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REGULAR ARTICLES

Growth rate and efficiency-related traits in Kermani lambs: estimations of (co)variance components and genetic parameters

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Abstract

Using Kermani sheep, the current study estimated (co)variance components and genetic parameters for average daily gain, Kleiber's ratio, growth efficiency, and relative growth rate. Data were analyzed by the average information restricted maximum likelihood (AI-REML) method using six animal models with different combinations of direct and maternal effects. The best-fitting model was determined after testing for improvement in log-likelihood values. The estimates of h^2 for average daily gain (ADG), Klieber's ratio (KR), growth efficiency (GE), and relative growth rate (RGR) in pre- and post-weaning phases were 0.13 ± 0.6 and 0.17 ± 0.02, 0.12 ± 0.04, and 0.16 ± 0.03; 0.05 ± 0.05 and 0.07 ± 0.03 and 0.06 ± 0.02 and 0.07 ± 0.01, respectively. Maternal heritabilities (m^2) ranged from 0.03 ± 0.01 for relative growth rate in pre-weaning phase to 0.11 ± 0.04 for average daily gain in post-weaning period. The maternal permanent environmental component (Pe^2) accounted for 3 to 13% to the phenotypic variance for all the studied traits. Estimated values of additive coefficient of variations (CV_A) ranged from 2.79% for relative growth rate at 6 months of age to 23.74% for growth efficiency at yearling age. Genetic and phenotypic correlations among traits were ranged from −0.687 to 0.946 and −0.648 to 0.918, respectively. The result indicated that selection for growth rate and efficiency-related traits would also be less effective in achieving genetic change, because there was little additive genetic variation among Kermani lambs.

Keywords Animal model · Genetic correlation · Growth trait · Heritability · Maternal effect

Introduction

In Iran, sheep are a critical sacrificial animal and better fit the environment and socioeconomic conditions. There are about 44.6 million sheep in the country, accounting for about half of Iran's livestock. The population of Kermani sheep is about 2.4 million animals, about 5.38% of the total sheep population of Iran (Sefidbakht, 2011). It is an indigenous breed with fat tails, medium-sized, longer legs, and white wool. It is found mainly in the southeastern areas of the country, especially in Kerman province. This sheep is a meat breed, but can also be valuable for its wool due to its high-quality wool (Tavakolian, 2000). Mutton is one of the most important sources of protein in Iran. However, the meat derived from sheep breeding does not meet the increasing consumer demand. Body weight and growth characteristics are among the most crucial economic parameters of meat production in sheep. One of the ways to increase meat production in sheep is to improve lamb growth performance and efficiency-related traits. Indeed, growth performance is a key factor in improving the profitability of the sheep industry, making lambs with faster growth and higher weight more desirable in terms of meat production (Tortereau et al., 2020; Ali et al., 2020). As noted by Boujenane and Diallo (2017), an increase in meat production can be achieved by selecting animals with the maximum genetic merit as parents of the next generation for growth traits. There are different factors affecting body weight and growth traits at different ages, including direct additive genetic, maternal genetic, and maternal permanent environmental effects.

For designing appropriate breeding programs to maximize genetic progress, estimates of genetic parameters and associations between different traits are major tools (Ghafouri-Kesbi and Abbasi, 2019; Bangar et al., 2020). Genetic parameters for the growth traits of Kermani sheep are readily available in the literature (Rashidi et al., 2008). However, there is insufficient information on genetic parameters for

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traits related to efficiency during pre-weaning and post-weaning periods in this breed. Therefore, this study was carried out to estimate variance components and heritabilities for growth rate and efficiency-related traits and determine phenotypic and genetic correlations between these traits in Kermani sheep.

Material and methods

Herd management

In suitable seasons of the year, pastures were the primary source of food. Flocks were grazed during the daytime and housed at night. Grazing is allowed for 4 h in the morning and 3 h in the afternoon. Rangeland consisted of green fodder and natural vegetation (shrubs and herbage). The quantity and quality of the pasture were low. Therefore, manual feeding was carried out mainly during the mating season and in winter. Sheep received supplemental feed composed of 1.5 kg alfalfa, 0.5 kg wheat straw, and 0.2 kg barely per head per day. Females remained in the herd for up to seven parities, while the rams were only kept for a maximum of three mating seasons. The average ewe weight in Kermani sheep is about 47 kg. Eighteen-month-old ewes were mated for the first time with the selected rams, and each ram was assigned a group of 25–35 ewes. The mating season began in mid-August and lasted until mid-September. The ewes gave birth to their young between January 15 and February 15. The newborn lambs were immediately weighed and ear-tagged within 24 h. Weights were precisely recorded on accurate dates at 3, 6, 9, and 12 months of age. The weaning of the lambs was enforced when they were about 3 months old.

Data and traits analyzed

The data used in this study were collected over 20 years (1991 to 2013) at the Kermani Sheep Breeding Station in Shahrebabak, Kerman Province, Iran. In the current study, body weight data at birth (WT0), weaning (WT3), 6 months of age (WT6), and 12 months of age (WT12) were used to calculate the traits. Four growth stages were defined: (1) birth to 3 months of age, (2) birth to 6 months of age, (3) weaning to 6 months of age, and (4) weaning to 12 months of age. Weight gains for the above growth phases were calculated as average daily gains (ADG1, ADG2, ADG3, ADG4), with total gain divided by the number of days in the period. ADG1, ADG2, ADG3, and ADG4 were then applied to calculate the corresponding Kleiber ratio as follows:

$KR1 = ADG1/WT3^{0.75}$, $KR2 = ADG2/WT6^{0.75}$, $KR3 = ADG3/WT6^{0.75}$, $KR4 = ADG4/WT12^{0.75}$. The Kleiber ratio (KR) is defined as the growth rate in a certain period divided by final body weight$^{0.75}$ (metabolic weight) (Kleiber 1947).

Growth efficiency, which indicates the rate of growth in a certain period (%), was calculated based on body weight at different ages (Ghafouri-Kesbi and Abbasi, 2019) as follows:

$$GE1 = \left[(WT3 - WT0)/WT0\right] \times 100$$

$$GE2 = \left[(WT6 - WT0)/WT0\right] \times 100$$

$$GE3 = \left[(WT6 - WT3)/WT3\right] \times 100$$

$$GE4 = \left[(WT12 - WT3)/WT3\right] \times 100$$

According to the following formula, body weights were also used to calculate the relative growth rate from birth to 3 months of age, (RGR1) from birth to 6 months of age (RGR2), from weaning to 6 months of age (RGR3), and from weaning to 12 months of age (RGR4):

$$RGR1 = \left[Loge\ (WT3) - Loge\ (WT0)\right]/90$$

$$RGR2 = \left[Loge\ (WT6) - Loge\ (WT0)\right]/180$$

$$RGR3 = \left[Loge\ (WT6) - Loge\ (WT3)\right]/90$$

$$RGR4 = \left[Loge\ (WT12) - Loge\ (WT3)\right]/275$$

Statistical analyses

The general linear model (GLM) method of the SAS package (SAS, 2009) was used to determine the fixed effects that significantly impacted the studied traits. For the traits considered, the model included the fixed effects of lamb sex (male and female), birth type (single and twin), dam age at lambing (2–7 years), and birth year (1993–2012). Tukey's procedure was used to identify means with significant differences ($P < 0.05$). Only significant ($P \leq 0.05$) fixed effects remained in the models and were used for subsequent genetic analysis. (Co)variance components were envisaged using the average information restricted maximum likelihood approach (AI-REML) by fitting an animal model with the software WOMBAT (Meyer, 2013). If the variance of the function values (-2log-L) in the simplex was less than 10^{-8}, it was assumed that convergence was present. The following six single-trait models were used to estimate (co)variance components and genetic parameters:

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

$$y = Xb + Zaa + Zpepe + e \quad (2)$$

$$y = Xb + Zaa + Zmm + e \quad Cov(a, m) = 0 \tag{3}$$

$$y = Xb + Zaa + Zmm + e \quad Cov(a, m) = A\sigma_{am} \tag{4}$$

$$y = Xb + Zaa + Zmm + Zpepe + e \quad Cov(a, m) = 0 \tag{5}$$

$$y = Xb + Zaa + Zmm + Zpepe + e \quad Cov(a, m) = A\sigma_{am} \tag{6}$$

Here, y denotes the vector of records; b is a vector of fixed effects with incidence matrix X; a, m, and pe are vectors of direct genetic, maternal genetic, and maternal permanent environmental effects with design matrices Z_a, Z_m, and Z_{pe}, respectively, and e is a vector of residual random effects. The variance and (co)variance structure of the random effects were as follows:

$$Var\begin{bmatrix} a \\ m \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{ma} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_d\sigma_{pe}^2 & 0 \\ 0 & 0 & 0 & I_n\sigma_e^2 \end{bmatrix}$$

where *A* is the additive genetic relationship matrix; σ_a^2, σ_m^2, σ_{pe}^2, and σ_e^2 are the direct genetic variance, maternal genetic variance, maternal permanent environmental variance, and residual variance, respectively; I_d and I_e are identities whose order corresponds to the number of ewes and records, respectively. In addition, σ_{am} represents the covariance between direct and maternal genetic effects. The best-fit model for estimating the variance components was determined using the log-likelihood ratio test (LRT). The chi-square test statistic was calculated using the following equation (Meyer, 1997):

$$\chi 2 = -2\left[ML(X)_r - ML(X)_f\right]$$

where $ML(x)_r$ is the maximum likelihood for the reduced model and $ML(x)_f$ is the maximum likelihood for the full model. The reduction of -2logL was calculated when a random effect was added. The random effect was considered significant if the reduction was greater than the chi-square value (df = 1, $P < 0.05$). However, when log-likelihoods were not significant ($P > 0.05$), the model with a small number of parameters was considered the most appropriate.

In addition, the bivariate models fitted based on the most appropriate single-animal models were used to estimate genetic and phenotypic correlations among traits. The direct additive genetic coefficient of variation (CV_A) as an indicator of genetic diversity was estimated using the additive genetic variance as described by Ghafouri-Kesbi and Eskandarinasab (2018):

$$CVA = \frac{\sqrt{\sigma_A^2}}{\overline{X}} \times 100$$

where σ_A^2 is the additive genetic variance and $\overline{X}$ denotes the mean of a trait.

Results

General considerations

Means, standard deviations, number of records, and phenotypic coefficient of variance (CV_P) for the traits considered are shown in Table 1. As shown, the number of records decreased with the age of the animals. In the pre-weaning period, the lambs had higher yields concerning the traits ADG, KR, GE, and RGR, while the value of these traits diminished in the post-weaning periods. Phenotypic coefficients of variation for the relevant traits ranged from 15.10% for ADG1 to 57.35% for RGR3. The smallest coefficients of variation were obtained for the traits in the pre-weaning growth periods.

Least squares mean and environmental effects

Based on various fixed effects, the least squares mean and respective standard errors for the studied traits are summarized in Tables 2 and 3. Lambs' growth rates generally decreased as their ages increased. In the pre-weaning phase, the highest ADG, KR, GE, and RGR were observed. The sex of lambs and birth year had a significant effect ($P < 0.01$) on all traits. Male lambs had higher ADG, KR, GE, and RGR than female lambs at each age, similar to those reported in other studies (Sallam et al., 2019; Gautam et al., 2019). Type of birth significantly affected pre-weaning ADG, KR, GE, and ADG ($P < 0.01$) but did not affect ADG4. Despite this, the post-weaning Kleiber ratios of twins and single lambs were similar ($P > 0.05$). Single lambs had a higher pre-weaning ADG, KR, GE, and RGR than twin lambs. Dam age was also an important source of variation for all traits except GE2, RGR2, and RGR4 ($P > 0.05$).

Model comparison

Table 4 provides the log-likelihoods of six different statistical models for traits studied in the research. In order to select the most suitable model for the dataset, the LRT method was applied. According to the study, model 5 was the most suitable model for ADG1, KR1, GE1, and RGR1 based on the LRT method. There is a direct genetic effect, maternal genetic effect, and maternal permanent environmental effect

Table 1 Statistics characteristics of the traits studied in Kermani sheep

Traits	Item					
	No. of records	No. of ewe	No. of ram	Mean	S.D.	CV_P (%)
ADG1	3890	2543	142	179.66	27.13	20.67
ADG2	1656	944	128	116.57	19.3	16.56
ADG3	2873	1760	133	48.65	21.48	44.15
ADG4	1017	548	65	14.88	6.73	45.23
KR1	3890	2543	142	17.55	4.43	25.24
KR2	1656	944	128	10.67	1.68	15.75
KR3	2873	1760	133	5.45	2.11	38.72
KR4	1017	548	65	3.46	1.02	29.48
GE1	3890	2543	142	519.27	131.22	25.27
GE2	1656	944	128	641.59	184.63	28.78
GE3	2873	1760	133	19.75	10.81	54.73
GE4	1017	548	65	20.83	11.46	55.02
RGR1	3890	2543	142	1.52	0.241	15.86
RGR2	1656	944	128	0.178	0.076	42.70
RGR3	2873	1760	133	0.211	0.121	57.35
RGR4	1017	548	65	0.158	0.054	34.18

ADG1 average daily gain from birth to weaning, *ADG2* average daily gain from birth to 6 months of age, *ADG3* average daily gain from 3 to 6 months of age, *ADG4* average daily gain from 3 to 12 months of age, *KR1* Kleiber's ratio from birth to weaning, *KR2* Kleiber's ratio from birth to 6 months of age, *KR3* Kleiber's ratio from 3 to 6 months of age, *KR4* Kleiber's ratio from 3 to 12 months of age, *GE1* growth efficiency from birth to weaning, *GE2* growth efficiency from birth to 6 months of age, *GE3* growth efficiency from 3 to 6 months of age, *GE4* growth efficiency from 3 to 12 months of age, *RGR1* relative growth rate from birth to weaning, *RGR2* relative growth rate from birth to 6 months of age, *RGR3* relative growth rate from 3 to 6 months of age, *RGR4* relative growth rate from 3 to 12 months of age; ADG1, ADG2, ADG3, and ADG4 in gr. GE1, GE2, GE3, and GE4 in %; *S.D.* standard deviation, CV_p phenotypic coefficient of variation

Table 2 Least squares mean and standard errors for growth rate (g day^{-1}) and Kleiber ratio (g/ kg of metabolic weight)

Fixed effects	Traits							
	ADG1	ADG2	ADG3	ADG4	KR1	KR2	KR3	KR4
Sex of lambs	**	**	*	**	**	**	**	*
Male	$146.32^a \pm 1.39$	$118.40^a \pm 1.21$	$55.35^a \pm 1.25$	$16.92^a \pm 1.19$	$20.69^a \pm 0.14$	$11.32^a \pm 0.08$	$3.78^a \pm 0.05$	$6.65^a \pm 0.31$
Female	$129.93^b \pm 1.68$	$108.17^b \pm 1.18$	$44.25^b \pm 1.18$	$12.06^b \pm 1.24$	$16.40^b \pm 0.18$	$10.08^b \pm 0.09$	$3.19^b \pm 0.07$	$5.05^b \pm 0.30$
Type of birth	**	**	*	ns	**	ns	ns	ns
Single	$143.50^a \pm 1.04$	$110.91^b \pm 1.10$	$49.48^b \pm 1.13$	$12.06^a \pm 1.29$	$20.57^a \pm 0.15$	$10.85^a \pm 0.05$	$3.54^a \pm 0.10$	$5.42^a \pm 0.44$
Twin	$134.18^b \pm 1.19$	$114.02^a \pm 1.05$	$51.69^a \pm 1.10$	$12.20^a \pm 1.34$	$16.42^b \pm 0.17$	$10.91^a \pm 0.08$	$3.64^a \pm 0.13$	$5.63^a \pm 0.33$
Age of dam	**	**	*	**	**	**	**	*
2	$138.32^b \pm 1.84$	$110.73^b \pm 1.20$	$53.13^a \pm 1.61$	$10.08^b \pm 1.18$	$19.01^b \pm 0.34$	$10.27^b \pm 0.08$	$3.03^b \pm 0.05$	$5.85^a \pm 0.23$
3	$129.22^c \pm 1.55$	$116.56^a \pm 1.24$	$51.51^{ab} \pm 1.80$	$10.71^a \pm 1.26$	$21.89^{ab} \pm 0.12$	$10.74^a \pm 0.07$	$3.59^a \pm 0.01$	$5.59^a \pm 0.14$
4	$132.45^a \pm 1.43$	$117.90^a \pm 1.33$	$51.11^{ab} \pm 2.11$	$10.44^a \pm 1.42$	$20.12^a \pm 0.12$	$10.54^b \pm 0.08$	$3.48^a \pm 0.05$	$5.69^a \pm 0.13$
5	$128.64^c \pm 2.38$	$116.98^a \pm 1.49$	$49.83^{ab} \pm 1.87$	$10.69^a \pm 1.31$	$19.21^b \pm 0.11$	$10.32^b \pm 0.06$	$2.90^b \pm 0.06$	$5.57^a \pm 0.19$
6	$146.10^a \pm 3.11$	$114.63^a \pm 2.50$	$50.62^{ab} \pm 2.48$	$10.45^a \pm 1.62$	$19.13^b \pm 0.13$	$10.24^{ab} \pm 0.08$	$3.69^a \pm 0.04$	$5.68^a \pm 0.22$
7	$138.51^b \pm 4.05$	$113.92^a \pm 3.63$	$43.51^b \pm 3.28$	$10.18^{ab} \pm 2.34$	$19.40^b \pm 0.19$	$10.10^b \pm 0.09$	$3.54^a \pm 0.05$	$5.28^b \pm 0.51$
Year of birth	**	**	**	**	**	**	**	**

Values within a column with different superscripts differ significantly at $P < 0.05$, $^{**}P < 0.01$, *ns* non-significant effects; *ADG1* average daily gain from birth to weaning, *ADG2* average daily gain from birth to 6 months of age, *ADG3* average daily gain from 3 to 6 months of age, *ADG4* average daily gain from 3 to 12 months of age, *KR1* Kleiber's ratio from birth to weaning, *KR2* Kleiber's ratio from birth to 6 months of age, *KR3* Kleiber's ratio from 3 to 6 months of age, *KR4* Kleiber's ratio from 3 to 12 months of age

Table 3 Least squares mean and standard errors for growth efficiency (%) and relative growth rate

	Traits							
	GE1	GE2	GE3	GE4	RGR1	RGR2	RGR3	RGR4
Overall mean	544.27	641.59	19.75	20.83	1.52	0.184	0.210	0.158
Sex of lambs	**	**	**	**	**	**	**	**
Male	$642.24^{a} \pm 12.12$	$545.75^{a} \pm 6.81$	$20.55^{a} \pm 0.48$	$20.02^{a} \pm 0.66$	$1.61^{a} \pm 0.018$	$0.196^{a} \pm 0.006$	$0.216^{a} \pm 0.009$	$0.172^{a} \pm 0.007$
Female	$634.39^{b} \pm 12.20$	$539.83^{b} \pm 7.08$	$18.39^{b} \pm 0.56$	$16.44^{b} \pm 0.87$	$1.58^{b} \pm 0.017$	$0.172^{b} \pm 0.009$	$0.198^{b} \pm 0.005$	$0.149^{b} \pm 0.009$
Type of birth	**	**	*	*	**	ns	*	*
Single	$624.31^{a} \pm 9.22$	$538.18^{a} \pm 4.69$	$17.69^{b} \pm 0.36$	$17.33^{b} \pm 0.73$	$1.60^{a} \pm 0.015$	$0.187^{a} \pm 0.007$	$0.201^{b} \pm 0.008$	$0.169^{b} \pm 0.010$
Twin	$612.72^{b} \pm 8.48$	$532.50^{b} \pm 5.25$	$21.48^{a} \pm 0.40$	$19.06^{a} \pm 0.78$	$1.40^{b} \pm 0.018$	$0.188^{a} \pm 0.006$	$0.208^{a} \pm 0.006$	$0.173^{a} \pm 0.011$
Age of dam	*	ns	**	**	**	ns	*	ns
2	$640.37^{b} \pm 16.27$	$541.93^{a} \pm 8.40$	$21.83^{a} \pm 0.61$	$18.42^{a} \pm 0.78$	$1.54^{a} \pm 0.008$	$0.189^{a} \pm 0.009$	$0.206^{a} \pm 0.008$	$0.167^{a} \pm 0.005$
3	$638.65^{b} \pm 14.43$	$542.37^{a} \pm 7.39$	$20.51^{ab} \pm 0.49$	$17.07^{ab} \pm 0.78$	$1.51^{a} \pm 0.006$	$0.177^{a} \pm 0.007$	$0.204^{a} \pm 0.006$	$0.161^{a} \pm 0.008$
4	$632.82^{c} \pm 14.28$	$542.70^{a} \pm 7.45$	$20.11^{ab} \pm 0.62$	$18.34^{a} \pm 1.42$	$1.48^{b} \pm 0.009$	$0.169^{a} \pm 0.006$	$0.195^{a} \pm 0.009$	$0.158^{a} \pm 0.007$
5	$648.08^{a} \pm 13.92$	$542.65^{a} \pm 8.24$	$19.83^{b} \pm 0.88$	$16.45^{b} \pm 1.64$	$1.49^{a} \pm 0.011$	$0.168^{a} \pm 0.008$	$0.198^{b} \pm 0.011$	$0.164^{a} \pm 0.009$
6	$644.35^{a} \pm 13.09$	$542.59^{a} \pm 8.39$	$19.62^{b} \pm 1.48$	$18.72^{a} \pm 1.21$	$1.46^{b} \pm 0.084$	$0.173^{a} \pm 0.008$	$0.205^{a} \pm 0.081$	$0.166^{a} \pm 0.008$
7	$645.22^{a} \pm 13.36$	$541.11^{a} \pm 8.68$	$17.51^{b} \pm 1.94$	$18.16^{a} \pm 2.44$	$1.40^{c} \pm 0.094$	$0.170^{a} \pm 0.009$	$0.204^{a} \pm 0.094$	$0.164^{a} \pm 0.009$
Year of birth	**	**	**	**	**	**	**	**

Values within a column with different superscripts differ significantly at $P < 0.05$, $^{**}P < 0.01$, *ns* non-significant effects; *GE1* growth efficiency from birth to weaning, *GE2* growth efficiency from birth to 6 months of age, *GE3* growth efficiency from 3 to 6 months of age, *GE4* growth efficiency from 3 to 12 months of age, *RGR1* relative growth rate from birth to weaning, *RGR2* relative growth rate from birth to 6 months of age, *RGR3* relative growth rate from 3 to 6 months of age, *RGR4* relative growth rate from 3 to 12 months of age

Table 4 The log-likelihood of six different models for studied traits in Kermani lambs

Traits	Model					
	1	2	3	4	5	6
ADG1	−12726.675	−12723.63	−12722.335	−12720.93	*−12718.01*	−12718.01
ADG2	−8827.61	*−8807.24*	−8820.94	−8817.05	−8816.9	−8807.25
ADG3	−10249.53	−10238.41	*−10214.06*	−10218.11	−10217.45	−10213.06
ADG4	*−7186.26*	−7191.31	−7194.39	−7188.28	−7186.23	−7185.21
KR1	−4887.35	−4885.61	−4885.13	−4885.1	*−4883.16*	−4883.13
KR2	−2932.15	*−2930.07*	−2932.67	−2931.99	−2932.93	−2930.05
KR3	−3994.56	−3984.13	*−3933.76*	−3933.98	−3934.04	−3933.71
KR4	*−7186.26*	−7187.31	−7186.89	−7187.28	−7187.23	−7185.21
GE1	−15484.6	−15483.8	−15483.21	−15483.18	*−15481.24*	−15481.22
GE2	−8293.4	*−8260.06*	−8261.86	−8262.89	−8259.77	−8259.81
GE3	−9759.44	−9752.10	*−9737.16*	−9743.48	−9740.66	−9736.15
GE4	*−8170.64*	−8175.16	−8174.93	−8174.92	−8175.82	−8170.56
RGR1	−4623.13	−4622.20	−4622.87	−4620.95	*−4617.71*	−4616.255
RGR2	−5324.07	*−5321.89*	−5323.93	−5322.83	−5322.35	−5321.43
RGR3	−4255.2	−4248.99	*−4236.66*	−4238.63	−4238.60	−4235.07
RGR4	*−5640.18*	−5640.94	−5640.43	−5641.23	−5641.89	−5639.70

ADG1 average daily gain from birth to weaning, *ADG2* average daily gain from birth to 6 months of age, *ADG3* average daily gain from 3 to 6 months of age, *ADG4* average daily gain from 3 to 12 months of age, *KR1* Kleiber's ratio from birth to weaning, *KR2* Kleiber's ratio from birth to 6 months of age, *KR3* Kleiber's ratio from 3 to 6 months of age, *KR4* Kleiber's ratio from 3 to 12 months of age, *GE1* growth efficiency from birth to weaning, *GE2* growth efficiency from birth to 6 months of age, *GE3* growth efficiency from 3 to 6 months of age, *GE4* growth efficiency from 3 to 12 months of age, *RGR1* relative growth rate from birth to weaning, *RGR2* relative growth rate from birth to 6 months of age, *RGR3* relative growth rate from 3 to 6 months of age, *RGR4* relative growth rate from 3 to 12 months of age. ADG1, ADG2, ADG3, and ADG4 in gr. GE1, GE2, GE3, and GE4 in %

but no direct-maternal genetic covariance is included in the model. Model 2, which includes direct genetic and maternal permanent environmental impact, was selected as the best model to describe ADG2, KR2, GE2, and RGR2. Based on the LRT for ADG3, KR3, GE3, and RGR3, models 3, 4, 5, and 6 had the highest log-likelihood, but there was no significant difference between them ($P > 0.05$). Therefore, the model with the smallest number of parameters (model 3) was chosen as the most appropriate. It contained direct genetic and maternal genetic effects without direct-maternal genetic covariance. For the traits ADG4, KR4, GE4, and RGR4, the model without maternal effects, i.e., model 1, was determined to be the most appropriate model.

Genetic parameters and additive coefficient of variations

Based on the best model, Table 5 presents the estimates of (co) variance components and genetic parameters for each trait. The estimates of heritability for growth-related traits ranged from 0.13 (ADG1) to 0.17 (ADG4). For efficiency-related traits, estimates of heritability were ranged between 0.04 (RGR2) and 0.16 (KR4). Pre-weaning traits were influenced by either maternal genetics or maternal permanent environmental factors. These results showed that maternal effects are an important contributor and should be considered in the breeding program.

Correlations between traits

Estimates of phenotypic (below the diagonal) and genetic (above the diagonal) correlations among traits are illustrated in Table 6. Genetic correlations between different trait combinations ranged from −0.687 (KR1-GE4) to 0.946 (ADG1-KR1), whereas phenotypic correlations varied from −0.648 for ADG1-GE4 to 0.918 for ADG3-KR3.

Discussion

Description of the traits

The phenotypic coefficient of variation for ADG, KR, GE, and RGR in the pre-weaning stage was lower than that for other periods, which indicates less influence of the environment on the pre-weaning traits ADG, KR, GE, and RGR compared with other traits. The mean value of the traits related to the pre-weaning period was higher than other traits. Compared to Vardhan Reddy et al. (2017)

Table 5 Genetic parameters and variance components for the studied traits based on the most appropriate model

Traits	Model	σ^2_a	σ^2_{pe}	σ^2_m	σ^2_e	σ^2_P	h^2	pe^2	m^2	CV$_A$
ADG1	5	168.86	120.13	145.95	902.26	1337.2	0.13 ± 0.06	0.09 ± 0.03	0.11 ± 0.03	9.30
ADG2	2	75.48	29.11	–	406.82	511.41	0.15 ± 0.03	0.06 ± 0.02	–	7.45
ADG3	3	19.08	–	11.05	106.4	136.53	0.14 ± 0.04	–	0.08 ± 0.04	8.98
ADG4	1	2.33	–	–	11.43	13.76	0.17 ± 0.02	–	–	10.04
KR1	5	0.88	0.98	0.75	4.98	7.59	0.12 ± 0.04	0.13 ± 0.05	0.10 ± 0.05	5.35
KR2	2	0.35	0.33	–	1.99	2.67	0.13 ± 0.03	0.12 ± 0.04	–	5.54
KR3	3	1.10	–	0.53	6.01	7.64	0.14 ± 0.04	–	0.07 ± 0.03	19.24
KR4	1	0.089	–	–	0.481	0.570	0.16 ± 0.03	–	–	8.62
GE1	5	679.25	982.12	655.45	10505.32	12822.14	0.05 ± 0.05	0.08 ± 0.03	0.05 ± 0.01	4.79
GE2	2	856.72	798.11	–	12002.64	13657.47	0.06 ± 0.05	0.06 ± 0.02	–	4.56
GE3	3	10.72	–	8.78	181.12	200.62	0.05 ± 0.04	–	0.04 ± 0.02	16.58
GE4	1	24.45	–	–	330.85	355.30	0.07 ± 0.03	–	–	23.74
RGR1	5	0.0018	0.0009	0.0014	0.0262	0.0303	0.06 ± 0.02	0.03 ± 0.01	0.05 ± 0.02	2.79
RGR2	2	0.0008	0.0006	–	0.0168	0.0182	0.04 ± 0.01	0.03 ± 0.01	–	16.85
RGR3	3	0.0007	–	0.0004	0.0123	0.0135	0.05 ± 0.03	–	0.03 ± 0.01	12.60
RGR4	1	0.0007	–	–	0.01	0.0107	0.07 ± 0.01	–	–	16.75

ADG1 average daily gain from birth to weaning, *ADG2* average daily gain from birth to 6 months of age, *ADG3* average daily gain from 3 to 6 months of age, *ADG4* average daily gain from 3 to 12 months of age, *KR1* Kleiber's ratio from birth to weaning, *KR2* Kleiber's ratio from birth to 6 months of age, *KR3* Kleiber's ratio from 3 to 6 months of age, *KR4* Kleiber's ratio from 3 to 12 months of age, *GE1* growth efficiency from birth to weaning, *GE2* growth efficiency from birth to 6 months of age, *GE3* growth efficiency from 3 to 6 months of age, *GE4* growth efficiency from 3 to 12 months of age, *RGR1* relative growth rate from birth to weaning, *RGR2* relative growth rate from birth to 6 months of age, *RGR3* relative growth rate from 3 to 6 months of age, *RGR4* relative growth rate from 3 to 12 months of age, CV_A additive genetic coefficient of variation

in brown Nellore sheep and Bangar et al. (2020) in Harnali sheep, our results are consistent with their findings in the pre-weaning growth phase. Similar results were also obtained in the study of Jafaroghli et al. (2021) on Moghani sheep. Differences in climatic conditions and management systems during different growth phases could be the main reason for different growth rates of lambs in pre- and post-weaning phases. According to Ali et al. (2021), during the pre-weaning period, lambs are less affected by environmental factors due to maternal support. After weaning, lambs lose maternal care and rely on themselves for feeding, some stress factors cause the lamb's growth rate to decrease.

Non-genetic effects

The growth rate of lambs decreased as they aged, which is in line with the results of other researchers (Jalil-Sarghale et al., 2014; Ghafouri-Kesbi and Gholizadeh, 2017). The reduced maternal effect as lambs grew old likely explains the lower growth rate. The sex of the lamb was significant ($P < 0.01$) for all traits recorded in the pre-and post-weaning phases. According to the results, male lambs had higher ADG, KR, GR, and RGR than female lambs, similar to those reported in other studies (Sallam et al., 2019; Gautam et al., 2019). The difference between the two sexes was also significant, indicating that sex from birth to yearling has a major influence on the growth traits of Kermani lambs. The observed difference between male and female lambs may be due to the effect of sex hormones and physiological and genetic differences between male and female lambs. The birth type of lambs significantly affected ADG1, KR1, GE1, and RGR1 ($P < 0.01$) and ADG3, GE3, RGR3, GE4, and RGR4 ($P < 0.05$), but this factor did not affect ADG4, KR2, KR3, RGR2, and KR4 ($P > 0.05$). Single-born lambs had higher ADG, KR, GE, and RGR ($P < 0.01$) than twin lambs before weaning, but their superiority was lost after weaning. The reason for the superiority of single-born lambs over twin-born lambs is that single lambs have better nutritional status than twin lambs in the mother's uterus and at birth. There were similar results reported on Baluchi sheep by Ghafouri-Kesbi and Gholizadeh (2017), and on Dorper sheep by Kiya et al. (2019). All traits considered except GE2, RGR2, and RGR4 were significantly influenced by the dam's age at lambing ($P < 0.01$), as observed by Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep. Several factors contribute to the significant effect of ewe age on the studied traits, including maternal effects, nursing, and mothering ability. The fixed effect of birth year on all studied traits was significant ($P < 0.01$). Likely, differences in agro-climatic conditions, management practices, and pasture quality and quantity play a major role in explaining why the birth year

Table 6 Genetic (above the diagonal) and phenotypic correlations (below the diagonal) ± S.E. among the studied traits

Traits	ADG1	ADG2	ADG3	ADG4	KR1	KR2	KR3	KR4	GE1	GE2	GE3	GE4	RGR1	RGR2	RGR3	RGR4
ADG1	–	0.859	0.904	0.891	0.946	0.899	0.921	0.324	0.492	0.304	−0.431	−0.049	0.621	0.441	0.203	0.201
		(0.14)	(0.17)	(0.12)	(0.13)	(0.10)	(0.22)	(0.03)	(0.09)	(0.11)	(0.07)	(0.01)	(0.10)	(0.14)	(0.05)	(0.02)
ADG2	0.682	–	0.825	0.547	0.831	0.911	0.435	0.229	0.664	0.778	0.548	0.401	−0.376	0.381	0.674	0.431
	(0.13)		(0.09)	(0.15)	(0.11)	(0.05)	(0.19)	(0.05)	(0.11)	(0.14)	(0.09)	(0.18)	(0.04)	(0.14)	(0.19)	(0.21)
ADG3	−0.332	0.626	–	0.845	0.323	0.642	0.939	0.628	0.401	0.299	0.354	0.397	0.711	0.632	0.764	0.589
	(0.03)	(0.10)		(0.11)	(0.14)	(0.11)	(0.13)	(0.20)	(0.09)	(0.13)	(0.14)	(0.10)	(0.06)	(0.14)	(0.11)	(0.08)
ADG4	−0.303	0199	0.454	–	0.389	0.425	0.384	0.912	0.289	0.625	0.344	0.661	−0.283	0.812	0.399	0.764
	(0.05)	(0.11)	(0.10)		(0.15)	(0.12)	(0.10)	(0.13)	(0.05)	(0.09)	(0.14)	(0.11)	(0.03)	(0.09)	(0.14)	(0.17)
KR1	0.845	0.701	−0.107	−0.225	–	0.849	−0.241	−0.389	0.829	0.841	−0.612	−0.687	0.761	0.631	−0.361	−0.531
	(0.14)	(0.17)	(0.02)	(0.02)		(0.11)	(0.03)	(0.05)	(0.10)	(0.15)	(0.06)	(0.05)	(0.11)	(0.14)	(0.04)	(0.07)
KR2	0.542	0.852	0.698	0.183	0.504	–	0.311	0.217	0.374	0.936	0.611	0.781	0.190	0.482	−0.312	−0.420
	(0.11)	(0.12)	(0.12)	(0.05)	(0.09)		(0.21)	(0.05)	(0.11)	(0.06)	(0.15)	(0.10)	(0.11)	(0.21)	(0.08)	(0.03)
KR3	−0.389	0.484	0.918	0.467	−0.381	0.494	–	0.428	0.382	0.801	0.762	0.824	−0.301	0.211	0.120	0.599
	(0.10)	(0.09)	(0.10)	(0.11)	(0.04)	(0.12)		(0.23)	(0.14)	(0.13)	(0.13)	(0.16)	(0.04)	(0.12)	(0.01)	(0.08)
KR4	−0.114	0.121	0.389	0.831	−0.442	0.148	0.618	–	−0.112	0.743	0.606	0.854	−0.411	−0.331	−0.206	0.131
	(0.02)	(0.06)	(0.06)	(0.15)	(0.02)	(0.03)	(0.13)		(0.02)	(0.10)	(0.10)	(0.14)	(0.08)	(0.03)	(0.05)	(0.10)
GE1	0.420	−0.334	−0.234	−0.202	0.855	−0.631	−0.090	−0.304	–	−0.211	0.052	−0.489	0.561	0.481	−0.099	−0.101
	(0.08)	(0.07)	(0.03)	(0.03)	(0.10)	(0.06)	(0.02)	(0.04)		(0.08)	(0.01)	(0.08)	(0.14)	(0.16)	(0.04)	(0.02)
GE2	−0.396	0.856	−0.456	0.542	−0.637	0.577	0.173	0.289	−0.334	–	0.189	0.164	0.088	0.351	0.124	0.084
	(0.04)	(0.10)	(0.08)	(0.09)	(0.04)	(0.09)	(0.09)	(0.10)	(0.09)		(0.10)	(0.08)	(0.04)	(0.13)	(0.06)	(0.03)
GE3	−0.614	0.498	0.860	0.515	−0.398	0.398	0.824	0.315	−0.479	0.646	–	0.739	−0.206	0.116	0.712	0.448
	(0.03)	(0.10)	(0.16)	(0.12)	(0.09)	(0.09)	(0.14)	(0.08)	(0.10)	(0.09)		(0.11)	(0.03)	(0.08)	(0.14)	(0.12)
GE4	−0.648	0.377	0.489	0.834	−0.274	0.425	0.587	0.813	−0.513	0.572	0.706	–	−0.463	0.321	0.208	0.498
	(0.09)	(0.14)	(0.11)	(0.09)	(0.03)	(0.09)	(0.11)	(0.14)	(0.05)	(0.09)	(0.11)		(0.03)	(0.12)	(0.10)	(0.13)
RGR1	0.678	−0.261	−0.181	0.139	0.802	0.099	−0.212	−0.279	0.874	−0.189	−0.241	−0.174	–	−0.369	0.251	−0.261
	(0.13)	(0.05)	(0.0.2)	(0.02)	(0.08)	(0.09)	(0.06)	(0.06)	(0.13)	(0.09)	(0.03)	(0.07)		(0.09)	(0.10)	(0.09)
RGR2	−0.398	0.712	0.678	0.584	−0.377	0.712	0.091	0.154	0.134	0.555	0.606	0.477	−0.510	–	0.316	0.272
	(0.08)	(013)	(0.14)	(0.12)	(0.09)	(0.09)	(0.09)	(0.06)	(0.06)	(0.09)	(0.14)	(0.12)	(0.09)		(0.14)	(0.11)
RGR3	−0.547	0.521	0.891	0.499	−0.191	0.329	0.612	0.243	0.234	0.249	0.773	0.734	−0.231	0.481	–	0524
	(0.06)	(0.17)	(0.10)	(0.13)	(0.06)	(0.09)	(0.10)	(0.09)	(0.09)	(0.09)	(0.10)	(0.08)	(0.04)	(0.11)		(0.13)
RGR4	−0.516	0.212	0.757	0.792	−0.387	0.288	0.521	0.783	−0.147	0.201	0.603	0.649	−0.218	0.611	0.716	–
	(0.04)	(0.10)	(0.09)	(0.15)	(0.02)	(0.09)	(0.15)	(0.11)	(0.02)	(0.09)	(0.10)	(0.15)	(0.02)	(0.10)	(0.13)	

ADG1 average daily gain from birth to weaning, *ADG2* average daily gain from birth to 6 months of age, *ADG3* average daily gain from 3 to 6 months of age, *ADG4* average daily gain from 3 to 12 months of age, *KR1* Kleiber's ratio from birth to weaning, *KR2* Kleiber's ratio from birth to 6 months of age, *KR3* Kleiber's ratio from 3 to 6 months of age, *KR4* Kleiber's ratio from 3 to 12 months of age, *GE1* growth efficiency from birth to weaning, *GE2* growth efficiency from birth to 6 months of age, *GE3* growth efficiency from 3 to 6 months of age, *GE4* growth efficiency from 3 to 12 months of age, *RGR1* relative growth rate from birth to weaning, *RGR2* relative growth rate from birth to 6 months of age, *RGR3* relative growth rate from 3 to 6 months of age, *RGR4* relative growth rate from 3 to 12 months of age

has a significant effect on the traits analyzed (Tesema et al., 2021; Areb et al., 2021).

Model selection

Based on LRT, model 5 was determined to be the most appropriate model to describe the variability in the pre-weaning ADG, KR, GE, and RGR. It was found that adding the maternal genetic effect and maternal permanent environmental effect to the model increased log-likelihood significantly ($P < 0.05$) when compared to other models. Similar to our results, Mohammadi et al. (2013), Mandal et al. (2015) and Javanrouh et al. (2021) proposed model 5 as the best model for ADG1, KR1, and GR1 traits in Makooei, Muzaffarnagari, and Iran-Black sheep breeds, respectively. The results indicate that maternal genetic effects and maternal permanent environmental effects significantly affect pre-weaning ADG, KR, GE, and RGR. Thus, growth rate and efficiency-related traits are considerably influenced by maternal effects. In contrast, Ghafouri-Kesbi and Gholizadeh (2017) offered model 3, which includes only direct genetic and maternal genetic effects as the most suitable model for the genetic evaluation of ADG1 and KR1. In addition, Sallam et al. (2019) recommended model 4, which contains direct genetic and maternal permanent environmental effects as the best model for estimating the variance components of pre-weaning ADG in Barki lambs. Based on the log-likelihood values, model 1, model 2, and model 3 were selected as the best model for the studied traits in the post-weaning growth periods. The addition of maternal genetic effect or maternal permanent environmental effect as a second random effect in the analysis models for ADG4, KR4, GE4, and RGR4 did not improve the log-likelihood ($P > 0.05$) compared with model 1, which included only the additive genetic effect. Therefore, model 1 was the most suitable model for the genetic analysis of ADG4, KR4, GE4, and RGR4. Javanrouh et al. (2021) proposed the model, including only the additive genetic effect as the best model for ADG4 and KR4 in Iran-Black sheep, which is consistent with the current results.

The inclusion of permanent maternal environmental effects in the simple model significantly improved log-likelihood. Therefore, model 2 was considered the best-fitting model for ADG2, KR2, GE2, and RGR2. This result implied the absolute importance of permanent maternal environmental effects for the genetic analysis of these traits in Kermani sheep. In agreement with the current results, Ghafouri-Kesbi and Abbasi (2019) proposed a similar model for the same traits in Makooei sheep. In addition, other authors have demonstrated that a model that incorporates direct genetic effects along with maternal permanent environmental effects (model 2) is the best model to explain the traits ADG2, KR2, and GE2 (Eskandarinasab et al., 2010; Mohammadi et al. 2015). When the maternal genetic effect was added to the simple model, the log-likelihood improved significantly and thus model 3 was determined to be the best model for ADG3, KR3, GE3, and RGR3. Mohammadi et al. (2013) in Makooei and Kiya et al. (2019) in Dorper sheep reported similar results.

Genetic parameter and heritability estimates

Direct heritability of growth rate before weaning was in the indicated range (0.01–0.38) for Sardi and Santa Ines sheep (Aguirre et al., 2016; Boujenane and Diallo, 2017). The estimate of h^2 for ADG1 (0.13) was consistent with the value proposed by Mohammadi et al. (2010) for Sanjabi sheep. However, lower values were obtained by Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi (0.06) and by Javanrouh et al. (2021) in Iran-Black (0.08) sheep. Conversely, higher estimates were reported by Sallam et al. (2019) in Barki lambs and Aguirre et al in Santa Ines sheep. For post-weaning ADG, literature estimates of h^2 range from 0.03 in Iran-Black sheep (Javanrouh et al., 2021) to 0.41 in Nellore sheep (Illa et al., 2018). The estimate of h^2 for ADG2 (0.15) was similar to that obtained in Lori sheep (Mohammadi et al., 2015), while Illa et al. (2018) obtained a higher estimate. The differences in the estimates of h^2 can be explained by differences in sheep breed and environmental and management conditions. As well as, recording conditions and data structure, the method used for estimation of (co)variance components and genetic parameters, and the models of data analysis also influence the results (Mohammadi et al., 2019).

For the ADG in the pre- and post-weaning phases, the estimates of CV_A were 9.30%, 7.45%, 8.98%, and 10.04%, respectively. Among these traits, the lowest estimate of heritability was related to ADG1, while ADG2 had the lowest CV_A. This result, confirms previous reports obtained by Ghafouri-Kesbi and Gholizadeh (2017), who estimated a CV_A of 9.29% for ADG in Baluchi sheep from weaning to 6 months of age and showed that traits with low heritability do not necessarily have a low CV_A. In another species, the Raini goat, Mokhtari et al. (2019) reported a CV_A for ADG1 of 8.37% which is consistent with the values obtained in this study. Due to environmental perturbations, a trait with low h^2 can have a high CV_A and vice versa. Houle (1992) showed that when the residual error variance for a trait is high, heritability does not provide a good means of measuring genetic variation and suggested the additive genetic coefficient of variations (CV_A). In such situation, CV_As can be high in traits with low heritability and vice versa. The estimates of heritability and variability (measured by CV_A) for growth rate at different stages showed low additive genetic variability. Traits with high heritability and variability are expected to have maximum genetic improvement. According to the estimates of CV_A, the growth rate in different growth phases has a slight additive genetic variability. Therefore, selection may not be the best strategy to improve ADG in Kermani lambs.

For efficiency-related traits, estimates of h^2 ranged from 0.05 (RGR2) to 0.16 (KR4). For pre-weaning KR, the h^2 value was estimated to be 0.12, which is in agreement with the value reported by Venkataramanan et al. (2016) and Ghafouri-Kesbi and Abbasi (2019) but lower than the value reported by Javanrouh et al. (2021) for Iran-Black sheep. Nevertheless, the estimate of h^2 for KR during the pre-weaning phase was higher than that reported by Mohammadi et al. (2010) for Sanjabi sheep, and by Bangar et al. (2020) for Harnali sheep. In agreement with the present results, Jafaroghli et al. (2021) in Moghani sheep reported the value of heritability for growth efficiency before and after weaning to be 0.07 and 0.06, respectively. Similar, low estimates of h^2, ranging from 0.02 to 0.06, were reported by Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep and Javanrouh et al. (2021) in Iran-Black sheep. These low estimates of h^2 for GEs in the pre- and post-weaning phases could be due to the management practices and flock structure over the years. In sheep, generally little literature on estimating heritability for RGR. Studies by Ghafouri-Kesbi and Abbasi (2019) in Makooei and Javanrouh et al. (2021) in Iran-Black of sheep also reported low estimates of h^2 for RGR at different phases. Similarly, Ghafouri-Kesbi and Rafiei-Tari (2015) studied RGR in Zandi sheep and reported h^2 estimates of 0.13 and 0.10 for pre- and post-weaning periods, which are slightly higher than the current values.

In Afshari sheep, heritability estimates were 0.15, 0.06, and 0.05 for RGR1, RGR3, and RGR4, respectively (Ghafouri-Kesbi and Eskandarinasab, 2018). In general, the estimated values of h^2 for efficiency-related traits were low and previous studies, including Ghafouri-Kesbi and Eskandarinasab (2018) in Makooe sheep, Jafaroghli et al. (2021) in Moghani sheep, and Javanrouh et al. (2021) in Iranian Black sheep, reported low estimates of h^2 for ADG, KR, GE, and RGR. Such low estimates of heritability reduce the rate of genetic gain by selection. In sheep production, however, KR, GE, and, RGR traits are highly valuable, and any improvement in these traits has a significant impact on profitability, especially in intensive systems where feed costs are high (Ghafouri-Kesbi and Gholizadeh, 2017).

In the present study, maternal components significantly affect all traits except ADG4, KR4, GE4, and RGR4. The estimated values of m^2 ranged from 0.03 for RGR3 to 0.11 for ADG1, and the ratio of maternal permanent environmental variance to phenotypic variance (pe2) was 0.03 for RGR1 and RGR2, and 0.13 for KR1. Similar findings were observed in Baluchi sheep by Ghafouri-Kesbi and Gholizadeh (2017). The traits related to the growth period before weaning were significantly affected by maternal genetic effects. It thus suggests that selecting these traits requires consideration of maternal genetic effects. The estimates of m^2 for pre-weaning ADG, KR, GE, and RGR were lower than h^2 estimates, indicating that genes controlling maternal performance were less influential than genes carried by lambs. The present estimate of m^2 for ADG1 (0.11) was similar to that reported for Mehraban sheep (Mohammadi et al., 2015), whereas Jafaroghli et al. (2021) reported a lower estimate.

Ghafouri-Kesbi and Abbasi (2019) reported a higher estimate of m^2 for ADG, KR, GE, and RGR of Makooei sheep in the growth phase before weaning than the present result as 0.16, 0.15, 0.13, and 0.13, respectively. Javanrouh et al. (2021) also determined that pre-weaning ADG, KR, GE, and RGR in Iran-Black sheep have maternal heritability estimates of 0.04, 0.06, 0.13, and 0.14, respectively. In Moghani sheep, Jafaroghli et al. (2021) reported m^2 for pre-weaning ADG, KR, and GE as 0.03, 0.07, and 0.04, respectively. According to our study, the influence of maternal genetic effects on the above traits decreased in the post-weaning stage. It is consistent with Tesema et al. (2021) who showed that maternal genetic factors affect the pre-weaning traits of lambs and its impact decreases as the lambs grew old. The permanent maternal environment (pe^2) for ADG1 was estimated to be 0.09 ± 0.03. Similar results were observed by Kamjoo et al. (2014) and Jalil-Sarghale et al. (2014) in different sheep breeds, while Mokhtari et al. (2013) reported a higher pe^2 value in Arman sheep. Nevertheless, lower estimates of pe^2 of ADG1 have been reported in other sheep breeds (Singh et al., 2016; Sallam et al., 2019). The pe^2 estimates of 0.06 and 0.13 for ADG2 and KR2, respectively, agreed well with the results of Ghafouri-Kesbi and Abbasi (2019) in Baluchi sheep. The value of permanent environmental variance decreased from 0.09 for ADG1 in the pre-weaning phase to 0.06 for ADG2 in the post-weaning phase. Similar to these results, Singh et al. (2016) worked on growth traits in Marwari sheep and showed that pe^2 for average daily gain decreased with growing lambs. A study conducted by Javanrouh et al. (2021) showed that for the traits related to efficiency, maternal influences are as important as their genetic potential and environmental factors. In order to achieve optimal development of ADG, KR, GE, and RGR in the pre-weaning period, both direct and maternal influences must be considered.

Genetic and phenotypic correlations

In general, our estimates were within the range reported in the literature for different trait combinations (Ghafouri-Kesbi and Gholizadeh, 2017; Jafaroghli et al., 2021; Javanrouh et al., 2021). There was a positive correlation between pre-weaning ADG and post-weaning growth rate and efficiency-related traits except for GE3 and GE4. Therefore, selecting any of these traits could result in a positive response to selection. Positive and high genetic correlations between ADGs and KRs indicate that lambs with higher growth rates are likely to be more efficient users of forage. Thus, selection for growth rate may improve both growth rate and feed utilization efficiency at different growth stages. The genetic correlations between the traits ADG1-KR1, ADG2-KR2, ADG3-KR3, and ADG4-KR4 were 0.941, 0.946, 0.939, and 0.912, respectively. It has been reported that Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep and Illa et al. (2018) in Nellore sheep have found similar high and positive estimates.

In general, positive genetic correlations indicated that some traits share some common genes, and selection based on one trait leads to the genetic evolution of another. Despite a positive genetic correlation among pre- and post-weaning ADGs, phenotypic correlations between ADG1–ADG3 and ADG1–ADG4 (−0.332 ± 0.03 and −0.301 ± 0.05, respectively) were negative, suggesting that lambs that grew faster in the pre-weaning phase grew slower in the post-weaning period and vice versa. Similar to our results, Mohammadi et al. (2015) in Lori sheep, Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep, and Illa et al. (2018) in Nellore sheep found a negative phenotypic correlation between pre- and post-weaning ADG -0.074, −0.265, and −0.08, respectively. Similarly, in Muzaffarnagari sheep, Mandal et al. (2015) reported a negative phenotypic correlation between pre- and post-weaning ADG.

A negative phenotypic correlation between pre- and post-weaning ADG with a positive genetic correlation could be due to the compensatory growth of some poorly reared lambs in the post-weaning period (Abegaz et al., 2005). The highest genetic and phenotypic correlations were observed between ADG1–KR1 (0.946 ± 0.13) and ADG3–KR3 (0.918 ± 0.10), which was consistent with the results of IlIa et al. (2018) in Nellore and Javanrouh et al. (2021) in Iran-Black sheep. Genetic and phenotypic correlations between pre-weaning RGR and post-weaning RGRs ranged from −0.369 (RGR1–RGR2) to 0.721 (RGR2–RGR4), respectively. Several researchers reported similar results (Ghafouri-Kesbi and Gholizadeh, 2017; Ghafouri-Kesbi and Eskandarinasab, 2018). Phenotypic correlations indicated that the traits with favorable association respond similarly to environmental conditions. Therefore, improving the herd's environmental conditions of the flock may increase animals' phenotypic mean due to a clear phenotypic correlation between the studied traits.

Conclusions

According to our findings, both direct additive genetic effects and maternal impacts played a significant role in the phenotypic variation of Kermani sheep ADG, KR, GE, and RGR traits. Thus, the model for the genetic evaluation of Kermani sheep must take into account maternal effects in addition to the direct genetic influences. The low heritabilities and additive genetic coefficient of variation for the traits studied indicated that selection would not be very effective in altering these traits, and relatively little genetic progress could be made by selection. Considering the low heritability and additive genetic coefficient of variation of the traits studied, selection would not be very effective in altering these traits.

Data availability Not applicable.

Declarations

Ethics approval This study did not require manipulation or modification of the usual handling of the animals, since we have worked directly with the routine records.

Consent to participate Not applicable.

Consent for publication The authors give their consent for publication.

Conflict of interest The authors declare no competing interests.

References

Abegaz, S., van Wyk, J. B., and Olivier, J. J. 2005. Model comparisons and genetic and environmental parameter estimates of growth and the Kleiber ratio in Horro sheep, South African Journal of Animal Science, 35 (1), 30-40.

Aguirre, E. L., Mattos, E. C., Eler, J. P., Barreto Neto, A. D., and Ferraz, J. B. 2016. Estimation of genetic parameters and genetic changes for growth characteristics of Santa Ines sheep, Genetics and Molecular Research, 15(3), 1–12.

Ali, A., Javed, K., Zahoor, I., and Anjum, K. M. 2020. Analysis of non-genetic and genetic influences underlying the growth of Kajli lambs, South African Journal of Animal Science, 50 (4), 613–625.

Areb, E., Getachew, T., Kirmani, M. A., Abate, Z., and Haile, A. 2021. Estimation of (co)variance components, genetic parameters, and genetic trends of growth traits in community-based breeding programs of Bonga sheep, Animal Bioscience, 34, 1451–1459.

Bangar, Y. C., Magotra, A., and Yadav, A. S. 2020. Estimates of covariance components and genetic parameters for growth, average daily gain and Kleiber ratio in Harnali sheep, Tropical Animal Health and Production, 52, 1–6.

Boujenane, I., and Diallo, I. T. 2017. Estimates of genetic parameters and genetic trends for pre-weaning growth traits in Sardi sheep, Small Ruminant Research, 146, 61–68.

Eskandarinasab, M., Ghafouri-Kesbi, F., and Abbasi, M. A. 2010. Different models for evaluation of growth traits and Kleiber ratio in an experimental flock of Iranian fat-tailed Afshari sheep. Journal of Animal Breeding and Genetics, 127, 26–33.

Gautam, L., Kumar Nagda, R. A., and Ashraf Waiz, A. 2019. Growth modeling and genetic analysis on growth traits of Sirohi goat under field conditions, Iranian Journal of Applied Animal Science, 9 (1), 115–124.

Ghafouri-Kesbi, F., and Abbasi, M. A. 2019. Autosomal and X-linked additive genetic effects on body weight, body measurements and efficiency-related traits in sheep, Small Ruminant Research, 180, 21–26.
Ghafouri-Kesbi, F., and Eskandarinasab, M. 2018. Heritability of relative growth rate and its relationship with growth-related traits in Afshari sheep, Gene Reports, 12, 225–229.
Ghafouri-Kesbi, F., and Gholizadeh, M. 2017. Genetic and phenotypic aspects of growth rate and efficiency-related traits in sheep, Small Ruminant Research, 149, 181–187.
Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics 130, 195–204.
Illa, S. K., Gollamoori, G., and Nath, S. 2018. Direct and maternal variance components and genetic parameters for average daily body weight gain and Kleiber ratios in Nellore sheep, Tropical Animal Health and Production, 5(1), 155–163.
Jafaroghli, M., Soflaee Shahrbabak, M., Ghafouri-Kesbi, F., and Mokhtari, M. 2021. Estimation of the autosomal and sex-linked genetic parameters for growth rate and efficiency-related traits in Moghani sheep, Journal of Livestock Science and Technologies, 9 (1), 69v75.
Jalil-Sarghale, A., Kholghi, M., Moradi Shahrebabak, M., Moradi Shahrebabak, M., Mohammadi, H., and Abdollahi-Arpanahi, R. 2014. Model comparisons and genetic parameter estimates of growth traits in Baluchi sheep, Slovak Journal of Animal Science, 47, 12–18.
Javanrouh, A., Baneh, H., and Ghafouri-Kesbi, F. 2021. Different models for genetic evaluation of growth rate and efficiency-related traits in Iran-Black sheep, Journal of Livestock Science and Technologies, 9 (2), 67–74.
Kamjoo, B., Baneh, H., Yousefi, V., Mandal, A., and Rahimi, G. 2014. Genetic parameter estimates for growth traits in IranBlack sheep, Journal of Applied Animal Research, 42 (1), 79–88.
Kesbi FG, Tari AR 2015. Relative growth rate in sheep: heritability and relationship with absolute growth rate and body weight, Songklanakarin Journal of Science and Technology, 37, 21–27.
Kiya, G. K., Pedrosa, V. B., Avelar Muniz, K. F., Gusmao, A. L., and Pinto, L. F. B. 2019. Estimates of the genetic parameters of a Dorper flock in Brazil, Small Ruminant Research 171, 57–62.
Kleiber, M. 1947. Body size and metabolic rate. Physiological Reviews, 27, 511–541.
Mandal, A., Karunakaran, M., Sharma, D. K., Baneh, H., and Rout, P. K. 2015. Variance components and genetic parameters of growth traits and Kleiber ratio in Muzaffarnagari sheep, Small Ruminant Research, 132, 79–85.
Meyer, K. 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. Livestock Production Science, 52, 187–199.
Meyer, K. 2013. WOMBAT. A tool for mixed model analysis in quantitative genetics by REML, J. Zhejiang Uni. SCIENCE B 8, 815–821. https://doi.org/10.1631/jzus.2007.B0815].
Mohammadi, Y., Rashidi, A., Mokhtari, M. S., and Esmailizadeh, A. K. 2010. Quantitative genetic analysis of growth traits and kleiber ratios in Sanjabi sheep, Small Ruminant Research, 93, 88–93.
Mohammadi, H., Shahrebabak, M. M., Vatankhah, M., and Shahrebabak, H. M. 2013. Direct and maternal (co)variance components, genetic parameters, and annual trends for growth traits of Makooei sheep in Iran, Tropical Animal Health and Production, 45(1), 185–191.
Mohammadi, K., Abdollahi-Arpanahi, R., Amraei, F., Mohamadi, E. M., and Rashidi, A. 2015 Genetic parameter estimates for growth and reproductive traits in Lori sheep, Small Ruminant Research, 131, 35–42.
Mohammadi, Y., Mokhtari, M. S., Saghi, D. A., and Shahdadi, A. R. 2019. Modeling the growth curve in Kordi sheep: The comparison of non-linear models and estimation of genetic parameters for the growth curve traits, Small Ruminant Research,177, 117–123.
Mokhtari, M. S., Moradi Shahrebabak, M., Moradi Shahrebabak, H., and Sadeghi, M. 2013. Estimation of (co) variance components and genetic parameters for growth traits in Arman sheep, Journal of Livestock Science and Technologies, 1 (1), 35–43.
Mokhtari, M., Razmkabir, M., Ghiasi, H., and Mohammadi, Y. 2019. Genetic evaluation of growth rate and efficiency related traits in Raeini Cashmere Goat, Iranian Journal of Applied Animal Science, 9 (2), 275–282.
Rashidi, A., Mokhtari, M. S., Safi Jahanshahi, A., and Mohammad Abadi, M. R. 2008. Genetic parameter estimates of pre-weaning growth traits in Kermani sheep, Small Ruminant Researh, 74,165–171.
Sallam, A. M., Ibrahim, A. H., and Samir, M. 2019. Estimation of genetic parameters and variance components of pre-weaning growth traits in Barki lambs, Small Ruminant Research, 173, 94–100.
SAS. 2009. User's Guide, 2nd SAS Institute, Cary NC, version 9.2.
Sefidbakht, N. 2011. Future aspect of sustainable animal production in Iran, focusing on the sheep and goat. Proceedings of the 1st Seminar Animal Production Tropical Environmental, Shahid Bahonar University of Kerman, Kerman, Iran.
Singh, H., Pannu, U., Narula, H. K., Chopra, A., Naharwara, V., and Bhakar, S. K. 2016. Estimates of (co)variance components and genetic parameters of growth traits in Marwari sheep, Journal of Applied Animal Research, 44, 27–35.
Tavakolian, J. 2000. An Introduction to Genetic Resources of Native Farm Animals in Iran. Animal Science Genetic Research Institute Press, Tehran.
Tesema, Z., Alemayehu, K., Kebede, K., Getachew, T., Deribe, B., Tilahun, M., Kefale, A., Lakew, M., Zegeye, A., Belayneh, N., Yizengaw, L., Shibeshi, M., Tiruneh, S., Worku, G., Kiros, S., and Bishaw, M. 2021. Evaluation of growth and efficiency-related traits of different levels of Boer x Central Highland crossbred goats, Heliyon, 7, 1–7.
Tortereau, F., Marie-Etancelin, C., Weisbecker, J. L., Marcon, D., Bouvier, F., Moreno-Romieux, C., and François, D. 2020. Genetic parameters for feed efficiency in Romane rams and responses to single-generation selection, Animal, 14, 681–687.
Vardhan Reddy, D., Sreenivas, D., Gnanaprakash, M., and Harikrishn, C. H. 2017. Genetic analysis of growth rates of Nellore brown sheep, International Journal of Current Microbiology and Applied Sciences, 6, 832–836.
Venkataramanan, R., Subramanian, A., Sivaselvam, S. N, Sivakumar, T., Sreekumar, C. 2016. Genetic parameters for Kleiber ratio and its relation to other body weight traits in Nilagiri and Sandyno sheep, Indian Journal of Animal Sciences, 86 (5), 559–563.

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