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Different models for genetic evaluation of growth rate and efficiency-related traits in Iran-Black sheep

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Abstract Six univariate animal models, including various combinations of the maternal effects, were used to estimate the (co)variance components and genetic parameters for growth rates from birth to weaning (GR1), weaning to six months of age (GR2) and weaning to 12 months of age (GR3), and the corresponding Kleiber ratios (KR1, KR2, KR3), efficiencies of growth (EF1, EF2, EF3) and relative growth rates (RGR1, RGR2, RGR3) in Iran-Black sheep. The most appropriate model for each trait was identified by the Akaike Information Criterion (AIC). In addition, bivariate analyses were used to estimate the (co)variance components between traits. Estimated values of the direct heritability (±S.E.) were 0.08±0.03, 0.07±0.03 and 0.05±0.03 for GR1, GR2, and GR3; 0.25±0.07, 0.05±0.02, and 0.01±0.01 for KR1, KR2 and KR3; 0.05±0.03, 0.04±0.02 and 0.00±0.01 for EF1, EF2 and EF3; and 0.09±0.04, 0.05±0.02 and 0.00±0.01 for RGR1, RGR2 and RGR3, respectively. There was little additive genetic variation in growth rate and efficiency-related traits in Iran-Black sheep and therefore, a small genetic progress would be expected through selection. All the studied traits were affected by maternal effects. Estimates of the maternal heritability ($\boldsymbol{m^2}$) ranged from 0.02 (GR3) to 0.13 (EF1) and estimates of the ratio of maternal permanent environmental variance to phenotypic variance ($\boldsymbol{c^2}$) ranged from 0.03 (GR2, GR3, KR2) to 0.09 (GR1, EF3). Genetic correlations between the studied traits varied from -0.63 (KR1 and EF3) to 0.99 (KR2 and EF3), and the phenotypic correlations ranged from -0.65 (GR1 and EF3) to 0.98 (EF2 and RGR2 and EF3 and RGR3). The study also showed the importance of inclusion of efficiency-related traits in selection programs to improve the biological characteristics of Iran-Black sheep.

Keywords: sheep, animal model, heritability, growth, Kleiber ratio.

Introduction

Sheep population in Iran is approximately 48.5 million, which comprises of 28 well recognized breeds and ecotypes (https://www.amar.org.ir). This large population plays a major role in the economy of rural communities of the country. Except Zel, other Iranian sheep breeds are fat-tailed, a desirable characteristic which provides a valuable energy source for the animal during migration and in winter (Emmam Jomeh Kashan et al., 2005). Iran-Black, the first composite sheep breed in Iran, was developed in 1975 by crossing of Baluchi ewes with Chios rams and *vice versa* at the Abbasabad Sheep Breeding Station (Kamjoo et al., 2014) with the aim of producing a breed with higher reproductive performance and greater tolerance to the harsh environmental conditions compared to Baluchi breed. Mokhtari et al. (2014) reported that Iran-Black had larger litter size, better growth performance, and tolerance to harsh environmental conditions compared to Baluchi sheep.

In Iran, the primary goal of the sheep breeding is to increase the efficiency of meat production because of the increasing demands for lamb and mutton as a direct consequence of population growth and improving the living standards. Selection for body weight, without considering the growth efficiency, will increase the nutritional requirements for expressing the genetic potential. It, consequently, increases the cost of meat production especially under intensive conditions. According to the reports, the price of meat and mutton has significantly increased over the recent years (Cheraghi and Gholipour, 2010), and there is a need for strategies aimed at decreasing the cost of sheep meat production. One efficient strategy would be to focus on both growth performance and efficiency of feed utilization simultaneously, because feed constitutes the greater part of meat production costs (Tortereau et al., 2020). It is known that individual sheep differ in their ability to utilize feed (Dass et al., 2004). This provides an opportunity for selecting the most efficient animals, those with lower maintenance requirements. Measures of feed efficiency such as the Kleiber ratio (Kleiber, 1947), growth efficiency (Dass et al., 2004), and relative growth rate (Fitzhugh and Taylor, 1971) can be used to achieve this goal. In order to design selection programs, knowledge of genetic parameters such as heritability and genetic correlations between traits is necessary. Although, genetic parameters for production and reproductive traits of Iran-Black sheep are available (Rashidi, 2013; Ahmadpanah et al., 2016), there is no reports on the genetic parameters for the traits related to efficiency in this breed. Hence, the aim of the present study was to estimate the genetic parameters for growth rate, Kleiber ratio, efficiency of growth and relative growth rate in Iran-Black sheep.

Materials and methods

Flock management

Data were obtained from the Abbasabad Sheep Breeding Station, located in Khorasan Razavi province of Iran. In mid 1970s, a breeding program was started in this station aiming to develop Iran-Black breed by crossing Baluchi rams and Chios ewes and *vice versa*. The first lamb was born in 1975 and the flock has been maintained as a close flock so far. In this flock, mating season starts from mid-August and continues to September. Young ewes are exposed to fertile rams for the first time at approximately 18 months of age. Groups of 10-12 ewes are allocated to a fertile ram. Lambing commences in mid-January and ends in February (Ahmadpanah et al., 2016). Upon birth, newborns are weighed and ear-tagged and identified to their parents (Kamjoo et al., 2014), and their birth date, sex and birth type are recorded. Lambs are weaned at approximately 3 months of age. After weaning, the ewes and lambs are reared separately. Ewes are kept in the flock for a maximum of 7 parities, and rams are used for 2-3 breeding seasons. From birth till 12 months of age, the lambs are weighed at three months intervals.

Traits studied

Data consisted of the birth weight (BW), weaning weight (WW), six-month weight (W6), and yearling weight (YW). Three growth phases were considered: 1) birth to weaning, 2) weaning to 6 months of age, and 3) weaning to 12 months of age. The gain in weights at each growth phase were used for calculations of the growth rate (GR1, GR2, GR3), as total gain divided by the number of days in the period. The estimates of GR1, GR2 and GR3 were used to calculate the corresponding Kleiber ratios as $KR1=GR1/WW^{0.75}$, $KR2=GR2/W6^{0.75}$ and $KR3=GR3/W12^{0.75}$. The lamb body weight was used to calculate the efficiency of growth as EF1= (WW-BW/BW) ×100, EF2= (W6-WW/WW) ×100 and EF3= (YW-WW/WW) ×100. Body weights were also used to calculate the relative growth rate from birth to weaning (RGR1), weaning to 6 months of age (RGR2) and weaning to yearling age (RGR3) as:

$$RGR1=Log_e(WW)–Log_e(BW)/90$$
$$RGR2=Log_e(W6)–Log_e(WW)/90$$
$$RGR3=Log_e(YW)–Log_e(WW)/275$$

Statistical analysis

Initially, least squares analyses were conducted using the GLM procedure (SAS, 2004) to identify the fixed effects to be included into the models. The model included the birth year, lamb sex, litter size and the age of the dam at lambing. All interactions between the fixed effects were non-significant and hence were not included in the model.

Six univariate linear animal models were fitted for each trait to estimate the (co)variance components and the corresponding genetic parameters. All models included an additive direct effect, and this was the only random factor in model 1. Model 2, included the maternal permanent environmental effect which was fitted as an additional random effect, uncorrelated with all other effects in the model. Model 3, included an additive maternal effect which was fitted as the second random effect. Model 4, was the same as model 3, but allowed for a direct-maternal genetic covariance. Model 5 and Model 6 included the maternal genetic and maternal permanent environmental effects, ignoring and fitting, respectively, the direct-maternal genetic covariance. The models were as follows:

$$\mathbf{y = Xb + Z_1a + e} \qquad \text{Model 1}$$
$$\mathbf{y = Xb + Z_1a + Z_2c + e} \qquad \text{Model 2}$$
$$\mathbf{y = Xb + Z_1a + Z_3m + e} \quad \mathbf{Cov (a, m) = 0} \qquad \text{Model 3}$$
$$\mathbf{y = Xb + Z_1a + Z_3m + e} \quad \mathbf{Cov (a, m) =} A\sigma_{a,m} \qquad \text{Model 4}$$

$y = Xb + Z_1a + Z_2c + Z_3m + e$ Cov (a, m) = 0 Model 5
$y = Xb + Z_1a + Z_2c + Z_3m + e$ Cov (a, m) = $A\sigma_{a,m}$ Model 6

where, ***y*** is the vector of phenotypic observations for all individuals. **b** is the vector of fixed effects fitted with design matrix **X**. $\mathbf{Z_1}$, $\mathbf{Z_2}$ and $\mathbf{Z_3}$ are the design matrices for the direct additive genetic effects, maternal permanent environmental and maternal additive genetic effects, respectively. The co(variance) structure for the random effects was:

$$V(a) = \boldsymbol{A}\sigma_a^2 \;;\quad V(m) = \boldsymbol{A}\sigma_m^2 \;;\quad V(c) = \boldsymbol{I}_{nd}\sigma_c^2 \;;\quad V(e) = \boldsymbol{I}_n\sigma_e^2$$

where, $\boldsymbol{I}_{nd}$ and $\boldsymbol{I}_n$ are identity matrices of order equal to the number of dams and number of records, respectively. σ_a^2, σ_m^2, σ_c^2 and σ_e^2 are direct additive genetic, maternal additive genetic, maternal permanent environmental and residual (temporary environment) variances, respectively. The vectors ***a***, ***m*** and ***c*** contain the direct additive genetic, maternal additive genetic, and maternal permanent environmental effects for each individual, respectively. ***A*** is the additive numerator relationship matrix obtained from the pedigree structure. $\sigma_{a,m}$ denotes the covariance between the direct and maternal genetic effects. (Co) variance components and genetic parameters were estimated by the restricted maximum likelihood (REML) procedure as implemented in the WOMBAT program (Meyer, 2013). The Akaike's information criterion (AIC) (1974) was computed to rank the examined models. With *p* denoting the number of random (co)variance parameters to be estimated and *Log L* is the maximum likelihood, then the information criterion is defined as: AIC = -2 *Log L* + 2*p*. The model yielding the smallest AIC fits the data best.

Bivariate analyses were done to estimate the (co)variances among the traits of interest. The models applied in bivariate analyses were those fitted for each of the underlying traits in the univariate analyses, i.e., the (co)variance between direct genetic effects was estimated among all traits and the (co)variances due to maternal permanent environmental effects and maternal additive genetic effects were estimated between traits which were significantly affected by the latter.

Results and discussion

The pedigree structure included 5081 animals distributed over 12 generations (Table 1). Descriptive statistics (mean, standard deviation and coefficient of variation) for the studied traits are presented in Table 2. In the pre-weaning growth phase, the growth rate was higher than post-weaning growth phase, and was well in agreement with the findings of Mokhtari et al. (2014), Jalil-Sarghale et al. (2014) and Singh et al. (2016) in Kermani, Baluchi and Marwari breeds of sheep, respectively. Similarly, higher Kleiber ratio, efficiency of growth, and relative growth rate were observed during the pre-weaning growth phase corroborating the findings of Ghafouri-Kesbi and Rafiei-Tari (2015). The higher growth rate, Kleiber ratio, and efficiency of growth during pre-weaning period indicated that lambs would utilize feed more efficiently compared with the post-weaning period. In the pre-weaning period, the growth of lambs were mostly dependent on their mother's milk production (Baneh and Hafezian, 2009) and less affected by the environmental factors. It is reflected in the lower phenotypic coefficient of variation which shows less respond to the environmental effects. After weaning, lamb growth is more affected by the environmental factors. In Iran, lambs are commonly weaned in summer and their post-weaning growth, concomitants with limited grazing resources, leads to decreased growth rate. In this study, among all traits, KR1 had the smallest coefficient of variation, which shows less response to the environmental factors. Male lambs showed higher growth rate and greater efficiency of feed utilization than ewe lambs (Table 3) as also reported in other sheep breeds (Eskandarinasab et al. 2010; Al-Bial et al. 2012), which might be due to difference in the endocrine milieu between the male and female sexes (Baneh and Hafezian, 2009). In the pre-weaning growth phase, single-born lambs exhibited higher growth rate and efficiency-related trait as compared to twins and triplets; however, after weaning, they lose their superiority. These findings were consistent with those of Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep, who suggested that "compensatory growth" may be responsible for this phenomenon. In our study, the effect of dam age was significant only on GR1, EF1, RGR1 and RGR2. Dams with different age groups have different body size, different uterine capacity and produce different amount of milk, which impact on the body size and other phenotypic characteristics of their progenies (Baneh and Hafezian, 2009; Al-Bial et al., 2012).

Table 1. Pedigree structure of the Iran-Black sheep

Item	N
No. of generations	12
No. of animals in the pedigree file	5081
No. of animals with progeny	1308
No. of animals without progeny	3773
No. of base animals	116
No. of non-base animals	4965
No. of sires	105
No. of dams	1203
No. of grand sires	79
No. of grand dams	656
Mean inbreeding in the whole population	7.54%

Based on the AIC values estimated for GR1, KR1, and RGR1, the model 6, the most comprehensive model, was selected as the best model. This model included all the random effects (direct and maternal additive genetic, direct-maternal genetic covariance, maternal permanent environmental and residual effects). For KR1, model 5 -

had the less AIC, whereas for other studied traits, model 2 was selected as the best model. This model included the direct additive genetic effect, maternal permanent environmental effect and residual effect as random effects. Later results showed that besides the direct genetic effect, all the traits studied were also controlled by the maternal effect, even those measured after weaning. Improvement in the Log L and AIC values after including the maternal effects in the model was also reported by Singh et al. (2016) and Mahala et al. (2020).

Table 2. Data structure of selected traits in Iran-Black sheep[a]

	Trait											
	GR1	**GR2**	**GR3**	**KR1**	**KR2**	**KR3**	**EF1**	**EF2**	**EF3**	**RGR1**	**RGR2**	**RGR3**
No. of animals	4207	3929	3201	4207	3929	3201	4207	3933	3202	4207	3933	3202
No. of sires with progeny	93	98	95	93	98	95	93	98	95	93	98	95
No. of sires with progeny and record	75	80	81	75	80	81	75	80	81	75	80	81
Average number of progeny per sire	56.09	49.11	39.51	56.09	49.11	39.51	56.09	49.16	39.51	56.09	49.16	39.51
No. of dams with progeny	1054	1066	1003	1054	1066	1003	1054	1066	1003	1054	1066	1003
No. of dams with progeny and record	899	956	896	899	956	896	899	956	896	899	956	896
Average number of progeny per dam	3.99	3.68	3.19	3.99	3.68	3.19	3.99	3.68	3.19	3.99	3.68	3.19
Mean	181.70	94.24	64.56	18.59	7.19	4.05	479.65	43.63	86.31	1.84	0.37	0.22
S.D	46.73	43.40	20.89	2.37	3.01	1.01	142.99	24.29	36.86	0.28	0.18	0.06
CV	25.71	46.10	32.36	12.76	41.87	24.90	29.59	52.67	42.71	15.27	47.94	31.67

[a]**GR1**: Growth rate from birth to weaning, **GR2**: Growth rate from weaning to 6 months of age, **GR3**: Growth rate from weaning to yearling age, **EF1**: Efficiency of growth from birth to weaning, **EF2**, Efficiency of growth from weaning to six months of age, **EF3**: Efficiency of growth from weaning to yearling age, **KR1**: Kleiber ratio at weaning, **KR2**: Kleiber ratio at six months of age, **KR3**: Kleiber ratio at yearling age, **RGR1**: Relative growth rate from birth to weaning, **RGR2**: Relative growth rate from weaning to six months of age, **RGR3**: Relative growth rate from weaning to yearling age, **GR1**, **GR2** and **GR3** in gr; **EF1**, **EF2** and **EF3** in %.

Table 3. Least squares means ± S.E and environmental effects for selected traits in Iran-Black sheep.

	Trait[1]											
Factor	**GR1**	**GR2**	**GR3**	**KR1**	**KR2**	**KR3**	**EF1**	**EF2**	**EF3**	**RGR1**	**RGR2**	**RGR3**
Year	**	**	**	**	**	**	**	**	**	**	**	**
SEX	**	**	**	**	**	**	**	**	**	**	**	**
Male	173.55±1.31^{a}	90.23±1.11^{a}	58.15±0.54^{a}	18.55±0.07^{a}	7.27±0.08^{a}	3.92±0.03^{a}	476.96±4.34^{a}	44.78±0.63^{a}	84.27±1.07^{a}	1.866±0.008^{a}	0.385±0.005^{a}	0.217±0.002^{a}
Female	190.21±1.32^{b}	102.12±1.13^{b}	71.21±0.56^{b}	18.97±0.07^{b}	7.55±0.08^{b}	4.31±0.03^{b}	495.22±4.38^{b}	46.54±0.64^{b}	94±1.10^{b}	1.887±0.008^{b}	0.393±0.005^{b}	0.235±0.002^{b}
Type of birth	**	ns	**	**	**	**	**	**	**	**	**	**
1	205.44±1.41^{a}	95.73±1.16^{a}	63.19±0.57^{b}	19.25±0.07^{a}	6.9±0.08^{a}	3.85±0.03^{b}	451.39±4.66^{c}	40.28±0.66^{b}	77.18±1.13^{c}	1.823±0.009^{b}	0.35±0.005^{b}	0.203±0.002^{c}
2	173.51±1.21^{b}	96.57±1.08^{a}	65.51±0.54^{a}	18.51±0.06^{b}	7.57±0.07^{b}	4.2±0.03^{a}	461.72±4.01^{b}	47.27±0.61^{a}	92.67±1.07^{b}	1.841±0.008^{a}	0.401±0.005^{a}	0.233±0.002^{b}
3	166.69±2.2^{c}	96.22±1.93^{a}	65.34±0.93^{a}	18.52±0.11^{b}	7.75±0.13^{b}	4.28±0.05^{a}	545.17±7.28^{a}	49.43±1.1^{a}	97.55±1.84^{a}	1.964±0.014^{a}	0.417±0.008^{a}	0.242±0.003^{a}
Dam age (year)	**	ns	ns	ns	ns	ns	**	ns	ns	**	*	ns
2	174.89±1.46^{c}	95.27±1.36^{a}	65.03±0.68^{a}	18.81±0.08^{a}	7.51±0.09^{a}	4.18±0.03^{a}	514.09±4.82^{a}	47.01±0.78^{a}	92.43±1.34^{a}	1.936±0.009^{a}	0.400±0.006^{a}	0.232±0.002^{a}
3	185.19±1.49^{a}	98.71±1.35^{a}	65.37±0.67^{a}	18.91±0.08^{a}	7.53±0.09^{a}	4.11±0.03^{a}	498.33±4.93^{b}	46.44±0.77^{a}	88.44±1.33^{a}	1.899±0.009^{b}	0.395±0.006^{ab}	0.224±0.002^{a}
4	186.46±1.63^{a}	95.16±1.21^{a}	65.25±0.59^{a}	18.77±0.08^{a}	7.27±0.08^{a}	4.11±0.03^{a}	496.12±5.41^{bc}	44.63±0.68^{a}	88.43±1.17^{a}	1.877±0.01^{bc}	0.382±0.005^{b}	0.225±0.002^{a}
5	185.35±1.95^{a}	95.95±1.78^{a}	64.89±0.89^{a}	18.8±0.10^{a}	7.27±0.12^{a}	4.1±0.05^{a}	481.42±6.45^{cd}	44.31±1.01^{a}	88.12±1.76^{a}	1.865±0.012^{cd}	0.380±0.007^{b}	0.224±0.003^{a}
6	183.45±2.53^{ab}	93.42±2.39^{a}	65.72±1.21^{a}	18.7±0.13^{a}	7.21±0.16^{a}	4.13±0.06^{a}	464.66±8.37^{d}	44.52±1.36^{a}	90.00±2.40^{a}	1.839±0.016^{d}	0.379±0.010^{b}	0.227±0.004^{a}
7	175.95±3.32^{bc}	98.55±3.09^{a}	61.83±1.52^{a}	18.57±0.17^{a}	7.67±0.21^{a}	4.05±0.08^{a}	461.94±11.01^{d}	47.05±1.75^{a}	87.38±3.01^{a}	1.841±0.021^{cd}	0.399±0.013^{ab}	0.223±0.006^{a}

*:*P*< 0.05, **:*P*< 0.01, ns: not significant.

[1] **GR1**: Growth rate from birth to weaning, **GR2**: Growth rate from weaning to 6 months of age, **GR3**: Growth rate from weaning to yearling age, **EF1**: Efficiency of growth during birth to weaning, **EF2**: Efficiency of growth from weaning to six months of age, **EF3**: Efficiency of growth from weaning to yearling age, **KR1**: Kleiber ratio at weaning, **KR2**: Kleiber ratio at six months of age, **KR3**: Kleiber ratio at yearling age, **RGR1**: Relative growth rate from birth to weaning, **RGR2**: Relative growth rate from weaning to six months of age, **RGR3**: Relative growth rate from weaning to yearling age, **GR1**, **GR2** and **GR3** in gr; **EF1**, **EF2** and **EF3** in %.

[a,b] Within columns, means with common superscript (s) are not different (*P*>0.05).

Variance components and genetic parameters for GRs, KRs, EFs and RGRs are listed in Tables 4 to 7. Estimated values of direct heritability (***h*²**) for GR1, GR2 and GR3 were 0.08, 0.07 and 0.05, respectively. In Baluchi sheep, Ghafouri-Kesbi and Gholizadeh (2017) reported identical estimates of ***h*²** for growth rate (birth to weaning, weaning to six months and weaning to yearling age) as 0.06, 0.03 and 0.10, respectively, which are close to the current estimates. In addition, Singh et al. (2016) reported estimates of ***h*²** for the pre- and post-weaning growth rates as 0.26 and 0.16, respectively. The current estimates of ***h*²** together with estimates of total heritability (h_T^2) showed low additive genetic variation in growth rate of Iran-Black sheep. In general, estimates of ***h*²** for GR in Iranian sheep are low, mostly lower than 0.2 (Eskandarinasab et al., 2010; Mohammadi et al., 2013).

Table 4. Estimates of variance components and genetic parameters for growth rates at different growth phases in Iran-Black sheep[a]

Trait	Model	σ_a^2	σ_{pe}^2	σ_m^2	$\sigma_{a,m}$	σ_e^2	σ_p^2	h^2	pe^2	m^2	$r_{a,m}$	h_T^2	AIC
GR1	1	704.247				1372.25	2076.50	0.34±0.04				0.34±0.04	32856.02
	2	268.730	272.616			1405.12	1946.46	0.14±0.04	0.14±0.02			0.14±0.04	32788.96
	3	142.863		388.566		1501.30	2032.73	0.07±0.03		0.19±0.03		0.17±0.03	32803.50
	4	138.263		271.300	147.560	1502.27	2059.39	0.07±0.03		0.13±0.03	0.76±0.22	0.24±0.04	32794.56
	5	197.492	219.819	86.9421		1439.13	1943.39	0.10±0.04	0.11±0.02	0.05±0.03		0.12±0.04	32786.44
	6	**157.147**	**182.384**	**84.3436**	**86.8979**	**1457.39**	**1968.16**	**0.08±0.03**	**0.09±0.02**	**0.04±0.02**	**0.76±0.31**	**0.17±0.04**	**32783.26**
GR2	1	106.635				1177.41	1284.05	0.08±0.03				0.08±0.03	29111.82
	2	**83.5601**	**34.5948**			**1160.81**	**1278.97**	**0.07±0.03**	**0.03±0.02**			**0.07±0.03**	**29110.10**
	3	93.4210		16.9943		1173.50	1283.92	0.07±0.03		0.01±0.01		0.09±0.03	29112.58
	4	103.765		21.4385	-12.5211	1169.89	1282.57	0.08±0.03	0.02±0.02		-0.27±0.38	0.08±0.03	29112.22
	5	83.5612	34.5926	0.213991		1160.81	1278.97	0.07±0.03	0.03±0.02	0.00±0.01		0.07±0.03	29112.10
	6	99.4053	40.0729	3.76050	-19.3324	1152.89	1276.80	0.08±0.03	0.03±0.02	0.00±0.01	-1.0±failed	0.06±0.03	29113.02
GR3	1	34.6337				266.328	300.962	0.12±0.04				0.12±0.04	19423.87
	2	21.5189	10.5450			265.416	297.480	0.07±0.03	0.04±0.02			0.07±0.03	19421.96
	3	16.1819		10.3417		271.268	297.792	0.05±0.03		0.04±0.02		0.07±0.03	19422.24
	4	11.6928		7.11315	9.11980	271.918	299.844	0.04±0.03		0.02±0.02	1.0±failed	0.09±0.03	19418.98
	5	**15.4897**	**7.69516**	**5.20695**		**268.326**	**296.718**	**0.05±0.03**	**0.03±0.02**	**0.02±0.02**		**0.06±0.03**	**19417.90**
	6	11.2527	5.41285	4.54794	7.15368	269.98	298.344	0.04±0.03	0.02±0.02	0.02±0.02	1.0±failed	0.08±0.03	19422.30

[a]**GR1**: Growth rate from birth to weaning, **GR2**: Growth rate from weaning to 6 months of age, **GR3**: Growth rate from weaning to yearling age.

Table 5. Estimates of variance components and genetic parameters for Kleiber ratio at different growth phases in Iran-Black sheep[a]

Trait	Model	σ_a^2	σ_{pe}^2	σ_m^2	$\sigma_{a,m}$	σ_e^2	σ_p^2	h^2	pe^2	m^2	$r_{a,m}$	h_T^2	AIC
KR1	1	1.27403				3.4406	4.71458	0.27±0.04				0.27±0.04	9554.54
	2	0.818796	0.432523			3.34075	4.59207	0.18±0.04	0.09±0.02			0.18±0.04	9512.56
	3	0.755625		0.522915		3.44461	4.72314	0.16±0.04		0.11±0.02		0.22±0.04	9517.96
	4	1.06123		0.675073	-0.26921	3.29332	4.76042	0.22±0.06		0.14±0.03	-0.32±0.16	0.21±0.04	9515.60
	5	0.749611	0.310123		0.193274	3.36426	4.61727	0.16±0.04	0.07±0.02	0.04±0.02		0.18±0.04	9508.10
	6	**1.16820**	**0.342005**	**0.292521**	**-0.291596**	**3.15651**	**4.66765**	**0.25±0.07**	**0.07±0.02**	**0.06±0.03**	**-0.50±0.18**	**0.19±0.04**	**9506.38**
KR2	1	0.344515				5.67295	6.01747	0.06±0.02				0.06±0.02	10031.42
	2	**0.277277**	**0.193255**			**5.53696**	**6.00750**	**0.05±0.02**	**0.03±0.02**			**0.05±0.02**	**10027.94**
	3	0.329806		0.030329		5.65933	6.01947	0.06±0.02		0.01±0.01		0.06±0.02	10033.22
	4	0.372922		0.048967	-0.045696	5.64111	6.01731	0.06±0.03		0.01±0.01	-0.34±0.58	0.05±0.02	10032.96
	5	0.277277	0.193252	0.00299		5.53696	6.00750	0.05±0.02	0.03±0.02	0.00±0.01		0.05±0.02	10029.94
	6	0.344411	0.206443	0.010583	-0.603687	5.50403	6.00510	0.06±0.03	0.03±0.02	0.01±0.01	-1.0±failed	0.04±0.02	10031.22
KR3	1	0.064737				0.66368	0.72842	0.09±0.03				0.09±0.03	2028.58
	2	0.024524	0.56067			0.63974	0.72033	0.03±0.02	0.08±0.02			0.03±0.02	2012.98
	3	0.0051323		0.05905		0.66103	0.72522	0.01±0.01		0.08±0.02		0.05±0.02	2005.94
	4	0.001483		0.05266	0.008754	0.66334	0.72624	0.01±0.01		0.07±0.02	0.99±failed	0.06±0.02	2005.68
	5	**0.005603**	**0.02913**		**0.03757**	**0.64886**	**0.72118**	**0.01±0.01**	**0.04±0.02**	**0.05±0.02**		**0.03±0.02**	**2004.90**
	6	0.0021375	0.029954	0.03083	0.00811	0.65081	0.72184	0.01±0.01	0.04±0.02	0.04±0.03	0.99±failed	0.04±0.02	2006.44

[a]**KR1**: Kleiber ratio at weaning, **KR2**: Kleiber ratio at six months of age, **KR3**: Kleiber ratio at yearling age.

For efficiency-related traits, the estimates of ***h*²** were between ≈0.00 (EF3 and RGR3) to 0.25 (KR1). In general, the efficiency-related traits measured in the pre-weaning phase had higher heritability as compared to that measured after weaning. For KR, the estimates of ***h*²** are abounding in the literature. In Deccani sheep, Bangar et al. (2018) reported that ***h*²** for pre- and post-weaning KRs were 0.04 and 0.16, respectively. Mahala et al. (2020) reported higher estimate of ***h*²** for KR of Avikalin sheep in the similar growth phases as the current study as 0.18, 0.14 and 0.11, respectively. For EF and RGR there is a general paucity in the literature regarding the - estimates of genetic parameters. Regarding EF, low estimates of ***h*²**, ranging from 0.05-0.06, were reported by Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep. Relative growth rate may be used as a criterion for modifying the shape of the growth curve in order to prevent undesirable consequences of selection for increased body weight (Fitzhugh and Taylor, 1971). In Zandi sheep, Ghafouri-Kesbi and Rafiei-Tari (2015) reported ***h*²** for RGR measured in the same growth phases as the current study as 0.13, 0.12 and 0.10, respectively. Furthermore, Ghafouri-Kesbi and Eskandarinasab (2018) obtained ***h*²** for RGR for Afshari sheep (0.15, 0.06 and 0.05, respectively) in the three different growth phases. The estimated values of h^2 for KR, EF and RGR showed that, only a small part of variation in the traits was explained by the additive genetic variation; therefore, a very low genetic progress would be expected through selection for these traits.

Table 6. Estimates of variance components and genetic parameters for efficiency of growth at different growth phases in Iran-Black sheep[a]

Trait	Model	σ_a^2	σ_{pe}^2	σ_m^2	$\sigma_{a,m}$	σ_e^2	σ_p^2	h^2	pe^2	m^2	$r_{a,m}$	h_T^2	AIC
EF1	1	5646.75	-	-	-	14052.9	19699.7	0.29±0.04	-	-	-	0.29±0.04	41616.36
	2	2051.41	2819.18	-	-	13868.6	18739.2	0.11±0.04	0.15±0.02	-	-	0.11±0.04	41535.32
	3	787.323	-	4214.18	-	14673.0	19674.5	0.04±0.02	-	0.21±0.02	-	0.14±0.02	41522.30
	4	696.887	-	3744.90	534.543	14733.1	19709.4	0.04±0.02	-	0.19±0.03	0.33±0.31	0.17±0.03	41526.28
	5	**901.241**	**1227.27**	**2529.22**		**14426.3**	**19084.0**	**0.05±0.03**	**0.06±0.03**	**0.13±0.04**		**0.11±0.03**	**41521.66**
	6	781.287	1266.31	1997.27	576.551	14489.1	19110.5	0.04±0.02	0.07±0.03	0.11±0.04	0.46±0.36	0.14±0.03	41522.26
EF2	1	24.6102				388.217	412.827	0.06±0.02				0.06±0.02	25129.70
	2	**17.6638**	**19.8434**			**374.567**	**412.074**	**0.04±0.02**	**0.05±0.02**			**0.04±0.02**	**25115.00**
	3	21.9366		3.84611		387.198	412.981	0.05±0.02		0.01±0.01		0.06±0.02	25116.51
	4	21.3091		3.55482	0.606106	387.515	412.985	0.05±0.03		0.01±0.01	0.07±0.1	0.06±0.02	25125.02
	5	17.6638	19.8435	0.00013		374.567	412.074	0.04±0.02	0.05±0.02	0.00±0.01		0.05±0.02	25117.00
	6	19.8666	20.2685	0.13231	-1.62126	373.447	412.093	0.05±0.03	0.05±0.02	0.00±0.01	-1.0±failed	0.04±0.02	25118.88
EF3	1	103.880				977.072	1080.95	0.10±0.03				0.10±0.03	23147.90
	2	20.4555	136.441			910.102	1067.00	0.02±0.02	0.13±0.02			0.02±0.02	23107.12
	3	0.001692		125.893		957.03	1082.92	0.00±0.01		0.12±0.02		0.06±0.02	23109.12
	4	8.20750		144.045	-22.6077	951.408	1081.05	0.01±0.01		0.13±0.03	-0.66±0.60	0.04±0.02	23108.60
	5	**0.00230**	**93.0813**	**54.8481**		**920.870**	**1068.80**	**0.00±0.01**	**0.09±0.03**	**0.05±0.03**		**0.03±0.02**	**23098.56**
	6	0.04224	92.7186	56.5491	-1.44741	920.855	1068.72	0.00±0.01	0.09±0.03	0.05±0.03	-0.94±failed	0.02±0.02	23100.56

[a]**EF1**: Efficiency of growth from birth to weaning, **EF2**: Efficiency of growth from weaning to six months of age, **EF3**: Efficiency of growth from weaning to yearling age.

Table 7. Estimates of variance components and genetic parameters for relative growth rate at different growth phases in Iran-Black sheep[a]

Trait	Model	σ_a^2	σ_{pe}^2	σ_m^2	$\sigma_{a,m}$	σ_e^2	σ_p^2	h^2	pe^2	m^2	$r_{a,m}$	h_T^2	AIC
RGR1	1	0.016549				0.05267	0.01654	0.24±0.04				0.24±0.04	-6637.46
	2	0.0061098	0.008372			0.05182	0.066307	0.09±0.03	0.12±0.02			0.09±0.03	-6705.34
	3	0.0044884		0.01185		0.05301	0.069358	0.07±0.03		0.17±0.02		0.15±0.03	-6725.14
	4	0.57423		0.01445	-0.00330	0.05233	0.692364	0.08±0.04		0.21±0.03	-0.36±0.18	0.12±0.03	-6727.84
	5	0.0046343	0.0033592	0.00760		0.05230	0.067905	0.07±0.03	0.05±0.02	0.11±0.03		0.12±0.03	-6729.68
	6	**0.005791**	**0.003313**	**0.00966**	**-0.00268**	**0.05172**	**0.06781**	**0.09±0.04**	**0.05±0.02**	**0.14±0.04**	**-0.36±0.20**	0.13±0.03	**-6731.90**
RGR2	1	0.14392				0.02093	0.022373	0.06±0.02				0.06±0.02	-9920.58
	2	**0.001047**	**0.0010628**			**0.02020**	**0.022318**	**0.05±0.02**	**0.05±0.02**			**0.05±0.02**	**-9929.54**
	3	0.0013012		0.00022		0.02085	0.022382	0.06±0.02		0.01±0.01		0.06±0.02	-9919.16
	4	0.0015217		0.00031	-0.000203	0.20748	0.022384	0.07±0.03		0.01±0.01	-0.29±0.46	0.06±0.02	-9919.36
	5	0.0012142	0.001459	0.000001		0.01993	0.022613	0.05±0.02	0.07±0.02	0.00±0.02		0.05±0.02	-9926.08
	6	0.0013599	0.1778	0.00001	-0.000154	0.02003	0.0230376	0.06±0.03	0.08±0.02	0.01±0.01	-0.97	0.05±0.02	-9921.94
RGR3	1	0.000372				0.00334	0.00372	0.10±0.03				0.10±0.03	-13248.48
	2	0.000089	0.000425			0.00315	0.003667	0.02±0.02	0.12±0.02			0.02±0.02	-13283.28
	3	0.0000012		0.00041		0.00329	0.003715	0.00±0.01		0.11±0.02		0.06±0.02	-13286.28
	4	0.0000209		0.00044	-0.000042	0.00328	0.003712	0.01±0.01		0.12±0.03	-0.43±0.68	0.05±0.02	-13286.44
	5	**0.0000044**	**0.000264**	**0.00020**		**0.00319**	**0.003673**	**0.00±0.01**	**0.07±0.03**	**0.06±0.02**		**0.03±0.02**	**-13293.00**
	6	0.006708	0.003874	0.002806	-0.00164	0.00211	0.01385	0.48±0.10	0.28±0.08	0.20±0.11	-0.38±0.20	0.40±0.08	-12283.46

RGR1: Relative growth rate from birth to weaning, **RGR2**: Relative growth rate from weaning to six months of age, **RGR3**: Relative growth rate from weaning to yearling age.

In the present study, maternal components significantly impacted on all traits. The estimates of maternal heritability (***m²***) ranged from 0.02 (GR3) to 0.13 (EF1) and the ratio of maternal permanent environmental variance to phenotypic variance (***c²***) varied from 0.03 (GR2, GR3, KR2) to 0.09 (GR1, EF3). Mohammadi et al. (2013) and Singh et al. (2016) found significant maternal effects on growth- and efficiency-related traits in different sheep breeds. When maternal genetic effects are present, total heritability (h_T^2) estimates are more informative than direct heritability to predict the phenotypic response to selection. In fact, the response to selection depends on the direct-maternal genetic correlation ($r_{a,m}$). In the case of positive correlation between direct and maternal genetic effects, total heritability is higher than direct heritability and selection for direct effects will improve the maternal effects of the trait. In contrast, when $r_{a,m}$ is negative, total heritability will be smaller than direct heritability, and phenotypic response to selection will be dampened.

Genetic correlations among the included traits ranged from -0.63 (KR1-EF3) to 0.99 (KR2-EF3) and the phenotypic correlations varied from -0.65 (GR1-EF3) to 0.98 (EF2-RGR2 and EF3-RGR3) (Table 8). The pre-weaning growth rate was positively correlated with post-weaning growth rate and efficiency-related traits except for EF3. Also, its relationship with RGR3 was low (0.05). Ghafouri-Kesbi and Gholizadeh (2017) reported negative genetic correlation between GR1 and RGR3 in Baluchi sheep. Therefore, selection for GR1 will result in genetic improvement of the growth rate and feed efficiency-related traits.

In general, the present findings showed that growth rate and efficiency-related traits in Iran Black sheep had low heritability; therefore, the expected genetic progress in these traits would be small. All the studied traits were influenced by the maternal effects; thus, maternal effects should be considered in the model of genetic evaluation. Otherwise, the accuracy of genetic evaluation will be low. Although, the heritability of efficiency-related traits were also low but by considering their importance, especially in the intensive production systems, they should be considered in selection programs in order to improve the biological efficiency of the Iran-Black sheep population.

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Conflict of interest statement

The authors declare no conflict of interest between authors and other people, institutions or organizations.

Table 8. Between-trait correlation in Iran-Black sheep[a]

Ttait 1	Trait 2	r_a	r_c	r_m	r_p
GR1	**GR2**	0.71	0.14	-	-0.02
GR1	**GR3**	0.83	-	-0.80	-0.08
GR2	**GR3**	0.97	-	-	0.53
KR1	**KR2**	-0.20	-0.16	-	-0.12
KR1	**KR3**	-0.37	-	0.35	-0.16
KR2	**KR3**	0.95	-	-	0.62
EF1	**EF2**	0.03	-0.52	-	-0.37
EF1	**EF3**	-0.42	-0.59	0.19	-0.45
EF2	**EF3**	0.79	0.88	-	0.74
RGR1	**RGR2**	-0.26	-0.06	-	-0.20
RGR1	**RGR3**	1.00	-	-0.94	0.13
RGR2	**RGR3**	0.96	-	0.99	0.72
KR1	**EF1**	-0.34	-0.06	0.37	0.37
KR1	**EF2**	-0.31	-0.31	-	-0.22
KR1	**EF3**	-0.66	-0.22	-0.07	-0.28
KR2	**EF1**	0.14	-0.44	-	-0.28
KR2	**EF2**	0.95	0.87	-	0.94
KR2	**EF3**	0.99	0.61	-	0.63
KR3	**EF1**	-0.08	-0.63	0.19	-0.38
KR3	**EF2**	0.78	0.91	-	0.66
KR3	**EF3**	0.91	0.99	0.98	0.92
EF1	**GR1**	0.36	0.45	-0.47	0.51
EF1	**GR2**	0.34	-0.02	-	-0.11
EF1	**GR3**	0.25	-	-0.43	-0.18
EF2	**GR1**	0.02	-	-0.83	-0.41
EF2	**GR2**	0.84	-	0.07	0.81
EF2	**GR3**	0.73	-	-	0.50
EF3	**GR1**	-0.04	-0.87	-0.70	-0.65
EF3	**GR2**	0.99	-0.15	-	0.44
EF3	**GR3**	0.89	-	0.99	0.77
KR1	**GR1**	0.75	0.52	0.85	0.70
KR1	**GR2**	0.25	0.09	-	0.01
KR1	**GR3**	0.37	-	0.31	-0.02
KR2	**GR1**	0.19	-0.62	-	-0.27
KR2	**GR2**	0.90	0.51	-	0.92
KR2	**GR3**	0.85	-	-	0.52
KR3	**GR1**	0.34	-0.93	-0.80	-0.39
KR3	**GR2**	0.92	-0.24	-	0.48
KR3	**GR3**	0.91	-	0.99	0.88
GR1	**RGR1**	0.60	0.08	0.10	0.60
GR1	**RGR2**	0.15	-0.90	-	-0.45
GR1	**RGR3**	0.05	-0.92	-0.58	-0.64
GR2	**RGR1**	-0.15	-0.05	-	-0.07
GR2	**RGR2**	0.77	0.41	-	0.87
GR2	**RGR3**	0.99	-0.11	-	0.46
GR3	**RGR1**	-0.31	-	0.39	0.09
GR3	**RGR2**	0.70	-	-	0.51
GR3	**RGR3**	0.56	-	-	0.80
KR1	**RGR1**	0.96	0.79	0.54	0.87
KR1	**RGR2**	-0.20	-0.29	-	-0.20
KR1	**RGR3**	-0.60	-0.21	-0.01	-0.26
KR2	**RGR1**	-0.20	-0.07	-	-0.15
KR2	**RGR2**	0.01	-	-	0.05
KR2	**RGR3**	0.99	0.68	-	0.64
KR3	**RGR1**	-0.42	0.03	0.08	-0.18
KR3	**RGR2**	0.89	0.92	-	0.66
KR3	**RGR3**	0.92	-	-	0.97
RGR1	**EF1**	-0.11	0.33	0.93	0.68
RGR1	**EF2**	-0.32	-0.06	-	-0.23
RGR1	**EF3**	-0.45	0.04	-0.21	-0.25
RGR2	**EF1**	-0.10	-0.48	-	-0.36
RGR2	**EF2**	0.97	0.98	-	0.98
RGR2	**EF3**	0.93	0.82	-	0.71
RGR3	**EF1**	-0.52	-0.61	-0.02	-0.46
RGR3	**EF2**	0.83	0.91	-	0.72
RGR3	**EF3**	0.99	0.98	0.99	0.98

[a] r_a: genetic correlation, r_c: maternal permanent environmental correlation, r_m: maternal genetic correlation, r_p: phenotypic correlation, **GR1**: Growth rate from birth to weaning, **GR2**: Growth rate from weaning to 6 months of age, **GR3**: Growth rate from weaning to yearling age, **EF1**: Efficiency of growth from birth to weaning, **EF2**: Efficiency of growth from weaning to six months of age, **EF3**: Efficiency of growth from weaning to yearling age, **KR1**: Kleiber ratio at weaning, **KR2**: Kleiber ratio at six months of age, **KR3**: Kleiber ratio at yearling age, **RGR1**: Relative growth rate from birth to weaning, **RGR2**: Relative growth rate from weaning to six months of age, **RGR3**: Relative growth rate from weaning to yearling age.

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