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Investigation of Maternal Effects on Early Growth Traits in Arabi Lambs, Using Single-Trait Animal Models

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Abstract: The aims of this study were to investigate the importance of maternal effects and to determine the most appropriate model of analyses for early growth traits of Arabi lambs. Records of 2445 lambs from 139 rams and 804 ewes for Birth Weight (BWT) on 2237 lambs from 127 rams and 784 ewes for Weaning Weight (WWT) and on 2098 lambs from 115 rams and 739 ewes for Average Daily Gain from birth to weaning (ADG) were used in this research. The data collected from Animal Science Research Station of Agricultural and Natural Resources Ramin (Khuzestan) University during 2001-2008. Genetic parameters were estimated by derivative free restricted maximum likelihood method. Six different animal models were fitted by including or excluding maternal genetic effect, maternal permanent environmental effect and covariance between direct-maternal genetic effects. On the basis of log likelihood ratio test results, Model 3 which included direct genetic and maternal genetic effects was determined to be the most appropriate model for all traits. The maternal genetic effects contributed about 74, 69 and 64% to the direct genetic effects and 15, 11 and 10% to the phenotypic variance for BWT, WWT and ADG, respectively. Depending on the model, the estimates of maternal heritability ranged from 0.074-0.146 for early growth traits of Arabi lambs. Results showed that maternal genetic effects were important for pre-weaning growth traits and should not be neglected from the model; therefore inclusion of maternal effects into the model for mentioned traits is necessary.

Key words: Maternal effects, variance components, lamb weights, arabi lamb, restricted maximum likelihood method, Iran

INTRODUCTION

Body weights and growth rates in pre-weaning are often considered as an early indicator of the late growth and economic benefit (Hanford *et al.*, 2006). Early growth traits in sheep are known to be influenced by direct and maternal genetic effects as well as by environmental effects. In general, growth traits, in particular until weaning are not only influenced by the genes of the individual for growth and environment under which it is raised but also by the maternal genetic composition and environment provided by the dam (Lewis and Beatson, 1999). In fact, maternal effects can be derived any influence from dam to progeny excluding the effects of directly transmitted genes (maternal genetic effect) and the factors consistent between each lambing of a dam but not genetic in origin (permanent environmental effect).

Therefore, the dam contributes to the phenotypic value of her offspring not only by a sample half of her genes but also through her genes responsible for maternal traits. Also, when growth traits are included in the breeding goal, both direct and maternal genetic effects should be taken into account in order to achieve optimum genetic progress. Hence, accurate estimates for the maternal genetic effects are required. The aim of this study were to determine the most appropriate model for the data set used and to investigate the importance of maternal genetic on early growth traits of Arabi lambs according to the determined model.

MATERIALS AND METHODS

Data and pedigree information of the Arabi sheep used in this study were obtained from the Animal Science Research Station of Agricultural and Natural Resources Ramin (Khuzestan) University during the period from 2001 until 2008. The traits analysed were Birth Weight (BWT), Weaning Weight (WWT) and Average Daily Gain from birth to weaning (ADG). Data set used for analyses consisted of 2445 records for BWT, 2237 records for

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WWT and 2098 records for ADG. The lambs were the progeny of 139 rams and 804 ewes for BWT, 127 rams and 784 ewes for WWT and 115 rams and 739 ewes for ADG. In this station all animals were raised under similar environmental, nutritional and management conditions. They were first exposed to rams at about 18 months of age and kept in the flock until death or the apparent infertility. The animals managed following semi-moving. They were grazed and supplemented by concentrates during the day and housed at night. The mating period began from early August to early October and continued as controlled. Lambing was from early January and continued until early February. Lambs were weighed and ear-tagged at birth. Weaning was at approximately 4 months of age. The descriptive statistics of mentioned traits are shown in Table 1. Variance components and genetic parameters and log likelihood values for traits were obtained using derivative-free restricted maximum likelihood procedures (DFREML3.1). To identify fixed effects to be included in the models, GLM procedure (SAS, 2003) was performed on a model including fixed effects (birth year, age of dam, sex and type of birth). All these fixed effects were significant and were included in the models. A simplex algorithm is used to search for variance components to minimize the function, -2 log likelihood (L). Convergence was assumed when the variance of the function values (-2 log L) of the simplex was $<10^{-8}$. A log likelihood ratio test was used to choose the most suitable random effects model for each trait.

The reduction in -2 log L when a random effect was added to the model was calculated. If this reduction was greater than the value of the chi-square distribution with one degree of freedom ($p<0.05$), the additional random effect fitted was considered significant. When log likelihoods did not differ significantly ($p>0.05$), the model that had the fewer number of parameters was selected as the most appropriate. Six different single-trait animal models were fitted for each trait by ignoring or including maternal genetic effect, covariance between direct-maternal effects, maternal permanent environmental effect and maternal temporary environmental effect that the six different models were: Model 1 was a model with animal additive genetic effects as the only random effect other than residuals:

$$y = Xb+Z_1a+e \qquad (1)$$

In model 2 we included a random effect of permanent maternal environment:

$$y = Xb+Z_1a+Z_3c+e \qquad (2)$$

Model 3 allowed for a genetic maternal effect to those of model 1:

$$y = Xb+Z_1a+Z_2m+e \quad \mathrm{Cov}\,(a,m) = 0 \qquad (3)$$

Model 4 was the same as model 3 but a non-zero correlation was assumed between direct and maternal genetic random effects:

$$y = Xb+Z_1a+Z_2m+e \quad \mathrm{Cov}\,(a,m) = A\sigma_{am} \qquad (4)$$

Models 5 and 6 included both permanent environmental and genetic maternal effects but allowing a genetic correlation between direct and maternal genetic random effects only for model 6:

$$y = Xb+Z_1a+Z_2m+Z_3c+e \quad \mathrm{Cov}\,(a,m) = 0 \qquad (5)$$

$$y = Xb+Z_1a+Z_2m+Z_3c+e \quad \mathrm{Cov}\,(a, m) = A\sigma_{am} \qquad (6)$$

where, y is a vector of records on the different traits b, a, m, c and e are vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects and the residual effects, respectively. X, Z_1, Z_2 and Z_3 are corresponding design matrices associating the fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects to vector of y. It is assumed that direct additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects and residual effects to be normally distributed with mean 0 and variance $A\sigma^2_a$, $A\sigma^2_m$, $I_d\sigma^2_c$ and $I_n\sigma^2_e$, respectively. That σ^2_a, σ^2_m, σ^2_c and σ^2_e are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance and residual variance, respectively. A is the additive numerator relationship matrix, I_d and I_n are identity matrices that have order equal to the number of dams and

Table1: Description of data set

Character	BWT[a]	WWT[a]	ADG[a]
Number of records	2445.00	2237.00	2098.000
Number of sire	139.00	127.00	115.000
Number of dams	804.00	784.00	739.000
Number of dam with own records	398.00	336.00	322.000
Average number of progeny per dam	3.04	2.85	2.840
Mean (kg)	4.18	20.06	0.137
SD (kg)	0.86	3.30	0.030
CV (%)	18.87	14.98	23.600

[a]BWT: Birth Weight, WWT: Weaning Weight, ADG: Average Daily Gain from birth to weaning, SD: Standard Deviation and CV: Coefficient of Variation

number of records, respectively and σ_{am} denotes the covariance between direct additive genetic and maternal additive genetic effects.

Depending on the model fitted, phenotypic variance (σ^2_p) direct additive genetic variance (σ^2_a), maternal genetic variance (σ^2_m), permanent environmental variance (σ^2_c), residual variance (σ^2_e), direct heritability (h^2_d), maternal heritability (h^2_m), genetic covariance between direct additive and maternal effects (σ_{am}) and correlation between direct and maternal additive effects (r_{dm}) were estimated, accordingly.

RESULTS AND DISCUSSION

The least-squares means and standard errors for mentioned traits are shown in Table 2. In the study on lamb weight at pre-weaning in Arabi sheep the effects of birth year, age of dam, sex and type of birth were highly significant on traits ($p<0.01$). As it is expected the single born and male lambs were heavier than lambs born as twin and female ones and lambs born from young ewes had lower weights than those born to adult ewes.

As well as, birth year had a significant effect on all body weight traits. These results are in agreement with those reported by other authors for other sheep breeds (Bahreini *et al*., 2007; Lavvaf *et al*., 2007; Lavvaf and Noshary, 2008; Rashidi *et al*., 2008; Mohammadi *et al*., 2010).

The log likelihood values under six different single-trait models with the most appropriate model (in bold) determined using log likelihood ratio tests regarding early growth traits of Arabi lambs are shown in Table 3 and heritability estimates based on the most appropriate model for growth traits are shown in Table 4.

In current study on early growth traits of Arabi lambs the inclusion of maternal genetic effects in model 3 led to a significant increase of the log likelihood function, in comparison with other models. On the other hand, in model 3 the maternal genetic effects (h^2_m) was significant and therefore this model was considered the most suitable for all traits.

In model (1) where maternal effects were ignored, heritability was biased upwards while the inclusion of maternal genetic effects in model 3 reduced the direct heritability about 40, 38 and 36% for BWT, WWT and ADG, respectively. In fact in model 3, in which both direct and maternal (indirect) genetic effects were taken into account, 14.6, 11.4 and 9.6% of the total variance was attributed to the maternal genetic effects for BWT, WWT and ADG, respectively.

Table 2: Least squares means and standard error for pre-weaning growth traits in Arabi lambs

	Traits[a]		
Fix effects	BWT (kg)	WWT (kg)	ADG
Sex	**	**	**
Male	4.30 ± 0.02^{a}	20.96 ± 0.09^{a}	0.146 ± 0.001^{a}
Female	4.07 ± 0.02^{b}	19.24 ± 0.10^{b}	0.129 ± 0.001^{b}
Birth type	**	**	**
Single	4.31 ± 0.02^{a}	20.22 ± 0.07^{a}	0.140 ± 0.000^{a}
Twin	3.74 ± 0.04^{b}	19.16 ± 0.18^{b}	0.123 ± 0.002^{b}
Dam's age (Year)	**	**	**
2	3.90 ± 0.04^{d}	19.58 ± 0.14^{d}	0.127 ± 0.001^{d}
3	4.07 ± 0.04^{c}	19.81 ± 0.15^{cd}	0.133 ± 0.002^{c}
4	4.22 ± 0.04^{b}	19.98 ± 0.19^{cd}	0.135 ± 0.002^{c}
5	4.34 ± 0.04^{ab}	20.16 ± 0.18^{bc}	0.140 ± 0.002^{b}
6	4.36 ± 0.04^{a}	20.52 ± 0.20^{ab}	0.144 ± 0.002^{b}
7	4.29 ± 0.05^{ab}	20.84 ± 0.18^{a}	0.151 ± 0.002^{a}
Birth year	**	**	**

Within column, within each factor, least square means with different superscripts are different at $p<0.01$, [a]BWT: Birth Weight, WWT: Weaning Weight, ADG: Average Daily Gain from birth to weaning, SD: Standard Deviation and CV: Coefficient of Variation; **$p<0.01$, **$p<0.01$

Table 3: Log likelihood values with the most appropriate model in bold for post-weaning traits

	Traits[a]		
Model	BWT	WWT	ADG
1	-1057.15	-5658.54	8263.15
2	-1043.88	-5653.77	8266.44
3	-1034.23	-5647.42	8273.38
4	-1039.12	-5651.04	8265.73
5	-1041.76	-5655.36	8266.05
6	-1052.17	-5656.95	8268.19[a]

[a]BWT: Birth Weight, WWT: Weaning Weight, ADG: Average Daily Gain from birth to weaning, SD: Standard Deviation and CV: Coefficient of Variation

When the maternal genetic effects were ignored, the total variance was attributed to the direct genetic variance, resulting in overestimation of the direct heritability.

Birth weight: The estimate of the direct heritability for BWT (0.194) was in agreement with the results reported by Dugoma *et al*. (2002) on Tygerhoek Merino lambs Abegaz *et al*. (2005) on Horro lambs and Ghafouri *et al*. (2008) on Mehraban lambs but Bahreini *et al*. (2007) obtained estimate for direct heritability 0.10 in Kermain lambs and Miraei-Ashtiani *et al*. (2007) obtained estimate for direct heritability 0.33 in Sangsari lambs which was lower and more than the estimate, respectively. Maternal heritability estimate (0.146) was similar to Lavvaf *et al*. (2007) on Moghani lambs; Riggio *et al*. (2008) on Scottish Blackface sheep and Refik *et al*., 2009 on Turkish Merino lambs. Miraei-Ashtiani *et al*. (2007) estimated very higher maternal heritability (0.65) in Sangsari lambs but the findings of Mandal *et al*. (2006) on Muzaffarnagari lambs (0.07) was lower than the finding.

Table 4: Variance components and genetic parameters estimated by DFREML using single-trait analysis

Traits[a]	Fitted model	σ^2_a	σ^2_m	σ^2_e	σ^2_p	h^2_d±SE	h^2_m±SE
BWT	3	0.0900	0.0677	0.3063	0.4640	0.194±0.041	0.146±0.033
WWT	3	1.6570	1.1589	7.3500	10.1659	0.163±0.035	0.114±0.039
ADG	3	0.00016	0.00011	0.00083	0.00110	0.149±0.038	0.096±0.034

Weaning weight: As WWT, model including maternal genetic effect (Model 3) had the highest log likelihood value and was determined to be the most suitable model for this trait. Maternal heritability about 22% reduced compared to birth weight. The direct heritability estimate here (0.163) was within the range reported from 0.06 (Maria *et al.*, 1993) on Romanov lambs to 0.35 (Lavvaf and Noshary, 2008) on Lori sheep and similar to the results reported by Miraei-Ashtiani *et al.* (2007). The estimate of maternal heritability for WWT was 0.114. Similar results were reported by Neser *et al.* (2001) on Dorper sheep and Lavvaf and Noshary (2008) on Lori sheep. In a study by Ozcan *et al.* (2005) on Turkish Merino lambs maternal heritability estimated (0.04) was lower than the estimate.

Average daily gain from birth to weaning: On the basis of the log likelihood ratio test results and number of parameters used in models, Model 3 was determined to be the most appropriate model for ADG. In present study the direct heritability estimate (0.149) was within the range of those published in the literature which varied from 0.03 (Miraei-Ashtiani *et al.*, 2007) to 0.27 (Dugoma *et al.*, 2002) for this trait. Maternal heritability estimate (0.096) was more than results reported by Yazdi *et al.* (1997) on Baluchi sheep and Matika *et al.* (2003) on Sabi sheep. Maternal heritability estimated for this trait is sparse. It is evident that maternal effects tend to diminish with age of progeny but might persist into the post-weaning growth period.

CONCLUSION

The results of the present study show that if maternal effects are present but not considered the estimate of additive genetic variance will include at least part of the maternal variance. Therefore, estimates of direct heritability will decrease when maternal effects are included. Also, the low maternal genetic influence on all traits was presumably due to poor quality of pasture, preventing the ewe's genetic ability to provide enough milk for her lamb(s). Thus, the lack of adequate pasture could be masking the expression of the maternal ability of the ewe.

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