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Study of sexual dimorphism in growth traits of Sangsari lambs: between-sex heritability and correlations

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Abstract This research examined the genetic aspects of sexual dimorphism (SXD) regarding body weights at birth (BW), weaning (WW), 6 months (6MW), 9 months (9MW), and 12 months (12MW) in Sangsari sheep. The records were retrieved from a dataset collected between 1986 and 2016 at the Sangsari sheep breeding station. The PROC GLM was applied to evaluate the environmental factors. The SXD levels were calculated as the average of male/female ratios at birth, weaning, six, nine and 12 months of age. Genetic analysis was accomplished using the AI-REML method of the WOMBAT software. Six univariate and bivariate animal models were employed for the genetic assessment of traits in combined sexes, as well as for male and female lambs separately. Male lambs weighed more than female lambs, with a weight difference of 0.21 kg (7.22%) at birth increasing to 3.91 kg (13.95%) at 12 months of age. Levels of SXD were relatively low, ranging from 1.07 for BW to 1.16 for 12MW. For all traits except 12MW, the σ^2_a, σ^2_e, σ^2_p, h^2, and CV_a were higher in male lambs than females. Direct heritability estimates for BW, 3MW, 6MW, 9MW, and 12MW in male lambs were 0.28, 0.17, 0.20, 0.16, and 0.18, respectively. The corresponding estimates for female lambs were 0.27, 0.17, 0.16, 0.13, and 0.23, respectively. Direct genetic correlations (r_g) between the sexes ranged from 0.89 for 6MW to 1.00 for 9MW and 12MW. Cross-sex maternal permanent environment correlations (r_{pe}) were 0.71 for 6MW and 0.98 for 3MW and 9MW. These results indicated that 6MW was the most dimorphic trait in the Sangsari lambs. High and positive genetic correlations between the sexes suggested that selection for body weight in males would result in a correlated response in females and vice versa, thereby preventing phenotypic divergence.

Keywords: body weight, cross-sex correlation, heritability, maternal effect, sheep

Introduction

Sexual dimorphism (SXD) refers to differences in phenotypic characteristics such as body weight, size, and the existence of distinctive morphological features in males and females of a particular species (Fairbairn and Roff, 2006; Gudex et al., 2009). This phenomenon arises from the confounding effects of several mechanisms, including selection, genetic variability, and sex-specific expression of genes found in males and females (Badyaev, 2002; Roulin and Jensen, 2015; Baneh et al., 2021). Additionally, Gatford et al. (1996) suggested that variations in the secretion and types of hormones and physical distinctions among both sexes of one species may account for sexual dimorphism. Because of the varying reproductive tasks of males and females, they exhibit differential selection for these roles, resulting in varied expression of phenotypic characteristics between the sexes (Polak and Frynta, 2010). There are various theories about how sexual dimorphism originated in different animal species, most of which can be classified into three primary influences that affect males and females within a population in different ways: sexual behavior, fertility, and natural selection (Yakubu and Akinyemi, 2010; Parés-Casanova, 2015). Improvement of genetic evaluation programs for economic traits may be possible by considering the contrasts in the genetic expression of traits between males and females and evaluating each trait separately based on the sex of individuals (Ghafouri-Kesbi et al., 2015). Hence, SXD can be exploited in breeding strategies through the use of genetic variations among males and females. Even though SXD is visible in various domesticated animals like sheep (Noorian et al., 2021), goats (Baneh et al., 2021), cattle (Polak and Frynta, 2010), and chickens (Maniatis et al., 2013), few attempts have been made to study its genetic background and investigate its possible application in sheep breeding program (Ghafouri-Kesbi and Notter, 2016; Ghafouri-Kesbi and Baneh, 2018). Challenges arise in sheep production when SXD is present, particularly when there are differences in heritabilities of the traits between genders, as well as when genetic associations between males and females are less than unity (Parker and Garant, 2005). Such differences complicate the estimation of breeding values and design and application of the most favorable multi-trait selection responses for each gender (Gudex et al., 2009; Ghafouri-Kesbi and Notter, 2016). Body weight in small ruminants is the best illustration of SXD amongst livestock. The sex difference in body weight traits can be attributed to genetic architecture. Genetic association among the lambs of males and females has been used by researchers in assessing the genetic control of SXD (Poissant et al., 2010). The presence of SXD in the growth traits of several sheep and goat breeds, including Afshari (Ghafouri-Kesbi and Notter, 2016), Iran Black (Ghafouri-Kesbi and Baneh, 2018), Baluchi (Noorian et al., 2021), and Jamunapari (Mandal et al., 2022) has been investigated. Overall, the results of these studies suggested that while there is sexual dimorphism in growth-related traits, there is also a strong and positive genetic correlation between the genders, and selection for certain traits in one sex can improve those traits in the other sex. The Sangsari sheep, a small-sized fat-tailed breed, is one of the indigenous breeds of central Iran, renowned for its remarkable adaptation to long drought periods (Kasiriyan et al., 2011). This breed showed a large variation in growth traits between both sexes; body weights at birth, weaning, and 6 months of age were higher in male lambs than in female lambs (Ehsaninia, 2021).

Considering the socio-economic effects, small ruminants play a significant role in the livelihoods of a considerable part of human population in the tropics from socio-economic aspects (Hajalizadeh et al., 2019; Jafari Ahmadabadi et al., 2023; Saadatabadi et al., 2023). Thus, combined trials with emphasis on administration and genetic progress to improve animal outputs are of decisive significance (Vahabzadeh et al., 2020; Amirteymoori et al. 2021; Mohammadabadi et al., 2023). Economical and biological efficiency of small ruminant production enterprises can be improved by increasing their productivity and reproductive performance (Mohammadabadi and Tohidinejad, 2017; Mohammadinejad et al., 2022; Safaei et al., 2022; Shokri et al., 2023). Various studies have been conducted on sexual dimorphism in sheep and goats across different breeds; however, there is no report on sexual dimorphism and its genetic aspects regarding the growth traits in Sangsari sheep. Hence the current study aimed to: (i) examine the existence of sexual dimorphism, (ii) analyze the variations in body weights between males and females from both phenotypic and genetic perspectives, (iii) estimate sex-specific heritabilities as well as inter-sex genetic and phenotypic correlations in Sangsari lambs.

Materials and methods

Data and management of animals

A dataset on the growth traits of Sangsari lambs was obtained from the Sangsari Sheep Breeding Station (SSBS) in Iran collected over 30 years (1986-2016). The primary objective of SSBS is to protect and improve this breed for meat production. The animals are reared on natural pasture during the spring and summer months (extensive migration) and at the station during the autumn and winter months (semi-intensive). The animals are allowed to graze on grass for approximately 6 to 8 hours daily and then housed in enclosures overnight. During the semi-intensive rearing phase, the animals are given a diet that includes alfalfa hay, barley grains, wheat straw, and concentrates. At approximately 18 months of age, the maiden ewes are joined with fertile rams (12 to 1 ratio). Rams are utilized for 2-3 breeding seasons, whereas ewes are bred until 8 years of age. At birth, the weight as well as the type and date of birth and parental identities are recorded. The lambs are weaned at approximately 3 months of age.

Traits considered

The data on weight included the body weights at birth (n=5613), 3-months (n=4788), 6-months (n=3985), 9-months (n=2775), and 12-months (n=2370) of age. Records outside the range of mean±3SD (standard deviations) and records of the lambs with unidentified dams, birth type, and year were excluded from the dataset.

Sexual dimorphism

Using the Lovich and Gibbons ratio (Lovich and Gibbons, 1992), the evaluation of SXD in body weight traits of Sangsari sheep was conducted. When males are heavier than females, as was in the present study, the SXD in body weight is calculated by the $\overline{\mathrm{M}}/\overline{\mathrm{F}}$ ratio where $\overline{\mathrm{M}}$ and $\overline{\mathrm{F}}$ are the means of male and female body weights, respectively. Each trait in male and female lambs was considered a distinct trait to identify SXD.

Statistical analysis

The generalized linear model (PROC GLM) of the SAS software (SAS, 2004) was applied to perform least square analyses for detection of the environmental factors. Means were compared using the Tukey's test. Environmental factors in the models were the year of birth in 30 levels (1986-2016), birth type in 2 levels (single and twin), and ewe age at lambing in 6 levels (2-7 years old). These fixed factors were found to significantly influence all of the traits that were analyzed ($P<0.01$) and were thus incorporated into the linear mixed models. However, interactions between the fixed effects were not significant and therefore excluded from the final models. A series of six univariate animal models was utilized to estimate the (co)variance components and genetic parameters, encompassing lambs of both sexes. Within these analyses, sex was integrated into the model as a fixed effect. By including the sex effects in the models, baseline estimates of variance components and genetic parameters were generated, predicated on the assumption that these sex effects do not influence the parameters under consideration. Following this, for the genetic analysis of SXD, six distinct bivariate animal models were employed. These models varied in their inclusion or exclusion of maternal additive genetic and maternal permanent environmental effects, as follows:

Model 1, $\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{a}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{a}2} \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix}$

Model 2, $\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{a}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{a}2} \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{pe}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{pe}2} \end{bmatrix} \begin{bmatrix} \mathrm{pe}_1 \\ \mathrm{pe}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix}$

Model 3, $\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{a}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{a}2} \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{m}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{m}2} \end{bmatrix} \begin{bmatrix} \mathrm{m}_1 \\ \mathrm{m}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix}, \mathrm{Cov}(\mathrm{a}, \mathrm{m}) = 0$

Model 4, $\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{a}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{a}2} \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{m}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{m}2} \end{bmatrix} \begin{bmatrix} \mathrm{m}_1 \\ \mathrm{m}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix}, \mathrm{Cov}(\mathrm{a}, \mathrm{m}) = \mathrm{A}\sigma_{\mathrm{a.m}}$

Model 5, $\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{a}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{a}2} \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{pe}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{pe}2} \end{bmatrix} \begin{bmatrix} \mathrm{pe}_1 \\ \mathrm{pe}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{m}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{m}2} \end{bmatrix} \begin{bmatrix} \mathrm{m}_1 \\ \mathrm{m}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix}, \mathrm{Cov}(\mathrm{a}, \mathrm{m}) = 0$

Model 6, $\begin{bmatrix} \mathrm{y}_1 \\ \mathrm{y}_2 \end{bmatrix} = \begin{bmatrix} \mathrm{X}_1 & 0 \\ 0 & \mathrm{X}_2 \end{bmatrix} \begin{bmatrix} \mathrm{b}_1 \\ \mathrm{b}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{a}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{a}2} \end{bmatrix} \begin{bmatrix} \mathrm{a}_1 \\ \mathrm{a}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{pe}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{pe}2} \end{bmatrix} \begin{bmatrix} \mathrm{pe}_1 \\ \mathrm{pe}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{Z}_{\mathrm{m}1} & 0 \\ 0 & \mathrm{Z}_{\mathrm{m}2} \end{bmatrix} \begin{bmatrix} \mathrm{m}_1 \\ \mathrm{m}_2 \end{bmatrix} + \begin{bmatrix} \mathrm{e}_1 \\ \mathrm{e}_2 \end{bmatrix}, \mathrm{Cov}(\mathrm{a}, \mathrm{m}) = \mathrm{A}\sigma_{\mathrm{a,m}}$

where, subscripts 1(2) represent traits of males and females, respectively; $\mathbf{y}_{1(2)}$ is a vector of observation for the studied traits, $\mathbf{b}_{1(2)}$ is a vector of fixed effects with incidence matrix $\mathbf{X}_{1(2)}$, $\mathbf{a}_{1(2)}$, $\mathbf{pe}_{1(2)}$ and $\mathbf{m}_{1(2)}$ are vectors of random effect with incidence matrices $\mathbf{Z}_{a1(2)}$, $\mathbf{Z}_{pe1(2)}$, and $\mathbf{Z}_{m1(2)}$, respectively.

It was assumed that $\mathbf{a} \sim \mathrm{N}(0, \mathbf{A}\sigma_{\mathrm{a}}^2), \mathbf{pe} \sim \mathrm{N}(0. \mathbf{I}_{\mathbf{pe}}\sigma_{\mathrm{pe}}^2)$, $\mathbf{m} \sim \mathrm{N}(0. \mathbf{A}\sigma_{\mathrm{m}}^2)$, and $\mathbf{e} \sim \mathrm{N}(0. \mathbf{I}_{\mathbf{n}}\sigma_{\mathrm{e}}^2)$. Here, **A** represents the additive numerator relationship matrix, $\mathbf{I}_{\mathbf{pe}}$ and $\mathbf{I}_{\mathbf{n}}$ are identity matrices of order equal to the number of dams and the number of records, respectively, and σ_{a}^2, σ_{m}^2, σ_{pe}^2 and, σ_{e}^2 are variances of the additive genetic, maternal additive genetic, maternal permanent environmental, and residual, respectively; $\sigma_{a,m}$ denotes the covariance between direct additive and maternal additive effects. Direct heritability (h^2), maternal heritability (m^2), and maternal permanent environmental effects (pe^2) were calculated as ratios of additive direct, additive maternal, and permanent environmental maternal variances to phenotypic variance, respectively. The best model was determined using the following equation (Akaike, 1974):

$AIC_i=-2\log L_i+2p_i$

Genetic parameters and (co)variance components were estimated by the average information-restricted maximum likelihood (AI-REML) algorithm using the WOMBAT program (Meyer, 2013). It has been suggested that heritability estimates, while easier to grasp, may not be reliable for comparing genetic variation across various traits, particularly when environmental variation levels vary between the traits of interest (Kruuk et al., 2000; Wilson et al., 2005). Using coefficients of variation is the preferred method for making such comparisons (Houle, 1992). The formula used to determine the additive genetic coefficient of variation (CV_a) for each characteristic is as follows:

$$\mathrm{CV}_{\mathrm{a}} = \frac{\sqrt{\sigma_{\mathrm{a}}^2}}{\overline{\mathrm{x}}} \times 100$$

where, σ_{a}^2 and $\overline{\mathrm{X}}$ are direct genetic variance and phenotypic mean of the trait.

Results

Descriptive statistics

Means, standard deviations, and coefficient of variations for the traits studied are presented in Table 1. At birth, weaning, and 6 months, 9 months, and 12 months of age, male lambs were 7.22%, 10.30%, 10.47%, 12.33%, and 13.95% heavier than females, respectively. At higher ages, the sexes recorded a greater variation in body weight traits. The means of body weight traits in male and female lambs increased by 10.24 and 9.46 folds from birth to 12 months of age. Male lamb CV values decreased from 21.47% for BW to 17.56% for 12MW, while female lamb CV values decreased from 20.27% to 15.07% for corresponding traits. As observed, the value of SD increased 7.76 times from birth to 12 months of age. Figure 1 illustrates the trend of SXD levels for the trait under investigation. The SXD levels for BW, 3MW, 6MW, 9MW, and 12MW were 1.07, 1.10, 1.10, 1.12, and 1.16, respectively.

Table 1. Description of data used in the analysis based on male and female lambs

	Traits^{a}									
	BW		3MW		6MW		9MW		12MW	
Item	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
No. of records	3061	2552	2442	2346	2032	1953	1415	1360	1201	1169
Mean (kg)	3.12	2.91	16.7	15.14	23.85	21.59	27.87	24.81	31.94	27.53
Minimum	1.85	1.73	5.85	4.73	11.21	11.94	13.75	14.8	16.11	16.82
Maximum	4.91	4.82	30.93	29.15	39.32	40.83	43.25	44.35	45.90	45.60
S.D.	0.67	0.59	3.93	3.31	4.90	4.26	5.03	4.63	5.61	4.15
C.V.(%)	21.47	20.27	23.53	21.86	20.55	18.57	18.05	18.66	17.56	15.07

^{a}BW: Birth weight; 3MW: 3-month weight; 6MW: 6-month weight; 9MW: 9-month weight; 12MW: 12-month weight. SD: standard deviation; CV: coefficient of variation.

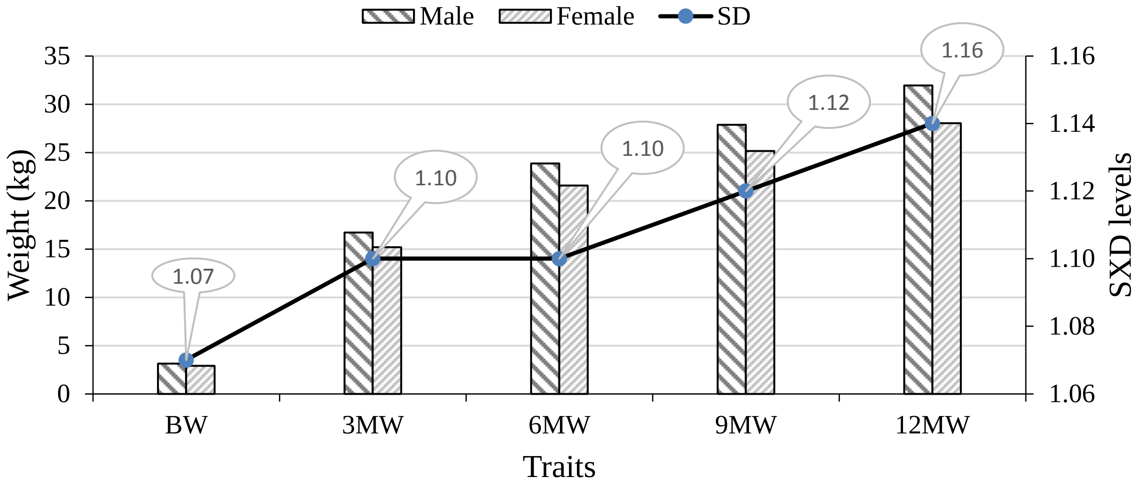

Figure 1. Sexual dimorphism (SXD) levels for body weight traits in Sangsari lambs

Environmental effects on growth traits

The least-square mean values (±SE) are presented in Table 2. The effect of dam age at lambing on all studied traits was significant in both males and females (P<0.01). Lambs born from ewes aged 2 and 7 years had lower weights than those born from ewes aged 3-6 years. At various ages, the body weights of male and female lambs were significantly affected by the year of birth (P<0.01). At all ages, male lambs were heavier than females. The birth type significantly impacted on all growth traits (P<0.01). At all ages and for both genders, singleton lambs were heavier than twins or triplets.

Animal model comparisons

Table 3 shows the AIC values for the characteristics examined with the bivariate animal models. Maternal effects impacted on all variables, except for 6MW and 12MW. Model 3, which was the most suitable for BW, incorporates both direct additive and maternal additive genetic effects, ignoring the covariance between these effects, while the best model for 3MW, involved direct genetic effects, maternal genetic effects, and maternal permanent environmental effects, without considering the covariance between them (Model 5). Both additive genetic effects and maternal permanent environmental effects had a significant impact on the variation of 9MW, hence, model 2 was considered the most appropriate for the 9MW trait. For 6MW and 12MW, Model 1, which solely considered direct additive genetic effects gave a lower AIC and proved to be the best model.

Table 2. The least-square means ± SE of body weight traits in male and female Sangsari lambs

Traits^{1}	BW		3MW		6MW		9MW		12MW	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Birth year	**	**	**	**	**	**	**	**	**	**
Birth type	**	**	**	**	**	**	**	**	**	**
Single	$3.44^{a}\pm0.03$	$3.22^{a}\pm0.04$	$16.65^{a}\pm0.14$	$14.48^{a}\pm0.16$	$23.91^{a}\pm0.24$	$21.82^{a}\pm0.30$	$27.98^{a}\pm0.29$	$24.92^{a}\pm0.23$	$32.08^{a}\pm0.29$	$28.49^{a}\pm0.35$
Twin	$2.97^{b}\pm0.04$	$2.61^{b}\pm0.04$	$15.16^{b}\pm0.12$	$14.16^{b}\pm0.16$	$21.75^{b}\pm0.23$	$20.31^{b}\pm0.45$	$25.45^{b}\pm0.31$	$22.87^{b}\pm0.21$	$29.84^{a}\pm0.27$	$26.87^{a}\pm0.30$
Dam age	**	**	**	**	**	**	**	**	**	**
2	$3.21^{c}\pm0.04$	$2.96^{c}\pm 0.04$	$15.89^{c}\pm0.23$	$14.12^{c}\pm0.26$	$23.72^{c}\pm0.29$	$19.92^{c}\pm0.31$	$26.14^{c}\pm0.32$	$23.81^{c}\pm0.35$	$29.77^{c}\pm0.29$	$27.79^{c}\pm0.32$
3	$3.38^{b}\pm0.04$	$3.21^{b}\pm 0.04$	$16.55^{b}\pm0.23$	$14.49^{b}\pm0.26$	$23.81^{b}\pm0.30$	$20.96^{b}\pm0.30$	$27.87^{ab}\pm0.32$	$24.86^{b}\pm0.35$	$30.90^{b}\pm0.28$	$28.91^{ab}\pm0.32$
4	$3.43^{b}\pm0.03$	$3.30^{ab}\pm0.04$	$16.68^{b}\pm0.20$	$14.58^{ab}\pm0.31$	$23.89^{ab}\pm0.31$	$21.05^{ab}\pm0.35$	$27.90^{a}\pm0.36$	$25.15^{ab}\pm0.39$	$31.15^{a}\pm0.39$	$28.95^{ab}\pm0.41$
5	$3.45^{ab}\pm0.05$	$3.41^{a}\pm0.06$	$16.74^{ab}\pm0.25$	$14.64^{ab}\pm0.37$	$23.95^{ab}\pm0.38$	$21.15^{ab}\pm0.34$	$27.80^{a}\pm0.39$	$25.19^{a}\pm0.44$	$30.95^{ab}\pm0.51$	$29.04^{ab}\pm0.48$
6	$3.50^{a}\pm 0.06$	$3.48^{a}\pm0.08$	$16.88^{a}\pm0.33$	$14.68^{a}\pm0.41$	$23.98^{a}\pm0.48$	$21.16^{a}\pm0.52$	$26.12^{c}\pm0.56$	$25.17^{ab}\pm0.64$	$31.10^{ab}\pm0.66$	$29.10^{a}\pm0.71$
7	$3.30^{b}\pm 0.08$	$3.29^{b}\pm0.09$	$16.49^{b}\pm0.33$	$14.14^{c}\pm0.41$	$23.69^{c}\pm0.48$	$20.05^{c}\pm0.52$	$26.10^{c}\pm0.56$	$24.85^{c}\pm0.64$	$29.80^{c}\pm0.66$	$27.84^{c}\pm0.78$

^{1}BW: birth weight; 3MW: 3-month weight; 6MW: 6-month weight; 9MW: 9-month weight; 12MW: 12-month weight. ^{a,b,c}: Within columns, mean values with common superscript (s) are not different (P>0.05; Tukey's test), **: P<0.01.

Table 3. Comparisons of bivariate animal models based on AIC values

Model	BW	3MW	6MW	9MW	12MW
Model 1	-6723.76	15839.97	**13621.64**	11775.32	**11225.45**
Model 2	-6764.92	15850.23	13684.18	**11844.28**	11231.87
Model 3	**-6894.35**	15841.70	13675.21	11854.79	11242.40
Model 4	-6885.54	15877.39	13663.42	11870.21	11256.31
Model 5	-6879.90	**15816.27**	13659.30	11865.55	11249.56
Model 6	-6877.76	15892.45	13654.11	11885.45	11279.75

[a]BW: birth weight; 3MW: 3-month weight; 6MW: 6-month weight; 9MW: 9-month weight; 12MW: 12-month weight.

Univariate analyses

Table 4 displays the results derived from univariate animal models that included the data from lambs of both sexes. Heritability values (h^2) for BW, 3MW, 6MW, 9MW, and 12MW were calculated as 0.27, 0.17, 0.18, 0.15, and 0.19, respectively. Maternal genetic and permanent environmental effects significantly influenced all the traits examined, except for 6MW and 12MW.

Bivariate analyses and genetic parameters

Estimates of genetic parameters from the best bivariate model are shown in Table 5. The additive genetic variance increased with age for all traits. Except for weight at 12 months of age, male lambs exhibited greater σ^2_a, σ^2_m, σ^2_{pe}, σ^2_e and, σ^2_p in all traits studied compared to females. Moreover, the estimates of h^2 and m^2 for BW, 3MW, 6MW, and 9MW were greater in males than in females. For 12MW the value of h^2 in females was greater than in males. The estimates of h^2 for BW, 3MW, 6MW, 9MW, and 12MW in male and female lambs were 0.28 and 0.27, 0.17 and 0.17, 0.20 and 0.17, 0.16 and 0.13, and 0.18 and 0.23, respectively. The values of m^2 in male and female lambs were 0.14 and 0.12 for BW and 0.12 and 0.10 for 3MW, respectively. Similar trends were observed for pe^2 values of 3MW, 6MW, and 9MW, although it was higher in females for the 3MW. The traits with the highest heritability in both sexes also had the highest CV_a.

Table 4. Estimates of variance components and genetic parameters for growth traits using a univariate analysis with both sexes included and with fitting of a fixed effect of the lamb sex

Trait[a]	model	σ^2_a	σ^2_m	σ^2_{pe}	σ^2_e	σ^2_P	h^2	m^2	pe^2
BW	3	0.117	0.061		0.251	0.429	0.27±0.02	0.14±0.02	
3MW	5	1.345	0.615	0.805	5.262	8.027	0.17±0.03	0.08±0.02	0.10±0.02
6MW	1	4.011			18.963	22.974	0.18±0.02		
9MW	2	5.998		1.715	32.783	40.496	0.15±0.03		0.04±0.01
12MW	1	8.886			38.461	47.347	0.19±0.02		

σ^2_a: additive genetic variance; σ^2_m: maternal genetic variance; σ^2_{pe}: maternal permanent environmental variance; σ^2_e: residual variance; σ^2_P: phenotypic variance; h^2: heritability; m^2: maternal heritability; pe^2: maternal environmental effect.
[a]BW: birth weight; 3MW: 3-month weight; 6MW: 6-month weight; 9MW: 9-month weight; 12MW: 12-month weight.

Table 5. Sex-specific estimates of variance components and genetic parameters for growth traits using bivariate analysis

Trait[a]	Sex	σ^2_a	σ^2_m	σ^2_{pe}	σ^2_e	σ^2_P	h^2	m^2	pe^2	CV_a
BW	Male	0.096	0.048		0.198	0.342	0.28±0.04	0.14±0.03		9.93
	Female	0.074	0.032		0.166	0.272	0.27±0.05	0.12±0.03		9.35
3MW	Male	1.410	0.978	0.799	4.980	8.167	0.17±0.05	0.12±0.04	0.10±0.03	7.11
	Female	0.809	0.501	0.528	3.060	4.898	0.17±0.06	0.10±0.05	0.11±0.03	5.94
6MW	Male	3.971			15.520	19.491	0.20±0.04			8.32
	Female	2.232			11.450	13.682	0.16±0.06			6.95
9MW	Male	5.931		2.312	29.790	38.033	0.16±0.05		0.05±0.04	8.74
	Female	4.282		1.117	28.110	33.509	0.13±0.05		0.03±0.04	8.34
12MW	Male	5.981			27.161	33.142	0.18±0.05			7.66
	Female	6.124			20.891	27.015	0.23±0.04			8.83

σ^2_a: additive genetic variance; σ^2_m: maternal genetic variance; σ^2_{pe}: maternal permanent environmental variance; σ^2_e: residual variance; σ^2_P: phenotypic variance; h^2: heritability; m^2: maternal heritability; pe^2: maternal environmental effect; CV_a: additive genetic coefficient of variation.
[a]BW: birth weight; 3MW: 3-month weight; 6MW: 6-month weight; 9MW: 9-month weight; 12MW: 12-month weight.

Sex-specific correlation estimates

The correlations between sexes for the traits studied are illustrated in Table 6. Positive direct genetic correlation (r_g) estimates were observed between males and females, ranging from 0.98 for BW and 3MW to 1.00 for 9MW and 12MW. Traits 9MW and 12MW had the highest genetic correlation value (1.00), while trait 6MW recorded the lowest one (0.89). The magnitude of maternal genetic correlation (r_m) between sexes was 0.93 for BW, and 0.98 for 3MW. The between-sex maternal permanent environmental correlation (r_{pe}) was 0.78 for 6MW and 0.98 for 3MW and 9MW. The phenotypic correlation (r_p) among male and female lambs varied from 0.21 for 6MW to 0.34 for BW.

Tale 6. Between-sex correlations for body weight traits in Sangsari lambs

Trait^a	r_g	r_m	r_{pe}	r_p
BW	0.98±0.13	0.93±0.06		0.34±0.08
3MW	0.98±0.10	0.98±0.05	0.98±0.10	0.29±0.06
6MW	0.89±0.09		0.78±0.14	0.21±0.07
9MW	1.00±0.08		0.98±0.19	0.24±0.05
12MW	1.00±0.07			0.30±0.05

r_g: direct genetic correlation; r_m: maternal genetic correlation; r_{pe}: maternal permanent correlation; r_p: phenotypic correlation.
^{a}BW: birth weight; 3MW: 3-month weight; 6MW: 6-month weight; 9MW: 9-month weight; 12MW: 12-month weight.

Discussion

Non-genetic effects and sexual dimorphism

Annual climatic and management conditions such as nutrition, healthcare, and housing could explain the significant effect of the birth of year. In this study, males were heavier than females at all ages, and the magnitude of this difference increased from 7.22% for BW to 13.95% for 12MW. Similar findings were reported by Maraveni et al. (2018) for Lori-Bakhtiari sheep. Single lambs typically receive more nutrients and attention from their mothers, leading to their larger size than twin lambs. This difference in weight can also be attributed to the competition for resources between twin lambs, resulting in slower growth rates. The age of the dam could potentially have a notable effect on body weight as a result of differences in milk production, nursing, and maternal behavior. As dams get older, their ability to produce milk may decrease, leading to potential changes in body weight for their lambs. Additionally, older dams may exhibit different nursing and maternal behaviors that can also influence the body weight of their young.

This study found that the sexual dimorphism in body weight varied from 1.07 to 1.16, depending on age, which is within the literature values. Likewise, there was a wide variation in SXD, ranging from 1.06 reported for Baluchi sheep (Noorian et al., 2021) to 1.67 for wild sheep (Polak and Frynta, 2009). Other authors working with different sheep breeds also reported similar findings (Ghafouri-Kesbi and Notter, 2016; Ghafouri-Kesbi and Baneh, 2018; Noorian et al., 2021). SXD values of 1.06, 1.09, 1.10, 1.10, and 1.09 for BW, 3MW, 6MW, 9MW, and 12MW were observed by Noorian et al. (2021) for Baluchi sheep. In Iran-Black sheep, the M/F ratios for BW, 3MW, 6MW, 9MW, and 12MW were 1.065, 1.098, 1.097, 1.105, and 1.142, respectively (Ghafouri-Kesbi and Baneh, 2018). For the traits studied, the low M/F ratios indicated a limited value of sexual dimorphism. A low M/F ratio suggests that there is little variation between the sexes in terms of the traits being studied. Contrary to us, Polak and Frynta (2009) reported higher levels of SXD for domestic (1.41) and wild sheep (1.67). The rise in dimorphism from birth to 12 months may be due to differences in steroids between males and females, along with distinct physiological characteristics (Aguirre et al., 2016; Mandal et al., 2022). Both testosterone and estrogen, have different effects on the growth of the sexes. Testosterone in males stimulates muscle growth by influencing the rate of protein synthesis, whereas estrogen in females restricts the long bone growth and causes females to be smaller than males (Mateescu and Thonney, 2002).

Scale effects (association between mean and variance) and physiological changes before sexual maturity are likely to explain the increase in sexual dimorphism before puberty. As noted by Mignon-Grasteau et al. (2000), animals may experience an increase in sexual dimorphism as they grow older and heavier, indicating a scale effect. Furthermore, sexual dimorphism becomes increasingly apparent as physiological changes associated with sexual maturation take place (Gatford et al., 1996; Badyaev, 2002). The process of domestication has resulted in a considerable reduction in the sexual dimorphism of domestic animals like sheep and goats where SXD decreased by about 18% in sheep and 36% in goats (Polak and Frynta, 2009). Sexual dimorphism may play a crucial role in breeding, making it possible to utilize the existing sexual dimorphism to create effective breeding programs for livestock.

(Co)variance components and genetic parameters

Identification of the genetic and phenotypic parameters is essential for selecting appropriate methods and evaluating the genetic gain in body weight traits. Univariate analysis (Table 4) demonstrate that the additive genetic variance for body weights increased with the increasing age of the animal. The heritability estimates ranged from 0.15 for 9MW to 0.27 for BW. The values of h^2 were almost in line with the average values reported previously for these traits (Singh et al., 2016; Noorian et al., 2021). The BW and 3MW displayed the least difference in variance component estimates between the univariate and bivariate methods. In contrast, the variance components for other traits demonstrated significant variation. Similar findings were reported by Ghafouri-Kesbi and Baneh (2018) in Iran-Black sheep. Variance components for all traits in both sexes exhibited heterogeneity; as the animal grew older, the estimates of σ_P^2 also increased for both males and females. The phenotypic variance for weight at 12 months showed a more pronounced difference between males and females. Comparable results were obtained for Iran-Black (Ghafouri-Kesbi and Baneh, 2018) and Baluchi (Noorian et al., 2021) sheep. Maria et al. (1993) found that males exhibited a higher phenotypic variation, mainly because of their larger size. In this study, for all traits except 12MW, there was a higher level of σ_a^2 in males than in females. For the 12MW, the σ_a^2 value was higher in females compared to males. Ghafouri-Kesbi and Baneh (2018), reported that Iran-Black male lambs showed a higher level of σ_a^2 in BW and WW, while female lambs exhibited a greater value of σ_a^2 in the 6MW, 9MW, and 12MW traits. Ghafouri-Kesbi et al. (2015) obtained high levels of σ_a^2 for 3MW and 6MW in male Zandi sheep, consistent with the results of this research. However, they found a higher estimate of σ_a^2 in the BW of females. Usually, males tended to exhibit more variation than females. Ghafouri-Kesbi and Nutter (2016) argued that higher values of σ_{pe}^2 and σ_e^2 in male lambs may indicate that they are more sensitive to the environmental factors. In a study of Scottish Blackface sheep, Riggio et al. (2008) found that the survival rate of male lambs was lower than that of female lambs. Therefore, males are more sensitive to environmental stresses, although they appear to be heavier and more robust than females (Ghafouri-Kesbi and Notter, 2016). For BW, WW, 6MW, 9MW, and 12MW traits, the estimates of h^2 for male lambs were 0.28, 0.17, 0.23, 0.15, and 0.18. The relevant values in female lambs were 0.27, 0.15, 0.16, 0.11, and 0.23, respectively. For all traits measured except 12MW, male lambs tended to have higher h^2 estimates than females. The h^2 values for BW and 3MW did not vary among males and females, while the estimates of h^2 for 6MW and 9MW differed between the two sexes and were higher in males. The higher h^2 for 12MW in females may be because they have less residual variance than males. The h^2 estimates for the traits studied in the male and female Sangsari lambs were within the range documented for other breeds of sheep (Ghafouri-Kesbi et al., 2015; Ghafouri-Kesbi and Notter, 2016; Noorian et al., 2021). In male lambs of Zandi breed sheep, the estimated heritabilities were 0.16 for BW, 0.08 for 3MW, and 0.17 for 6MW but in female lambs were 0.10 for BW, 0.13 for 3MW, and 0.09 for 6MW (Ghafouri-Kesbi et al., 2015), which are lower than the estimated values in the present research. Noorian et al. (2021) observed that the heritability values of BW, 3MW, 6MW, 9MW, and 12MW in male Baluchi lambs were 0.07, 0.08, 0.05, 0.19, and 0.19, 0.10, 0.13, 0.09, 0.16, and 0.24, respectively in females.

Ghafouri-Kesbi and Notter (2016) found that the heritability estimates for BW of male and female Afshari lambs were 0.39 and 0.29, and for 3MW were 0.15 and 0.22, respectively. These values were higher than those found in the current research. Heritability estimates for body weight traits in sheep vary greatly across breeds and populations. Furthermore, the h^2 values may be influenced by various factors, such as the methods of parameter estimation, the genetic variation within the population, and the structure of the data (Ghavi Hossein-Zadeh and Ghahremani, 2018). Heritabilities for BW, 3MW, 6MW, and 9MW in male lambs were 3.18%, 4.53%, 24.05%, and 18.97% more than female lambs. For 12MW, the heritability in females was 23.83% higher than in males. Similar trends were found for the values of CVa. The highest CVa values in both male and female lambs were related to BW and therefore a greater response would be expected for this trait. Similar results were reported by Ghafouri-Kesbi et al. (2015) regarding BW. Generally, variations in CV_a showed a trend comparable to h^2, and the values of these parameters indicated the presence of a relatively small genetic variability between the genders. The development of body weight in sheep, especially at an early age, is significantly influenced by maternal effects (Illa et al., 2018). Furthermore, these researches showed ignoring the mothering effects, if they are present, may lead to overestimation of h^2, as the estimated of σ_a^2 will encompass at least part of the maternal variation. Both BW and 3MW were influenced by maternal effects, indicating the need to consider them in the genetic evaluation of Sangsari lambs for these traits. In both male and female Sangsari lambs, the maternal heritability values for BW and 3MW were 0.14 and 0.12, and 0.12 and 0.10, respectively.

According to a study by Noorian et al. (2021), the m^2 values of BW in males and females of Baluchi lambs were 0.13 and 0.06, respectively, which are partially lower than the estimates in the current study. Ghafouri-Kesbi and Baneh (2018) calculated the maternal heritability of BW in male and female lambs of Iran-Black sheep to be 0.42 and 0.45, which are higher than estimates in the current study. The values of pe^2 for 3MW and 9MW in male and female lambs were 0.10 and 0.11, and 0.05 and 0.03, respectively. Males had higher pe^2 values than females for 3MW and 9MW, although differences between sexes were not significant, consistent with Noorian et al. (2021). The values of pe^2 for 3MW were higher in females than in males that are in line with the findings in Australian Coopworth sheep (Gudex et al., 2009). As expected, there were no maternal effects on the 12MW of Sangsari lambs, likely because the lambs were weaned and separated from their mother.

Between-sex correlation estimates

The potential for genetic improvement is greatly influenced by the genetic variation in a trait and how it correlates with other traits. Genetic correlations show that genes influencing one trait affect others (Mandal et al., 2022). This parameter also assists in defining the relationship between the sets of genes that contribute to the genetic aspect of variation in the two correlated traits. There was a direct genetic correlation of 1.00 between sexes for 6MW, 9MW, and 12MW, suggesting that the same genes are responsible for controlling these traits in both sexes. An estimate of 0.98 was determined for r_g between sexes for BW and 3MW, indicating that several common genes influence these traits in both sexes of Sangsari lambs. Thus, selection for growth traits in one gender would cause a correlated response in the other gender. Comparable results regarding BW and 3MW in Afshari sheep were also noted by Ghafouri-Kesbi and Notter (2016). In the Zandi sheep breed, the r_g between male and female lambs were 0.82 for BW and 0.92 for WW (Ghafouri-Kesbi et al., 2015), which are smaller than our estimates. In other research (Ghafouri-Kesbi and Notter, 2016), the cross-sex genetic correlation for

BW in Afshari lambs was reported to be 0.98, which is in agreement with the current findings.

In the present study, the estimated r_g value between the sexes for 6MW was 0.85 which is smaller than the corresponding values in Baluchi (1.00; Noorian et al., 2021) and Zandi sheep (0.92; Ghafouri-Kesbi and Notter, 2016). This shows that 6MW is a dimorphic trait and thus the genetic makeup of the male and female lambs may differ. Since the direct genetic correlation for 6MW in both sexes is less than unity, divergent selection may be effective. This implies that selecting for 6MW in male or female lambs will not result in a strongly correlated response in the other sex. Maternal genetic correlations for birth and weaning weights were 0.93 and 0.98, respectively, indicating some differences in maternal genetic effects of the ewe on lamb's birth weight depending on sex. Ghafouri-Kesbi and Baneh (2018) and Noorian et al. (2021) found the value of r_m for birth weight of males and females in Iran-Black and Baluchi breeds to be 0.99, which is greater than the estimate in this research.

Maternal permanent environment correlations between sexes were 0.98 for 3MW and 9MW. Noorian et al. (2021) reported r_{pe} between sexes as 0.99 for 3MW and 9MW in Baluchi lambs, concordant with the present findings. The estimate of r_{pe} for 6MW was 0.78, implying that maternal effects on male and female lambs are different. The estimated value of r_{pe} between sexes for 6MW in Iran-Black lambs was 0.66, consistent with Ghafouri-Kesbi and Baneh (2018). The lower genetic and permanent environmental correlations between the sexes for 6MW indicate that this is the most dimorphic trait among Sangsari lambs. This finding is interesting because it identifies a specific trait with a significant difference between sexes, which could have implications for management and genetic selection strategies. Therefore, regarding the maternal effects on 6MW, a possible sexual dimorphism is also considered. The values of cross-sex phenotypic correlations for the traits under investigation were lower than those estimated for r_g, r_m and r_{pe}. Similarly, for BW, 3MW, 6MW, 9MW, and 12MW in Baluchi lambs, Noorian et al. (2021) obtained between-sex r_p of 0.28, 0.22, 0.19, 0.27, and 0.31.

Conclusions

In Sangsari lambs, the level of sexual dimorphism in body weights was found to be relatively low. Male lambs exhibited greater birth weights, experienced faster growth rates up to weaning, and consequently were heavier at weaning than their female counterparts. The body weights in both sexes, spanning from birth to six months of age, were influenced by maternal effects. Intra-sexual maternal permanent and additive genetic correlations for 6MW in Sangsari lambs were lower than unity, indicating that this trait is the strongest dimorphism within this breed. High and positive genetic correlations between the sexes reveal that selection for body weight in male lambs would produce a correlated response in females and, consequently, would inhibit phenotypic divergence.

Conflict of interest

The authors declare that they have no conflict of interest.

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