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Genetic parameter estimates for growth and reproductive traits in Lori sheep

Kourosh Mohammadi[a,*], Rostam Abdollahi-Arpanahi[b], Fatemeh Amraei[c], Ebrahim Mirza Mohamadi[d], Amir Rashidi[d]

[a] Department of Animal Science, Ferdowsi University of Mashhad, Mashhad, Iran
[b] Department of Animal and Poultry Science, Abureyhan Campus, University of Tehran, Pakdasht, Iran
[c] Department of Animal Science, Faculty of Agriculture, University of Zabol, Zabol, Iran
[d] Department of Animal Science, Faculty of Agriculture, University of Kurdistan, Sanandaj, Iran

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ABSTRACT

Lori sheep is one of the well adapted and relatively heavy breeds in mountainous regions of Iran, primarily reared for mutton production. The current study was conducted to estimate the (co) variance components and genetic parameters by restricted maximum likelihood method using six univariate models for growth and four univariate models for reproductive traits. Data and pedigree information were collected at Agricultural Organization of Lorestan province, west of Iran from 2001 to 2012. Studied growth traits were birth weight (BW), weaning weight (WW), 6-month weight (6MW), average daily gain from birth to weaning (ADG_{0-3}), average daily gain from birth to 6-month (ADG_{0-6}), average daily gain from weaning to 6-month (ADG_{3-6}), and corresponding Kleiber ratio (KR_{0-3}, KR_{0-6}, KR_{3-6}). Reproductive traits were litter size at birth (LSB), litter size at weaning (LSW), litter mean weight per lambing (LMWL), litter mean weight per lamb weaned (LMWLW), total litter weight at birth (TLWB) and total litter weight at weaning (TLWW). Moreover, multivariate analyses were performed to estimate covariance between traits. Direct heritability estimates (h^2_a) for growth traits ranged from 0.000 (ADG_{0-3} and KR_{0-3}) to 0.156 (6MW). Maternal heritability (h^2_m) decreased from 0.110 at birth to 0.022 at 6-month weight. The ratio of maternal permanent environmental variance to phenotypic variance (pe^2) persisted into the post-weaning growth period and it was 0.115, 0.080, 0.087 and 0.081, for BW, ADG_{0-6}, KR_{0-3} and KR_{0-6}, respectively. Estimates of h^2_a for reproductive traits were significant for LSB, LSW, LMWL and LMWLW being 0.175, 0.213, 0.088 and 0.034, respectively, while TLWB and TLWW were more affected by the permanent environmental effects of ewes. Service sire effects (S^2) were significant for LMWL. Genetic correlations between growth traits ranged from −0.425 (BW-KR_{0-3}) to 1.000 (6MW-ADG_{0-3}, 6MW-KR_{0-3}, ADG_{0-3}–ADG_3–ADG_{3-6}-KR_{0-3} and KR_{0-3}–KR_{0-6}), and phenotypic correlations ranged from −0.341 (ADG_{0-3}–KR_{3-6}) to 0.990 (6MW–ADG_{0-6}). Genetic correlations between reproductive traits were higher than phenotypic ones, and ranged from −0.986 (LSB-LMWLW) to 0.999 (LMWLW-TLWB).

1. Introduction

Small ruminants play an important role to enhance husbandry economy of Iran. Increasing growth and reproductive performance depend on the precisely genetic evaluation through appropriate parameter values affecting profitability in meat production and improve breeding efficiency. Breeders can reduce the rearing time to achieve a desired body weight by increasing the growth rate of lambs, and ameliorate the efficiency of production through reduced maintenance costs (Li and Purvis, 2012). In sheep production, heavier weaning weight and higher post-weaning growth rate are desirable as they guarantee higher income of the production system.

In mammalian species, maternal genetic and environmental components influence growth performance of the lambs, especially until weaning, and may eventually affect their reproductive performance. Maternal effects tend to decrease with ageing of the offspring, but may sustain into the post-weaning growth period or throughout its life (Mohammadi et al., 2011, 2013a; Abbasi et al., 2012; Kamjoo et al., 2014).

Lori sheep is an important fat-tailed mutton breed, numbering approximate 2.5 million heads and distributed mainly in Zagros

* Corresponding author at: Department of Animal Science, Faculty of Agriculture, Ferdowsi University of Mashhad, Mashhad, P.O: Box 91775-1163, Iran. Tel.: +98 912 644 7209.
E-mail address: kouroshmhd@hotmail.co.uk (K. Mohammadi).

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Mountains in Lorestan province. Also they are found in some areas of Khuzestan, Kermansheh and Ilam provinces. This breed has an average litter size of 1.25 and its growth rate is noticeable compared to other Iranian sheep breeds. Average mature live weight in this breed is 62 kg (137 lbs) for ewe and 67 kg (148 lbs) for ram. Milk yield ranges from 80 to 85 kg in an approximate 3-month period, with annual greasy fleece weight between 1.5–2 and 2–3 kg in ewes and rams, respectively (Jalali Zonour, 2010). The coat color for this breed is yellowish and white, but brown spots are found on the forehead. This breed is mainly valued due to its superiority over other breeds in terms of disease resistance, tolerance to harsh environmental conditions and adaptability to mountainous regions of the western zone of country (Tavakkolian, 1999).

The literature, to our knowledge, did not report on genetic parameter estimates for the growth and reproductive traits of Lori sheep breed. Therefore, this is the first study in which different animal models were compared to plan optimum selection designs for Lori breed. Correlations between traits were also estimated.

2. Materials and methods

2.1. Animal and data collection

Data and pedigree information used in the current study were collected on Lori lambs born from 2001 to 2012 at the Agricultural Organization of Lorestan province, Khorramabad, Iran. Maiden ewes were randomly mated to the rams for the first time at approximately 18 months of age. Ewes usually remained in the flock for 6 parities. The selected rams were typically 3–4 years old and kept separately from ewes. During the breeding season (early-October until mid-November), single-sire pens were used to allocate 20–25 ewes per ram. Lambing was restricted to one season, from mid-February until late March. At birth and/or 24 h afterwards, lambs were weighed and ear-tagged, and then pedigree and birth information were recorded. After lambing, ewes and their lambs were placed in separate pens and kept for few days. Lambs were allowed to suckle dams and with dry alfalfa twice a day at morning and evening from 3 weeks of age until weaning. The suckling stage lasted for 90 days on average. All lambs were weaned at the same day, i.e. not necessarily at the same age. They were separately raised from older animals until 1 year of age. Some of lambs were sold after weaning due to poor growth or health problems. Animals were kept on natural pasture during spring and summer seasons. During autumn both lambs and ewes grazed on stubble-fields of wheat and barley and were kept indoors during the winter months and fed with a ration composed of wheat and barley straw and dry alfalfa.

2.2. Traits studied

Body weight was recorded at birth (BW), weaning (WW) and 6 months of age (6MW). Average daily gain from birth to weaning (ADG_{0-3}), from birth to 6-month (ADG_{0-6}), and from weaning to 6-month (ADG_{3-6}) were calculated and analyzed as additional traits. These average daily gains were also used to calculate the corresponding Kleiber ratio. The WW was adjusted to 90-days of age, whereas the 6MW records were adjusted to 180-days of age using the following formulas (Khorsand et al., 2014):

$$\mathrm{WW} = \left(\frac{\text{Actual WW} - \text{BW}}{\text{Registerd age(days)for WW}}\right) \times 90 + \text{BW}$$

$$\mathrm{6MW} = \left(\frac{\text{Actual 6MW} - \text{Actual WW}}{\text{Registerd age(days)for 6MW} - \text{Registerd age(days)for WW}}\right) \times (180 - \text{Registerd age(days)for WW}) + \text{Actual WW}$$

Recorded and derived reproductive traits were classified as basic and composite ones. Basic traits were litter size at birth (LSB, the number of lambs born alive per ewe lambing within a specific year, coded as 1 or 2), litter size at weaning (LSW, the number of lambs weaned per ewe lambing within a specific year, coded as 0 for dead lambs and 1 or 2 for alive lambs at weaning), litter mean weight per lambing (LMWL, the average birth weight of lambs per ewe lambing), litter mean weight per lamb weaned (LMWLW, the average weaning weight of lambs per ewe lambing). Composite traits were total litter weight at birth (TLWB, the sum of the birth weights of all lambs born per ewe lambing) and total litter weight at weaning (TLWW, the sum of the weights of all lambs weaned per ewe lambing).

2.3. Statistical models for growth traits

The general linear model (GLM) procedure of SAS (SAS Institute, 2009) was used to determine the significance of the environmental effects, such as lamb sex (2 levels, male or female), birth type (2 levels, single or twin), dam age at lambing (6 levels, 2–7 years old), and year of birth (12 levels, 2001–2012) for growth traits.

(Co) variance components and corresponding genetic parameters for aforementioned traits were estimated using WOMBAT software (Meyer, 2007). Six animal models were fitted as follows:

$$y = \boldsymbol{Xb} + \boldsymbol{Z_a a} + \boldsymbol{e} \quad \text{Model 1}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{W_{pe}pe} + \boldsymbol{e} \quad \text{Model 2}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{Z_m m} + \boldsymbol{e} \ (\boldsymbol{cov}_{\boldsymbol{a,m}} = 0) \quad \text{Model 3}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{Z_m m} + \boldsymbol{e} \ (\boldsymbol{cov}_{\boldsymbol{a,m}} = \boldsymbol{A}\sigma_{\boldsymbol{a,m}}) \quad \text{Model 4}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{Z_m m} + \boldsymbol{W_{pe}pe} + \boldsymbol{e} \ (\boldsymbol{cov}_{\boldsymbol{a,m}} = 0) \quad \text{Model 5}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{Z_m m} + \boldsymbol{W_{pe}pe} + \boldsymbol{e} \ (\boldsymbol{cov}_{\boldsymbol{a,m}} = \boldsymbol{A}\sigma_{\boldsymbol{a,m}}) \quad \text{Model 6}$$

where $\boldsymbol{y}$, is a vector of observations on the different traits; $\boldsymbol{b}$, $\boldsymbol{a}$, $\boldsymbol{m}$, $\mathbf{pe}$ and $\boldsymbol{e}$ are vectors of fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental and residual effects, respectively; $\boldsymbol{X}$, $\boldsymbol{Z_a}$, $\boldsymbol{Z_m}$ and $\boldsymbol{W_{pe}}$ are incidence matrices relating observations to the corresponding fixed and random effects, respectively.

It was assumed that direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects and residual effects are normally and independently distributed with mean 0 and variance $\boldsymbol{A}\sigma^2{}_{\mathrm{a}}$, $\boldsymbol{A}\sigma^2{}_{\mathrm{m}}$, $\boldsymbol{I_d}\sigma^2{}_{\mathrm{pe}}$ and $\boldsymbol{I_n}\sigma^2{}_{\mathrm{e}}$, respectively, where $\sigma^2{}_{\mathrm{a}}$, $\sigma^2{}_{\mathrm{m}}$, $\sigma^2{}_{\mathrm{pe}}$ and $\sigma^2{}_{\mathrm{e}}$ are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance and residual variance, respectively, $\boldsymbol{A}$ is the additive numerator relationship matrix, $\boldsymbol{I_d}$ and $\boldsymbol{I_n}$ are identity matrices that have order equal to the number of dams and records, respectively, and σ_{am} denotes the covariance between direct additive genetic and maternal additive genetic effects.

In order to choose the most suitable model for each trait, Akaike's Information Criterion (AIC) was applied (Akaike, 1974) as follows:

$$\mathrm{AIC_i} = -2\log \mathrm{L_i} + 2\mathrm{p_i}$$

where, $\log L_{\mathrm{i}}$ is the maximized log likelihood of model i at convergence and p_{i} is the number of parameters obtained from each model. Model with the lowest AIC was chosen as the most appropriate model.

Table 1
Data structure for growth and reproductive traits of Lori sheep.

Traits[a]	No. of records	No. of sires	No. of dams	No. of dams with own records and progeny	No. of progenies/sire	No. of progenies/dam	No. of service sires	Overall mean ± S.E.	Coefficient of variation (%)
BW (kg)	3079	95	1101	706	32.41	2.80	–	3.73 ± 0.01	17.50
WW (kg)	2523	93	991	625	27.13	2.55	–	21.73 ± 0.08	19.47
6MW (kg)	2009	86	809	523	23.36	2.48	–	31.79 ± 0.12	17.49
ADG_{0-3} (g/d)	2523	93	991	625	27.13	2.55	–	199.83 ± 0.89	22.30
ADG_{0-6} (g/d)	2009	86	809	523	23.36	2.48	–	155.52 ± 0.69	19.29
ADG_{3-6} (g/d)	2009	86	809	523	23.36	2.48	–	108.81 ± 0.94	38.63
KR_{0-3}	2523	93	991	625	27.13	2.55	–	19.69 ± 0.03	9.05
KR_{0-6}	2009	86	809	523	23.36	2.48	–	11.55 ± 0.02	6.90
KR_{3-6}	2009	86	809	523	23.36	2.48	–	8.02 ± 0.06	32.18
LSB	1481	65	339	256	–	–	80	1.12 ± 0.008	29.35
LSW	1481	65	339	256	–	–	80	0.91 ± 0.013	55.32
LMWL (kg)	1481	65	339	256	–	–	80	3.80 ± 0.016	16.46
LMWLW (kg)	1222	63	321	238	–	–	79	21.50 ± 0.116	18.80
TLWB (kg)	1481	65	339	256	–	–	80	4.21 ± 0.029	26.40
TLWW (kg)	1222	63	321	238	–	–	79	23.28 ± 0.172	25.80

[a] BW: Birth weight; WW: weaning weight; 6MW: 6-month weight; ADG_{0-3}: average daily gain from birth to weaning; ADG_{0-6}: average daily gain from birth to 6-month weight; ADG_{3-6}:average daily gain from weaning to 6-month weight; KR_{0-3}: Kleiber ratio from birth to weaning; KR_{0-6}: Kleiber ratio from birth to 6-month weight; KR_{3-6}: Kleiber ratio from weaning to 6-month weight; LSB: litter size at birth; LSW: litter size at weaning; LMWL: litter mean weight per lambing; LMWLW: litter mean weight per lamb weaned; TLWB: total litter weight at birth; TLWW: total litter weight at weaning; S.E.: standard error.

The total heritability (h^2_t, Willham, 1972) and repeatability of the ewe performance (t_m, Notter, 1998) were calculated as follows:

$$h_t^2 = \frac{\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}}{\sigma_p^2}$$

$$t_m = \frac{1}{4}h_a^2 + h_m^2 + pe^2 + (mr_{am}h)$$

2.4. Statistical models for reproductive traits

The fixed effects for reproductive traits were ewe age at lambing (5 levels, 2–6 years old) and lambing year (10 levels, 2003–2012). Moreover, the data for TLWB, LMWL, TLWW and LMWLW were pre-adjusted for effect of lamb sex by multiplicative adjustment factors (van Wyk et al., 2003). The adjustment factors were determined using least squares mean (LSM) of male and female lambs and then records of birth and weaning weight were accordingly adjusted. The following models were applied to each trait:

$$y = \boldsymbol{Xb} + \boldsymbol{Z_a a} + \boldsymbol{e} \quad \text{Model 1}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{W_{pe}pe} + \boldsymbol{e} \quad \text{Model 2}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{Z_s s} + \boldsymbol{e} \quad \text{Model 3}$$

$$\boldsymbol{y} = \boldsymbol{Xb} + Z_{\boldsymbol{a}}\boldsymbol{a} + \boldsymbol{Z_s s} + \boldsymbol{W_{pe}pe} + \boldsymbol{e} \quad \text{Model 4}$$

where, all terms are as in Models 1–6 for growth traits, with the exception of pe and *s* that denotes vectors of the permanent environmental effects related to repeated records of the ewes and service sire, with corresponding design matrices $\boldsymbol{W_{pe}}$ and $\boldsymbol{Z_s}$. It was assumed that ewe permanent environmental and service sire effects were normally distributed with mean 0 and variance $\boldsymbol{I_d}\sigma^2_{pe}$ and $\boldsymbol{I_s}\sigma^2_s$, respectively, where σ^2_{pe}, σ^2_s are ewe permanent environmental variance and service sire variance and $\boldsymbol{I_d}$ and $\boldsymbol{I_s}$ are identity matrices with the order equal to the number of ewes and service sires.

Repeatability (r) was calculated using the following formula:

$$r = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_p^2}$$

In order to estimate genetic, phenotypic and environmental correlations, multivariate analyses were carried out with the most appropriate models derived from univariate analyses. Thresholds to define whether convergence had been achieved were 10^{-8} and 10^{-5} for univariate and multivariate analyses, respectively. A Bivariate Bayesian threshold–threshold model was applied to estimate genetic parameters for LSB and LSW using Gibbs sampling by thrgibbsf90 software (Misztal et al., 2002). Gibbs sampling consisted of 100,000 samples and the first 10,000 samples were discarded as burn-in period. A thinning interval of 10 was used for computing features of the posterior distribution.

3. Results and discussion

3.1. Descriptive statistics and fixed effects

Data structure and descriptive statistics are summarized in Table 1. The sex ratio in the lambs (♂: ♀) and birth type ratio (single: twin) were 1.22: 1 and 4.36: 1, respectively. The coefficients of variation (CV) for growth traits ranged from 6.90% (KR_{0-6}) to 38.63% (ADG_{3-6}), and for reproductive traits ranged from 16.46% (LMWL) to 55.32% (LSW). This was in agreement with the findings reported by Ghafouri-Kesbi et al. (2011) and Mohammadi et al. (2013b). Growth traits were significantly affected by dam age ($P < 0.05$), birth type and birth year ($P < 0.01$). In particular, different climatic conditions, choice of rams, quality and quantity of pastures and feedstuff availability, especially during late pregnancy might lead to a significant effect of year of birth (Miraei-Ashtiani et al., 2007; Abbasi et al., 2012; Mohammadi et al., 2013a). Significant influences of lamb sex were also observed ($P < 0.01$) for most of the traits. These fixed effects were reported to be significant in previous studies (Ghafouri-Kesbi et al., 2011; Abbasi et al., 2012; Mohammadi et al., 2013b; Kamjoo et al., 2014).

All reproductive traits were significantly influenced by dam age and lambing year ($P < 0.01$; results not shown). This is in agreement with those reported for other sheep breeds (Rashidi et al., 2011; Mohammadi et al., 2012, 2013b; Amou Posht-e- Masari et al., 2013; Nabavi et al., 2014). However, Mokhtari et al. (2010) reported non-significant effect of dam age on LSB and LSW of Kermani sheep.

3.2. (Co) variance components and genetic parameters for growth traits

Findings obtained in the current study were noticeable due to more than 2 lambing records per dam and 64% of dams having own

Table 2
(Co) variance components and genetic parameters for growth traits fitting the most appropriate model.

Traits[a]	Model fitted	σ^2_a	σ^2_{pe}	σ^2_m	σ_{am}	σ^2_e	σ^2_p	$h^2_a \pm$ S.E.	$pe^2 \pm$ S.E.	$h^2_m \pm$ S.E.	r_{am}	h^2_t	t_m	AIC value
BW	6	0.030	0.037	0.035	0.022	0.197	0.322	0.094 ± 0.03	0.115 ± 0.03	0.110 ± 0.03	0.689	0.250	0.318	−665.542
WW	3	0.056	–	1.172	–	7.699	8.928	0.006 ± 0.02	–	0.131 ± 0.03	–	0.072	0.132	8036.130
6MW	4	2.266	–	0.316	0.844	11.056	14.482	0.156 ± 0.04	–	0.022 ± 0.02	0.998	0.252	0.119	7313.210
ADG_{0-3}	3	0.206	–	100.148		879.055	979.408	0.000 ± 0.02	–	0.102 ± 0.02	–	0.051	0.102	19820.894
ADG_{0-6}	2	59.768	33.111	–	–	319.621	412.500	0.145 ± 0.04	0.080 ± 0.02	–	–	0.145	0.116	14021.034
ADG_{3-6}	1	83.704	–	–	–	879.337	963.041	0.087 ± 0.02	–	–	–	0.081	0.022	15747.030
KR_{0-3}	2	0.000	0.142	–	–	1.498	1.641	0.000 ± 0.02	0.087 ± 0.03	–	–	0.000	0.087	3833.320
KR_{0-6}	2	0.034	0.024	–	–	0.245	0.303	0.111 ± 0.03	0.081 ± 0.02	–	–	0.111	0.109	−330.404
KR_{3-6}	1	0.295	–	–	–	3.434	3.729	0.079 ± 0.03	–	–	–	0.079	0.020	4691.798

σ^2_a: Direct genetic variance; σ^2_{pe}: maternal permanent environmental variance; σ^2_m: maternal genetic variance; σ_{am}: covariance between direct and maternal genetic effects; σ^2_l: common litter variance; σ^2_e: residual variance; σ^2_p: phenotypic variance; h^2_a: direct heritability; pe^2: ratio of maternal permanent environmental variance on phenotypic variance; h^2_m maternal genetic heritability; r_{am}: correlation between direct and maternal genetic effects; l^2: ratio of common litter effects to phenotypic variance; h^2_t: total heritability; t_m: repeatability of the ewe performance.

[a] For trait abbreviations see footnote of Table 1.

records (Table 1). It has been indeed shown that complete data sets with more associations between dam performance records and offspring records as well as more progeny per dam affected the accuracy of partitioning maternal effects into genetic and environmental components (Boligon et al., 2012).

Variance components and genetic parameters for growth traits, obtained from the most suitable model for each trait, are presented in Table 2. Direct heritabilities ranged from 0.000 for ADG_{0-3} and KR_{0-3} to 0.156 for 6MW. The h^2_a for BW was 0.094, in agreement with that reported by Mohammadi et al. (2010) in Sanjabi sheep. However, it differed from estimates reported in other studies (Mohammadi et al., 2011; Ved Prakash et al., 2012; Mohammadi et al., 2013b; Kamjoo et al., 2014). Such a low h^2_a estimate is possibly due to the inclusion of the maternal effects in the model and showed that direct additive genetic effects constitute a negligible part of phenotypic variance for BW of Lori lambs, suggesting that little genetic progress would be expected through direct selection. Estimated pe^2 and h^2_m for BW (0.115 and 0.110, respectively) were incompatible with those observed by Kamjoo et al. (2014) and Khorsand et al. (2014) in Iran-Black and Afshari sheep, respectively. In the current study, positive r_{am} was obtained for BW (0.689). Such estimate was also reported by Abbasi et al. (2012). Understanding the correlations between direct and maternal additive genetic effects (r_{am}) would facilitate formulation of optimum breeding programs and improve selection efficiency (Robison, 1981), as negative and positive r_{am} can diminish and accelerate response to selection, respectively (Wolf et al., 1998).

For WW, the h^2_a estimate was 0.006. Higher h^2_a estimates were reported by Bahreini Behzadi et al. (2007), Mohammadi et al. (2013a) and Khorsand et al. (2014). The h^2_m was estimated as 0.131 for WW and was substantially higher than the h^2_a. Higher h^2_m estimates were also reported in the literature (Bahreini Behzadi et al., 2007; Mohammadi et al., 2010; Li and Purvis, 2012). However, lower h^2_m estimate (0.05) was achieved by Kamjoo et al. (2014). In the Lori sheep, lambs are fed with their mother's milk during the day. Thus, lambs' pre-weaning performance is under the control of the environment provided by the dams. From weaning to 6-month of age, the influence of maternal effects on the growth of lambs decreased in agreement with other reports (Miraei-Ashtiani et al., 2007; Mohammadi et al., 2010). The estimated h^2_a for 6MW (0.156) was consistent with estimates of Mohammadi et al. (2013b) and Kamjoo et al. (2014), but lower values were also reported by Mohammadi et al. (2010) and Abbasi et al. (2012). Miraei-Ashtiani et al. (2007) also suggested a similar model (Model 4) for 6MW in Sangsari sheep, obtaining higher estimates ($h^2_a = 0.49$, and $h^2_m = 0.11$). The increase of h^2_a for 6MW is due to post-weaning feed conditions; as lambs experienced relative favorable range conditions. Therefore, direct additive genetic variance component increased faster than the environmental variance component. In addition, in the post-weaning period, when animals live separately from their mothers, direct additive genetic effects become more important than maternal additive genetic effects. A similar finding was obtained for the Malpura sheep by Gowane et al. (2010). Maternal effects never completely disappeared after weaning (Maniatis and Pollott, 2002), but declined as lambs became independent of their mother. The h^2_m estimate for 6MW was low (0.022), but similar to the value obtained by Abbasi et al. (2012) in Baluchi sheep. Maternal genetic effects was a considerable source of phenotypic variance for 6MW (0.25) of Kermani sheep in the study of Bahreini Behzadi et al. (2007). As the proportion of dams without record has a substantial effect on the accuracy of r_{am} estimation (Heydarpour et al., 2008), current estimate of r_{am} (+0.998) for 6MW should be overestimate making interpretation difficult because h^2_m is low. Similarly, Miraei-Ashtiani et al. (2007) and Abbasi et al. (2012) reported positive estimates of r_{am} in Sangsari and Baluchi sheep, respectively.

Table 3
Estimates of correlations between growth traits in Lori lambs.

Trait[a] 1	Trait 2	r_{a12}	r_{pe12}	r_{m12}	r_{e12}	r_{p12}
BW	WW	0.995 ± 0.22	–	0.788 ± 0.11	0.392 ± 0.03	0.394 ± 0.02
BW	6MW	0.300 ± 0.12	–	0.997 ± 0.25	0.320 ± 0.05	0.292 ± 0.02
BW	ADG_{0-3}	0.975 ± 0.33	–	0.488 ± 0.15	0.166 ± 0.03	0.220 ± 0.02
BW	ADG_{0-6}	0.457 ± 0.18	0.087 ± 0.21	–	0.099 ± 0.04	0.151 ± 0.02
BW	ADG_{3-6}	0.016 ± 0.25	–	–	0.037 ± 0.03	0.029 ± 0.02
BW	KR_{0-3}	−0.155 ± 0.06	−0.366 ± 0.18	–	−0.082 ± 0.03	−0.100 ± 0.02
BW	KR_{0-6}	−0.080 ± 0.24	−0.591 ± 0.22	–	−0.109 ± 0.04	−0.143 ± 0.02
BW	KR_{3-6}	-0.425 ± 0.24	–	–	-0.038 ± 0.03	−0.070 ± 0.02
WW	6MW	0.975 ± 0.15	–	1.000 ± 0.06	0.671 ± 0.02	0.710 ± 0.01
WW	ADG_{0-3}	0.992 ± 0.10	–	0.960 ± 0.01	0.988 ± 0.00	0.983 ± 0.00
WW	ADG_{0-6}	0.940 ± 0.05	–	–	0.640 ± 0.02	0.680 ± 0.01
WW	ADG_{3-6}	0.936 ± 0.31	–	–	−0.141 ± 0.03	−0.065 ± 0.02
WW	KR_{0-3}	0.758 ± 0.20	–	–	0.905 ± 0.01	0.859 ± 0.01
WW	KR_{0-6}	0.789 ± 0.16	–	–	0.588 ± 0.02	0.565 ± 0.02
WW	KR_{3-6}	0.656 ± 0.23	–	–	−0.401 ± 0.03	−0.336 ± 0.02
6MW	ADG_{0-3}	1.000 ± 0.16	–	1.000 ± 0.07	0.650 ± 0.02	0.690 ± 0.01
6MW	ADG_{0-6}	0.995 ± 0.00	–	–	0.992 ± 0.00	0.990 ± 0.00
6MW	ADG_{3-6}	0.903 ± 0.07	–	–	0.688 ± 0.02	0.704 ± 0.01
6MW	KR_{0-3}	1.000 ± 0.09	–	–	0.608 ± 0.02	0.615 ± 0.01
6MW	KR_{0-6}	0.942 ± 0.03	–	–	0.916 ± 0.01	0.895 ± 0.01
6MW	KR_{3-6}	0.637 ± 0.20	–	–	0.498 ± 0.03	0.483 ± 0.02
ADG_{0-3}	ADG_{0-6}	0.978 ± 0.04	–	–	0.649 ± 0.02	0.686 ± 0.01
ADG_{0-3}	ADG_{3-6}	1.000 ± 0.33	–	–	−0.152 ± 0.03	-0.074 ± 0.01
ADG_{0-3}	KR_{0-3}	0.876 ± 0.10	–	–	0.951 ± 0.00	0.931 ± 0.00
ADG_{0-3}	KR_{0-6}	0.913 ± 0.11	–	–	0.635 ± 0.02	0.630 ± 0.01
ADG_{0-3}	KR_{3-6}	0.999 ± 0.37	–	–	−0.406 ± 0.03	−0.341 ± 0.02
ADG_{0-6}	ADG_{3-6}	0.961 ± 0.05	–	–	0.723 ± 0.01	0.707 ± 0.02
ADG_{0-6}	KR_{0-3}	1.000 ± 0.15	0.822 ± 0.14	–	0.634 ± 0.02	0.656 ± 0.01
ADG_{0-6}	KR_{0-6}	0.946 ± 0.03	0.846 ± 0.07	–	0.956 ± 0.01	0.944 ± 0.01
ADG_{0-6}	KR_{3-6}	0.946 ± 0.02	–	–	0.971 ± 0.00	0.945 ± 0.00
ADG_{3-6}	KR_{0-3}	1.000 ± 0.34	–	–	−0.115 ± 0.03	−0.043 ± 0.02
ADG_{3-6}	KR_{0-6}	0.999 ± 0.05	–	–	0.674 ± 0.02	0.694 ± 0.01
ADG_{3-6}	KR_{3-6}	0.941 ± 0.02	–	–	0.959 ± 0.00	0.944 ± 0.00
KR_{0-3}	KR_{0-6}	1.000 ± 0.19	0.955 ± 0.10	–	0.698 ± 0.02	0.721 ± 0.01
KR_{0-3}	KR_{3-6}	0.999 ± 0.39	–	–	−0.356 ± 0.03	−0.285 ± 0.02
KR_{0-6}	KR_{3-6}	0.901 ± 0.13	–	–	0.511 ± 0.02	0.527 ± 0.02

r_{a12}: Genetic correlation between trait 1 and 2; r_{pe12}: maternal permanent environmental correlation between traits 1 and 2; r_{m12}: maternal genetic correlation between traits 1 and 2; r_{l12}: common litter correlation between traits 1 and 2; r_{e12}: environmental correlation between traits 1 and 2; r_{p12}: phenotypic correlations between traits 1 and 2.

[a] For trait abbreviations see footnote of Table 1.

Although Model 3 was suitable to explain the variation of ADG_{0-3}, no evidence for the direct additive genetic effect was observed. This indicated that the trait is highly influenced by environmental factors. Literature estimates of h^2_a for ADG_{0-3} ranged from 0.03 (Miraei-Ashtiani et al., 2007) to 0.23 (Ved Prakash et al., 2012). In terms of h^2_m, the present estimate (0.102) was similar to that reported for Mehraban sheep (Ghafouri-Kesbi, 2013), whereas Abbasi et al. (2012) reported a lower estimate.

Estimate of h^2_a for ADG_{0-6} (0.145) was similar to that observed in Zandi sheep (Ghafouri-Kesbi et al., 2011), whereas higher estimate was reported by Ved Prakash et al. (2012). The estimate of pe^2 (0.080) was almost half of h^2_a. A similar result was observed by Miraei-Ashtiani et al. (2007), whereas Eskandarinasab et al. (2010) reported higher pe^2 (0.16) in Afshari sheep. The h^2_a estimate for ADG_{3-6} (0.087) was in agreement with previous reports (Mohammadi et al., 2010; Ghafouri-Kesbi et al., 2011). However, higher estimates were also reported (Ved Prakash et al., 2012).

An indirect criterion to evaluate feed conversion to achieve maximum output is applying Kleiber ratio (KR), defined as growth rate/body weight$^{0.75}$ (Kleiber 1947; Scholtz et al., 1990) due to its high relationship at the phenotypic level with feed efficiency (Scholtz and Roux, 1988). Indeed, animals with higher KR require lower maintenance energy. Similar to ADG_{0-3}, the h^2_a estimate for KR_{0-3} was near to zero, whereas a higher estimate (0.20) was reported by Ved Prakash et al. (2012). In agreement with our results, Abegaz et al. (2005) and Mohammadi et al. (2010) reported that permanent environmental effects of the dam dominated KR_{0-3}. Our estimate of pe^2 (0.087) differed from that reported by Mohammadi et al. (2010), but it agreed with those reported by Abegaz et al. (2005) and Ghafouri-Kesbi (2013).

Our estimate of h^2_a for KR_{0-6} was 0.111 and consistent with that reported by Ghafouri-Kesbi et al. (2011). This estimate falls in the range reported in literature (e.g., Eskandarinasab et al., 2010; Ved Prakash et al., 2012). The estimate of pe^2 for KR_{0-6} (0.081) was lower than that reported by Eskandarinasab et al. (2010) in Afshari sheep.

For KR_{3-6} the magnitude of h^2_a was estimated being 0.079 consistent with that reported by Mohammadi et al. (2010), but lower than that reported by Ved Prakash et al. (2012). Nonetheless, Abegaz et al. (2005) and Mohammadi et al. (2011) obtained the similar h^2_a estimate (0.01) for KR in the same growth phase.

When maternal effects contribute significantly in the phenotype of progenies, prediction of selection response should be done by estimating h^2_t (Willham, 1972). This parameter is useful to estimate response to selection based on phenotypic values (Abegaz et al., 2005). The h^2_t estimates ranged from 0.000 (KR_{0-3}) to 0.252 (6MW) (Table 2). The h^2_t for BW (0.250) and 6MW (0.252) were noticeable suggesting that mass selection would be effective in improving these traits. These were in agreement with those reported by Bahreini Behzadi et al. (2007) and Gowane et al. (2010). Future performance of the ewes is predictable using repeatability of the ewe performance (t_m). Also this parameter is useful to identifying and culling less-productive ewes. According to Table 2, the t_m estimates showed a decreasing trend from BW to 6MW for repeatability of the

Table 4
(Co) variance components and genetic parameters for reproductive traits fitting the most appropriate model.

Traits[a]	Model fitted	σ^2_a	σ^2_{pe}	σ^2_s	σ^2_e	σ^2_p	$h^2_a \pm SE$	$pe^2 \pm SE$	$S^2 \pm SE$	r	AIC value
LSB[b]	2	0.225	0.030	–	1.00	1.25	0.175 ± 0.06	0.024 ± 0.01	–	0.204	−1754.136
LSW[b]	1	0.279	–	–	1.00	1.279	0.213 ± 0.07	–	–	0.213	−533.956
LMWL	4	0.032	0.078	0.005	0.248	0.363	0.088 ± 0.052	0.215 ± 0.055	0.014 ± 0.009	0.303	−50.554
LMWLW	1	0.322	–	–	9.058	9.380	0.034 ± 0.027	–	–	0.034	3976.900
TLWB	2	0.571×10^{-3}	0.188	–	0.936	1.124	0.000 ± 0.024	0.167 ± 0.040	–	0.168	1681.552
TLWW	2	0.213	3.583	–	22.841	26.637	0.008 ± 0.028	0.134 ± 0.048	–	0.142	5220.140

[a] For trait abbreviations see footnote of Table 1.
[b] LSB and LSW were analyzed by threshold models.

ewe performance. These findings were consistent with the results reported by Ved Prakash et al. (2012).

3.3. Correlation estimates between growth traits

Genetic, phenotypic and environmental correlations among the growth traits are presented in Table 3. Generally, our estimates were in the range reported in the literature for different trait combinations (Eskandarinasab et al., 2010; Mohammadi et al., 2011, 2013b; Abbasi et al., 2012).

The patterns of direct genetic, phenotypic and environmental correlations are similar to each other, as they were higher between adjacent weights than between non-adjacent ones. Similar findings have been reported by Eskandarinasab et al. (2010) and Li and Purvis (2012). With the exception of observed negative genetic correlations between BW–KR_{0-3} (−0.155), BW–KR_{0-6} (−0.080) and BW–KR_{3-6} (−0.425), genetic correlations between different growth trait combinations were positive and high. Therefore, selection for any of these traits could bring positive response to selection. The negative genetic correlations between BW with KRs imply that different genetic mechanisms are involved in expressing these traits at different stages of growth. Positive and high genetic correlations between ADGs with KRs indicate that lambs with higher growth rate are supposed to be more efficient users of feed. Therefore, selection for growth rate may ameliorate both growth rate and efficiency of feed utilization in different growth phases.

Estimates of positive and high maternal genetic correlations between BW–WW (0.788), BW–6MW (0.997) and WW–6MW (1.000) indicate the presence of common favorable maternal genes for these traits. The negative phenotypic correlation between BW and KRs may be of the reason for negative values of KR_{3-6} for some animals. In spite of highly positive genetic correlation between ADG_{0-3} and ADG_{3-6}, phenotypic and environmental correlations were negative, indicating that lambs that grew faster in the pre-weaning period, grew more slowly during post-weaning period and vice versa. Similarly, Abegaz et al. (2005) found negative phenotypic and environmental correlations between ADG_{0-3}–ADG_{3-6} (−0.11 and −0.18, respectively) and between ADG_{0-3}–KR_{3-6} (−0.27 and −0.39, respectively).

3.4. (Co) variance components and genetic parameters for reproductive traits

Estimates of (co) variance components and genetic parameters for the reproductive traits obtained from the most suitable model are presented in Table 4. Current estimates of h^2_a using threshold models for LSB and LSW were 0.175 and 0.213, respectively; and using linear models they were estimated to be 0.000. Numerous literature have reported the lower h^2_a estimates using linear models (Mokhtari et al., 2010; Rashidi et al., 2011; Mohammadi et al., 2012, 2013b; Amou Posht-e- Masari et al., 2013). Although direct genetic variances for LMWL, TLWB, and TLWW were 0.032, 0.571×10^{-3} and 0.213, respectively, the effect of ewe permanent environment (pe^2) on these traits were remarkable being 0.215, 0.167 and 0.134, respectively. According to the findings reported in the literature (Mokhtari et al., 2010; Rashidi et al., 2011; Mohammadi et al., 2012, 2013a; Amou Posht-e- Masari et al., 2013), the most appropriate model for LSB, TLWB, and TLWW included both direct genetic and permanent environmental effects related to the ewes. The inclusion of service sire effects (s^2) together with direct genetic effects and permanent environmental effects of ewe significantly affected Log likelihoods of LMWL; however, our s^2 estimate was negligible (0.014). TLWW is an important economic composite trait, reflecting the combined influences of reproductive and mothering abilities of ewes, pre-weaning growth, and survival of lambs. A negligible estimate of h^2_a was obtained for TLWW (0.008), lower than other reports ranging from 0.03 in Shall sheep (Amou Posht-e- Masari et al., 2013) to 0.18 in Kermani sheep (Mokhtari et al., 2010). Estimates of pe^2 were higher than the corresponding h^2_a for reproductive traits and higher than the pe^2 estimates reported in the literature by Mokhtari et al. (2010), Rashidi et al. (2011) and Mohammadi et al. (2012, 2013b) for the same traits. Repeatability estimates were similar to the h^2_a or pe^2 estimates, with the exception of LMWL. These findings indicated that using more records is required for more accurate genetic evaluation. However, the repeatability value for LMWL was 0.303; thus, the selection accuracy ought to be medium in the first lambing. Low h^2_a estimates for the reproductive traits with the exception of litter traits is probably due to the greater influence of environmental effects such as nutrition and management conditions, and therefore little improvement by selection would be expected.

3.5. Correlation estimates between reproductive traits

Genetic, phenotypic and environmental correlation estimates among reproductive traits are shown in Table 5. Response to direct selection for litter size is restricted by low heritability of the trait, due to its discrete phenotypic expression (Hill, 1985). However, positive genetic correlation estimates between LSB–LSW, LSB–TLWB, LSB–TLWW and LSW–TLWW could help to improve litter size indirectly, in agreement with the report by Amou Posht-e-Masari et al. (2013). On the other hand, genetic, environmental and phenotypic correlations for LSB–LMWL and LSB-LMWLW were all negative (−0.337 and −0.128, −0.174 and −0.986, −0.157 and −0.161, respectively), suggesting that single lambs tend to be heavier than twins and therefore selection for large LSB would lead to a reduction in litter mean weight per lambing and per lamb weaned. Mohammadi et al. (2013a) reported similar results. The highly positive genetic correlations between LMWL–TLWB (0.998), LMWLW–TLWB (0.999) and LMWLW–TLWW (0.967) imply that the ewes which have lambs with high mean birth weight are likely to produce more TLWB and TLWW. The positive and high genetic correlation between TLWB with other reproductive traits with the exception of LSW (Table 5) was in the same line with the report of Rashidi et al. (2011). TLWB was positively and highly correlated with TLWW in terms of genetic effects. Similar results were also reported by Mokhtari et al. (2010) and Mohammadi et al. (2012, 2013b). The negative environmental correlations observed

Table 5
Estimates of correlations between reproductive traits in Lori sheep.

Trait[a] 1	Trait 2	r_{a12}[b]	r_{pe12}	r_{e12}	r_{p12}
LSB[c]	LSW[c]	0.990 ± 0.02	–	0.980 ± 0.02	0.957 ± 0.02
LSB	LMWL	−0.998 ± 0.23	0.337 ± 0.08	−0.128 ± 0.04	−0.174 ± 0.02
LSB	LMWLW	−0.986 ± 0.36	–	−0.157 ± 0.03	−0.161 ± 0.02
LSB	TLWB	0.962 ± 0.02	–	0.294 ± 0.01	0.359 ± 0.02
LSB	TLWW	0.894 ± 0.22	–	0.200 ± 0.02	0.226 ± 0.01
LSW	LMWL	0.773 ± 0.34	–	−0.121 ± 0.03	−0.095 ± 0.02
LSW	LMWLW	0.562 ± 0.22	–	90.127 ± 0.03	−0.120 ± 0.02
LSW	TLWB	−0.963 ± 0.16	–	0.127 ± 0.00	0.174 ± 0.02
LSW	TLWW	0.949 ± 0.62	–	0.200 ± 0.03	0.210 ± 0.02
LMWL	LMWLW	0.998 ± 0.46	–	0.200 ± 0.04	0.267 ± 0.05
LMWL	TLWB	0.998 ± 0.40	0.292 ± 0.06	0.142 ± 0.05	0.197 ± 0.02
LMWL	TLWW	0.193 ± 0.28	0.341 ± 0.05	−0.026 ± 0.04	0.010 ± 0.03
LMWLW	TLWB	0.999 ± 0.41	–	−0.040 ± 0.03	-0.014 ± 0.02
LMWLW	TLWW	0.967 ± 0.13	–	0.187 ± 0.05	0.236 ± 0.01
TLWB	TLWW	0.774 ± 0.39	0.277 ± 0.06	0.200 ± 0.03	0.224 ± 0.02

[a] For trait abbreviations see footnote of Table 1.
[b] For correlation abbreviations see footnote of Table 3.
[c] Parameters were estimated using a bivariate threshold–threshold model.

between LSB–LMWL (−0.337) and LSB–LMWLW (−0.986) indicated that unfavourable temporary environmental effects tended to decline LSB and thereby decreasing LMWL and LMWLW. These findings were comparable with the results reported by Amou Posht-e-Masari et al. (2013).

4. Conclusion

Our results confirmed the importance of implementing the appropriate animal model for the estimation of (co) variance components and suggested that both direct additive genetic effects and maternal effects played a considerable role in phenotypic variation of growth traits. Higher heritabilities for 6MW, ADG_{0-6}, and KR_{0-6} and strong and high genetic correlation between 6MW–ADG_{0-6} (0.995), 6MW–KR_{0-6} (0.942) and ADG_{0-6}–KR_{0-6} (0.946), as well as measuring feed efficiency by Kleiber ratio allow us to improve the efficiency of feed utilization. The low heritability and repeatability estimates for reproductive traits indicated that genetic improvement for considered traits by direct selection might be difficult and would not be achieved without improving environmental factors. Results from the current study can be used by breeders to improve growth and reproductive performances of Lori sheep.

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