Estimates of (co)variance components and genetic parameters for pre-weaning body weight traits and Kleiber ratio in Sangsari sheep breed

Jamshid Ehsaninia

Department of Agriculture, Minab Higher Education Center, University of Hormozgan, Bandar Abbas, Iran

ABSTRACT

The current study aimed to estimate (co)variance components and heritability for pre-weaning body weight traits and Kleiber ratio in Sangsari sheep. Data used in this research were collected over 30 years (1986–2016) at the breeding station of Sangsari sheep. Traits considered were birth weight (BW), weaning weight (WW), pre-weaning daily gain (PWDG), and Kleiber ratio (KR). Genetic parameters were estimated by the average information restricted maximum likelihood (AI-REML) procedure, using six animal models. The most suitable model was selected using the Akaike information criterion (AIC) for each trait. Direct heritability estimates for BW, WW, PWDG and KR were 0.30 ± 0.04, 0.20 ± 0.03, 0.15 ± 0.02, and 0.13 ± 0.05, respectively. Maternal heritability estimates varied from 0.06 ± 0.02 for PWDG to 0.12 ± 0.03 for BW. The maternal permanent environmental effects for the traits of KR, WW and PWDG account for about 7%, 9% and 12% of the phenotypic variance. The estimates of the direct genetic ($r_d$) and maternal genetic ($r_m$) correlations among pre-weaning growth traits were positive and ranged from 0.21 (BW-KR) to 0.98 (WW-PWDG) and 0.27 (WW-PWDG) to 0.48 (BW-WW), respectively. Therefore, to have an accurate genetic evaluation, maternal effects need to be considered in any program aimed at improving pre-weaning growth traits. In addition, due to the existence of genetic variation for early growth traits and generally positive and medium to high genetic correlations among them, it can be concluded that in the Sangsari breed of sheep, genetic progress for these traits is possible by selection.

HIGHLIGHTS

- Genetic parameters (direct and maternal heritability) were estimated for the Sangsari breed of sheep.
- The low to moderate estimate of heritability for pre-weaning body weights and Kleiber ratio indicate that genetic improvement of these traits is possible by selection.
- Considerable genetic correlations among early body weights, pre-weaning daily weight gain, and Kleiber ratio in Sangsari sheep were estimated.

Introduction

The latest statistics indicate that the population of Iranian sheep is about 50 million heads (Molaei et al. 2019). There are 27 recognised different sheep breeds in Iran which account for almost half of livestock production (Khodabakhshzadeh et al. 2016). The Sangsari sheep is an important fat-tailed breed in the centre of Iran and is reared in the north of Semnan province, in an area called Sangsar. The main purpose of rearing this breed is lamb and mutton production. The Sangsari sheep have good fattening performance and their meat yield is about 60% of the weight before slaughter (Sheikhlu et al. 2017; Lima et al. 2019). The animals of this breed are relatively small-sized and known to be well adapted to the high ranges, long drought periods and long-distance travelling (Miraei-Ashtiani et al. 2007; Kasiryan et al. 2011). Growth performance is one of the main factors that influence the efficiency and profitability of the meat production system. A strategy to improve the efficiency of sheep production is the selection of animals based on the efficiency of feed utilisation (Ghafouri-Kesbi et al. 2011). The profitability of any sheep meat production enterprise can be influenced by factors such as early growth traits, growth rate and Kleiber ratio (Mandal et al. 2012; Jafari and Razzagzadeh 2016). Consequently,
these traits are usually used as selection criteria to increase economic efficiency. Among these, the trait of growth rate has been used as the main selection criterion in most breeding schemes for meat production. In any breeding program, an important method to get maximum returns in sheep breeding flocks is to improve the performance of growth traits by selection. This is possible by including traits such as early growth traits and Kleiber ratio in selection programs (Amarilho-Silveira et al. 2017; Ghavi Hossein-Zadeh and Gahramehani 2018). Kleiber ratio is an indirect selection method for measuring feed conversion. Several studies stated that pre-weaning growth traits are influenced by direct and maternal effects (Mohammadi et al. 2013; Mirhoseini et al. 2015). The results of these studies have shown that including the maternal effects into models caused a more accurate estimation of (co)variance and genetic parameter of these traits. Therefore, pre-weaning body weight traits are particularly important (Gholizadeh and Ghafoori-Kesbi 2015; Jannoune et al. 2015), as the maternal effect decreases with increasing age (Mohammadi et al. 2015). Taking these factors into account prevents selection bias, which may decrease the efficiency of a breeding program. Knowledge about the inheritance of important economic growth traits is needed to obtain maximum genetic improvement, taking the best animal selection program into account (Baneh et al. 2010). The heritability estimates for early body weight traits ranged from 0.01 to 0.48 (Jawasreh et al. 2018; Varkoohi et al. 2018) and for growth rate and Kleiber ratio varied from 0.01 to 0.52 (Boujenane and Diallo 2017; Latifi and Mohammadi 2018). These values indicate that they can be improved through selection. However, only a few attempts have been made to estimate genetic parameters in Sangsari sheep, and there have been limited published results on the estimates of genetic parameters for pre-weaning traits in Sangsari sheep. To our knowledge, no genetic parameters for Kleiber ratio have been reported for this breed. Therefore, the present study was performed at aiming estimation of genetic parameters for pre-weaning body weight traits and Kleiber ratio as well as the genetic correlations among these traits in Sangsari sheep.

Materials and methods

Breed and flock management

The Sangsari sheep are well adapted to arid and semi-arid areas in the centre of Iran. The native and natural pastures have an important role in their feeding animals so that flocks were grazed on natural pastures during the daytime and housed at night. Besides grazing, animals are fed with a diet comprising of alfalfa, barley gains, wheat straw and concentrate especially during winter and late pregnancy. During the mating period, each fertile ram was randomly mated with 12 ewes. The mating season took place from August to September and lambing commenced from January to February. Lambs were kept indoors and carefully managed and fed. At birth, all lambs were ear-tagged and weighted within 24 h after birth. The lambs were weaned at about 3 months of age. All lambs were weaned on the same days, but not necessarily at the same age. The identities of newborns and their parents, birth date, sex, type of birth, and birth weight were recorded.

Data

The dataset used in the current research was obtained from 1986 to 2016 at the Sangsari sheep breeding station in Damghan, Semnan province, Iran. A total of 5686 lambing records from 178 sires and 1987 dams were used in this study. The average weaning age was 90 days. Bodyweight at birth (BW), pre-weaning average daily weight gain from birth to weaning (PWDG), weaning weight at 3 months of age (WW), and pre-weaning Kleiber ratio (KR) were investigated. The structure of data used in the analysis is given in Table 1.

The increases in weight from birth to weaning were used to calculate PWDG. Kleiber ratio (KR) for the pre-weaning (birth to 3-months) period was calculated as follows:

$$KR = \frac{PWDG}{WW^{0.75}}$$

Statistical and genetic analysis

At first, a least-squares analysis was conducted using the PROC GLM procedure of the SAS software

Table 1. Characteristics of the data structure for early growth traits of Sangsari sheep.

| Item                  | BW, kg | WW, kg | PWDG, g | KR |
|-----------------------|--------|--------|---------|----|
| No. of records        | 5686   | 4981   | 4981    | 4981          |
| No. of animals        | 6048   | 5481   | 5481    | 5481          |
| No. of sires          | 178    | 169    | 169     | 169           |
| No. of dams           | 1987   | 1895   | 1895    | 1895          |
| No. of records per sires | 31.94   | 28.94   | 28.94   | 28.94          |
| No. of records per dam | 2.86    | 2.58    | 2.58    | 2.58           |
| Mean                  | 3.03   | 15.98  | 143.23  | 17.49         |
| S.D                   | 0.68   | 4.65   | 2.39    | 10.62         |
| C.V (%)               | 17.05  | 20.93  | 26.82   | 10.62         |

Abbreviations. BW: birth weight; PWDG: pre-weaning daily gain from birth to weaning; WW: weaning weight; KR: pre-weaning Kleiber ratio (PWDG/WW^{0.75}); S.D.: standard deviation; C.V.: coefficient of variation.
Table 2. The random (co)variance components used in the six models.

| Model number | (Co)variance components$^a$ | $\sigma_a^2$ | $\sigma_m^2$ | $\sigma_{pe}^2$ | $\sigma_{am}^2$ | $\sigma_e^2$ |
|--------------|-----------------------------|------------|-----------|-------------|-------------|----------|
| 1            |                             |           |           |             |             |          |
| 2            | $\checkmark$                |           |           |             |             |          |
| 3            | $\checkmark$                | $\checkmark$ |           |             |             |          |
| 4            | $\checkmark$                |           | $\checkmark$ |             |             |          |
| 5            | $\checkmark$                |           |           | $\checkmark$ |             |          |
| 6            | $\checkmark$                |           |           |             | $\checkmark$ |          |

$^a\sigma_a^2$: direct additive genetic variance; $\sigma_m^2$: maternal genetic variance; $\sigma_{pe}^2$: maternal permanent environmental variance; $\sigma_{am}^2$: direct-maternal additive genetic covariance; $\sigma_e^2$: residual variance.

(SAS 2009) to determine the significant environmental effects to be included in the model. The fixed effects included in the statistical model were the type of birth (single and twin), sex (male and female), year of lambing (1986–2014) and age of dam at lambing (2–7 years old). Age of lamb at weaning (in days) was used as a covariate effect for the trait of WW. The (co)variance components and genetic parameters were obtained by the average information restricted maximum likelihood (AI-REML) and fitting six animal models throughout using the VCE program (Groeneveld et al. 2010). The variance components included in each model are presented in Table 2. The models used were as follows:

$y = Xb + Z_a a + Z_m m + e$  \hspace{1cm} (1)
$y = Xb + Z_a a + Z_{pe} pe + e$ \hspace{1cm} (2)
$y = Xb + Z_a a + Z_m m + e \quad \text{Cov}(a,m) = 0$ \hspace{1cm} (3)
$y = Xb + Z_a a + Z_m m + Z_{pe} pe + e \quad \text{Cov}(a,m) = A \sigma_{am}$ \hspace{1cm} (4)
$y = Xb + Z_a a + Z_m m + Z_{pe} pe + e \quad \text{Cov}(a,m) = A \sigma_{am}$ \hspace{1cm} (5)
$y = Xb + Z_a a + Z_m m + Z_{pe} pe + e \quad \text{Cov}(a,m) = A \sigma_{am}$ \hspace{1cm} (6)

Where $y$ is a vector of observations for the studied traits, $b$ is a vector of fixed effects with incidence matrix $X$, $a \sim N(0, A \sigma_a^2)$ and $m \sim N(0, A \sigma_m^2)$, are vectors of direct and maternal genetic effects with incidence matrices $Z_a$ and $Z_m$, respectively, $pe \sim N(0, I_6 \sigma_{pe}^2)$ is a vector of random maternal permanent environmental effects with incidence matrix $Z_{pe}$, and $e \sim N(0, I_n \sigma_e^2)$ is a vector of residual effects. It was assumed that:

\[
\begin{bmatrix}
A \sigma_a^2 & A \sigma_{am} & 0 & 0 \\
A \sigma_{ma} & A \sigma_m^2 & 0 & 0 \\
0 & 0 & I_6 \sigma_{pe}^2 & 0 \\
0 & 0 & 0 & I_n \sigma_e^2
\end{bmatrix}
\]

Where $\sigma_a^2$ is the direct additive genetic variance, $\sigma_m^2$ is the maternal additive genetic variance, $\sigma_{pe}^2$ is the maternal permanent environmental variance, $\sigma_e^2$ is the residual variance. Also, $A$ is the additive relationship matrix, $I_6$ and $I_n$ are identity matrices of records equal to the number of dams and number of records, $\sigma_{am}$ is the covariance between direct and maternal additive genetic effects, respectively. The convergence was assumed when the variance of the function values (−2 log L) in the simplex was less than $10^{-8}$. Direct heritability ($h^2_d$), maternal heritability ($h^2_m$) and maternal permanent environmental effects ($pe^2$) were estimated as ratios of additive direct, additive maternal, and permanent environmental maternal variances to phenotypic variance, respectively.

The Akaike information criterion (AIC) was used to determine the most appropriate model for each trait as follows (Akaike 1974):

\[\text{AIC}_i = -2 \log L_i + 2p_i\]

where $\log L_i$ is the maximised log-likelihood of the model at convergence and $p_i$ is the number of parameters obtained from each model. The model with the smallest AIC was preferred as the most appropriate model.

Total heritability ($h^2_T$, Willham 1972) was calculated according to the following formula:

\[h^2_T = \frac{\sigma_a^2 + 0.5 \sigma_m^2 + 1.5 \sigma_{am}}{\sigma_p^2}\]

where $\sigma_a^2$, $\sigma_m^2$, $\sigma_{am}$ and $\sigma_p^2$ are direct additive genetic variance, maternal additive genetic, the covariance between direct and maternal additive genetic and phenotypic variance, respectively. Estimation of genetic, phenotypic, and environmental correlations was carried out using bivariate analysis applying the most suitable model which was determined in univariate analysis.

Results and discussion

Non-genetic effects

As shown in Table 1, the coefficients of variations for the studied traits were ranged from 10.62% for KR to 26.82% for PWDG. Comparing those results with the results obtained from other Iranian sheep breeds, observations for BW and WW were similar to the result reported by Mohammadi et al. (2015) and Gholizadeh and Ghafouri-Kesbi (2017). Contrary to those, Jawasreh et al. (2018) reported greater values of CV% for BW and WW in Romney sheep than the values in the current study. The least-squares means and their standard errors for the traits are given in Table 3. The results revealed that the sex, birth type, birth year of lambs and age of dam had significant effects on BW, WW and PWDG ($p<.01$). The significant effects of the age of the dam could be attributed to their nursing, maternal behavior and maternal abilities of the dam
at different ages. Also, differences in management, food availability, diseases, condition of climate and raising systems in different years, probably are reasons for significant effects of the year on pre-weaning traits in Sangsari sheep. All the considered fixed effects except for dam age had a significant effect on KR ($p < .01$), which is in line with previous reports in Afshari sheep (Eskandarinasab et al. 2010), Kourdi sheep (Shahdadi and Saghi 2016) and Deccani sheep (Bangar et al. 2018). Contrary to us, the significant effect of dam age on KR was obtained for Muzaffarnagari sheep (Mandal et al. 2015), Lori-Bakhtiari lambs (Ghafouri-Kesbi and Gholizadeh 2017) and Makuie sheep (Latifi and Mohammadi 2019). The different effect of non-genetic factors on pre-weaning body weight traits and KR can be attributed to the endocrine system of male and female lambs, limited uterine space during pregnancy and inadequate vailability of nutrients during pregnancy and early lactation, competition for milk consumption between twin lambs and differences in the maternal behaviour and mothering ability of the ewes in different parities (Rashidi et al. 2008; Gowane et al. 2011).

Higher early body weights, pre-weaning daily gain and Kleiber ratio were also found in male lambs than females. The weight difference between male and female lambs increased from 0.17 kg (5%) at birth to 1.47 kg (9%) at weaning, indicating that males are more responsive to improvements in the environmental factors, which is also in agreement with the results of Kamjoo et al. (2014) and Faid-Allah et al. (2017) studies. Single-born lambs had higher pre-weaning body weights and pre-weaning daily gain than twins, which is in agreement with results from previous studies in other sheep breeds (Boujenane et al. 2015; Boujenane and Diallo 2017). Singles have more desirable conditions for growth and hence receive more nutrients in the womb of their dams than the twins. Therefore, the type of birth has a significant influence on the weight at birth and weaning. Similar results have been reported by other researchers (Zhang et al. 2009; Mandal et al. 2012).

Model comparisons

Akaike information criterion (AIC) values under six different models with the most appropriate model (in bold-face) are given in Table 4. For all the studied traits Model 1, which included the direct additive genetic effect as the unique known random effect had the highest AIC value. The results showed that considering either maternal additive genetic effects and/or maternal permanent environmental effect in models decreased the AIC values in comparison with Model 1. Based on AIC, the most suitable model for BW was model 3, which included direct and maternal additive genetic effects, without considering covariance between them. In accordance with this study, Khorsand et al. (2014) and Amarilho-Silveira et al. (2017) suggested a similar model for BW in Texel and Afshari sheep breeds, respectively.

The appropriate model for WW and PWDG had direct additive genetic, maternal additive genetic and permanent environmental maternal effects but did not include the additive direct-maternal covariance (model 5). Similarly, Abbasi et al. (2012) proposed the same model for these traits in Baluchi sheep. The model that included only direct additive genetic effects and

Table 3. Least-squares means ± S.E for studied traits.

| Fixed effects | BW, kg | WW, kg | PWDG, g/d | KR |
|---------------|--------|--------|-----------|----|
| Birth year    |        |        |           |    |
| Birth type    |        |        |           |    |
| Sex           |        |        |           |    |
| Dam age, years|        |        |           |    |

Abbreviations. BW: birth weight; PWDG: pre-weaning daily gains from birth to weaning; WW: weaning weight; KR: pre-weaning Kleiber ratio (PWDG/WW^0.75); ns: non-significant ($p > .05$). Means with different letters in each subclass within a column differ significantly from another.

*p < .05; **p < .01.
maternal permanent environmental effects (model 2) was adequate to explain the observed variation in KR. Likewise, Mandal et al. (2015) applied the same model for KR in Muzaffarnagari sheep. Maternal permanent environmental effects had a considerable impact on variation for WW, PWDG and KR. These results are consistent with the findings of Roshanfekr (2014) in Arabi sheep and Mohammadi et al. (2013) in Shal sheep.

**Genetic parameters**

The (co)variance components and corresponding genetic parameters for pre-weaning growth traits are summarised in Table 5. Direct heritability ($h^2_d$) estimates for BW, WW, PWDG and KR were 0.30, 0.20, 0.15 and 0.13, respectively. The range of $h^2_d$ estimates for BW vary substantially from 0.01 (Amarilho-Silveira et al. 2017) to 0.49 (Varoochi et al. 2018). An estimate of $h^2_d$ for BW in the present study (0.30) was approximately in line with those of 0.32 by Safi et al. (2017) in Harnali sheep, 0.30 by Jawasreh et al. (2018) in Awassi sheep and 0.32 by Latifi and Mohammadi (2018) in Afshari sheep. However, higher direct heritabilities for BW were obtained by Gizaw et al. (2007) in Menz sheep (0.48) and Lalit et al. (2016) in Harnali sheep (0.40) and differed with the results of this study. Contrary to the result found here, the lower direct heritability estimate was reported by various scientists in different breed sheep. Neser et al. (2001) and Senemari et al. (2011) reported the estimate of 0.09 and 0.05 for Zandi and Dorper breed of sheep in Iran and South Africa. The birth weight had an important role in the profitability of sheep enterprise by influencing survival and pre-weaning growth (Rashidi et al. 2008).

The $h^2_d$ estimate of WW obtained in the current research (0.20) was within the range reported from 0.08 by Ghafouri-Kesbi and Eskandarinasab (2008) to 0.40 by Gowane et al. (2015). Similar estimates were obtained by Aguirre et al. (2016) in Santa Ines, Safi et al. (2017) in Harnali and Kiya et al. (2019) in Droper sheep breeds. The direct heritability estimate for WW in the current study was slightly lower than those reported by Lalit et al. (2016) in Harnali sheep (0.38) and Gowane et al. (2015) in Malpura sheep (0.40). In an earlier study, Miraei-Ashtiani et al. (2007) estimated a value of 0.13 for $h^2_d$ of WW in Sangsari lambs. The difference between results obtained could be explained by the model used for analysis and environmental conditions.

Literature estimates of direct heritability for early body weights have shown a decreasing trend for direct heritability with age (Abbasi et al. 2012; Ceyhan et al. 2015). After weaning where lambs experience poor environmental condition, it could result in lambs not expressing their genetic potential and consequence lower values of heritability (Abbasi et al. 2012). The moderate estimates of heritability for BW and WW in our study show that these traits have moderately heritable variation. Therefore, genetic gain in these traits may result from selection designs (Illa et al. 2019).

Likewise, the direct heritability estimate of PWDG (0.15) in the current study was in accordance with the estimated values reported by Mandal et al. (2015), Jafari et al. (2014) and Sallam et al. (2019) in Muzaffarnagari, Makuie and Barki sheep, respectively. However, these results were incompatible with those obtained by Lalit et al. (2016) in Harnali (0.40), Illa et al. (2019) in Nellore (0.37) and Latifi and Mohammadi (2019) in Afshari (0.37) sheep, who reported higher values. Other authors have also reported lower values.

---

**Table 4. AIC for studied traits under different models with the best model in bold face.**

| Model | BW | PWDG | WW | KR |
|-------|----|------|----|----|
| 1     | -20646.76 | 34385.36 | 43879.85 | 55594.34 |
| 2     | -20648.12 | 34381.45 | 43854.41 | 55583.23 |
| 3     | -20674.50 | 34378.58 | 43869.81 | 55589.74 |
| 4     | -20662.82 | 34383.88 | 43873.02 | 55587.09 |
| 5     | -20651.45 | 34376.74 | 43856.34 | 55593.89 |
| 6     | -20655.18 | 34384.08 | 43877.19 | 55588.65 |

**Table 5. Estimates of (co)variance components and genetic parameters for traits studied.**

| Components | BW | PWDG | WW | KR |
|-----------|----|------|----|----|
| $\sigma^2_a$ | 0.095 | 180.970 | 1.190 | 0.498 |
| $\sigma^2_m$ | 0.039 | 101.650 | 0.418 | 0.140 |
| $\sigma^2_e$ | 0.185 | 372.490 | 3.820 | 3.060 |
| $\sigma^2_{pe}$ | 0.319 | 1205.370 | 6.030 | 3.810 |
| $h^2_d$ | 0.300 ± 0.040 | 0.150 ± 0.020 | 0.200 ± 0.030 | 0.130 ± 0.040 |
| $h^2_m$ | 0.120 ± 0.030 | 0.060 ± 0.010 | 0.100 ± 0.020 | 0.070 ± 0.010 |
| $h^2_t$ | 0.360 | 0.190 | 0.240 | 0.130 |

Abbreviations. BW: birth weight; PWDG: pre-weaning daily gains from birth to weaning; WW: weaning weight; KR: pre-weaning Kleiber ratio (PWDG/WW 0.75).

[a] The best model is indicated in bold face.
for the mentioned trait compared to those estimated in the present study (Boujenane and Diallo 2017; Gholizadeh and Ghafouri-Kesbi 2017; Bangar et al. 2018).

The obtained direct heritability estimate of 0.13 for KR at weaning in the present study was similar to the findings of Roshanfekr (2014) for Arabi, Faid-Allah et al. (2017) for Romney and Ismail (2017) for Barki sheep. In contrast to our study, Abegaz et al. (2005) in Horro sheep, Eskandarinasab et al. (2010) in Afshari sheep and Ghafooriresi and Gholizadeh (2017) in Baluchi sheep reported lower estimates for this trait. The variations in these reports of literature may be due to the differences in sheep breed, environment and management. Additionally, factors such as genetic diversity of populations, methods used for estimating the parameters, within-population genetic variations and data structure also affect the results (Ghavi Hossein-Zadeh and Gahreman 2018). Literature estimates of direct heritability have revealed that the Kleiber ratio is a low heritable trait. The Kleiber ratio is proposed as an efficient criterion for feed efficiency under low-input range conditions and provides a good indication of how economically an animal grows (Mohammadi et al. 2011). Results of the current study indicate the presence of low additive genetic variation for Kleiber ratio in this breed. Therefore, relatively low genetic progress will be expected following selection. Despite the low estimates of $h^2_m$ for Kleiber ratio, the utilisation of Kleiber ratio in order to improve the efficiency of feed utilisation, and in consequence, a decrease in the costs of the production system, is recommended.

The estimated values for maternal heritability of BW, WW and PWDG were 0.12, 0.08 and 0.06, respectively. According to our study, the $h^2_m$ decreased as lambs grew old. This result was similar to the estimates of Ghafouri-Kesbi et al. (2011) in Zandi sheep and Mokhtari et al. (2013) in Arman sheep. Estimates of maternal heritability for BW in the present study were in accordance with those obtained by other workers (Aguirre et al. 2016; Boujenane and Diallo 2017) in different sheep breeds. However, Shahdadi and Saghi (2016) in Kourdi sheep, Maraveni et al. (2018) in Lori-Bakhteyari sheep and Kiya et al. (2019) in Dorper sheep reported higher $h^2_m$ for BW (0.20–0.59). Mohammadi, Shahrebabak, Vatankhah, et al. (2013) and Nemutandani et al. (2018) estimated lower maternal heritability estimates for BW in Makooei and South African Merino sheep, respectively. Low maternal heritability value obtained for WW (0.08) was in general agreement with Mohammadi, Shahrebabak, Vatankhah, et al. (2013) in Makooei sheep (0.08), Jafaroghi et al. (2013) in Baluchi sheep (0.07) and Latifi and Mohammadi (2018) in Afshari sheep (0.07). However, Kiya et al. (2019) in Dorper Flock (0.16) and Faid-Allah et al. (2017) in Romney sheep (0.41) reported greater maternal heritability than the value estimated in the present study. The maternal heritability was lower for WW than this estimated for BW, which emphasises the hypothesis of decreasing the maternal effect with WW (El Fadili et al. 2000) and the importance of maternal effect on young mammals (Robison 1981). In the current study, the low estimate of maternal heritability for WW may be due to pre-weaning feed conditions. Lambs receiving limited supplies of ewe’s milk may be encouraged to start eating creep feed earlier. In such a situation, the importance of milk yield of dams would decrease more rapidly when lambs were offered a high-quality pasture or grass hay and concentrate. This presumably would lead to a smaller estimate of maternal heritability at weaning (Ghafouri-Kesbi and Eskandarinasab 2008). Gowane et al. (2010) also reported that the maternal genetic effects expressed during gestation and lactation are expected to have a diminishing influence on weight as the lambs grow. These results confirm that maternal effects are as important as the additive effects, this is because of lambs in the pre-weaning period are completely dependent on their mothers.

The maternal permanent environmental (pe$^2$) effects for the traits of KR, WW and PWDG account for about 7%, 9% and 12% of the phenotypic variance. The maternal permanent environmental effect obtained for WW (0.10) was similar to the estimate reported in previous studies (Jalil-Sarghale et al. 2014; Singh et al. 2016; Boujenane and Diallo 2017). In contrast to the present estimate, Mokhtari et al. (2013) in Arman sheep (0.06) and Sallam et al. (2019) in Barki sheep (0.06) published lower values. The estimate of pe$^2$ for PWDG in our study (0.12) was similar to the reported estimates of Abegaz et al. (2005) in Horro sheep and Mandal et al. (2015) in Muzaffarnagari sheep. However, Aguirre et al. (2016) published an estimate of 0.48 for maternal permanent environmental effect of PWDG in Santa Ines sheep, which was higher than our estimate. The pe$^2$ for KR was lower (0.07) than that obtained by Abegaz et al. (2005) for Horro sheep (0.19). Similar results were also reported by other workers (Savar-Soi et al. 2011; Mandal et al. 2015; Mohammadi et al. 2015).
The permanent environmental effect (pe²) may be due to the effects of the uterine environment, the feeding level in late gestation of the ewe and maternal bevior (Kamjoo et al. 2014). The moderate pe² estimate for weaning weight indicates the importance of maternal permanent environment and maternal care during the period from birth to weaning, as lambs remained with their dams longer. Ghafouri-Kesbi et al. (2009) reported that estimates of pe² are high at birth, when direct effects are the least important, but they decrease sharply after weaning and at the highest age this effect is negligible. However, Al-Shorepy et al. (2002) found opposing results and related that although the permanent environmental effects had a higher influence on weaning weight than on birth weight, the genetic basis for these effects could not be interpreted. In addition, Meyer (2001) reported that breed differences in the importance of maternal environmental effects are important and in some breeds lower pe² is due to an earlier decline of the lactation curve than in other breeds. Results suggest that the maternal effects were maximum at weaning stage and accounted for a significant portion of the total genetic variance and then declined as the animal became independent of the mother. Therefore, these effects should be considered in breeding programs for pre-weaning traits in the Sangsari breed of sheep.

The total heritability (h²) estimates for BW, WW, PWDG and KR were 0.36, 0.24, 0.19 and 0.13, respectively. The estimate of h² for BW was high in magnitude (0.36), indicating that mass selection would be effective for improving this trait. Total heritability estimates are model sensitive (Gowane et al. 2010). Where maternal genetic effects are present, the potential response to selection might better be expressed by h² (Abegaz et al. 2005). The h² for BW in our study was similar to those obtained by Mohammadi et al. (2015) in Lori sheep (0.32) and Rashidi (2013) in Iran-Black sheep (0.34). However, higher (Gamasae et al. 2010; Aguirre et al. 2016) and lower (Mohammadi et al. 2013; Jafaroghl et al. 2013) estimates of total heritability were also reported. An estimate of h² for WW was moderate (0.19), which was in agreement with the reports of Kushwaha et al. (2009) for Chokla sheep and Gowane et al. (2010) for Malpura sheep. Since maternal genetic effects are heritable, the h² of BW and WW will be somewhat higher than the estimates of direct heritability reported. Presence of maternal genetic variance would increase the total heritability and hence the potential response to selection. Therefore, as a result, phenotypic response to selection may be accelerated by maternal genetic effects.

Table 6. Correlation estimates between studied traits under bivariate animal models.

| Trait 1 | Trait 2 | r_g | r_m | r_e | r_p |
|---------|---------|-----|-----|-----|-----|
| BW      | WW      | 0.67±0.12 | 0.48±0.09 | 0.41±0.07 | 0.35±0.07 |
| BW      | PWDG    | 0.58±0.10 | 0.30±0.08 | 0.16±0.08 | 0.14±0.09 |
| BW      | KR      | 0.21±0.05 | 0.19±0.07 | 0.09±0.04 | 0.19±0.06 |
| WW      | PWDG    | 0.98±0.09 | 0.27±0.10 | 0.81±0.19 | 0.93±0.09 | 0.84±0.10 |
| WW      | KR      | 0.81±0.12 | 0.55±0.11 | 0.69±0.09 | 0.79±0.12 |
| PWDG    | KR      | 0.92±0.10 | 0.43±0.08 | 0.57±0.12 | 0.65±0.10 |

**Correlation estimates**

Estimates of different correlations between the investigated traits are shown in Table 6. Direct additive genetic correlation estimates were higher than those of phenotypic and environmental ones. Direct additive genetic correlations among all traits were positive, ranging from low (0.21) for BW-KR to high (0.98) for WW-PWDG. A low direct additive genetic correlation value was reported for BW-KR which was in agreement with the estimates of Mohammadi et al. (2013) in Shal sheep and Mandal et al. (2015) in Muzzafarnagari sheep. The direct additive genetic correlation of 0.67 for BW-WW was similar to the estimate of 0.61 by Gholidze and Ghafouri-Kesbi (2015) in Baluchi sheep and 0.65 by Kiya et al. (2019) in Dorper sheep. The birth weight had a positive and medium genetic correlation with PWDG (0.58). Mandal et al. (2015) reported a similar value of 0.53 in Muzzafarnagari sheep. The correlations between WW and PWDG were quite high and positive for all types of correlations. A high direct genetic correlation estimate was obtained for WW-PWDG (0.98) which was in agreement with those obtained by Roshanfekr (2014) in Arabi sheep (0.89) and Mandal et al. (2015) in Muzzafarnagari sheep (0.98). They pointed out that WW and PWDG are genetically the same traits, and selection can be carried out based on one of them. The high genetic correlation between WW and PWDG indicated that quite similar genetic factors influence these traits. This indicates that selection on one of these traits will have a high genetic change on the other one. Such correlations should be considered in any sheep breeding program. The direct genetic correlation of weaning weight with KR (0.81) was high and positive, which indicates that they are controlled by similar genes and selection for WW will increase KR and the efficiency of feed utilisation in Sangsari lambs.

The additive genetic correlation estimate of 0.92 for PWDG-KR was similar to the estimate of 0.91 by
Ghafouri-Kesbi (2013) in Mehraban sheep and 0.93 by Ghafouri-Kesbi and Gholizadeh (2017) in Baluchi sheep. These results indicate that selection for Kleiber ratio increases PWDG and then indirectly the feed efficiency, which is difficult to measure individually and select based on it as a criterion. Therefore, breeders could improve KR at weaning by selecting lambs with high weaning weight. On the other hand, selection for Kleiber ratio also led to the improvement of feed efficiency. Measuring feed efficiency and selecting based on it as a criterion is costly, then by selecting based on the KR, the mean of feed efficiency is better.

Medium estimates of maternal genetic correlations for BW-WW (0.48), BW-PWDG (0.30) and WW-PWDG (0.27) were generally lower than those obtained by Jalil-Sarghale et al. (2014) but generally agreed with Mokhtari et al. (2013). Estimates of maternal permanent environmental correlation were high and positive, ranging from 0.65 (PWDG-KR) to 0.81 (WW-PWDG) among early growth traits. Environmental correlations ranged from 0.25 for BW-KR to 0.89 for WW-PWDG. Mokhtari et al. (213) reported results similar to our estimates in Arman sheep. Lower values of environmental correlation were obtained by Khorsand et al. (2014) in Afshari sheep. The environmental correlations between the studied traits in the present study are probably due to the greater similarity of environmental and management conditions. All the phenotypic correlation estimates among studied traits were positive and changed from 0.14 for BW–PWDG to 0.84 for WW–PWDG. The phenotypic correlation estimates between traits indicated the presence of desirable association among pre-weaning traits.

Conclusions

The low to moderate estimate of direct heritability for pre-weaning growth traits indicated the presence of genetic variability within the Sangsari sheep breed and genetic progress of these traits is possible by selection. The maternal genetic effects seemed to have a significant effect on the early growth traits except for KR, however, permanent environmental maternal effects were important for PWDG, WW and KR. Thus, both direct and maternal effects were found to be important for the genetic evaluation of early growth traits in this breed. The moderate to high estimates of genetic correlation among early growth traits indicated that selection for one of these traits would probably bring out a positive response of selection in the correlated one.

Ethical 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 provided by the breeding station of Sangsari sheep.

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Jamshid Ehsaninia http://orcid.org/0000-0003-1169-2973

References

Abegaz S, van Wyk JB, Olivier JJ. 2005. Model comparisons and genetic and environmental parameter esti-mates of growth and the Kleiber ratio in Horro sheep. South African J Anim Sci. 35:30–40.
Aguirre EL, Mattos EC, Eler JP, Barreto Neto AD, Ferraz JB. 2016. Estimation of genetic parameters and genetic changes for growth characteristics of Santa Inês sheep. Genet Mol Res. 15(3):1–12.
Akaike H. 1974. A new look at the statistical model identifi-cation. IEEE Trans Automat Contr. 19(6):716–723.
Al-Shorepy SA, Alhadrami GA, Abdulwahab K. 2002. Genetic and phenotypic parameters for early growth traits in Emirati goat. Small Rumin Res. 45(3):217–223.
Amarilho-Silveira F, Laurino Dionello NJ, Mendonça G, Freitas Motta J, Tiago Albandes Fernandes T, Silveira Silva N. 2017. Genetic components of birth weight of texel sheep reared in extensive system. Acta Sci Anim Sci. 40:e36481.
Baneh H, Hafezian S H, Rashidi A, Gholizadeh M, Rahimi G. 2010. Estimation of Genetic Parameters of Body Weight Traits in Ghezel Sheep. Asian Australas J Anim Sci. 23(2):149–153.
Bangar YC, Lawar VS, Nimbalkar CA, Shinde OV, Nimase RG. 2018. Heritability estimates for average daily gain and Kleiber ratio in Deccani sheep. Ind J Small Rumin. 24(1):18–21.
Boujenane I, Chikhi A, Ilbnelbachry M, Mouh FZ. 2015. Estimation of genetic parameters and maternal effects for body weight at different ages in D’man sheep. Small Rumin Res. 130:27–35.
Boujenane I, Diallo IT. 2017. Estimates of genetic parameters and genetic trends for pre-weaning growth traits in Sardi sheep. Small Rumin Res. 146:61–68.
Ceyhan A, Moore K, Mrodé R. 2015. The estimation of (co)variance components growth, reproduction, carcass, FECS and FECN traits in Lleyn sheep. Small Rumin Res. 131:29–34.
El Fadili M, Michaux C, Detilleux J, Leroy PL. 2000. Genetic parameters for growth traits of the Moroccan Timahdit breed of sheep. Small Rumin Res. 37:203–208.
Eskandarinasab M, Ghafouri-Kesbi F, Abbasi MA. 2010. Different models for evaluation of growth traits and Kleiber ratio in an experimental flock of Iranian fat-tailed Afshari sheep. J Anim Breed Genet. 127(1):26–33.
Faid-Allah E, Ghoneim E, Ibrahim AHM. 2017. Estimated variance components and breeding values for pre-eaning growth criteria in Romney sheep. JIVT. 21(2):73–82.

Gamasae VA, Hafezian SH, Ahmadi A, Banesh H, Farhadi A, Mohamadi A. 2010. Estimation of genetic parameters for body weight at different ages in Mehraban sheep. African J Biotech. 32:5218–5223.

Ghafouri-Kesbi F. 2013. (Co)variance components and genetic parameters for growth rate and Kleiber ratio in fat-tailed Mehraban sheep. Arch Anim Breed. 56(1):564–572.

Ghafouri-Kesbi F, Abbasi MA, Afrad F, Babaei M, Banesh H, Abdollahi Arpanahi R. 2011. Genetic analysis of growth rate and Kleiber ratio in Zandi sheep. Trop Anim Health Prod. 43(6):1153–1159.

Ghafouri-Kesbi F, Eskandarinasab MP. 2008. An evaluation of maternal influences on growth traits: the Zandi sheep breed of Iran as an example. J Anim Feed Sci. 17(4):519–529.

Jafari S, Hashemi A, Darvishzadeh R, Manafiazar G. 2014. Genetic parameters of live body weight, body measurements, greasy fleece weight, and reproduction traits in Makuie sheep breed. Spanish J Agric Res. 12:653–663.

Jafari S, Razzagzadeh S. 2016. Genetic analysis and the estimates of genetic and phenotypic correlation of growth rates, Kleiber ratios, and fat-tail dimensions with birth to weaning live body weight traits in Makuie sheep. Trop Anim Health Prod. 48(3):667–672.

Jafaroghli M, Rashidi A, Mokhtari MS, Mirzamohammadi E. 2013. Estimation of genetic parameters for body weight traits in Baluchi sheep. J Livest Sci Tech. 128:1–18.

Jannoune A, Boujenane I, Falaki M, Dergaoui L. 2015. Genetic analysis of live weight of Sardie sheep using random regression and multi-trait animal models. Small Rumin Res. 130:1–7.

Jawasreh K, Ismail ZB, Iya F, Cañá-Medina-Bustos VJ, Valencia-Posadas M. 2018. Genetic parameter estimation for pre-weaning growth traits in Jordan Awassi sheep. Vet World. 11(2):254–258.

Kamjoo B, Banesh H, YOUSEF V, Mandal A, Rahimi G. 2014. Genetic parameter estimates for growth traits in Iran-Black sheep. J Appl Anim Res. 42(1):79–88.

Kasiriyan MM, Hafezian SH, Hassan N. 2011. Genetic polymorphism BMP15 and GDF9 genes in Sangsfari sheep of Iran. Int J Genet Mol Biol. 3:31–34.

Khodabakhshzadeh R, Mohammadabadi MR, Esmaillizadeh AK, Moradi Shahrebabak H, Bordbar F, Ansari Namin S. 2016. Identification of point mutations in exon 2 of GDF9 gene in Kermani sheep. Pol J Vet Sci. 19(2):281–289.

Khosand A, Hafezian SH, Teimouri-Yansari A, Farhadi A. 2014. Genetic parameters of direct and maternal effects for growth traits of Afshari sheep. Iranian J Appl Anim Sci. 4:69–74.

Kiya GK, Pedrosa VB, Avelar Muniz KF, Gusmão AL, Pinto LFB. 2019. Estimates of the genetic parameters of a Dorper flock in Brazil. Small Rumin Res. 171:57–62.

Kushwaha BP, Mandal A, Arora AL, Kumar R, Kumar S, Notter DR. 2009. Direct and maternal (co)variance components and heritability estimates for body weights in Chokla sheep. J Anim Breed Genet. 126(4):278–287.

Latifi M, Moghaddam A. 2018. Analysis of genetic parameters and genetic trends for early growth traits in Iranian Afshari sheep. Bio Anim Hosp. 34(3):289–301.

Latifi M, Mohammadi A. 2019. Estimation of genetic parameters of Autosomal and sex-linked pre-weaning traits in Makuie sheep using multivariate analysis. Genetika. 51(2):365–375.

Lima MJ, Rokouei M, Dashab GR, Seyedalani AR, Faraji-Aroukh H. 2019. Genetic and non-genetic analysis of lamb
survival in Sangsari sheep by Gibbs sampling method. Small Rumin Res. 177:56–60.

Mandal A, Dass G, Rout PK. 2012. Model comparisons for estimation of genetic parameters of pre-weaning daily weight gains in Muzaffarnagari sheep. Small Rumin Res. 106(2–3):118–124.

Mandal A, Karunakaran M, Sharma DK, Baneh H, Rout PK. 2015. Variance components and genetic parameters of growth traits and Kleiber ratio in Muzaffarnagari sheep. Small Rumin Res. 132:79–85.

Maraveni M, Vatankhah M, Eydivandi S. 2018. Phenotypic and genetic analysis of Lori-Bakhtiari lamb’s weight at different ages for autosomal and sex-linked genetic effects. Iranian J Appl Anim Sci. 8:67–75.

Meyer K. 2001. Estimates of direct and maternal covariance functions for growth of Australian beef calves from birth to weaning. Genet Sel Evol. 33(5):487–514.

Mirhoseini SZ, Zare J, Ghavi Hossein-Zadeh N, Khanzadeh H, Seidavi A, Laudadio V, Cataldo C, Tufarellic V, Selvaggic M. 2015. Estimation of genetic parameters for body weight traits and pelt quality score in Iranian Karakul sheep. Small Rumin Res. 132:67–71.

Mohammadi K, Abdollahi-Arpanahi R, Amraei F, Mirza Mohamadi E, Rashidi A. 2015. Genetic parameter estimates for growth and reproductive traits in Lori sheep. Small Rumin Res. 131:35–42.

Mohammadi H, Shahrebabak MM, Shahrebabak HM, Bahrami A, Dorostkar M. 2013. Model comparisons and genetic parameter estimates of growth and the Kleiber ratio in Shal sheep. Arch Anim Breed. 56(1):264–275.

Mohammadi H, Moradi Shahrebabak M, Vatankhah M, Moradi Shahrebabak H. 2013. Direct and maternal (co)variance components, genetic parameters, and annual trends for growth traits of Makooei sheep in Iran. Trop Anim Health Prod. 45(1):185–191.

Mohammadi K, Rashidi A, Mokhtari MS, Beigi Nassiri MT. 2011. The estimation of (co) variance components for growth traits and Kleiber ratios in Zandi sheep. Small Rumin Res. 99(2–3):116–121.

Mokhtari MS, Moradi-Shahrebabak M, Moradi-Shahrebabk H, Sadeghi M. 2013. Estimation of (co)variance components and genetic parameters for growth traits in Arman sheep. J Livest Sci Tech. 1:38–47.

Molaei V, Otarod V, Abdollahi D, Lühken G. 2019. Lentivirus susceptibility in Iranian and German sheep assessed by determination of TMEM154 E35K. Animals. 9(9):685–614.

Nemutandani KR, Snyman MA, Olivier WJ, Visser C. 2018. Estimation of genetic parameters and comparison of breeding values for body weight with different models in a South African Merino stud. Small Rumin Res. 106(2–3):118–124.

Neser F, Erasmus GJ, Van Wyk JB. 2001. Genetic parameter estimates for pre-weaning weight traits in Dorper sheep. Small Rumin Res. 40(3):197–202.

Rashidi A. 2013. Genetic parameter estimates of body weight traits in Iran-Black sheep. J Livest Sci Tech. 1:50–56.

Rashidi A, Mokhtari MS, Safi JA, Mohammad AMR. 2008. Genetic parameter estimates of pre-weaning growth traits in Kermani sheep. Small Rumin Res. 74(1–3):165–171.

Robison OW. 1981. The influence of maternal effects on the efficiency of selection; a review. Livest Prod Sci. 8(2):121–137.

Roshanfekr H. 2014. Estimation of genetic parameters for Kleiber ratio and trends for weight at birth and weaning in Arabi sheep. Int J Adv Biol Biom Res. 2:2830–2836.

SAS Institute, 2009. SAS User’s Guide Version 9.1: Statistics. SAS Institute Inc., Cary, NC.

Safi AS, Ali Kaleri H, Muhammad G, Raja Kaleri R, Kaleri A, Safi MA, Ullah A, Kamal Uddin Mandokhial KU, Siddiq M. 2017. Effect of genetic parameters on some growth performance traits of Harnai sheep. J Basic Appl Sci. 13: 60–62.

Sallam AM, Ibrahim AH, Samir M. 2019. Estimation of genetic parameters and variance components of pre-weaning growth traits in Barki lambs. Small Rumin Res. 173:94–100.

Savar-Sofla S, Nejati-Javaremi A, Abbasi MA, Vaez-Torshizi R, Chamani M. 2011. Investigation on direct and maternal effects on growth traits and the Kleiber ratio in Moghani Sheep. World Appl Sci J. 14:1313–1319.

Senemari M, Kalantar M, Khalajzadeh S, Gholizadeh M. 2011. Genetic and phenotypic parameters of body weight in Zandi sheep. African J Biotech. 10(68):15444–15449.

Shahdadi AR, Sagihi DA. 2016. Estimating genetic parameters of body weight traits in Kourdi sheep. Iranian J Appl Anim Sci. 6:657–663.

Sheikhoul M, Ahmadi M, Shakhoseini M. 2017. Pedigree analysis of the closed nucleus of Iranian Sangsari sheep. J Res Agric and Anim Sci. 4:1–7.

Singh H, Pannu U, Narula HK, Chopra A, Naharwara V, Bhakar SK. 2016. Estimates od (co)variance components and genetic parameters of growth traits in Marwari sheep. J Appl Anim Res. 44(1):27–35.

Varkoohi S, Bani-Saadat SH, Razzagh-Zadeh S. 2018. Estimation of genetic parameters for growth and body measurement traits in different ages in Iranian Makuei sheep. Iranian J Appl Anim Sci. 8:77–82.

Willham RL. 1972. The role of maternal effects in animal breeding. 3. Biometrical aspects of maternal effects in animals. J Anim Sci. 35(6):1288–1293.

Zhang CY, Zhang Y, Xu DQ, Li X, Su J, Yang LG. 2009. Genetic and phenotypic parameter estimates for growth traits in Boer goat. Livest Sci. 124(1–3):66–71.