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Genetic Parameters of Early Growth Traits in Mehraban Breed of Sheep

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Abstract: Genetic parameters were estimated for birth weight (BWT), weaning weight (WWT) and pre-weaning Average Daily Gain (ADG) using Restricted Maximum Likelihood (REML) procedures. Six different animal models were fitted, differentiated by including or excluding maternal effects. The direct heritability estimates (h^2) ranged from 0.26 to 0.53, 0.18 to 0.32 and 0.15 to 0.33 for BWT, WWT and ADG, respectively. The estimates were substantially higher when maternal effects, either genetic or environmental, were ignored from the model. The maternal heritability (m^2) for BWT was the highest (0.25) when maternal genetic effect alone was fitted in the basic model. It was decreased to 0.14 when the maternal permanent environmental effect (c^2) was employed.

Key words: Early growth, direct heritability, maternal effects, Mehraban sheep

INTRODUCTION

Mehraban breed of sheep is originated in the western provinces of Iran which are Hamadan, Zanjan and Kordestan. In Hamadan province, more than 2 millions of sheep are raised which 40% of them are Mehraban. Estimates of genetic parameters for early growth traits are important in the design of appropriate breeding programme aimed for maximizing genetic improvement. In mammals, growth is influenced by the genes of the individual for growth, by the environment provided by the dam and other environmental effects (Albuquerque and Meyer, 2001). The main activities of sheep breeding are estimation of genetic parameters for different traits, estimation of genetic trends of flocks in stations, estimation of economic values and selection criterias and improvement of carcass quality. Authors were not able to find any structured breeding program, breeding objectives and/or selection criteria, for Mehraban breed. The objectives of this study were to estimate genetic parameters for birth weight, weaning weight and average daily gain to weaning from 20 different Mehraban flocks as an indicator for possible improvement through selection.

MATERIALS AND METHODS

Mehraban breed of sheep could be classified as a fat-tailed and large frame size breed (Fig. 1). They are the most common native breed of Iran adapted to harsh and rocky environments in the western parts of the country including Hamadan, Zanjan and Kordestan provinces. The study was conducted at Hamadan city, which is



Fig. 1: A picture of a male Mehraban sheep breed

located at 48° 30' N latitude and an altitude of 1830 m above sea level. This breed reared primarily for meat production. They are mostly light-brown color and head, face and throat are devoided of wool. They are normally raised on pasture in spring and summer while they have access to farm residual feeds during autumn. In winter time on cold and windy days, they have access to dry hay and wheat straw as well as barley grain. A total of 15555 performance records of 5043 animals were available from 20 different flocks from 1993 to 2004 in Hamadan province. The flocks were under a recording system of newly established Mehraban Sheep Genetic Evaluation Program. The maximum and minimum number of sheep in flocks were ranging from 211 to 1089 sheep with an average of 570 sheep. Most of the flocks were practiced a kind of selection procedure which was consisted of the

Table 1: Summary of data description in the present study

Traits	Records (No.)	Mean (kg)	Min. (kg)	Max. (kg)	Standard deviation	Variation coefficient
Birth Wt.	5043	3.88	1.75	7.20	0.75	14.92
Weaning Wt.	3141	21.58	11.00	38.00	2.63	18.30
6 month Wt.	2115	33.27	15.00	54.00	3.30	23.52
Daily gain to weaning	3141	0.197	0.072	0.583	0.06	20.75
Daily gain to 6 month Wt.	2115	0.141	0.026	0.470	0.04	29.75

heaviest rams and ewes as parents for the next generation. Ewes were culled for old age or failure to conceive. Primary analysis of data which was performed by SAS (1996) procedures is summarized in Table 1.

Statistical analysis: The General Linear Model (GLM) procedures of SAS (1996) were determined whether any of the effects or interactions have an influence on the traits ($p < 0.05$). Those having an effect ($p < 0.05$) were fitted in the subsequent models to estimate the genetic parameters. The fitted fixed effects were lambing year (1993 to 2004), sex (male, female), birth type (single, multiple), age of dam and herd (20 flocks). Genetic parameters were estimated by derivative-free REML (Meyer, 1998). The following models were used:

- Model 1 $y = X\beta + Z_1a + \varepsilon$
- Model 2 $y = X\beta + Z_1a + Z_2c + \varepsilon$
- Model 3 $y = X\beta + Z_1a + Z_2m + \varepsilon$ with $\text{cov}(a, m) = 0$
- Model 4 $y = X\beta + Z_1a + Z_2m + \varepsilon$ with $\text{cov}(a, m) = A \delta m$
- Model 5 $y = X\beta + Z_1a + Z_2m + Z_3c + \varepsilon$ with $\text{cov}(a, m) = 0$
- Model 6 $y = X\beta + Z_1a + Z_2m + Z_3c + \varepsilon$ with $\text{cov}(a, m) = A \delta m$

Where: y is the vector of observations, β is the vector of fixed effects, a and m are the vectors of random direct and maternal additive genetic effects, c is the vector of random maternal permanent environmental effects and ε is the vector of residuals. X , Z_1 , Z_2 and Z_3 are the incidence matrices for β , a , m and c , respectively. $E(y)$ is $X\beta$, $V(a)$, $V(m)$, $V(c)$ and $V(\varepsilon)$ are, δ^2a , δ^2m , $I_{N_d} \delta^2c$ and $I_N \delta^2\varepsilon$, respectively, where N_d is the number of dams, N is the number of records, A is the numerator of the relationship matrix among animals and I is an identity matrix. Heritability estimates were obtained as $\frac{\delta^2a}{\delta^2p}$, $\frac{\delta^2m}{\delta^2p}$, respectively, for direct and maternal genetic effects, where δ^2p , is the sum of all variance components estimated by the model of analysis.

RESULTS AND DISCUSSION

Estimates of (co) variance components, direct (h^2) and maternal (m^2) heritabilities and values for the maternal permanent environmental effects (c^2) are shown in Table 2. For comparisons, published heritability estimates for BWT and WWT are summarized in Table 3 and 4, respectively. The log likelihood values obtained using

six different models of analyses are shown for each trait in Table 2. In this study, fitting the maternal genetic effects as the only random effect in addition to the direct genetic effect resulted in larger log likelihood ratios than in the models that ignored the maternal genetic effects. The estimates of h^2 were also larger than both the m^2 and c^2 estimates for BWT, WWT and ADG. The h^2 estimates for BWT ranged from moderate to high ($h^2 = 0.26$ to 0.53). In Model 1, where maternal effects were ignored, the h^2 estimates were higher and most likely biased upwards. However, fitting either or both of the maternal effects reduced δ^2a and h^2 estimates from 0.18 to 0.09 and from 0.53 to 0.26, respectively. Likewise, failure to account for maternal permanent environmental effects (c^2) resulted in a higher maternal genetic variances (δ^2m) and the corresponding m^2 estimates. Thus, when the maternal permanent environmental effect (c^2) was ignored, the total variance was attributed to the maternal genetic variance (δ^2m), probably resulting in an overestimation of m^2 . Thus, it is an evident that the relative values of h^2 and m^2 were greatly influenced by the model used in the analysis. As in BWT, h^2 estimates for WWT decreased when either of the maternal effects was fitted in the model. When the maternal permanent environmental effects (c^2) were fitted in the model, the variance due to the maternal genetic effects (δ^2m) and the corresponding estimate of m^2 decreased. As opposed to BWT, both the maternal genetic and maternal permanent environmental effects were smaller than the direct genetic effects under all models. For ADG, the estimates of the direct and maternal genetic and maternal permanent environmental variances followed the same pattern as for WWT and they were of approximately similar magnitude.

Estimates of h^2 for BWT obtained in the present study are within the range of the animal model estimates, which varied from 0.07 (Tosh and Kemp, 1994) to 0.62 (Behzadi and Eftekhari-Shahroodi, 2002) (Table 3). Estimates of h^2 for WWT obtained from the different models were also within the ranges of published values. The h^2 estimates for WWT in the literature ranged from 0.067 (Khalili *et al.*, 2002) to 0.59 (Behzadi and Eftekhari-Shahroodi, 2002) (Table 4). The estimates for ADG ranged from 0.03 (Seid Alian *et al.*, 2004) to 0.48 (Behzadi and Eftekhari-Shahroodi, 2002).

Table 2: Estimation of variance components for pre-weaning traits

Model	δ^2a	δ^2m	δ^2c	δ_{am}	δ^2e	δ^2p	h^2 (se)	m^2 (se)	c^2 (se)	r_{am}	Log L
Birth weight											
1	0.18				0.16	0.34	0.53±0.05				93.77
2	0.12		0.07		0.15	0.34	0.35±0.05		0.11±0.03		90.78
3	0.10	0.08			0.16	0.34	0.28±0.04	0.25±0.03			122.47
4	0.09	0.05		0.05	0.15	0.33	0.27±0.04	0.23±0.03		0.06	121.86
5	0.09	0.07	0.02		0.16	0.34	0.26±0.04	0.20±0.03	0.03±0.03		148.21
6	0.08	0.04	0.02	0.02	0.15	0.31	0.26±0.04	0.14±0.03	0.08±0.03	0.4	147.42
Weaning weight											
1	8.72				18.85	27.57	0.32±0.04				6692.00
2	6.30		2.41		18.83	27.54	0.23±0.04		0.04±0.03		6586.00
3	6.06	2.65			18.85	27.57	0.22±0.03	0.09±0.03			7442.00
4	6.00	2.19		0.27	18.84	27.30	0.22±0.03	0.08±0.03		0.07	7386.00
5	5.02	2.42	1.28		18.85	27.57	0.18±0.03	0.08±0.04	0.02±0.02		9604.00
6	5.02	2.05	1.34	0.11	18.84	27.36	0.18±0.03	0.07±0.04	0.02±0.02	0.03	9509.00
Average daily gain											
1	1122				2298	3420	0.33±0.04				14117.00
2	809		313		2298	3420	0.24±0.04		0.04±0.02		14081.00
3	787	335			2298	3420	0.23±0.03	0.09±0.03			14606.00
4	788	345		-5.69	2298	3425	0.23±0.03	0.10±0.03		-0.01	14568.00
5	517	333	272		2297	3420	0.15±0.05	0.08±0.03	0.03±0.03		15362.00
6	574	341	232	-24.4	2297	3444	0.16±0.05	0.08±0.03	0.03±0.03	0.04	15345.00

δ^2a = Direct Additive var., δ^2m = Maternal additive var., δ^2c = Permanent maternal environmental var., δ_{am} = Direct maternal genetic covar., δ^2e = Residual var., h^2 (se) = Direct heritability, m^2 (se) = Maternal heritability, c^2 (se) = Ratio of permanent maternal environmental var. to total var., r_{am} = Correlation of additive genetic effect and maternal genetic effect and log L = The highest value shows the best model for each trait

In all three traits, estimates of h^2 ranging from 0.15 to 0.35 were computed after maternal effects were taken into account. In contrast, failure to take account of these effects gave estimates ranging from 0.33 to 0.53. This indicates the extent to which estimates of h^2 can be biased if maternal effects, either genetic or environmental, are ignored using an animal model. The h^2 of BWT in particular was halved when either or both of the maternal effects were fitted compared to the estimate obtained under Model 1 ($h^2 = 0.53$). Several corresponding results have been reported in the literature (Torshizi *et al.*, 1996; Ligda *et al.*, 2000; Edriss *et al.*, 2002). Snyman *et al.* (1995) reported that ignoring maternal effects, if these effects have a significant influence, leads to the over-estimation of direct as well as total heritabilities. In the present study, the magnitude of the h^2 estimates obtained for BWT was greater than for both the m^2 and c^2 estimates. In some other investigations, c^2 also tended to be higher than both the h^2 and m^2 estimates (Table 3). In the present study, the m^2 estimates were, however, lower than the h^2 estimates for both WWT and ADG. In general, the values for m^2 in the present study varied from low to medium and were influenced by the model fitted (Table 2). It accounted for about 0.25 of the phenotypic variance when the maternal permanent environmental effect was ignored from the model, but was reduced to 0.14 when the latter was fitted in the model. Snyman *et al.* (1995) also indicated that the exclusion of the maternal permanent environmental effect, when it has a significant influence, could cause estimates of m^2 to be biased upwards. The maternal permanent environmental effect (c^2) for BWT (Model 2) was lower than the direct genetic effect (h^2), which is in accordance

with results of several other studies (Table 3). The c^2 estimates were in agreement with some of the estimates reported for WWT (Table 3). Both Snyman *et al.* (1995) and Nesar *et al.* (2001) reported an estimate of 0.12, while Edriss *et al.* (2002) found an estimate of 0.07 for the permanent environmental effect of the dam in BWT. They ascribed this value of the permanent environmental effect to the influence of the uterus and the effect of multiple births. Relatively large c^2 estimates for WWT and ADG most likely reflected differences in rearing abilities of dams that might be influenced by environmental fluctuations between years or her birth/weaning status.

Generally, results showed a trend of increasing direct variance ratios and maternal variance ratios from birth to weaning. The increasing h^2 of lamb weight at weaning is most likely caused by an increased expression of genes with direct effects on body development (Yazdi *et al.*, 1997). This also confirms the idea of Snyman *et al.* (1995), who concluded that maternal effects in mammals diminish with age. In general, results of this study showed that maternal, genetic and environmental, factors are important for BWT and need to be considered in selection.

The correlation estimates between direct and maternal genetic effects (r_{am}) for BWT of Mehraban sheep are higher than most of the previously reported estimates (Table 3). The estimate of -0.43 reported by Torshizi *et al.* (1996) for BWT contradicts the positive estimates found in this study. This study reported positive correlation estimates for WWT. In the present study, the signs of these estimates for WWT were in agreement with

Table 3: Summary of reported direct (h^2), maternal genetic (m^2), permanent environmental (c^2) estimates and correlations between direct and maternal genetic effects (r_{am}) for birth weight

Breed	h^2	m^2	c^2	r_{am}	References
Zandi	0.18-0.28	0.12	0.10	-0.41	Kalantar and Torshizi (2002)
Baluchi	0.125	0.08		0.47	Khalili <i>et al.</i> (2002)
Kermani	0.10-0.62	0.23		0.35	Behzadi and Eftekhar Shahroodi (2002)
Bakhtiari	0.18-0.48	0.21-0.29	0.07	0.05	Edriss <i>et al.</i> (2002)
Sang sari	0.33	0.65		-0.40	Seid Alian <i>et al.</i> (2004)
Chios	0.13-0.38	0.13-0.33	0.16-0.28	-0.44	Ligda <i>et al.</i> (2000)
Horro	0.18-0.32	0.10-0.26		-0.64	Abegaz <i>et al.</i> (2002)
Romanov	0.07	0.13	0.32	-0.13	Tosh and Kemp (1994)
Australian Merino	0.30	0.29		-0.43	Torshizi <i>et al.</i> (1996)
Dorper sheep	0.11	0.10	0.12	0.35	Neser <i>et al.</i> (2001)
Merino	0.19-0.38	0.25-0.38	0.10-0.27	-0.23	Duguma <i>et al.</i> (2002)
Mehraban	0.26-0.53	0.14-0.25	0.03-0.11	0.40	Present study

h^2 = Direct heritability, m^2 = Maternal heritability, c^2 = Ratio of Permanent maternal environmental var. to total var., r_{am} = Correlation of additive genetic effect and maternal genetic effect

Table 4: Summary of reported direct (h^2), maternal genetic (m^2), permanent environmental (c^2) estimates and correlations between direct and maternal genetic effects (r_{am}) for weaning weight

Breed	h^2	m^2	c^2	r_{am}	References
Zandi	0.16-0.24	0.14-0.16	0.20	-0.42	Kalantar and Torshizi (2002)
Baluchi	0.067	0.08		0.34	Khalili <i>et al.</i> (2002)
Kermani	0.19-0.59	0.11		0.56	Behzadi and Eftekhar-Shahroodi (2002)
Bakhtiari	0.12-0.30	0.09-0.23	0.12-0.18	-0.16	Edriss <i>et al.</i> (2002)
Sang sari	0.17	0.80		-0.53	Seid Alian <i>et al.</i> (2004)
Chios	0.15-0.29	0.05-0.16	0.08-0.12	-0.26	Ligda <i>et al.</i> (2000)
Horro	0.10-0.26	0.19-0.24		-0.42	Abegaz <i>et al.</i> (2002)
Romanov	0.14	0.02	0.12	0.43	Tosh and Kemp (1994)
Australian Merino	0.28	0.41		-0.59	Torshizi <i>et al.</i> (1996)
Dorper sheep	0.20	0.10	0.08	-0.58	Neser <i>et al.</i> (2001)
Merino	0.25-0.36	0.05-0.11	0.06-0.10	0.05	Duguma <i>et al.</i> (2002)
Mehraban	0.18-0.32	0.07-0.09	0.02-0.04	0.03-0.07	Present study

h^2 = Direct heritability, m^2 = Maternal heritability, c^2 = Ratio of Permanent maternal environmental var. to total var., r_{am} = Correlation of additive genetic effect and maternal genetic effect

those reported by Duguma *et al.* (2002), Snyman *et al.* (1995) and Yazdi *et al.* (1997). However, the positive genetic correlations ranging from 0.05 to 0.56 reported by these authors were higher than those reported in this study, which were very small, ranging from 0.03 to 0.07. This suggest, that selection for increased live weight of the lamb would not negatively affect the maternal ability of the ewe. Cloete *et al.* (2001) also found no significant correlation between the direct and the maternal effects in Merino flocks. The estimates for ADG ranged from -0.01 to 0.04, slightly higher than the -0.17 reported range by Seid-Alian *et al.* (2004). Edriss *et al.* (2002) reported negative estimates ranging from -0.23 to -0.33 for ADG.

A negative estimate of the direct and maternal genetic covariance has mostly been observed in field data while it has by and large been absent in experimental data sets (Meyer, 1997), which has indicated that this could have been attributed to factors like more uniform management and lack of preferential treatment. Alternatively, it may also reflect better identification of contemporary or management groups. Early growth traits in sheep are mostly characterized by negative r_{am} estimates

(Table 3 and 4). These estimates may be considerable and could be affected by small data sets (El Fadili *et al.*, 2000; Al-Shorepy, 2001), the models fitted or poor pedigree structure for estimation of both the direct and maternal heritabilities and the genetic correlations between animal effects (Lee *et al.*, 2000). The antagonism between the effects of an individual's genes for growth and those of its dam for a maternal contribution may also be due to natural selection for an intermediate optimum (Tosh and Kemp, 1994). Heritability estimates of early growth traits from the different models ranged from moderate to moderately high. It seems that, ignoring maternal effects, both maternal genetic and environmental effects lead to an overestimation of the h^2 estimates. Likewise, exclusion of maternal permanent environmental effects of the dam resulted in overestimation of m^2 estimates, particularly for BWT. Thus, they need to be considered when carrying out genetic evaluations of early growth traits, in addition to the direct genetic effects. The absence of a genetic antagonism for WWT obtained between the direct and the maternal genetic effects, suggests that genetic improvement could be obtained in both direct and maternal performances if selection is based on individual weaning weight performance.

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