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Estimation of genetic parameters for body weight traits in Baluchi sheep

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Abstract Genetic parameters for birth weight (BW), weaning weight (WW), 6 months weight (6MW), 9 months weight (9MW) and yearling weight (YW) in Baluchi sheep were estimated using data collected during a 26-year period (1984-2010). Estimates of (co)variance components were obtained by REML procedures by fitting a linear mixed animal model. Significant random effects for each trait were explored by fitting direct additive genetic effects, maternal additive genetic effects, covariance between direct additive and maternal additive genetic effects, maternal permanent environmental effects and common litter effects in different models. The Akaike's information criterion (AIC) test was applied to determine the most appropriate model for each trait. The estimated direct heritabilities for BW, WW, 6MW, 9MW and YW were 0.34, 0.09, 0.06, 0.12 and 0.16, respectively. Corresponding maternal heritability estimates were 0.12, 0.07, 0.05, 0.03 and 0.01, respectively. The variance ratios due to maternal permanent environment (c^2) decreased from 0.06 in BW to 0.02 for YW. The variance ratios due to litter component were 0.23, 0.07, 0.08 and 0.12 for BW, WW, 9MW and YW, respectively. Direct genetic correlations between body weight traits were positive and high and ranged from 0.52 for BW-YW to 0.96 for 9MW-YW.

Keywords: heritability, growth traits, genetic correlation, sheep

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Introduction

The sheep population in Iran, reported at 54 million heads in 2011, accounts for 36.8% of total red meat production (Iranian Ministry of Agriculture, 2011). Mutton is the traditional source of animal protein in Iran, but its supply does not satisfy the increasing demand from consumers (Rashidi et al., 2008). Baluchi sheep is the main sheep breed constituting some 30% of the total sheep population. It is well adapted to dry and hot climatic conditions and is mainly kept under low-input production systems. Although Iranian native breeds of sheep are multi-purpose types (meat, milk and wool), lamb production is of primary importance, and profitability of sheep enterprise depends to a large extent on the body weights of the lamb. Within breed selection is a suitable tool for genetic improvement of sheep under low input pastoral systems (Kosgey et al., 2006). Design of optimal breeding strategies for genetic improvement of growth in Baluchi sheep requires accurate estimate of heritability as well as genetic relationships among growth traits and between these trait and other economically important ones. Genetic parameters for growth traits have been reported by Yazdi et al. (1997) without fitting litter effect in the statistical model. Given a 30% twin birth rate in the current data set, it is of interest not only to estimate the contribution of litter effect to the total variance, but also determine the possible impact of its inclusion in the model on other random effect components and in particular on the contribution from direct genetic effects. Therefore, the main objective of the present study was to test the significance of a range of variance components such as maternal, permanent environment, and litter effects and the covariance between direct and maternal genetic effects and their impacts on the estimates of genetic parameters for body weight traits in Iranian Baluchi sheep. Such estimates are important in designing breeding strategies for Baluchi sheep population.

Materials and methods

Flock management and data collection

Data were collected from 1984 to 2010 at the Abbasabad Sheep Breeding Station, located in Khorasan Razavi province, north-eastern, Iran. Breeding rams and ewes were selected based on the weaning weight, breed characteristics (white coat color with black pigment in the head and legs), visual body conformation, wool quality scores and birth type (twin preference). Before mating, estrous ewes were identified by teaser rams. Annually, around 30 rams were randomly allocated to mate with 15 to 25 ewes each and 55% of sires were used once and the rest were kept for 2 to 3 mating seasons. To establish genetic links between flocks, some of the rams were used in both flocks. Ewes were kept for a maximum of 7 parities (8 years of age). The annual ewe replacement rate was 25-30%. The breeding season started from late August to late October. Maiden ewes were first exposed to fertile rams at approximately 18 months of age and lambing was commenced in late January to late March. After lambing, lambs were ear-tagged and weighed. The ewes and their lambs were kept in separate pens. The lambs were fed on natural pastures, mainly *Festuca*and *Poa*, and kept together until weaned at approximately three months of age. The lambs were weaned on the same day, not necessarily at same age. During spring and summer, flocks were kept on pastures and in autumn were fed on wheat and barley stubble. Supplementary feed was offered during winter and late pregnancy and included a diet composed of wheat and barley straw, alfalfa hay, dry sugar beet pulp, and concentrate. The supplementary diet contained 2.0 Mcal ME per kg, 11.5% crude protein, 1.02% calcium and 0.28% phosphorus on dry matter basis (NRC, 1985). All animals had free access to mineral blocks and fresh water. The traits analyzed were weights at birth (BW), weaning (at 3 months of age; WW), 6 months (6MW), 9 months (9MW), and yearling weight (YW). The descriptive statistics and data structure are presented in Table 1.

Table 1. Descriptive statistics and data structure for birth weight (BW), weaning weight (WW), six-month weight (6MW), nine-month weight (9MW) and yearling weight (YW)

Traits	No. of Records (lambs)	Mean (kg)	S.D. (kg)	No. of dams	No. of sires	Average No. of records per		No. of dams with records	No. of sires with records
						dam	sire		
BW	14030	4.25	0.70	4371	444	4.65	51.62	2988	182
WW	10541	22.19	4.98	3225	331	3.90	43.60	2313	151
6MW	8635	31.39	5.49	2987	325	3.26	36.75	2156	147
9MW	7741	34.34	5.44	2833	320	3.13	32.72	2059	141
YW	6948	38.94	6.56	2655	315	2.65	28.43	1962	139

S.D.: Standard deviation.

Statistical analysis

The fixed effects in the analytical model were sex of the lamb (male and female), birth year in 26 classes (1984–2010), dam age at lambing in 7 classes (2-8 years old), birth type in 3 classes (single, twin and triplet), and lamb age (in days) as a linear covariate for WW, 6MW, 9MW and YW, respectively**.** The interactions between fixed effects were not significant, thus excluded from the models. The (Co)variance components and corresponding genetic parameters were obtained by the restricted maximum likelihood (REML) procedure under nine different animal models using WOMBAT software(Meyer,2010). The full linear mixed models were:

Table 2. Changes in the AIC values as deviation from the model with the lowest AIV value under different models for birth weight (BW), weaning weight (WW), six-month weight (6MW), nine- month weight (9MW) and yearling weight (YW)

Model	BW	WW	6MW	9MW	YW
1	507.76	94.40	66.00	45.90	33.22
2	246.32	27.46	13.80	18.48	16.00
3	256.20	10.96	4.08	15.72	18.64
4	237.88	12.70	3.02	4.90	11.08
5	219.36	5.50	1.00	14.04	15.86
6	203.24	7.26	0.00	4.14	9.70
7	26.70	3.18	3.52	10.58	7.38
8	12.32	0.00	1.44	10.44	7.20
9	0.00	1.72	0.44	0.00	0.00

Model 1		$y = Xb + Z_a a + e$
Model 2		$y = Xb + Z_a a + Z_c c + e$
Model 3	Cov (a,m) = 0	$y = Xb + Z_a a + Z_m m + e$
Model 4	Cov (a,m) = $A\sigma_{am}$	$y = Xb + Z_a a + Z_m m + e$
Model 5	Cov (a,m) = 0	$y = Xb + Z_a a + Z_c c + Z_m m + e$
Model 6	Cov (a,m) = $A\sigma_{am}$	$y = Xb + Z_a a + Z_c c + Z_m m + e$
Model 7		$y = Xb + Z_a a + Z_l l + Z_c c + e$
Model 8	Cov (a,m) = 0	$y = Xb + Z_a a + Z_l l + Z_c c + Z_m m + e$
Model 9	Cov (a,m) = $A\sigma_{am}$	$y = Xb + Z_a a + Z_l l + Z_c c + Z_m m + e$

where ***y*** is a vector of observations for different traits; ***b, a, m***, ***c***, ***l*** and***e*** are vectors of fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental, litter and residual effects, respectively. ***X***, $\boldsymbol{Z_a}$, $\boldsymbol{Z_m}$, $\boldsymbol{Z_c}$and $\boldsymbol{Z_l}$are the incidence matrices relating the observations to the fixed, direct additive genetic, maternal additive genetic, maternal permanent environmental and litter effects, respectively.

It was assumed that direct additive genetic, maternal additive genetic, maternal permanent environmental, litter and residual effects were normally distributed with mean of zero and variance of $A\sigma_a^2$, $A\sigma_m^2$,$I_d\sigma_c^2$, $I_l\sigma_l^2$ and $I_n\sigma_e^2$, respectively; where, σ_a^2, σ_m^2, σ_c^2, $\sigma_l^2$and σ_e^2were direct additive genetic, maternal additive genetic, maternal permanent environmental litter and the residual variance components, respectively. ***A*** is the additive numerator relationship matrix, $\boldsymbol{I_d}$, $\boldsymbol{I_l}$ and $\boldsymbol{I_n}$ were identity matrices with the order equal to the number of dams, litters and number of records, respectively; and $\boldsymbol{\sigma_{am}}$ refers to the covariance between direct additive genetic and maternal additive genetic effects.

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

$$AIC_i = -2 \log L_i + 2 p_i \qquad (1)$$

where $\log L_i$ is the maximized log likelihood of themodel at convergence and p_i is the number of parameters obtained from each model; the model with the lowest AIC was chosen as the most appropriate model. Total heritability was estimated according to the following formula (Willham, 1972):

$$h_t^2 = \sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{a,m}/\sigma_p^2 \qquad (2)$$

Maternal across year repeatability for ewe performance (t_m) was calculated as follows:

$$t_m = 1/4 h_a^2 + h_m^2 + c^2 + (mr_{am}\, h) \qquad (3)$$

Genetic and phenotypic correlations were estimated using multivariate analyses applying the most appropriate models from the univariate analysis. If the value of -2 log likelihood variance in the AIREML function was smaller than 10^{-8}, it was assumed that convergence had been achieved.

Results and discussion

Model selection

The model with minimum AIC value for BW, 9MW and YW was the full model (Model 9) in contrast to Model 8 for WW and model 6 for 6MW (Table 2). The results provide no support for the inclusion of covariance between direct additive and maternal additive genetic effects for WW, as well as litter effect for 6MW in this data set. These results are consistent with the findings of Safari et al. (2007) on BW and YW but not on WW where a similar model with the inclusion of covariance between direct additive and maternal additive genetic effects was reported to be significant in the Australian Merino sheep.

Genetic parameter estimates

Variance components and genetic parameter estimates are presented in Table 3. Low to high heritability values were estimated for growth traits. Direct heritability estimates decreased from birth (0.34) to wean

Table 3. Estimates of (co)variance components and genetic parameters (± s.e.) for birth weight (BW), weaning weight (WW), six-month weight (6MW), nine-month weight (9MW) and yearling weight (YW) from the best model

Trait	Model	σ^2_a	σ^2_m	σ^2_c	σ^2_l	$\sigma^2_{a.m}$	σ^2_e	σ^2_p	h^2_a±S.E	m^2±S.E	c^2±S.E	l^2±S.E	$r_{a,m}$±S.E	h^2_t	t_m
BW	9	0.114	0.040	0.019	0.078	-0.025	0.112	0.338	0.34±0.02	0.12±0.02	0.06±0.01	0.23±0.02	-0.37±0.07	0.29	0.19
WW	8	1.047	0.878	0.420	0.807	-	8.941	12.093	0.09±0.02	0.07±0.01	0.04±0.02	0.07±0.01	-	0.12	0.13
6MW	6	0.990	0.895	0.722	-	0.431	14.830	17.868	0.06±0.02	0.05±0.01	0.04±0.01	-	0.46±0.20	0.12	0.13
9MW	9	2.198	0.480	0.417	1.483	0.950	13.373	18.901	0.12±0.02	0.03±0.02	0.02±0.01	0.08±0.03	0.92±0.37	0.20	0.13
YW	9	3.948	0.333	0.484	2.838	1.056	15.580	24.239	0.16±0.02	0.01±0.01	0.02±0.02	0.12±0.02	0.92±0.60	0.24	0.11

σ_a^2: direct additive genetic variance: σ_m^2: maternal additive genetic variance: σ_c^2: maternal permanent environmental variance; σ_l^2: common litter variance; $\sigma_{a.m}$: covariance between direct and maternal additive genetic effects; σ_e^2: residual variance; σ_p^2: phenotypic variance; h_a^2: direct heritability: m^2: maternal heritability; c^2: ratio of maternal permanent environmental variance to phenotypic variance; l^2: ratio of common litter variance to phenotypic variance; S.E: standard error; h_t^2: total heritability; $t_{m:}$ Maternal across year repeatability for ewe performance.

ing (0.09) and six months of age (0.06), increasing afterwards to 0.12 at nine months of age and 0.16 at yearling. The heritability estimates for BW in our study (0.34) was much higher than estimates by Yazdi et al. (1997) for flock 1 (0.14) and flock 2 (0.20). In contrast to our estimates, Yazdi et al. (1997) reported a higher estimates for WW (0.19, 0.13), 6MW (0.23, 0.32) and YW (0.32, 0.26) for flock 1 and flock 2, respectively. The heritability estimate for BW was similar to the estimates by Miraei-Ashtiani et al. (2007) in Sangsari sheep. Birth weight plays an important role in the profitability of sheep enterprise by influencing survival and pre-weaning growth (Rashidi et al., 2011; Al-Shorepy, 2001). The estimated direct heritability for WW is also consistent with estimates by Abegaz et al. (2005) in Horro and Jafaroghli et al. (2010) for Moghani sheep populations. Similar low heritability estimates were reported for 6MW by Eskandarinasab et al. (2010) in Afshari sheep. The heritability estimates at 9MW and YW fall within the range reported by other researchers (Mokhtari et al., 2008; Snyman et al., 1995).

Generally an increasing trend was expected for the magnitude of heritability estimates from birth to yearling age based on estimates from across population studies (e.g. Safari et al., 2005; Safari et al., 2007), and from the findings by Yazdi et al. (1997) in Baluchi sheep. Drought and poor quality pastures during the last two decades, higher accuracy of parameter estimate due to genetic link, and larger combined data set are among the possible contributing factors to the lower heritability estimates in this study compared to those of Yazdi et al. (1997).

The maternal heritability decreased from birth to yearling age (Table 3). This was expected and is in agreement with an across population review by Safari et al. (2005;2007) in Australian Merino sheep. The estimate of maternal heritability for BW is in general agreement with the estimate by Mohammadi et al. (2010) for Sanjabi sheep. Similar maternal heritability estimates were reported by Ligda et al. (2000) and Vatankhah and Talebi (2008) for WW and Nasholm and Danell (1996) for 6MW. However, maternal heritability estimates for 6MW were unexpectedly higher than those for 9MW and YW.

The estimates of maternal permanent environmental variance as a proportion of phenotypic variance are shown in Table 3. The estimates for BW and WW were in agreement with those by Matika et al. (2003) in Sabi sheep and Safari et al. (2005) in wool and dual-purpose sheep breeds. Maternal permanent environmental effects can be ascribed to the uterine environmental conditions, milk production, feeding level at the late stages of gestation and maternal behavior of the ewe (Maria et al., 1993; Snyman et al., 1995). Based on results from the present study, accurate genetic evaluation of growth traits in Baluchi sheep requires adopting models with direct, maternal genetic and maternal environmental effects. A significant maternal effect was observed for all traits. This may be due to carry-over maternal effects from weaning. Such carry-over effect beyond weaning is of biological importance, especially when pre-weaning lamb growth is restricted by low milk production of dam, either due to larger litter size or seasonal feed shortage (Snyman et al., 1995).

The significant impact of litter on growth traits is consistent with other studies (Tosh and Kemp, 1994; Al-Shorepy and Notter, 1998; van Vleck et al., 2003; Safari et al., 2007). The litter contribution decreased from 23% of the phenotypic variance for BW to 12% for YW. This was expected and is a reflection of increasing independence of lambs on their dams. High litter estimate was also reported by van Wyk et al. (2003)

Table 4. Estimates (±s.e.) of additive genetic (r_a), maternal genetic (r_m), maternal permanent environmental (r_c), litter (r_l), phenotypic (r_p) and environmental correlations among birth weight (BW), weaning weight (WW), six-month weight (6MW), nine-month weight (9MW) and yearling weight (YW)

Pair traits[a]	r_a	r_m	r_c	r_l	r_p	r_e
BW-WW	0.79±0.05	0.57±0.13	0.45±0.18	0.41±0.10	0.39±0.01	0.33±0.01
BW-6MW	0.76±0.07	0.62±0.13	0.21±0.24	-	0.32±0.01	0.30±0.01
BW-9MW	0.62±0.07	0.82±0.14	0.12±0.28	0.21±0.10	0.31±0.01	0.19±0.03
BW-YW	0.52±0.07	0.74±0.21	0.41±0.31	0.34±0.09	0.28±0.01	0.11±0.04
WW-6MW	0.88±0.05	0.98±0.04	0.98±0.11	-	0.68±0.01	0.67±0.01
WW-9MW	0.72±0.07	0.98±0.04	0.95±0.16	0.60±0.18	0.60±0.01	0.53±0.02
WW-YW	0.76±0.06	0.98±0.06	0.94±0.18	0.42±0.17	0.54±0.01	0.53±0.01
6MW-9MW	0.94±0.03	0.99±0.02	0.96±0.13	-	0.76±0.01	0.73±0.01
6MW-YW	0.95±0.03	0.99±0.04	0.95±0.16	-	0.76±0.01	0.70±0.01
9MW-YW	0.96±0.02	0.99±0.02	0.96±0.16	0.91±0.08	0.77±0.01	0.78±0.01

for BW in Eslenburg Dormer sheep. The greater litter effect for BW is due to the fact that Baluchi sheep are mainly kept on sparse pasture and under low-input production system where greater competition between-lambs in the same litter for limited nutritional resources in-utero is expected. The estimate of covariance between direct genetic and maternal genetic effects for BW is consistent with the estimate by Tosh and Kemp (1994) in Polled Dorset sheep.

The total heritability (h^2_t) estimates (Table 3) were in general agreement with the estimates reported by Gowane et al. (2010) in Malpura sheep for BW and WW and Mohmmadi et al. (2010) for post weaning weight. Total heritability estimate is shown to be model sensitive (Gowane et al., 2010). Abegaz et al. (2005) suggested that total heritability value is more useful than direct heritability in the presence of significant maternal additive genetic and covariance between direct and maternal additive genetic effects. In such cases, use of total heritability instead of direct heritability resulted in higher similarity between expected and observed response to selection. The maternal across year repeatability or ewe performance (t_m) estimates were moderate and the magnitude decreased from birth to yearling (Table 3). Similar results were reported by Mohammadi et al., (2011) for BW and WW in Zandi sheep, and for post-weaning body weight by Gowane et al. (2010) in Malpura sheep.

Correlation among growth traits

Direct additive genetic correlations among body weight at different ages were high and positive and ranged from 0.52 for BW-YW to 0.96 for 9MW-YW (Table 4), in agreement with estimates by Mohammadi et al. (2010). High estimates were also reported for correlation of 6MW with 9MW and YW (Gowane et al., 2010). Among traits, maternal additive genetic correlation estimates were high, suggesting that maternal additive genetic effects, which favor fetal growth, could also have some beneficial effect on post-natal growth traits. The estimated values for maternal genetic correlations in the present study were similar to those reported in the Horro sheep (Abegaz et al., 2005). High maternal permanent environmental correlation (0.98) was found between WW and 6MW, suggesting that maternal ability and favorable maternal behavior at weaning have positive influences on post-weaning body weights. The litter effect correlations between growth traits were positive and ranged from 0.21 for BW-9MW to 0.91 for 9MW-YW.

Among traits phenotypic correlations were positive, ranging from 0.28 for BW-YW to 0.77 for 9MW-YW, and generally lower than those of direct genetic ones. Estimates of phenotypic correlation between BW and other traits were low and decreased with increasing age. Among traits, environmental correlations were positive, medium to high in magnitude and in agreement with estimates by Yazdi et al. (1997) and Mohammadi et al. (2010).

Conclusions

This study provided estimates of heritability and other variance components for five body weight traits in Baluchi sheep. The estimates of heritability point to the availability of considerable additive genetic variation for birth weight that can be exploited by sheep breeders. But other traits showed law level of genetic variation, perhaps due to drought, poor quality pastures and law input production system.

This study also highlighted the significance of maternal effect for all traits, and litter effect for birth, weaning, nine month and yearling weights. The magnitude of the maternal, as well as litter effects, decreased from birth to yearling age. The covariance between direct and maternal genetic effect had a significant impact for all traits with the exception of weaning weight. The results also showed positive and strong genetic correlations between body weight traits, suggesting that there is no major antagonism between body weight traits, and that use of an appropriate selection index could lead to simultaneous improvements in all traits.

Excluding the litter effect from the model for genetic evaluation may not affect the estimates of direct and maternal genetic components; it will affect the weighting of contribution of birth and weaning information from multiple births in predicting breeding values, as pointed out by Al-Shorepy and Notter (1998).

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