

Paper type: Original Research

A model including parent-of-origin genetic effects to analyze sexual size dimorphism in body weight of sheep

Farhad Ghafouri-Kesbi^{1*}, Ahmad Ahmadi¹, Mohsen Gholizadeh²

¹Department of Animal Science, Faculty of Agriculture, Bu-Ali Sina University, Hamedan, Iran

²Department of Animal Science, Faculty of Animal and Aquatic Science, Sari Agricultural Sciences and Natural Resources University, Sari, Iran

*Corresponding author,
E-mail address:
f.ghafouri@basu.ac.ir

Received: 26 Feb 2025,
Received in revised form: 24 Mar
2025,
Accepted: 10 Apr 2025,
Published online: 11 Apr 2025,
© The authors, 2025.

ORCID

Farhad Ghafouri-Kesbi
0000-0002-2219-055X
Ahmad Ahmadi
0000-0003-0276-9027
Mohsen Gholizadeh
0000-0003-4544-1566

Abstract So far, the parent-of-origin genetic effects have not been accounted for analyzing the sexual size dimorphism (SSD) in sheep. Therefore, genetic analysis of sexual size dimorphism in Baluchi sheep was performed with models incorporating the parent-of-origin genetic effects. Body weights at birth (**BW**), weaning (**WW**), 6 (**W6**), 9 (**W9**) and 12 (**W12**) months of age were analyzed with twelve bivariate animal models including the male and female body weight records as different traits. Male lambs were 0.26, 1.92, 3.049, 3.228, and 4.695 kg heavier than females at birth, weaning, and 6, 9 and 12 months of age, respectively. The SSD level (expressed as male/female ratio) was 1.062, 1.085, 1.11, 1.11 and 1.13 for **BW**, **WW**, **W6**, **W9** and **W12**, respectively. For all traits studied, a model that contained the maternal imprinting effects was selected as the most appropriate one. For **BW** and **WW**, maternal imprinting heritability (h_{mi}^2) was higher in males (0.25 and 0.12) compared to females (0.21 and 0.11), but for **W6**, **W9** and **W12**, females recorded higher h_{mi}^2 (0.24, 0.34, 0.27 vs. 0.12, 0.22, 0.17). The estimates of direct heritability (h_a^2) were almost equal in both sexes ranging from 0.02 (**W6**) to 0.15 (**W12**) in males and 0.03 (**W6**) to 0.16 (**W12**) in females. For all traits studied, maternal permanent environmental and residual variances were greater in males than females, indicating greater environmental sensitivity of male lambs. Cross-sex additive genetic correlation, maternal imprinting correlation, and maternal permanent environmental correlations were close to unity indicating absence of sexual dimorphism for direct additive, maternal imprinting, and maternal permanent environmental effects on the traits studied. Therefore, divergent selection could not be recommended because selection for either male or female weights would result in a strongly correlated response in the other sex.

Keywords: sheep, body weight, sexual size dimorphism, heritability, correlation

Introduction

In almost all domestic and wild mammalian species, males are larger than females, a phenomenon which is called sexual size dimorphism (SSD; Roulin and Jensen, 2015). The SSD is more evident in larger species, *i.e.*,

as the species size increases, the difference between the body size of males and females (SSD level) increases. In addition, because of the power of sexual selection in the wild, SSD is more prevalent in wild species compared to domestic species (Polák and Frynta, 2009). The

mechanisms for maintaining sexual dimorphism in a population are not completely understood but may involve interaction between the sex chromosomes and autosomes. For example, the *Sry* locus on the Y chromosome plays an important role in sex determination and dimorphism (McLaren, 1990). In addition, several autosomal loci are expressed differentially in males and females with concomitant effects on sexual dimorphism (McMahon et al., 2003; Salih et al., 2005).

Recent reports show that SSD is present at a considerable level in different breeds of sheep. For example, Ghafouri-Kesbi and Baneh (2018) reported an increasing trend for SSD in Iran-Black sheep from birth (3.50kg vs 3.73kg) to yearling age (36.81kg vs 42.04kg). Gudex et al. (2009) reported that SSD has a genetic background. A general requirement for SSD to evolve is that the trait of interest should be controlled by genes differently expressed in the two sexes and that the cross-sex correlations should be lower than unity (Merilä et al., 1998). Many researchers including Maniatis et al. (2013), Ghafouri-Kesbi and Notter (2016), Ghafouri-Kesbi and Baneh (2018), Mokhtari et al. (2022), and Mandal et al. (2022) estimated sex-specific genetic variance and cross-sex genetic correlations in different sheep breeds. However, they only included animal and maternal effects in the genetic model and ignored other genetic components such as imprinting effects. Imprinting is an epigenetic modification that is parental origin-specific, leading to preferential expression of a specific parental allele in the somatic cells of the offspring. Mechanisms such as DNA methylation, RNA-associated silencing, and histone modification cause relative silencing of a specific parental allele (Fradin et al., 2010). Complete imprinting causes the monoallelic expression of a diploid locus, either maternal or paternal, *i.e.*, not both of them. Consider *Aa* and *aA* genotypes, the first allele is transferred from the father, and the second is transferred from the mother. Although classic quantitative genetics consider the two heterozygotes (*Aa* and *aA*) equal, because of imprinting, their product can be different (Cheveroud et al., 2008). Partial imprinting is also possible. In such cases, the expression of a specific allele is not entirely monoallelic but is instead influenced by imprinting in a way that can result in variable or intermediate levels of expression. Recent studies have shown the contribution of imprinting effects to the phenotypic variation of body weight in sheep (Amiri-Roudbar et al., 2018; Mokhtari et al., 2022; Ghafouri-Kesbi et al., 2022). However, the role of genomic imprinting in the evolution of sexual dimorphism in sheep has not been investigated. Therefore, this study was conducted to analyze sexual dimorphism in the body weight of Baluchi sheep using models that included the imprinting effects.

Materials and methods

Data

The data used in the present study were obtained from the Abbasabad Sheep Breeding Station (flock 1), Mashhad, Khorasan Razavi, Iran. This experimental population of Baluchi sheep was founded in the early 1960s. Data included the following traits: birth weight (**BW**) and body weights at weaning (**WW**), 6 months (**W6**), 9 months (**W9**), and 12 months of age (**W12**). In order to account for the differences among animals with different ages, weaning weight, 6-month weight, 9-monthly weight, and 12-month weight were adjusted to 90, 180, 270, and 365 days of age, respectively. Errors in the pedigree were detected and edited with CFC software (Sargolzaei et al., 2006). The final pedigree included 11658 animals which were progenies of 258 sires and 3137 dams (Table 1).

Table 1. Pedigree structure of the Baluchi sheep

No. of Generations (including base generation)	17
No. of Animals in the pedigree file	11658
No. of Animals with progeny	3395
No. of Animals without progeny	8263
No. of Non-base animals	10827
No. of Non-base animals with known sire and dam	10494
No. of Non-base animals only with known sire	13
No. of Non-base animals only with known dam	320
No. of Sire	258
No. of Dam	3137
No. of Grand sire	210
No. of Grand dam	588
No. of Great grand sire	181
No. of Great grand dam	980

Statistical analysis

The generalized linear model (GLM) of SAS (2004) was fitted to the data to identify the fixed effects of the model. The effect of year of birth, age of dam at lambing, and birth type were significant ($P < 0.01$) for all traits studied. Lovich and Gibbons ratio (Lovich and Gibbons, 1992) was used to measure the SSD level as M/F, where M and F are the mean body weight of males and females, respectively. Preliminary analysis showed that paternal imprinting effects were almost zero for all the traits studied. Therefore, paternal imprinting effects were ignored in subsequent analyses. A series of 12 bivariate animal models was fitted including the observations on male and female lambs as different traits. The bivariate models were as follows:

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

$$\text{Model 2: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{mi1} & 0 \\ 0 & Z_{mi2} \end{bmatrix} \begin{bmatrix} mi_1 \\ mi_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

$$\text{Model 3: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

$$\text{Model 4: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} Z_{mi1} & 0 \\ 0 & Z_{mi2} \end{bmatrix} \begin{bmatrix} mi_1 \\ mi_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

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

$$\text{Model 6: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} Z_{mi1} & 0 \\ 0 & Z_{mi2} \end{bmatrix} \begin{bmatrix} mi_1 \\ mi_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix};$$

$$\text{Cov}(a, m) = 0$$

$$\text{Model 7: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}; \text{Cov}(a, m) = A\sigma_{a,m}$$

$$\text{odel 8: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} Z_{mi1} & 0 \\ 0 & Z_{mi2} \end{bmatrix} \begin{bmatrix} mi_1 \\ mi_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix};$$

$$\text{Cov}(a, m) = A\sigma_{a,m}$$

$$\text{Model 9: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}; \text{Cov}(a, m) = 0$$

$$\text{odel 10: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} Z_{mi1} & 0 \\ 0 & Z_{mi2} \end{bmatrix} \begin{bmatrix} mi_1 \\ mi_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix};$$

$$\text{Cov}(a, m) = 0$$

$$\text{Model 11: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}; \text{Cov}(a, m) = A\sigma_{a,m}$$

$$\text{Model 12: } \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_{a1} & 0 \\ 0 & Z_{a2} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_{c1} & 0 \\ 0 & Z_{c2} \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 \\ 0 & Z_{m2} \end{bmatrix} \begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} Z_{mi1} & 0 \\ 0 & Z_{mi2} \end{bmatrix} \begin{bmatrix} mi_1 \\ mi_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix};$$

$$\text{Cov}(a, m) = A\sigma_{a,m}$$

where, subscripts 1 and 2 refer to male and female traits, respectively; $y_{1(2)}$ is $n_{1(2)} \times 1$ vector of observations; $b_{1(2)}$ is a $p \times 1$ vector of fixed effects where p denotes the total number of fixed effect classes; $a_{1(2)}$ is a $q \times 1$ vector of additive genetic effects where q denotes the total number of animals in the pedigree; $c_{1(2)}$ is a $k \times 1$ vector of maternal permanent environmental effects where k is the number of dams with offspring; $m_{1(2)}$ is a $d \times 1$ vector of maternal genetic effects where d is the total number of females; $mi_{1(2)}$ is a $d \times 1$ vector of maternal imprinting genetic effects where d is the total number of animals; $\text{Cov}(a, m)$ is direct-maternal additive genetic covariance.; $e_{1(2)}$ is an $n_{1(2)} \times 1$ vector of residuals corresponding to temporary environment effects; and $X_{1(2)}$, $Z_{a1(2)}$, $Z_{c1(2)}$, $Z_{m1(2)}$, and $Z_{mi1(2)}$ denote incidence matrices relating observations to fixed effects, additive animal effects, maternal permanent environmental effects, maternal additive genetic effects, and maternal imprinting effects, respectively. Direct additive genetic, maternal permanent environmental, maternal genetic, maternal imprinting and residual effects were assumed to be normally distributed with mean 0 and variances $A\sigma_a^2$, $I_{nd}\sigma_c^2$, $A\sigma_m^2$, $G\sigma_{mi}^2$ and $I_e\sigma_e^2$ and, respectively, where A

is the additive numerator relationship matrix and G is the gametic relationship matrix. The I_{nd} and I_e are identity matrices of order equal to the number of dams and the number of records, respectively. The δ_a^2 , δ_c^2 , δ_m^2 , δ_{mi}^2 and δ_e^2 are direct additive genetic, maternal permanent environmental, maternal additive genetic, maternal imprinting and residual variances, respectively. The WOMBAT program of Meyer (2020) was used to estimate the variance components and genetic parameters. The Akaike's information criteria (AIC; Akaike, 1974) were computed to identify the best models as follows:

$$\text{AIC} = -2\log L + 2p,$$

where, p is the number of model parameters, and $\log L$ is the natural logarithm of the likelihood function. The model with the smallest AIC was selected as the best model.

Results

Table 2 presents descriptive statistics for the studied traits in male and female lambs. Male lambs were 0.26, 1.92, 3.049, 3.228, and 4.695 kg heavier than females at birth, weaning, 6 months, 9 months, and 12 months of age, respectively. There was an increasing trend for SSD level (expressed as M/F) from birth until 12 months of age (Figure 1), being 1.062, 1.085, 1.11, 1.11 and 1.13 for **BW**, **WW**, **W6**, **W9** and **W12**, respectively.

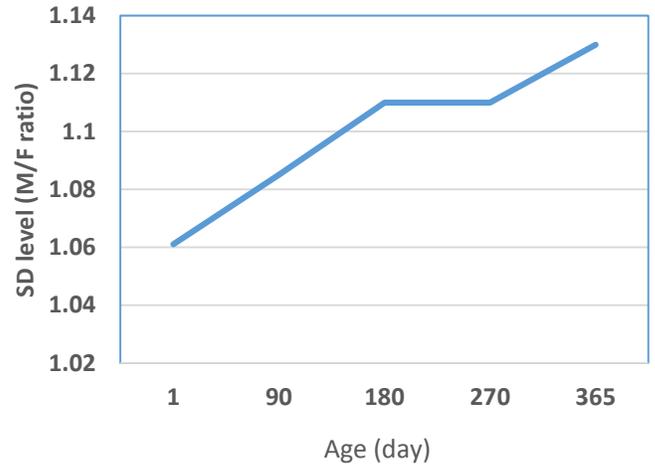


Figure 1. Increase in SD level (M/F ratio) with age in Baluchi sheep

Table 2. Descriptive statistics for weight traits in Baluchi sheep¹

Item	BW		WW		W6		W9		W12	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
No of records	3754	3585	3702	3601	2931	2953	2962	2961	2340	2272
Mean	4.344	4.085	24.460	22.54	31.941	28.892	32.077	28.849	41.437	36.742
Minimum	1.600	1.500	10.11	10.00	15.24	15.180	12.40	11.190	21.970	20.02
Maximum	6.500	6.500	37.97	37.68	45.10	43.250	51.560	43.250	60.220	58.96
SD	0.727	0.685	5.12	4.482	5.473	4.543	5.668	4.614	6.78	5.530
CV (%)	16.7	16.8	20.9	19.80	17.1	15.7	17.7	15.9	16.3	15.1

¹ **BW**: birth weight; **WW**: weaning weight; **W6**: 6-month weight; **W9**: 9-month weight; **W12**: 12-month weight; SD: Phenotypic standard deviation; CV: Phenotypic coefficient of variation.

Table 3 shows the least square means (\pm SE) for the traits studied. Effects of year of birth, birth type, and age

of dam at lambing were significant in both sexes ($P < 0.01$). In both sexes, single lambs were heavier than

twins at all ages. Lambs from 3- to 6-year-old ewes were heavier than those from 2- or > 6-year-old dams.

Estimates of variance components and genetic parameters are shown in Table 4. According to AIC values, for **BW**, **WW**, and **W6**, model 4 which included the direct additive genetic effect, maternal permanent environmental effect and maternal imprinting effect provided the lowest AIC value which was selected as the most appropriate model. For **W9** and **W12**, model 2 which included direct additive genetic effects and maternal imprinting effects fitted the data better than other models and therefore selected as the most appropriate model. For birth weight and weaning weight, the additive genetic variance was greater in females, but afterward, the additive genetic variance was greater in males. However, similar trends were not observed for the direct heritability (h_a^2) due to sex differences

regarding other variance components. For both sexes, a significant maternal permanent environmental effect (h_c^2) was detected ranging between 0.07 (**W6**) to 0.09 (**BW**) in males and 0.03 (**W6**) to 0.08 (**BW**) in females. For all traits studied, maternal imprinting effects were significant with greater estimates of maternal imprinting heritability (h_{mi}^2) in females (0.11-0.34) compared to males (0.12-0.25). For all traits, the estimates of maternal imprinting heritability were also greater than direct heritability. Direct genetic correlations (r_a) between sexes were 0.96, 1.00, 0.99, 0.99 and 0.96 for **BW**, **WW**, **W6**, **W9** and **W12**, respectively (Table 5). Maternal permanent environmental correlations (r_c) between sexes were 0.99, 0.96 and 0.99 for **BW**, **WW**, and **W6**, respectively. Maternal imprinting correlations (r_{mi}) between sexes were 1.00 for **BW**, 0.99 for **WW**, 1.00 for **W6**, 1.00 for **W9** and 0.91 for **W12**.

Table 3. Least-squares means and standard errors of body weight at different ages in male and female Baluchi sheep¹

	BW		WW		W6		W9		W12	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Birth Year	**	**	**	**	**	**	**	**	**	**
Birth type	**	**	**	**	**	**	**	**	**	**
Single	4.56±0.03 ^a	4.29±0.02 ^a	26.52±0.12 ^a	24.11±0.17 ^a	35.65±0.19 ^a	32.63±0.24 ^a	36.75±0.20 ^a	34.31±0.23 ^a	45.29±0.26 ^a	41.37±0.24 ^a
Twin	4.16±0.04 ^b	3.91±0.04 ^b	23.15±0.13 ^b	23.43±0.18 ^b	33.54±0.18 ^b	31.24±0.27 ^b	34.22±0.19 ^b	32.35±0.27 ^b	42.64±0.27 ^b	39.35±0.25 ^b
Triplet	3.83±0.04 ^c	3.64±0.05 ^c	20.76±0.17 ^c	20.19±0.22 ^c	30.64±0.32 ^c	28.57±0.30 ^c	31.69±0.33 ^c	30.61±0.37 ^c	39.09±0.35 ^c	37.33±0.31 ^b
Damage (y)	**	**	**	**	**	**	**	**	**	**
2	3.62±0.02 ^c	3.39±0.02 ^d	20.34±0.17 ^c	19.65±0.21 ^b	29.787±0.18 ^c	27.36±0.24 ^b	31.24±0.32 ^b	28.76±0.31 ^c	38.09±0.25 ^c	36.99±0.26 ^b
3	3.81±0.02 ^b	3.45±0.03 ^c	20.73±0.19 ^{ab}	20.16±0.20 ^b	29.89±0.18 ^c	27.39±0.23 ^b	31.96±0.36 ^a	29.16±0.32 ^b	38.18±0.25 ^b	36.87±0.27 ^a
4	3.84±0.03 ^{ab}	3.59±0.03 ^b	21.66±0.21 ^{ab}	22.01±0.24 ^a	30.25±0.19 ^c	28.64±0.24 ^a	32.24±0.29 ^a	30.68±0.33 ^b	39.66±0.27 ^b	37.55±0.27 ^a
5	3.95±0.03 ^a	3.60±0.04 ^b	21.67±0.22 ^a	21.44±0.28 ^a	31.11±0.21 ^b	29.37±0.29 ^a	32.74±0.30 ^a	31.72±0.35 ^a	40.03±0.33 ^b	38.45±0.35 ^a
6	3.95±0.04 ^a	3.73±0.04 ^a	22.45±0.27 ^{ab}	21.54±0.29 ^a	32.15±0.28 ^a	30.05±0.32 ^a	32.37±0.35 ^a	30.28±0.44 ^b	41.63±0.42 ^a	38.13±0.44 ^a
7	3.89±0.06 ^{ab}	3.70±0.05 ^a	21.37±0.33 ^{bc}	20.37±0.37 ^b	31.42±0.36 ^b	29.65±0.47 ^a	31.26±0.43 ^b	30.13±0.54 ^b	41.09±0.51 ^a	37.49±0.63 ^b
8	3.80±0.07 ^{ab}	3.81±0.07 ^a	21.09±0.45 ^{bc}	20.56±0.51 ^b	31.14±0.44 ^b	29.43±0.61 ^a	31.30±0.54 ^b	30.22±0.63 ^b	41.14±0.72 ^a	37.24±0.75 ^b

¹ **BW**: birth weight; **WW**: weaning weight; **W6**: 6-month weight; **W9**: 9-month weight; **W12**: 12-month weight. Within columns, means with common superscript(s) are not different ($P>0.05$); **: $P<0.01$.

Table 4. Estimates of (co)variance components for body weight at different ages in male and female Baluchi sheep¹

Trait	Sex	δ_a^2	δ_c^2	δ_{mi}	δ_e^2	δ_p^2	h_a^2	h_c^2	h_{mi}^2
BW	Male	0.018	0.032	0.089	0.219	0.357	0.05±0.02	0.08±0.02	0.25±0.05
	Female	0.019	0.030	0.068	0.212	0.327	0.06±0.02	0.08±0.02	0.21±0.04
WW	Male	1.048	1.694	2.200	13.120	18.067	0.06±0.03	0.09±0.03	0.12±0.04
	Female	1.386	0.662	1.552	10.056	13.660	0.10±0.03	0.05±0.02	0.11±0.04
W6	Male	0.449	1.485	2.450	0.749	31.250	0.02±0.02	0.07±0.02	0.12±0.04
	Female	0.428	0.483	3.995	0.651	14.079	0.03±0.02	0.03±0.02	0.24±0.04
W9	Male	0.547	-	5.120	0.981	22.852	0.03±0.03	-	0.22±0.04
	Female	0.316	-	4.952	0.534	14.759	0.02±0.04	-	0.34±0.04
W12	Male	4.219	-	4.749	19.254	28.223	0.15±0.04	-	0.17±0.05
	Female	3.024	-	5.201	11.012	19.239	0.16±0.05	-	0.27±0.05

¹ **BW**: birth weight; **WW**: weaning weight; **W6**: 6-month weight; **W9**: 9-month weight; **W12**: 12-month weight; δ_a^2 : additive genetic variance; δ_c^2 : maternal permanent environmental variance; δ_{mi} : maternal imprinting variance; δ_e^2 : residual variance; δ_p^2 : phenotypic variance; h_a^2 : direct heritability; h_c^2 : maternal environmental effect; h_{mi}^2 : maternal imprinting heritability; h_e^2 : maternal environmental effect.

Discussion

Several studies have examined the impact of fixed effects on body weight traits in sheep (Al-Bial et al., 2012; Khojastehkey and Aslaminejad, 2013; Petrovic et al., 2015; Sharif et al., 2022). The differences in nutrition and agro-climatic conditions that affect the growth rate

are the origins of year of birth effects (Al-Bial et al., 2012; Khojastehkey and Aslaminejad, 2013; Petrovic et al., 2015; Sharif et al., 2022). Sharif et al. (2022) reported that the effect of type of birth was significant on weight traits in lambs to yearling age. The singleton body weight at all ages was higher than twins weight because of the competition between twins in obtaining the dam's milk

resulting in receiving less milk compared to the singleton lambs. The dam's age significantly affected the body weight at all ages. However, lambs from 3-6 years old ewes were heavier than those from 2- or > 6-yr-old ewes. Younger dams are still under development, limiting the availability of nutrients for growth of the fetus (Babar et al., 2004). Also, younger dams produce less milk because their udder has not yet been completely developed (Sharif et al., 2022). The ewes older than 6 years of age may also suffer from health problems. For example, some may lose their teeth and their feed intake decreases, thus decreasing the fetal intake of nutrients.

Table 5. Between-sex direct and maternal correlations in Baluchi sheep¹

Trait	r_a	r_c	r_{mi}	r_p
BW	0.96±0.18	0.99±0.28	1.00±0.17	0.26±0.17
WW	1.00±0.19	0.96±0.21	0.99±0.09	0.36±0.09
W6	0.99±0.19	0.99±0.29	1.00±0.16	0.36±0.16
W9	0.99±0.31	-	1.00±0.18	0.30±0.18
W12	0.96±0.11	-	0.91±0.13	0.34±0.13

¹**BW**: birth weight; **WW**: weaning weight; **W6**: 6-month weight; **W9**: 9-month weight; **W12**: 12-month weight; r_a : genetic correlation between males and females; r_c : maternal permanent environmental correlation between males and females; r_{mi} : maternal imprinting correlation between males and females, r_p : phenotypic correlation between males and females.

The M/F ratios (1.06 to 1.13, Figure 1) were in the range of other reports. Ghafouri-Kesbi et al. (2014) in Zandi sheep, reported SSD levels for **BW**, **WW** and **W6** as 1.11, 1.07 and 1.09, respectively. In addition, in Afshari sheep, Ghafouri-Kesbi and Notter (2016) reported SSD levels for **BW** and **WW** as 1.07 and 1.14, respectively. Furthermore, Ghafouri-Kesbi and Baneh (2018) reported SSD levels for **BW**, **WW**, **W6**, **W9** and **W12** in Iran-Black sheep as 1/07, 1.10, 1.10, 1.11 and 1.14, respectively. These estimates show that males are heavier than females at birth, and because of greater growth rate during the pre- and post-weaning growth periods, they would be heavier at older ages. Khojastehkey and Aslaminejad (2013) in Zandi sheep, Petrovic et al. (2015) in cross-bred sheep and Sharif et al. (2022) in Luha sheep reported heavier male lambs compared to female lambs at birth and thereafter. Benyi et al. (2006) stated that male lambs grow faster in the uterus than females. Similarly, Babar et al. (2004) reported that pregnancy duration for male lambs is slightly longer than for females. Another possible explanation for the variation in gender weights is hormonal differences, especially sexual hormones, leading to differences in growth rate. Estrogens limit the development of long bones in females; this could be one of the reasons why females have smaller bodies and are lighter than the males (Petrovic et al., 2015).

In our study, until weaning, the additive genetic variance (δ_a^2) was greater in females but for body weight measured after weaning it was greater in males. Ghafouri-Kesbi et al. (2014) reported higher δ_a^2 for **WW** and **W6** of male Zandi lambs, while it was higher for the birth weight of female lambs. Concerning the birth weight of Afshari lambs, Ghafouri-Kesbi and Notter (2016)

reported higher δ_a^2 for the birth weight of male lambs compared to females. However, for weaning weight and pre-weaning growth rate, they reported higher δ_a^2 in females. Moreover, in the study by Ghafouri-Kesbi and Baneh (2018), δ_a^2 was higher for the ram lamb at birth and weaning weights; however for body weight at 6, 9, and 12 months of age, δ_a^2 was greater in females. In all cases, maternal permanent environmental variance and residual variances were greater in males compared to females. According to Ghafouri-Kesbi and Notter (2016), high values of δ_c^2 and δ_e^2 in males show greater environmental sensitivity in males. This means that male lambs are more affected by harsh environmental effects which can be evidenced by more abortion cases and mortality rate in male lambs compared to females.

The estimated values of h_a^2 for the studied traits in both sexes were close to each other and were in the range reported for other breeds of sheep (Singh et al., 2016; Amiri Roudbar et al., 2017; Amiri Roudbar et al., 2018; Sharif et al., 2022; Mokhtari et al., 2022). The low h_a^2 values indicated that following selection, a low response would be expected in the body weight of Baluchi lambs. Ghafouri-Kesbi and Notter (2016) reported estimates of 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, which are higher than our findings. Maternal permanent environmental effect (h_c^2) was higher in males compared to females, in line with Ghafouri-Kesbi and Notter (2016).

Except for **BW**, **WW** and **W9**, for other traits studied, maternal imprinting variance and its ratio to phenotypic variance (h_{mi}^2) was higher in females. In maternal imprinting, the maternal allele is silenced (imprinted), and the active allele is paternally expressed and paternally transmitted down through the generations; therefore, the male offspring transmit the active allele to sons and daughters in each subsequent generation, while female offspring only transfer the inactivated copy of the allele. Therefore, half of the daughters' children (both sons and daughters) will have the inactive (silenced) copy of the allele (Jonsson et al., 2023). Maternal imprinting shuts down the genes that enhance the embryo's growth whereas paternal imprinting silences the genes that limit growth and development. Therefore, maternal imprinting favors smaller offspring and paternal imprinting favors the production of larger offspring (Hunter, 2007). The estimates of h_{mi}^2 for studied traits in both sexes were higher than other reports. Amiri Roudbar et al. (2017) in Iran-Black sheep reported estimates h_{mi}^2 for weaning weight and six months weight as 0.22 and 0.21, respectively. In addition, Amiri Roudbar et al. (2018), studying the Lori-Bakhtiari sheep, reported estimates of h_{mi}^2 as 0.23, 0.10, 0.13 for the birth weight, weaning weight and nine months weight, respectively. Ghafouri-Kesbi et al. (2022) estimated h_{mi}^2 for the efficiency of growth and relative growth rate in Zandi sheep as 0.06 and 0.06, respectively. In Kermani sheep, Mokhtari et al. (2022)

reported h_{mi}^2 for growth traits in a range from 0.05 (average daily gain) to 0.24 (6-month weight). Our results together with previous reports show that because maternal imprinting effects are significant on body weight in sheep, these effects should be included in the model for genetic evaluation of body weight in sheep. Otherwise, the accuracy of genetic evaluation would be low.

Cross-sex additive genetic correlation determines the extent to which the similarities in male and female phenotypes are co-inherited (Poissant et al., 2010). For all traits studied, the additive genetic correlation between sexes was almost unity indicating that body weight in male and female lambs is controlled by similar genes. Ghafouri-Kesbi and Baneh (2018) reported r_a for **BW**, **WW**, **W6**, **W9**, and **W12** in Iran-Black sheep as 1.00 which is inconsistent with our results. When r_a is less than 1.0, divergent selection could be effective because selection for either male or female weights wouldn't result in a strongly correlated response in the other sex (Ghafouri-Kesbi and Baneh, 2018). This is in line with Merilä et al. (1998) who stated that since the genetic correlations between the sexes are usually high for morphometric traits, a slow evolutionary rate of SSD should be expected. Except for **W12**, for other traits, maternal imprinting correlation (r_{mi}) between sexes was close to one. It shows that similar imprinted genes in female and male lambs affect body weight in a similar direction. At the age of twelve months, r_{mi} was less than unity which indicated that male and female lambs experience differential maternal imprinting effects.

Conclusions

While male lambs were heavier than females at all ages, a low level of SSD (measured as male/female ratio) was observed in the body weight of Baluchi lambs. Maternal imprinting effects contributed significantly to the phenotypic variation in body weight of Baluchi lambs in both sexes, being greater than animal additive genetic effects. However, genetic correlations between the body weight of male and female lambs were close to unity, which indicated that male and female lambs share the same genes and that there is no need or opportunity for divergent selection strategies.

Acknowledgment

The staff of Abbasabad Baluchi Sheep Breeding Station are gratefully acknowledged for providing the data.

References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716-723.
- Al-Bial, A., Singh, J., Singh, D.P., Niwas, R., 2012. Environmental and genetic factors on growth traits of Black Bangal sheep in Yemen. *The Bioscan* 7, 185-188, 2012.
- Amiri Roudbar, M., Abdollahi-Arpanahi, R., Ayatollahi Mehrgardi, A., Mohammadabadi, M., Taheri Yeganeh, A., Rosa, G.J.M., 2018. Estimation of the variance due to parent-of-origin effects for productive and reproductive traits in Lori-Bakhtiari sheep. *Small Ruminant Research* 160, 95-102.
- Amiri Roudbar, M., Mohammadabadi, M., Mehrgardi, A.A., Abdollahi-Arpanahi, R., 2017. Estimates of variance components due to parent-of-origin effects for body weight in Iran-Black sheep. *Small Ruminant Research* 149, 1-5.
- Babar, M.E., Ahmad, Z., Hussain, A., 2003. Heritability estimates of birth and weaning weight in Lohi sheep. *Pakistan Journal of Agricultural Science* 40, 214-216.
- Babar, M.E., Ahmad, Z., Nadeem, A., 2004. Yaqoob, M. Environmental factors affecting birth weight in Lohi sheep. *Pakistan Veterinary Journal* 24, 5-8.
- Benyi, K., Norris, D., Karbo, N., Kgomo, K.A., 2006. Effects of genetic and environmental factors on pre-weaning and post-weaning growth in West African crossbred sheep. *Tropical Animal Health and Production* 38, 547-554.
- Cheverud, J.M., Hager, R., Roseman, C., Fawcett, C., Wang, B., Wolf, J.B., 2008. Genomic imprinting effects on adult body composition in mice. *Proceedings of the National Academy of Sciences of the United States of America* 105, 4253-4258.
- Fradin, D., Cheslack-Postava, K., Ladd-Acosta, C., Newschaffer, C., Chakravarti, A., Arking, D.E., Feingerg, A., Fallin, M.D., 2010. Parent-of-origin effects in autism identified through genome-wide linkage analysis of 16,000 SNPs. *PLoS One* 5, e12513.
- 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., Rahimi, G.H., Hafeziyan, H., Ansari, Z., Baneh, H., Solimani, B., 2014. A genetic study on sexual dimorphism of body weight in sheep. *Animal Production Science* 55, 101-106.
- Ghafouri-Kesbi, F., Zamani, P., Mokhtari, M., 2022. Relative contribution of imprinting, X chromosome and litter effects to phenotypic variation in economic traits of sheep. *Journal of Animal Breeding and Genetics* 139, 611-622.
- Gudex, B.W., Condro, C., Marshal, K., and van der Werf, J.H.J., 2009. The genetics of sexual dimorphism in sheep, Proc. Assoc. Advance. *Journal of Animal Breeding and Genetics* 18, 14-17.
- Hunter, P., 2007. The silence of genes. Is genomic imprinting the software of evolution or just a battleground for gender conflict? *EMBO Reports* 8, 441-443.
- Jønsson, V., Awan, H., Johannesen, T.B., Tjønnfjord, G.E., 2023. Maternal and paternal imprinting in the segregation of malignant blood disorders. *Clinics in*

- Oncology* 8,1986.
- Khojastehkey, M., Aslaminejad, A.A., 2013. Study of the environmental, genetic and phenotypic trends for pelt traits and body weight traits in Zandi sheep. *Journal of Applied Animal Research* 41, 356-361.
- Lovich, J.E., Gibbons, J.W., 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Development and Aging* 56, 269-281.
- McLaren, A., 1990. What makes a man a man? *Nature* 346, 216.
- McMahon, C.D., Popovic, L., Jeanplong, F., Oldham, J.M., Kirk, S.P., Osepchook, C.C., Wong, K.W., Sharma, M., Kambadur, R., and Bass, J.J., 2003. Sexual dimorphism is associated with decreased expression of processed Myostatin in males. *American Journal of Physiology-Endocrinology and Metabolism* 284, 377-381.
- Mandal, A., Baneh, H., Rout, P.K., Notter, D.R., 2022. Genetic analysis of sexual dimorphism in growth of Jamunapari goats of India. *Journal of Animal Breeding and Genetics* 139, 1-14.
- Maniatis, G., Demiris, N., Kranis, A., Banos, G., and Kominakis, A., 2013. Genetic analysis of sexual dimorphism of body weight in broilers. *Journal of Applied Genetics* 54, 61-70.
- Merila, J., Sheldon, B.C., Ellegren, H., 1998. Quantitative genetics of sexual size dimorphism in the collared flycatcher, *Ficedula albicollis*. *Evolution* 52, 870-876.
- Meyer, K., 2020. WOMBAT: A tool for estimation of genetic parameters--highlights and updates. The 6th International Conference on Quantitative Genetics, 3-13 November, Brisbane, Queensland, Australia.
- Mokhtari, M., Barazandeh, A., Roudbari, Z., Ghafouri-Kesbi, F., Amiri-Roudbar, M., 2022. Quantifying parent-of- origin variation in growth and reproductive traits of Kermani sheep. *Journal of Agricultural Science* 160, 391-396.
- Petrović, M.P., Caro-Petrović V., Ružić-Muslić D., Maksimović, N., Petrović, M.M., Ilić, Z., Stojković J., 2015. Effect of genetic and environmental factors on the phenotype characteristics of lambs. *Biotechnology in Animal Husbandry* 31,223-233
- 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.
- Polák, J., Frynta, D., 2009. Sexual size dimorphism in domestic goats, sheep, and their wild relatives. *Biological Journal of the Linnean Society* 98, 872-883.
- Roulin, A., Jensen, H., 2015. Sex-linked inheritance, genetic correlations and sexual dimorphism in three melanin-based colour traits in the barn owl. *Journal of Evolutionary Biology* 28, 655-666.
- Salih, D.A., Mohan, S., Kasukawa, Y., Tripathi, G., Lovett, F.A., Anderson, N.F., Carter, E.J., Wergedal, J.E., Baylink, D.J., and Pell, J.M., 2005. Insulin-like growth factor-binding protein-5 induces a gender-related decrease in bone mineral density in transgenic mice. *Endocrinology* 146, 931-940.
- Sargolzaei, M., Iwaisaki, H., Colleau, J. J., 2004. CFC: a tool for monitoring genetic diversity. Proceedings of the 8th World Congress on Genetics Applied to Livestock Production, 13-18 August, Belo Horizonte, Minas Gerais, Brazil.
- SAS, 2004. User's Guide, version 9. SAS Institute, Cary, NC.
- Sharif, N., Ali, A., Dawood, M., Khan, M.I.R., Do, D.N., 2022. Environmental effects and genetic parameters for growth traits of Lohi sheep. *Animal* 12, 3590.
- 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.