Genetic aspects of sexual size dimorphism in a synthesized breed of sheep

Farhad Ghafouri-Kesbi[a,*], Hasan Baneh[b]

[a] Department of Animal Sciences, Faculty of Agriculture, Bu-Ali Sina University, Hamedan, Iran
[b] Department of Animal Breeding and Genetics, Animal Science Research Institute of Iran, Karaj, Iran

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ABSTRACT

The aim was to study genetic aspects of sexual size dimorphism in Iran-Black synthetized breed of sheep. Traits evaluated were birth weights (BW), weaning weights (WW) and post-weaning body weights measured at 6 months (W6), 9 months (W9) and 12 months (W12) of age. A series of six bivariate animal models including direct and maternal components were used to measure phenotypic variance and its constituent components in male and female lambs. Male lambs were heavier than female lambs by 6%, 10%, 9%, 10% and 14% at birth, weaning, six-month, 9-month and 12 months of age, respectively. SD levels (expressed as M/F) for BW, WW, W6, W9 and W12 were 1.065, 1.098, 1.097, 1.105 and 1.142, respectively. From birth until weaning, additive genetic variance was greater in males but at 6, 9 and 12 months of age females expressed more additive genetic variance. Concerning direct heritability (h_a^2), males and females expressed almost equal heritability for BW and WW, but for traits measured after weaning, heritability estimates were higher in females. In nearly all cases, maternal variances and residual variance were greater in males compared to females indicating greater environmental sensitivity in males compared to females. However, concerning direct and maternal effects, none of the differences between two sexes were significant, indicating no need for sexual selection. Between-sex additive genetic correlations (r_a) were almost 1.00 for all the traits studied. Deviation of maternal permanent environmental correlations (r_c) between sexes from unity for W6 showed presence of sexual dimorphism for maternal effects on W6.

1. Introduction

Nearly all of mammal species show phenotypic differences regarding size and weight between males and females. This phenotypic difference between two sexes is termed "sexual dimorphism" (SD; Polak and Frynta, 2009, 2010; Gudex et al., 2009). Due to strong sexual selection, sexual dimorphism is more prevalent in wild species where body size of males is one of the most important components of fitness (Polak and Frynta, 2009), resulting a higher Lovich and Gibbons (1992) ratios in wild species: M/F for male larger species and 2-F/M for female larger species; where M and F are the mean male and female body mass, respectively. In domestic populations because matings depends on breeders decisions, thus, selection on strong, heavy rams by females, i.e., sexual selection is much reduced.

In recent years, exploring genetic aspects of sexual size dimorphism in animal breeding has retained the attention of animal breeders (Gudex et al., 2009; Maniatis et al., 2013; Ghafouri-Kesbi et al., 2015; Ghafouri-Kesbi and Notter, 2016). The main reason is that when SD is present, especially if heritability for traits measured on males and females are unequal and (or) genetic correlations between the sexes are

significantly less than unity, accurate estimation of breeding values could not be obtained and the definition and realization of optimal multiple-trait selection response for each sex are challenges (Gudex et al., 2009; Ghafouri-Kesbi and Notter, 2016).

In different sheep breeds, SD is very evident. Reports shows that differences in body weight of rams and ewes has a wide range from 22 kg in the West African Dwarf to 130 kg in the Mutton Merino. However, among mammalian species, SD is lower in domestic sheep compared to other species such as dog and horse (Arés-Casanovanthetic sheep breed originated from Baluchi rams and Chios ewes. It is developed in the breeding station of Abbasabad, north-east of Iran in order for improving production and reproduction performances as well as tolerance to harsh environmental conditions of Baluchi sheep (Mokhtari et al., 2014). Although, genetic parameters for production and reproduction traits of Iran-Black sheep are available (Rashidi, 2013; Ahmadpanah et al., 2016), there is no previous reports regarding genetic and phenotypic aspects of SD in this breed. Therefore, the present study was conducted to study phenotypic and genetic differences in body weights of male and female Iran-Black lambs as well as to estimate the between-sex genetic correlations.

* Corresponding author.
E-mail address: farhad_ghy@yahoo.com (F. Ghafouri-Kesbi).

2. Material and methods

2.1. Flock management

In the mid-1970s a breeding program was designed in Abbasabad sheep breeding station, Khorasan province, to develop Iran-Black breed by crossing Baluchi rams and Chios ewes and vice versa. The first lambs were born in 1975 and the flock was maintained as a close flock so far. In the flock, matings started from mid-August and continued to September. Two years old rams are mated with ewes for the first time. The ewes were exposed to fertile rams at approximately 18 months of age and usually 10–12 ewes are allocated to a fertile ram. Lambing commenced in mid-January and ends in February. Upon lambing, lambs are weighed and ear-tagged and identified to their parents (Kamjoo et al., 2014). Lambs are weaned from their mothers at approximately 3 months of age. After weaning, ewes and young animals are kept in the separate flocks. Ewes were kept in the flock for a maximum of 7 parities (until 8 years of age) while the rams were used for 2 breeding seasons. From birth till 12 months of age, the lambs were weighed at three months intervals, and the date of each weight is recorded.

2.2. Evaluated traits

Data included birth weight (BW), 3-month weight (weaning weight, W3), 6-month weight (W6), 9-month weight (W9) and 12-month weight (W12). 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 90, 180, 270 and 365 days of age, respectively.

2.3. Statistical analysis

First of all, Shapiro-Wilk procedure of SAS (2004) was used to test normality of data. Then, to identify fixed effects, least square analyses were conducted using the Generalized Linear Model (GLM; SAS, 2004) with a model that included fixed effects of year of birth, age of dam at lambing and type of birth. Lovich and Gibbons ratio (Lovich and Gibbons, 1992) was used to measure SD as M/F, where M and F are the mean male and female body weight, respectively. A series of six bivariate animal models was fitted including observations on male and female lambs as different traits. An animal model partitions each individual animal's phenotype for a given trait into a linear sum of different fixed and random effects, with specific variance structures specified for the different random effects (Schaeffer, 2010). The bivariate models were:

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

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

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

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

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

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

where subscripts 1 and 2 refer to 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 ($p = 33$ classes of fixed effects); $a_{1(2)}$ is a $q \times 1$ vector of additive genetic effects where q denotes the total number of animals in the pedigree (q = 5127 animals); $c_{1(2)}$ is a $k \times 1$ vector of maternal permanent environmental effects where k is the number of dams with offspring (k = 1202 dams); $m_{1(2)}$ is a $d \times 1$ vector of maternal genetic effects where d is the total number of females (d = 2561 females); $Cov(a,m)$ is direct-maternal additive genetic covariance which was used to estimate direct-maternal additive genetic correlation ($r_{a,m}$) as $r_{a,m} = cov(a,m)/\sqrt{\delta_a^2} \times \sqrt{\delta_m^2}$; $e_{1(2)}$ is an $n_{1(2)} \times 1$ vector of residuals corresponding to temporary environment effects; and $X_{1(2)}$, $Z_{a1(2)}$, $Z_{c1(2)}$ and $Z_{m1(2)}$ denote incidence matrices relating observations to fixed effects, additive animal, maternal permanent environmental effects and maternal additive genetic effects, respectively. Direct additive genetic, maternal permanent environmental, maternal genetic and residual effects were assumed to be normally distributed with mean 0 and variances $A\sigma_a^2$, $I_{nd}\sigma_c^2$, $A\sigma_m^2$ and $I_e\sigma_e^2$, respectively, where A is the additive numerator relationship matrix containing individual elements $A_{ij} = 2\Theta_{ij}$ and Θ_{ij} is the coefficient of co-ancestry (kinship) between individuals i and j; I_{nd} and I_e are identity matrices of order equal to the number of dams and number of records, respectively; and δ_a^2, δ_c^2, δ_m^2 and δ_e^2 are additive genetic, maternal permanent environmental, maternal additive genetic and residual variances, respectively. (Co)variance components and genetic parameters were estimated using the WOMBAT program of Meyer (2007) by the restricted maximum likelihood procedure (REML). Convergence was assumed when the variance of likelihood values was less than 10^{-8}. In addition, a restart of each analysis was performed with different starting values to attempt to avoid convergence to local maxima. Only when global convergence occurred, (co)variance components were extracted. Computing time was under 1 min for all models. The Bayesian Information Criterion (BIC) of Schawarz (1978) were computed to rank the models as follow:

$$BIC = -2logL + p\log(N - r)$$

where p is the number of model parameters, N is the total number of records, r is the rank of the fixed effect incidence matrix in the model, and log L is the natural logarithm of the likelihood function.

3. Results

Descriptive statistics for the traits studied are listed in Table 1. As observed, differences between males and females regarding body weight increased with age in a way that male lambs were 6%, 10% and 9%, 10% and 14% heavier than females at birth, weaning, six-month, 9-month and 12 months of age, respectively. Evolution of SD levels (expressed as M/F ratio) during the period studied is shown in Fig. 1. As observed there is an increasing trend for SD from birth until yearling age. For BW, WW, W6, W9 and W12, the SD levels were 1.065, 1.098, 1.097, 1.105 and 1.142, respectively. Least square means (± SE) for the traits studied are shown in Tables 2. Effects of year of birth, birth type and age of dam at lambing were significant in both sexes ($P < .01$). Male lambs were heavier than female lambs in all cases. In addition, in both male and female lambs, single lambs were heavier