Iranian Society of Animal Science

Journal of Livestock Science and Technologies

Shahid Bahonar University of Kerman

ISSN: 2322-3553 (Print) ISSN: 2322-374X (Online)

Paper type: Original Research

Estimation of genetic parameters for sexual dimorphism in body weight of Baluchi sheep

Milad Noorian[1], Sahereh Joezy-Shekalgorabi[2*], Nasser Emam Jomeh Kashan[1]

[1]*Department of Animal Science, Science and Research Branch, Islamic Azad University, Tehran, Iran.*
[2]*Department of Animal Science, Shahr-e-Qods Branch, Islamic Azad University, Tehran, Iran.*

*Corresponding author,
E-mail address:
Joezy5949@gmail.com

Received: 24 Jun. 2021,
Accepted: 26 Aug. 2021,

Abstract The objective of this study was to estimate genetic parameters for sexual dimorphism (SD) in birth weights (BW), weaning weights (WW), 6-month weight (W6), 9-month weight (W9) and 12-month weight (W12) of Baluchi sheep. Data were collected during 1981-2011 from Baluchi sheep flock (flock No. 1) of Abbas Abad Sheep Breeding Station located in Mashhad, Iran. The data set included 7339, 7303, 5884, 5162 and 4691 records of birth weight, weaning weight, 6-month weight, 9-month weight and 12-month weight, respectively. Six bivariate animal models were used to estimate variance components and corresponding genetic parameters in male and female lambs separately. The SD levels (ratio of Male/Female) increased from 1.06 at birth to 1.13 at yearling age. Except for W9 in which additive genetic variance and direct heritability ($\boldsymbol{h_a^2}$) were greater in males, for the other studied traits, females experienced higher additive genetic variance and $\boldsymbol{h_a^2}$. In both sexes, maternal effects contributed significantly to phenotypic variations in body weights with greater contribution to body weights measured early in life. The maternal genetic effect was greater in females but the maternal permanent environmental effect was greater in males, which together with higher estimates of residual variances revealed greater sensitivity of male lambs to environmental conditions. Cross-sex additive genetic correlation ($\boldsymbol{r_a}$) was 0.86 for BW and 1.00 for the other studied traits. Maternal correlations between sexes were close to 1.00 indicating lack of sexual dimorphism for maternal effects on body weights of Baluchi lambs. Based on an approximate 95% confidence intervals, the difference between sexes regarding direct heritability were not significant, indicating no need or opportunity for different selection strategies in two sexes. Therefore, a model including the lambs of both sexes and with sex effects included in the model can be used for genetic evaluation.

Keywords: body weight, heritability, sexual dimorphism, sheep

Introduction

The difference between males and females of the same species in their body weight, size, color, and structure is termed sexual dimorphism (SD) (Badyaev, 2002). Darwin (1871) stated that because of different reproductive roles of sexes, they are selected differentially to do these roles. This causes variations in phenotypic trait exp-

DOI: 10.22103/JLST.2021.17787.1372

pression in different sexes. Badyaev (2002) reported that sexual dimorphism is the outcome of the combined effects of sex specific selection pressure, sex-biased phenotypic and genetic variation and cross-sex genetic correlations. Further, Ghafouri-Kesbi et al. (2015) reported that SD may arise due to the differences in the amount and type of hormone secretion as well as physical structure between the two sexes in a species. Generally, SD is more prominent in larger species and less related species (Ghafouri-Kesbi and Notter, 2016). Several hypotheses have been suggested to explain SD, of which the Rensch's rule (Rensch, 1950) is more accepted. According to this rule, the slope of the allometric relationship between male and female body size is higher than one, i.e., larger species have relatively larger males. The SD has been studied in many wild species (see for example Poissant et al., 2008; Polak and Frynta, 2009; Mallon, 2017; McLean et al., 2018). However, in domestic species, little effort has been made to investigate SD (Gudex et al., 2009; Maniatis et al., 2013; Ghafouri-Kesbi et al., 2015; Ghafouri-Kesbi and Notter, 2016; Ghafouri-Kesbi and Baneh, 2018). van der Heide et al. (2016) stated that despite the potential consequences of sexual dimorphism, genetic evaluation of economically important traits in males and females was undertaken considering both traits as a single trait by most breeding companies, assuming a genetic correlation of unity between phenotypes measured in both sexes. Besides, the effect of SD may be increased through selection, when SD is not taken into consideration in selection programs (Mignon-Grasteau et al., 2000). The main reason for studying the SD in domestic animals is that when SD is present, accurate estimation of breeding values could not be achieved and the definition and recognition of ideal multiple-trait selection response for each sex is challenged (Gudex et al., 2009; Ghafouri-Kesbi and Notter, 2016).

Baluchi is an Iranian native breed of sheep. Historically, Baluchi breed is originated from southwest Pakistan, eastern Iran and southern Afghanistan (Kamalzadeh and Shabani, 2007). They are small sized and fat-tailed and mainly raised for meat production. There is a large population of Baluchi sheep in Iran, comprising of 12% of the total sheep population (Bahreini-Behzadi et al., 2014). Although, the growth and efficiency-related traits of Baluchi sheep have been studied (Bahreini-Behzadi et al., 2014; Ghafouri-Kesbi and Gholizadeh, 2017), the SD in body weight of the breed has not been studied so far. Therefore, this study was designed to estimate the genetic parameters for sexual dimorphism in body weight of Baluchi sheep.

Materials and methods

Data

Body weight records and pedigree information collected during 1981-2015 were obtained from flock No. 1 of Baluchi Sheep Breeding Station of Abbasabad, Mashhad, Khorasan Razavi, Iran. The flock was managed as follows: each year, breeding season started in August and continued to September, with February lambing. Shortly after birth, the birth date and birth weights of lambs were recorded. Ear tags are used to identify the newborns. Suckling period lasted for approximately 90 days. After weaning, the ewes and young animals grazed on natural pasture. The animals were kept indoors during late autumn and winter months and received a ration consisted of wheat and barley straw, alfalfa hay, sugar beet pulp and concentrates. Rams and ewes were kept in the flock for a maximum of three and six breeding years, respectively; however, infertile ewes and extra rams were culled sooner.

Evaluated traits

Birth weight (BW), 3-month weight (weaning weight, W3), 6-month weight (W6), 9-month weight (W9) and 12-month weight (W12) were evaluated in this study. In order to account for the differences among animals with different ages, weaning weight, 6-month weight, 9-month weight and 12-month weight were adjusted to standard 90, 180, 270 and 365 days of age, respectively. To correct the weaning weight for the standard age of 90 days, first the average daily gain from birth to weaning was calculated for each animal and then multiplied by 90 and added to the birth weight of each animal. To correct the six-month weight for the standard age of 180 days, the average daily gain from weaning to six months was calculated for each animal and then multiplied by 90 and added to the weaning weight. To correct the 9-month weight for the standard age of 270 days, the average daily gain from 6 to 9 months for each animal was calculated and then multiplied by 90 and added to the 6-month weight. To correct the weight of 12 months for the standard age of 365 days, the average daily gain from 9 to 12 months for each animal was estimated and then multiplied by 95 and added to the 9- month weight.

correct the weaning weight for the standard age of 90 days, first the average daily gain from birth to weaning was calculated for each animal and then multiplied by 90 and added to the birth weight of each animal. To correct the six-month weight for the standard age of 180 days, the average daily gain from weaning to six months was calculated for each animal and then multiplied by 90 and added to the weaning weight. To correct the 9-month weight for the standard age of 270 days, the average daily gain from 6 to 9 months for each animal was calculated and then multiplied by 90 and added to the 6-month weight. To correct the weight of 12 months for the standard age of 365 days, the average daily gain from 9 to 12 months for each animal was estimated and then multiplied by 95 and added to the 9- month weight.

Statistical analysis

Least squares analyses were applied using the generalized linear model (GLM) of SAS software (2004) to test the importance of the fixed effects. Year of birth, month of birth, and age of dam at lambing and type of birth, and their interaction were included in the model. The effects of year of birth, age of dam at lambing and type of birth were significant ($P<0.05$) and therefore were included in the model of analysis. The Lovich and Gibbons ratio (Lovich and Gibbons, 1992) was used to measure the SD as M/F, where M and F are the average body weight of male and female lambs, respectively.

To estimate the (co)variance components and genetic parameters, a series of 6 univariate animal models including lambs of both sexes, and with sex effects included in the model were fitted to provide baseline estimates of variance components and genetic parameters under the assumption that sex effects do not influence these parameters. Then six bivariate animal models were fitted in which body weights of male and female lambs were considered as different traits. The bivariate models were (Ghafouri-Kesbi and Baneh, 2018):

$$Model\ 1, \begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{a2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$$

$$Model\ 2, \begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{a2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{c1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{c2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{c_1} \\ \boldsymbol{c_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}$$

$$Model\ 3, \begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{a2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{m1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{m2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{m_1} \\ \boldsymbol{m_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}, \boldsymbol{Cov(a,m) = 0}$$

$$Model\ 4, \begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{a2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{m1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{m2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{m_1} \\ \boldsymbol{m_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}, \boldsymbol{Cov(a,m) = A\sigma_{a,m}}$$

$$Model\ 5, \begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{a2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{c1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{c2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{c_1} \\ \boldsymbol{c_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{m1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{m2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{m_1} \\ \boldsymbol{m_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix}, \boldsymbol{Cov(a,m) = 0}$$

$$Model\ 6, \begin{bmatrix} \boldsymbol{y_1} \\ \boldsymbol{y_2} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X_1} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{X_2} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{a1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{a2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_1} \\ \boldsymbol{a_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{c1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{c2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{c_1} \\ \boldsymbol{c_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_{m1}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{Z_{m2}} \end{bmatrix} \begin{bmatrix} \boldsymbol{m_1} \\ \boldsymbol{m_2} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \end{bmatrix} \boldsymbol{Cov(a,m) = A\sigma_{a,m}}$$

where, subscripts 1 and 2 denote to male and female traits, respectively; $\mathbf{y}_{1(2)}$ is $n_{1(2)} \times 1$ vector of observations; $\mathbf{b}_{1(2)}$ is a p × 1 vector of fixed effects where p refers to the total number of fixed effect classes; $\mathbf{a}_{1(2)}$ is a q × 1 vector of additive genetic effects where q refers to the total number of animals in the pedigree; $\mathbf{c}_{1(2)}$ is a k × 1 vector of maternal permanent environmental effects where k is the number of dams with offspring; $\boldsymbol{m}_{1(2)}$ is a d × 1 vector of maternal genetic effects where d is the total number of females. $\mathbf{e}_{1(2)}$ is an $n_{1(2)} \times 1$ vector of residuals effects. $\mathbf{X}_{1(2)}$ is a design matrix relating observations to fixed effects. $\mathbf{Z}_{a1(2)}$, $\mathbf{Z}_{c1(2)}$ and $\mathbf{Z}_{m1(2)}$ are incidence matrices relating observations direct additive genetic effects, maternal permanent environmental effects and maternal additive genetic effects, respectively. (Co)variance structure for direct additive genetic, maternal permanent environmental, maternal genetic and residual effects were, respectively, $\mathbf{A}\sigma_a^2$, $\boldsymbol{I}_{nd}\sigma_c^2$, $\mathbf{A}\sigma_m^2$ and $\boldsymbol{I}_e\sigma_e^2$, where **A** is the additive numerator relationship matrix; $\boldsymbol{I}_{nd}$ and $\boldsymbol{I}_e$ are identity matrices of order equal to the number of dams and number of records, respectively; and $\boldsymbol{\delta_a^2}$, $\boldsymbol{\delta_c^2}$, $\boldsymbol{\delta_m^2}$ and $\boldsymbol{\delta_e^2}$ are additive genetic, maternal permanent environmental, maternal additive genetic and residual variances, respectively. The WOMBAT program (Meyer, 2007) was used to estimate (co)variance components and genetic parameters using the REML procedure. The Akaike's information criterion (AIC) was used to select the best model (Akaike, 1974).

Results

Table 1 shows the descriptive statistics for the traits studied. As shown, male lambs were heavier than female lambs with greater differences at higher ages. This resulted in an increasing trend from 1.06 (BW) to 1.13 (W12) for the SD level (i.e., the ratio of male to females body weights, Figure 1).

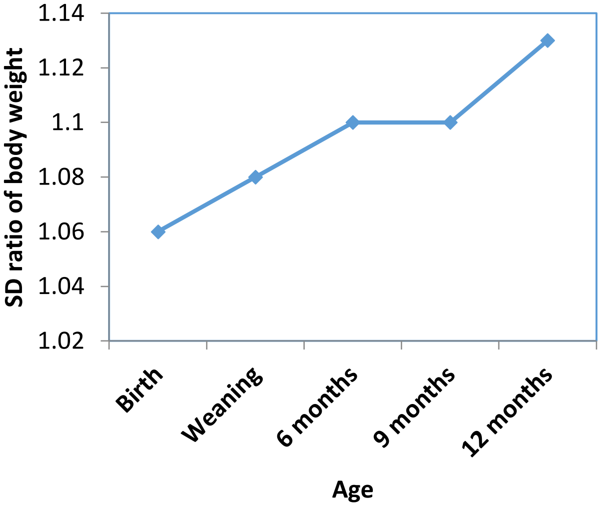

Figure 1. Sexual dimorphism (SD; the ratio of males to femasle) of body weights from birth to yearling age in Baluchi sheep

Results of univariate animal models including the data from lambs of both sexes are shown in Table 2. Direct heritability estimates ($\boldsymbol{h_a^2}$) for BW, WW, W6, W9 and W12 were 0.08, 0.10, 0.08, 0.17 and 0.23, respectively. Both maternal genetic and environmental effects were significant on all traits studied.

Estimates of variance components and genetic parameters for male and female lambs together with AIC values are listed in Tables 3 to 7. For BW, model 6 which was the most complete model and included the direct and maternal effects was selected as the most suitable model. For WW, W6 and W9 and W12, model 5 which included direct and maternal additive genetic effects and maternal permanent environmental effects was selected as the best model. Except for W9 for which additive genetic variance and direct heritability were greater in males, for other studied traits, females experienced higher additive genetic variance and direct heritability. However, approximate standard errors and resulting 95% confidence intervals for direct heritability did not indicate significant differences between sexes.

Table 1. Descriptive statistics for body weight from birth to yearling age in Baluchi sheep

	BW		**WW**		**W6**		**W9**		**W12**	
Variable	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
No of records	3585	3754	3601	3702	2953	2931	2612	2550	2368	2323
Mean (kg)	4.08	4.34	22.54	24.46	28.89	31.94	32.45	35.75	36.73	41.38
Minimum(kg)	1.500	1.600	10.00	10.11	15.18	15.24	18.15	15.12	17.21	21.97
Maximum(kg)	6.500	6.500	37.68	37.97	43.25	45.100	48.82	56.07	58.96	62.80
SD(kg)	0.68	0.72	4.48	5.11	4.54	5.47	4.63	5.51	5.55	6.75
CV(%)	10.46	11.07	11.88	13.45	10.49	12.13	9.48	9.41	9.41	10.74

***SD**: Phenotypic standard deviation; **CV**: Phenotypic coefficient of variation. **BW**: birth weight; **WW**: weaning weight; **W6**: 6-month weight; **W9**: 9-month weight; **W12**: 12-month weight.

In both sexes, maternal effects contributed significantly to phenotypic variations in all the studied traits. For BW and WW, maternal heritability (h_m^2) was higher in males but for W6, W9 and W12, h_m^2 was greater in females. At birth, maternal permanent environmental effect (h_c^2) was almost equal in both sex, but was greater in males thereafter.

Cross-sex direct genetic correlation (r_a) was 0.86 for birth weight and 1.00 for other traits studied. Cross-sex maternal genetic correlation (r_m) was 0.99 for all traits studied. Cross-sex maternal permanent environmental correlation (r_c) was 0.97 for BW and 0.99 for WW, W6 and W9 and W12 (Table 8).

Table 2. Estimates of variance components and genetic parameters for body weight from birth to yearling age in Baluchi sheep

Trait	Model	δ_a^2	δ_m^2	δ_c^2	$\delta_{a,m}$	δ_e^2	δ_p^2	h_a^2	h_m^2	h_c^2	$r_{a,m}$
BW	6	0.042	0.044	0.063	0.016	0.341	0.506	0.08(0.02)	0.09(0.02)	0.12(0.02)	0.46(0.11)
WW	5	1.922	0.471	2.576	-	15.412	20.381	0.10(0.02)	0.02(0.01)	0.12(0.02)	-
W6	6	1.636	0.335	2.075	0.462	15.153	19.810	0.08(0.02)	0.01(0.01)	0.10(0.02)	0.98(0.23)
W9	5	3.895	0.914	2.100	-	16.265	23.176	0.17(0.02)	0.03(0.02)	0.10(0.02)	-
W12	5	6.824	0.806	1.572	-	20.845	30.046	0.23(0.03)	0.03(0.02)	0.05(0.02)	-

δ_a^2: additive genetic variance; δ_c^2:maternal permanent environmental variance; δ_m^2 :maternal genetic variance; δ_e^2: residual variance; δ_p^2: phenotypic variance; $\delta_{a,m}$: direct-maternal additive genetic (co)variance; h_a^2: direct heritability; h_m^2 : maternal heritability; h_c^2: maternal environmental effect; $r_{a,m}$: direct-maternal additive genetic correlation; BW: birth weight; WW: weaning weight; W6: 6-month weight; W9: 9-month weight; W12: 12-month weight.

Table 3. Estimates of (co)variance components for the birth weight in male and female Baluchi lambs (best model in bold)[a]

Model	**Sex**	δ_a^2	δ_m^2	δ_c^2	$\delta_{a,m}$	δ_e^2	δ_p^2	h_a^2	h_m^2	h_c^2	$r_{a,m}$	**AIC**
1	Male	0.191				0.207	0.399	0.48±0.04				-771.274
	Female	0.123				0.213	0.337	0.37±0.03				
2	Male	0.076		0.058		0.234	0.369	0.21±0.04		0.16±0.02		-887.05
	Female	0.078		0.041		0.210	0.330	0.24±0.04		0.13±0.02		
3	Male	0.032	0.090			0.258	0.381	0.08±0.03	0.24±0.03			-903.732
	Female	0.035	0.057			0.233	0.326	0.10±0.03	0.18±0.02			
4	Male	0.028	0/079		0.014	0.267	0.389	0.07±0.03	0.20±0.03		0.31±0.26	-912.428
	Female	0.026	0.038		0.025	0.239	0.330	0.08±0.02	0.12±0.02		0.80±0.46	
5	Male	0.037	0.045	0.032		0.253	0.331	0.10±0.02	0.12±0.03	0.09±0.03		-907.068
	Female	0.038	0.035	0.026		0.230	0.369	0.12±0.03	0.11±0.03	0.08±0.03		
6*	**Male**	**0.026**	**0.051**	**0.026**	**0.015**	**0.263**	**0.383**	**0.07±0.03**	**0.13±0.03**	**0.07±0.02**	**0.41±0.28**	**-920.078**
	Female	**0.032**	**0.018**	**0.022**	**0.019**	**0.231**	**0.324**	**0.10±0.03**	**0.06±0.02**	**0.07±0.02**	**0.81±0.39**	

[a] δ_a^2: additive genetic variance; δ_c^2: maternal permanent environmental variance; δ_m^2 : maternal genetic variance; δ_e^2: residual variance; δ_p^2: phenotypic variance; $\delta_{a,m}$: direct-maternal additive genetic (co)variance; h_a^2: direct heritability; h_m^2 : maternal heritability; h_c^2: maternal environmental effect; $r_{a,m}$: direct-maternal additive genetic correlation; **AIC**: Akaike's information criterion. *****The best model.

Table 4. Estimates of (co)variance components for the weaning weight in male and female Baluchi lambs (Best model in bold)[a]

Model	Sex	δ_a^2	δ_m^2	δ_c^2	$\delta_{a,m}$	δ_e^2	δ_p^2	h_a^2	h_m^2	h_c^2	$r_{a,m}$	AIC
1	Male	5.604				13.315	18.920	0.30±0.04				27212.682
	Female	3.916				10.235	14.154	0.28±0.03				
2	Male	2.159		2.365		13.589	18.114	0.12±0.03		0.13±0.02		27146.316
	Female	2.559		0.988		10.222	13.770	0.19±0.03		0.07±0.02		
3	Male	1.212	2.454			14.676	18.344	0.07±0.03	0.13±0.02			27157.772
	Female	1.566	1.496			10.802	13.866	0.11±0.03	0.11±0.02			
4	Male	0.952	2.073		0.508	14.835	18.370	0.05±0.02	0.11±0.03		0.36±0.40	27163.002
	Female	1.502	1.111		0.383	10.884	13.882	0.11±0.03	0.08±0.02		0.29±0.26	
5*	**Male**	**1.363**	**0.844**	**1.805**		**14.031**	**18.040**	**0.08±0.03**	**0.05±0.02**	**0.10±0.03**		**27144.342**
	Female	**1.818**	**0.684**	**0.639**		**10.563**	**13.705**	**0.13±0.03**	**0.04±0.02**	**0.05±0.02**		
6	Male	1.088	0.686	1.877	0.408	14.306	18.365	0.06±0.02	0.04±0.03	0.10±0.03	0.39±0.39	27150.080
	Female	1.669	0.447	0.594	0.340	10.710	13.761	0.12±0.04	0.03±0.02	0.04±0.02	0.47±0.23	

[a] δ_a^2: additive genetic variance; δ_c^2:maternal permanent environmental variance; δ_m^2 :maternal genetic variance; δ_e^2: residual variance; δ_p^2: phenotypic variance; $\delta_{a,m}$: direct-maternal additive genetic (co)variance; h_a^2: direct heritability; h_m^2 : maternal heritability; h_c^2: maternal environmental effect; $r_{a,m}$: direct-maternal additive genetic correlation; **AIC**: Akaike's information criterion. *****The best model.

Table 5. Estimates of (co)variance components for the 6-month body weight in male and female Baluchi lambs (Best model in bold)[a]

Model	Sex	δ_a^2	δ_m^2	δ_c^2	$\delta_{a,m}$	δ_e^2	δ_p^2	h_a^2	h_m^2	h_c^2	$r_{a,m}$	AIC
1	Male	4.765				17.199	21.964	0.22±0.04				22496.558
	Female	4.474				10.087	14.562	0.31±0.03				
2	Male	2.035		2.135		17.162	21.333	0.09±0.03		0.10±0.02		22457.346
	Female	2.804		1.311		10.010	14.126	0.20±0.04		0.09±0.02		
3	Male	0.987	1.939			18.467	21.404	0.05±0.02	0.09±0.02			22454.936
	Female	1.120	2.138			10.904	14.163	0.08±0.03	0.15±0.03			
4	Male	1.237	2.334		-0.395	18.583	21.759	0.06±0.03	0.10±0.04		-0.23±0.38	22453.916
	Female	0.728	1.661		0.882	11.225	14.497	0.05±0.03	0.11±0.03		0.80±0.41	
5*	**Male**	**1.035**	**0.819**	**1.663**		**17.710**	**21.228**	**0.05±0.02**	**0.04±0.02**	**0.08±0.03**		**22451.436**
	Female	**1.316**	**1.379**	**0.598**		**10.705**	**14.000**	**0.09±0.04**	**0.10±0.03**	**0.04±0.03**		
6	Male	0.806	1.096	1.667	0.030	17.953	21.598	0.04±0.03	0.05±0.03	0.08±0.03	0.03±0.06	22452.428
	Female	1.031	1.139	0.480	0.866	11.070	14.564	0.07±0.03	0.07±0.03	0.03±0.03	0.81±0.42	

[a] δ_a^2: additive genetic variance; δ_c^2:maternal permanent environmental variance; δ_m^2 :maternal genetic variance; δ_e^2: residual variance; δ_p^2: phenotypic variance; $\delta_{a,m}$: direct-maternal additive genetic (co)variance; h_a^2: direct heritability; h_m^2 : maternal heritability; h_c^2: maternal environmental effect; $r_{a,m}$: direct-maternal additive genetic correlation; **AIC**: Akaike's information criterion. *****The best model.

Table 6. Estimates of (co)variance components for 9-month body weight in male and female Baluchi lambs (Best model in bold)[a]

Model	Sex	δ_a^2	δ_m^2	δ_c^2	$\delta_{a,m}$	δ_e^2	δ_p^2	h_a^2	h_m^2	h_c^2	$r_{a,m}$	AIC
1	Male	7.367				15.370	22.737	0.32±0.05				19998.712
	Female	5.382				10.937	16.319	0.33±0.04				
2	Male	4.597		2.032		15.428	22.057	0.21±0.05		0.09±0.03		19970.664
	Female	4.030		1.461		10.474	15.966	0.25±0.04		0.09±0.03		
3	Male	4.454	1.435			16.295	22.184	0.20±0.05	0.06±0.02			19967.548
	Female	2.275	2.200			11.449	15.924	0.14±0.04	0.14±0.02			
4	Male	3.292	1.919		0.323	16.637	22.174	0.15±0.05	0.09±0.03		0.13±0.33	19969.554
	Female	2.152	1.720		0.640	11.496	16.010	0.13±0.04	0.11±0.03		0.33±0.36	
5*	**Male**	**4.123**	**0.400**	**1.846**		**15.600**	**21.970**	**0.19±0.04**	**0.02±0.02**	**0.08±0.03**		**19963.558**
	Female	**2.519**	**1.407**	**0.665**		**11.172**	**15.765**	**0.16±0.04**	**0.09±0.03**	**0.04±0.03**		
6	Male	3.384	0.872	1.517	0.442	15.987	21.923	0.15±0.05	0.04±0.03	0.07±0.03	0.09±0.44	19968.338
	Female	2.368	1.197	0.622	0.161	11.210	15.840	0.15±0.05	0.08±0.03	0.04±0.03	0.26±0.29	

[a] δ_a^2: additive genetic variance; δ_c^2:maternal permanent environmental variance; δ_m^2 :maternal genetic variance; δ_e^2: residual variance; δ_p^2: phenotypic variance; $\delta_{a,m}$: direct-maternal additive genetic (co)variance; h_a^2: direct heritability; h_m^2 : maternal heritability; h_c^2: maternal environmental effect; $r_{a,m}$: direct-maternal additive genetic correlation; **AIC**: Akaike's information criterion. *****The best model.

Table 7. Estimates of (co)variance components for 12-month body weight in male and female Baluchi lambs (Best model in bold)[a]

Model	Sex	δ_a^2	δ_m^2	δ_c^2	$\delta_{a,m}$	δ_e^2	δ_p^2	h_a^2	h_m^2	h_c^2	$r_{a,m}$	AIC
1	Male	8.482				20.185	28.667	0.30±0.05				19120.396
	Female	8.611		3.533		11.515	20.127	0.43±0.04				
2	Male	6.046		0.959		18.539	28.118	0.21±0.04		0.13±0.03		19100.340
	Female	7.837				11.100	19.897	0.39±0.05		0.05±0.02		
3	Male	5.802	1.915			20.538	28.256	0.20±0.05	0.07±0.02			19103.54
	Female	5.913	1.784			12.011	19.708	0.30±0.05	0.09±0.03			
4	Male	3.894	2.231			21.199	28.191	0.14±0.04	0.08±0.03		0.29±0.35	19101.828
	Female	4.947	1.184		0.865	12.569	19.734	0.25±0.05	0.06±0.03		0.43±0.29	
5*	**Male**	**5.359**	**0.618**	**3.149**	**1.032**	**18.882**	**28.009**	**0.19±0.04**	**0.02±0.02**	**0.11±0.03**		**19097.272**
	Female	**6.114**	**1.523**	**0.114**		**11.892**	**19.644**	**0.24±0.05**	**0.08±0.03**	**0.01±0.02**		
6	Male	3.949	1.222	2.666	0.524	19.571	27.933	0.14±0.05	0.04±0.03	0.09±0.03	0.24±0.43	19099.230
	Female	5.199	1.084	0.049	1.011	12.369	19.715	0.26±0.05	0.05±0.03	0.01±0.03	0.42±0.30	

[a] δ_a^2: additive genetic variance; δ_c^2:maternal permanent environmental variance; δ_m^2 :maternal genetic variance; δ_e^2: residual variance; δ_p^2: phenotypic variance; $\delta_{a,m}$: direct-maternal additive genetic (co)variance; h_a^2: direct heritability; h_m^2 : maternal heritability; h_c^2: maternal environmental effect; $r_{a,m}$: direct-maternal additive genetic correlation; **AIC**: Akaike's information criterion. *The best model.

Table 8. Between-sex direct and maternal correlation coefficients in Baluchi sheep[a]

Trait	r_a	r_m	r_c	r_p
BW	0.86	0.99	0.97	0.28
WW	1.00	0.99	0.99	0.22
W6	1.00	0.99	0.99	0.19
W9	1.00	0.99	0.99	0.27
W12	1.00	0.99	0.99	0.31

a**ra*: genetic correlation between males and females; ***rm: maternal genetic correlation between males and females; ***rc***: maternal permanent environmental correlation between males and females; ***rp***: phenotypic correlation

Discussion

Our estimates of the M/F ratios showed a relatively low level of sexual dimorphism for the studied traits. In general, previous reports indicated low level of SD in body weight of domestic sheep. For example, Ghafouri-Kesbi et al. (2015) in Zandi sheep, reported SD levels of 1.11, 1.07 and 1.09 for BW, WW and W6, respectively. Furthermore, in Afshari sheep, Ghafouri-Kesbi and Notter (2016) reported M/F ratios for BW as 1.07 and for WW as 1.14. In addition, Ghafouri-Kesbi and Baneh (2018) estimated M/F ratios for BW, WW, W6, W9 and W12 in Iran-Black sheep as 1.065, 1.098, 1.097, 1.105 and 1.142, respectively. Increasing trend for M/F ratio after birth until yearling age may be explained by endocrine differences between the sexes and occurrence of sexual puberty. Steroids such as testosterone and estrogen affect the growth of males and females differently. In males, testosterone accelerates muscle growth by affecting the rate of protein synthesis, while in females estrogen dampens growth by limiting the length of long bones leading to smaller body size than males (Mateescu and Thonney, 2002).

The extent to which a trait is improved depends on the degree of additive genetic variance in the population. The additive variance is often measured as heritability (h_a^2), the fraction of the total phenotypic variance that is additive (Ghafouri-Kesbi and Notter, 2016). Heritability estimates for the studied traits were close to the average reported values for these traits in models that fitted maternal effects (Safari et al., 2005). However, according to heritability estimates, a relatively small response to selection would be expected, especially for BW, WW and W6. Maternal effects were significant for all the studied traits in the present work. Therefore, to increase the accuracy of genetic evaluation, these effects should be included in the model.

The estimates of direct heritability for studied traits in both sexes were in the range reported for other breeds of sheep (see Singh et al., 2016 and references therein). Higher additive genetic variance and direct heritability in female lambs was in agreement with Gudex et al. (2009) who reported higher additive genetic variance in females than males for weaning and post-weaning body weights in three Australian sheep breeds (Coopworth, Poll Dorset and White Suffolk). In the study by Ghafouri-Kesbi et al. (2015) on Zandi sheep, while additive genetic variance in BW of female lambs was higher than males, greater additive genetic variance was observed for WW and W6 in male lambs. In Afshari lambs, Ghafouri-Kesbi and Notter (2016) reported higher additive genetic variance in birth weight of male lambs. But in weaning weight and pre-weaning growth rate, they reported higher additive genetic variance in females. In Iran-Black sheep, Ghafouri-Kesbi and Baneh (2018) reported higher additive genetic variance in birth weight and weaning weight of male lambs, while at 6, 9 and 12 months of age, females expressed more additive genetic variance. While estimates of h_a^2 for studied traits varied between sexes, the differences between sexes were not significaant (P>0.05). Gudex et al. (2009) who worked on Australian Coopworth, Poll Dorset and White Suffolk breeds of sheep, reported higher heritability estimates for post-weaning body weights in female lambs, although in most cases the differences were not significant. Ghafouri-Kesbi and Notter (2016) reported estimates of $\boldsymbol{h_a^2}$ for BW and WW of Afshari sheep as 0.39 and 0.15 in males and 0.29 and 0.22 in females, respectively. In the study by Ghafouri-Kesbi and Baneh (2018) on Iran-Black sheep, while males and females expressed almost equal heritability for BW and WW, but for traits measured after weaning, heritability estimates were higher in females, though the differences were non-significant. However, non-significant differences between sexes regarding direct heritability indicated that sexual selection cannot be used to alter the phenotype of males and females in different directions (Parés-Casanova, 2016). If the differences were significant, sex-specific selection strategies could be applied.

Previous reports including those of Singh et al. (2016), Maraveni et al. (2018), Latifi and Mohammadi (2019) and Latifi and Bohlouli (2020) showed that in sheep, maternal effects play a key role in development of body weight especially at earlier ages. These reports also showed that ignoring maternal effects when they are actually present will result in an upward bias in estimates of direct heritability because estimated additive genetic variance will capture at least part of the maternal variation. As maternal additive genetic and maternal permanent environmental effects were significant in both male and female lambs, these effects should be included in the model of genetic evaluation of body weights of both sexes to obtain more accurate estimates of genetic parameters and breeding values. In all the studied traits, maternal permanent environmental variance and residual variances were greater in male lambs compared to female lambs. Ghafouri-Kesbi and Notter (2016) reported that greater values of δ_c^2 and δ_e^2 in males showed that male lambs are more sensitive to environmental conditions in agreement with Riggio et al. (2008) who reported lower survival rates for male lambs compared to female lambs. It means that while males are heavier and seem to be stronger than females, they are also more sensitive to environmental stresses. Therefore, for males, abortion cases and mortality rate should be higher than females as reported in human studies (Cunningham et al., 2010).

For BW, cross-sex additive genetic correlation was 0.86. It shows that birth weight is controlled by genes that are differently expressed in male and female lambs. It provides opportunity for divergent selection. By applying sex-specific selection we can increase birth weights of females to improve perinatal survival, without changing birth weights in males to avoid increases in difficult births. For other body weights, the $\boldsymbol{r_a}$ was close to 1.00 which showed no opportunity for sexual selection. Ghafouri-Kesbi et al. (2015) estimated genetic correlations between sexes of Zandi lambs for BW, WW and W6 as 0.82, 0.92 and 0.92, respectively. Moreover, Ghafouri-Kesbi and Notter (2016) who worked on Afshari sheep estimated $\boldsymbol{r_a}$ as 0.98 and 0.99 for BW and WW, respectively. In addition, Ghafouri-Kesbi and Baneh (2018) estimated $\boldsymbol{r_a}$ for body weight at birth, weaning, 6, 9 and 12 months of age in Iran-Black sheep as 1.00. Poissant et al. (2010) found that, except for fitness-related traits, genetic correlations between homologous traits expressed in males and females were predominantly large and positive. Because of genotype–environment interactions, $\boldsymbol{r_a}$ is environment-specific, and, due to differences in allele frequencies, estimates of $\boldsymbol{r_a}$ are also population-specific (Poissant et al., 2010). Between sexes maternal correlations ($\boldsymbol{r_m}$ and $\boldsymbol{r_c}$) were close to 1.00 which indicated that the phenotypes of male and female offspring are equally influenced by maternal effects. Ghafouri-Kesbi and Notter (2016) reported estimates of $\boldsymbol{r_c}$ for BW, WW and W6 in Afshari lambs as 0.72, 0.98 and 0.96, respectively. They reported that deviation of $\boldsymbol{r_c}$ from unity for birth weight might be because of pre-natal programming events and epigenetic modifications that can affect future progeny birth weights in mammalian species.

Conclusions

Relatively low levels of sexual dimorphism were observed in body weights of Baluchi lambs. None of the observed differences in direct heritability between sexes were significant, indicating no need or opportunity for sex-specific selection strategies. In both sexes, body weights from birth until yearling age were under control of maternal effects. Estimates of maternal permanent environmental and residual variances showed greater environmental sensitivity in male lambs. Except for birth weight, between-sex genetic correlation was 1.00 which indicated that these traits share similar genes.

References

Akaike, H., 1974. A new look at the statistical model identification. *Transactions on Automatic Control* 19, 716-723.

Badyaev, A.V., 2002. Male and female growth in sexually dimorphic species: harmony, conflict, or both? *Comments on Theoretical Biology* **7**, 11–33.

Bahreini-Behzadi, M.R., Aslaminejad, A., Sharifi, A.R., Simianer, H., 2014. Comparison of mathematical models for describing the growth of Baluchi sheep. *Journal of Agricultural Science and Technology* 14, 57-68.

Cunningham, F., K, Leveno, S, Bloom., J, Hauth., D., Rouse., Spong, C., 2010. William's Obstetrics. 23rd Edition, McGraw-Hill, New York, USA.

Darwin, C., 1871. The descent of man, and selection in relation to sex. Murray, London, UK.

Ghafouri-Kesbi, F., Baneh, H., 2018. Genetic aspects of sexual size dimorphism in a synthesized breed of sheep. *Meta Gene* 17, 177-183.

Ghafouri-Kesbi, F., Gholizadeh, M., 2017. Genetic and phenotypic aspects of growth rate and efficiency-related traits in sheep. *Small Ruminant Research* 149, 181-187.

Ghafouri-Kesbi, F., Notter, D.R., 2016. Sex influence on genetic expression of early growth in Afshari lambs. *Archiv Tierzukht* 59, 9-17.

Ghafouri-Kesbi, F., Rahimi, G.H., Hafeziyan, H., Ansari, Z., Baneh, H., Solimani, B., 2015. A genetic study on sexual dimorphism of body weight in sheep. *Animal Production Science* 55, 101-106.

Gudex, BW., Condro C., Marshal, K., van der Werf, J.H.J., 2009. The genetics of sexual dimorphism in sheep. *Proceedings* of the 18th *Association for the Advancement of Animal Breeding and Genetics Conference* 18, 14-17.

Kamalzadeh, A., Shabani, A., 2007. Maintenance and growth requirements for energy and nitrogen of Baluchi sheep. *International Journal of Agricultural Biology* 4, 535-539.

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, 365-375.

Latifi, M., Bohlouli, M., 2020. Estimation of growth curve parameters in Mehraban sheep using different non-linear models. *Genetika* 52, 815-823.

Lovich, J.E., Gibbons, J.W., 1992. A review of techniques for quantifying sexual size dimorphism. *Growth, Development and Aging* 56, 269-281.

Maniatis, G., Demiris, N., Kranis, A., Banos, G., Kominakis, A., 2013. Genetic analysis of sexual dimorphism of body weight in broilers. *Journal of Applied Genetics* 54, 61-70.

Mateescu, R.G., Thonney, M.L., 2002. Gene expression in sexually dimorphic muscles in sheep. *Journal of Animal Science* 80, 1879-1887.

McLean, C., Garwood R.J., Brassey, C.A., 2018. Sexual dimorphism in the Arachnid orders. *Peer Journal* 6, 5751.

Mallon, J.C., 2017. Recognizing sexual dimorphism in the fossil record: lessons from non-avian dinosaurs. *Paleobiology* 43, 495-507.

Maraveni, M., Vatnkhah, 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 Journal of Applied Animal Research* 8, 67-75.

Meyer, K., 2007. WOMBAT: a program for mixed model analyses by restricted maximum likelihood. User notes.

Mignon-Grasteau, S., Piles, M., Varona, L., De Rochambeau, H., Poivey, J., Blasco, A., Beaumont, C., 2000. Genetic analysis of growth curve parameters for male and female chickens resulting from selection on shape of growth curve. *Journal of Animal Science* 78, 2515-2524.

Polak, J., Frynta, D., 2009. Sexual size dimorphism in domestic goats, sheep, and their wild relatives. *Biological Journal of the Linnaean Society* 98, 872-883.

Parés-Casanova, P.M., 2015. Discrete sexual size dimorphism in domestic sheep. *Annals of Biology* Research 6, 43-48.

Poissant, J., Wilson, A. J., Coltman, D.W., 2010. Sex-specific genetic variance and the evolution of sexual dimorphism: A systematic review of cross-sex genetic correlation. *Evolution* 64, 97-107.

Poissant, J.M., Wilson, AJ., Festa-Bianchet, M., Hogg, J.T., Coltman, D.W., 2008. Quantitative genetics and sex-specific selection on sexually dimorphic traits in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences* 275, 623-628.

Rensch, B., 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner zoologische Beiträge* 1, 58-69.

Riggio, V., Finocchiaro, R., Bishop, S.C., 2008. Genetic parameters for early lambs survival and growth in Scottish Blackface sheep. *Journal of Animal Science* 86, 1758-1764.

Safari, E., Fogarty, N.M., Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livestock Production Science* 92, 271-289.

SAS. 2004. User's Guide, version 9.SAS Institute, Cary, NC.

Singh, H., Pannu, U., Narula, H.K., Chopra, A., Naharwara, V., Bhakar S.K., 2016. Estimates of (co)variance components and genetic parameters of growth traits in Marwari sheep. *Journal of Applied Animal Research* 44, 27-35.

van der Heide, E. M. M., Lourenco, D. A. L., Chen, C. Y., Herring, W. O., Sapp, R. L., Moser, D. W., Tsuruta, S., Masuda, Y., Ducro, B. J., Misztal, I., 2016. Sexual dimorphism in livestock species selected for economically important traits. *Journal of Animal Science* 94, 3684-3692.