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Original scientific paper

ESTIMATION OF GENETIC PARAMETERS OF AUTOSOMAL AND SEX-LINKED PRE-WEANING TRAITS IN MAKUIE SHEEP USING MULTIVARIATE ANALYSIS

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The objective of this study was to determine the genetic parameters of autosomal and sex-linked effects for birth weight (BW), weaning weight (WW), average daily gain from birth to weaning (ADG) and kleiber ratio (KR) of Makuie sheep. The data set used in this study was collected at Makuie sheep breeding station in West Azerbaijan province, Iran, between 1994 and 2011. The fixed effects included herd-year, sex (male or female), birth type (single or twin), and age of dam (five classes, 2-6 years old). The three multivariate linear animal models including direct (autosomal and sex-linked) and maternal effects were used to analyze data. The 2nd model (including direct additive genetic effects of animal (autosomal and sex-linked) and permanent environmental effects), with the lowest AIC value was considered as the most appropriate model. Based on the most appropriate fitted model, direct autosomal and sex-linked heritabilities of BW, WW, ADG and KR were 0.12±0.04 and 0.03±0.03, 0.18±0.04 and 0.05±0.03, 0.37±0.04 and 0.04±0.03, and 0.52±0.05 and 0.07±0.04, respectively. The magnitude of sex-linked variances as a proportion of phenotypic variance obtained by the best model were 4%, 4.5%, 3% and 5.7% for BW, WW, ADG and KR, respectively. Also, the autosomal and sex-linked chromosomes, maternal permanent environmental and phenotypic correlations were ranged from -0.20 to 0.96, 0.11 to 0.84, -0.34 to 0.89 and -0.20 to 0.91, respectively. The results of this study indicated that the sex-linked chromosomes have an affect like

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maternal effects, and it could contribute to a more accurate estimation of the direct autosomal heritability.

Keywords: Sheep, Autosomal and sex-linked heritabilities, Pre-weaning traits, Multivariate analysis

INTRODUCTION

The Makuie sheep population in Iran is a total of approximately three million heads distributed mainly in Azerbaijan Province. Also, in Turkey country, this sheep is known as White Karaman (GHAFOURI-KESBI, 2012). It is a medium-sized and fat-tailed sheep that is adapted to cold and highland environments conditions and raised for mutton, producing milk and wool. Lamb weights and daily gains are important components of market lamb production Growth rate (FADILI *et al*., 2005) and kleiber ratio (KR) has been suggested to be a useful indicator of growth efficiency and an important selection criterion for efficiency of growth (KÖSTER *et al*., 1994).

Estimating genetic parameters is important to determine breeding strategies and to select superior animals as parents. In recent decades, researchers have been using statistical methods such as Bayesian and REML, and different animal models in genetic parameter estimation of quantitative traits. Accurate estimation of these genetic parameters and in particular genetic correlations requires large across-generation data sets and effective genetic analytical methods - considering all potential effects (DI *et al*., 2011). There are many studies in mammals showing that important economic traits are influenced by direct genetic effect, maternal genetic effect and other environmental effects (ZAMANI and MOHAMMADI, 2008; MOHAMMADI *et al*., 2015). So, in order to obtain an optimal genetic progress in a selection scheme, including maternal effects will decrease the bias of predicted responses to selection. In genetic evaluation of animals, it is generally assumed that only autosomal chromosomes are involved and the effect of sex chromosomes is usually ignored.

Sex-linked genetic variation might inflate the estimate of autosomal additive genetic variance, but may also be pooled with the residual variance, that both situations are not desirable (HUSBY *et al*., 2012). VATANKHAH *et al*. (2016) stated that the proportion of the variance related to the sex-linked effect was similar to the proportion of variance attributed to maternal effect. A study by LARSEN *et al*. (2014) using simulation was showed that the animal model accounting both autosomal and sex-linked effect provides accurate inference on the variance components of pigmentation in Swiss barn owl. Several studies have conducted on body weight traits in Makuie sheep (MOHAMMADI *et al*., 213; JAFARI *et al*., 2012; GHAFOURI-KESBI and BANEH, 2012), but no previous information on the sexual chromosomal heritability is available in this breed. Therefore, the objectives of this study were to compare different multivariate models and estimation of genetic parameters of autosomal and sex-Linked pre-weaning traits in Makuie sheep.

MATERIALS AND METHODS

Data and management

The data set used in this study was collected at Makuie sheep breeding station in West Azarbaijan province, Iran between 1994 and 2011. The details of flock management and the environmental condition were presented by GHAFOURI-KESBI and BANEH, (2012). Briefly, Ewes were first exposed to rams at approximately 18 months. Mating season was from October to November, with February to March lambing. At birth, lambs were identified and date of birth, sex and type of birth were recorded at birth. The suckling stage lasts approximately for 3 months. The analyzed traits were birth weight (BW), weaning weigh (WW), average daily gain from birth to weaning (ADG) and kleiber ratio (KR) from birth to weaning. The data structure and descriptive statistics are summarized in Table 1.

Table 1. The summary of data set in Makuie sheep

Item	BW (Kg)	WW (Kg)	ADG (gr)	KR (gr)
No. of records	7081	7081	7061	7061
Average weight	4.01	22.44	197.19	18.99
Standard deviation	0.86	3.82	53.32	3.66
Coefficient of variation (%)	21.44	17.01	26.94	19.27
Number of sire with records	259	259	259	259
Number of dams with records	4945	4945	4940	4940

BW: birth weight, WW: weaning weight, ADG: average daily gain from birth to weaning and KR: Kleiber ratio

Statistical analysis

The GLM procedure of SAS software was applied to identify the fixed effects which should be considered in the animal models (SAS, 2004). The fixed effects included herd-year, sex (male or female), birth type (single or twin), age of dam (five classes, 2-6 years old). The age of lamb at weaning weight (in days) was used as a covariate for WW ($P < 0.001$).

(Co)Variance components and genetic parameters were estimated with different multivariate models using the Restricted Maximum Likelihood (REML) methodology by WOMBAT software (MEYER, 2013). The three multivariate linear animal models were fitted for all traits:

1st Model: $\boldsymbol{y}_i = \boldsymbol{X}_i\boldsymbol{b}_i + \boldsymbol{Z}_{1i}\boldsymbol{a}_i + \boldsymbol{Z}_{1i}\boldsymbol{s}_i + \boldsymbol{e}_i$

2nd Model: $\boldsymbol{y}_i = \boldsymbol{X}_i\boldsymbol{b}_i + \boldsymbol{Z}_{1i}\boldsymbol{a}_i + \boldsymbol{Z}_{1i}\boldsymbol{s}_i + \boldsymbol{Z}_{3i}\boldsymbol{pe}_i + \boldsymbol{e}_i$

3rd Model: $\boldsymbol{y}_i = \boldsymbol{X}_i\boldsymbol{b}_i + \boldsymbol{Z}_{1i}\boldsymbol{a}_i + \boldsymbol{Z}_{1i}\boldsymbol{s}_i + \boldsymbol{Z}_{2i}\boldsymbol{m}_i + \boldsymbol{e}_i$

Where $\boldsymbol{y}_i$, $\boldsymbol{b}_i$, $\boldsymbol{a}_i$, $\boldsymbol{s}_i$, $\boldsymbol{m}_i$, $\boldsymbol{pe}_i$ and $\boldsymbol{e}_i$ are vectors of observations, fixed effects, direct additive genetic effects in autosomal chromosomes, direct additive genetic effects in sex-linked, maternal additive genetic effects, maternal permanent environmental effects and residual effects for trait *i*, respectively. X_1, Z_1, Z_2 and Z_3 are incidence matrices relating records for trait *i*, respectively. Assumptions for variances (V) and matrices involving random effects were:

V(a) = $A\sigma_a^2$, V(S) = $S\sigma_F^2$, V(m) = $A\sigma_m^2$, V(pe) = $I_d\sigma_{pe}^2$ and V(e) = $I_n\sigma_e^2$

Where, A and S are the additive numerator relationship matrix and matrix whose elements are functions of co-ancestries between relative for X-chromosomal loci, respectively; I_d and I_n are identity matrices that have order equal to the number of dams and records, respectively; and σ_a^2, σ_F^2, σ_m^2, σ_{pe}^2 and σ_e^2 are variance of additive genetic values for autosomal loci, additive genetic variance for X-chromosomal loci for non-inbred females (FERNANDO and

GROSSMAN, 1990), maternal additive genetic variance, maternal permanent environmental variance and residual variance, respectively.

Akaike's Information Criterion (AIC) was used to choice the best model. AIC is defined as: $AIC = -2\,\log L + 2\,p$

Where logL is the maximized likelihood and p is the number of parameters obtained from each model. The model with the lowest AIC is considered as the most appropriate model. Also, (Co)variances and correlations among traits were estimated using the best model for multivariate analysis.

RESULTS

Fixed effects and models comparison

The least square means and standard errors for the studied traits are presented in Table 2. Herd-year as interactions significantly affected all studied traits (*P < 0.001*). Gender and birth type had a significant effect on BW, WW and ADG traits (*P < 0.001*) except KR. All traits were significantly influenced by age of dam (*P < 0.001*) except BW. Indeed, the age of lamb as a covariate had a significant effect on WW (*P < 0.001*). Based on the AIC values, model 2 including direct additive genetic effects of animal (autosomal and sex-linked) and permanent environmental effects was considered to be the most appropriate model (Table 3).

Table 2. Number of observations and least square means ±SE of growth traits in Makuie sheep

Fixed effects	Trait			
	BW (Kg)	WW (Kg)	ADG (gr)	KR (gr)
Herd*Year	**	**	**	**
Gender	**	**	**	ns
Male	3.64±0.02[a]	21.99±0.09[a]	192.30± 1.22[a]	18.85 ±0.29[a]
Female	3.44±0.02[b]	21.06±0.09[b]	186.12± 1.22[b]	18.78 ±0.29[a]
Birth type	**	**	**	ns
single	3.97±0.01[a]	22.15±0.06[a]	18.37±0.09[a]	18.86 ±0.07[a]
twin	3.10±0.01[b]	20.91±0.12[b]	16.94±0.10[b]	18.77 ±0.13[a]
Age of dam (Year)	ns	**	**	**
2	3.51±0.02[a]	21.26±0.10[b]	180.42±1.48[c]	18.08±0.11[c]
3	2.53±0.02[a]	21.30±0.09[b]	187.43±1.27[b]	18.78±0.09[b]
4	2.53±0.02[a]	21.58±0.10[a]	191.91±1.40[a]	19.08±0.11[a]
5	2.52±0.03[a]	21.61±0.13[ab]	194.81±1.86[a]	19.20±0.14[a]
6	2.60±0.03[a]	21.70±0.15[a]	191.48±2.19[ab]	18.94±0.16[ab]

; Significant at P < 0.05;; Significant at P < 0.001;Ns; Not significant (P >0.05).*
A same letter in each column means not-significant difference of least square means in letters are not significant at P < 0.05.

Table 3. Genetic parameter estimates and AIC values for pre-weaning traits in Makuei sheep by Multivariate analysis (The best model in bold).

Model	Traits	σ^2_a	σ^2_s	σ^2_m	σ^2_{pe}	σ^2_e	σ^2_p	h^2_a	h^2_s	h^2_m	pe^2	AIC
	BW	0.07	0.02	-	-	0.16	0.24	0.27 ± 0.05	0.09 ± 0.04	-	-	
1	WW	1.23	0.30	-	-	3.59	5.13	0.24 ± 0.04	0.06 ± 0.03	-	-	55662.99
	ADG	390.52	44.81	-	-	489.71	925.05	0.42 ± 0.05	0.05 ± 0.04	-	-	
	KR	3.19	0.52	-	-	1.73	5.44	0.58 ± 0.05	0.10 ± 0.04	-	-	
	BW	0.02	0.01	-	0.05	0.15	0.25	0.12 ± 0.04	0.03 ± 0.03	-	0.22 ± 0.02	
2	WW	0.95	0.26	-	0.43	3.57	5.22	0.18 ± 0.04	0.05 ± 0.03	-	0.08 ± 0.02	***55507.93***
	ADG	342.83	33.19	-	61.52	483.97	922.25	0.37 ± 0.04	0.04 ± 0.03	-	0.07 ± 0.02	
	KR	2.85	0.36	-	4.57	1.72	5.41	0.52 ± 0.05	0.07 ± 0.04	-	0.09 ± 0.02	
	BW	0.03	0.01	0.04	-	0.17	0.25	0.13 ± 0.04	0.03 ± 0.03	0.16 ± 0.02	-	
3	WW	1.11	0.24	0.22	-	3.68	5.25	0.21 ± 0.05	0.05 ± 0.03	0.04 ± 0.02	-	55602.84
	ADG	351.13	28.50	46.84	-	496.48	922.99	0.38 ± 0.05	0.03 ± 0.03	0.05 ± 0.02	-	
	KR	2.83	0.31	0.46	-	1.81	5.41	0.52 ± 0.05	0.06 ± 0.04	0.09 ± 0.02	-	

σ^2_a, σ^2_s σ^2_m, σ^2_{pe}, σ^2_e *and* σ^2_p*: additive genetic variance for autosomal loci, additive genetic variance for sex-linked loci, maternal additive genetic variance, maternal permanent environmental variance, residual variance and phenotypic variance, respectively;* h^2_a, h^2_s, h^2_m *and* pe^2*: direct autosomal heritability, direct sex-linked heritability, maternal heritability, maternal permanent environmental effect, respectively.*

Variance components and correlation estimates

Variance components, genetic parameters and correlation coefficients estimates for pre-weaning traits, obtained from the most appropriate model are shown in Table 3 and 4, respectively. Based on the most appropriate model (2^{nd} model), the autosomal heritability estimates for BW, WW, ADG and KR were 0.12±0.04, 0.18±0.04, 0.37±0.04 and 0.52±0.05, respectively. Furthermore, the estimates of sex-linked heritabilities of BW, WW, ADG and KR were 0.03±0.03, 0.05±0.03, 0.04±0.03 and 0.07±0.04, respectively. The maternal permanent environmental effects had a considerable effect on variation of BW (0.22±0.02) but reduced in WW, ADG and KR traits (0.08±0.02, 0.07±0.02 and 0.09±0.02, respectively). Estimated maternal heritability ranged from 0.04±0.02 to 0.16±0.02 for WW and BW, respectively (By 3^{rd} model).

The autosomal genetic correlations between pre-weaning traits were varied and ranged from -0.20 between BW and KR to 0.96 between ADG and KR. The estimates of sex-linked genetic correlations among studied traits were positive, low to high and ranged from 0.11 for BW-KR to 0.84 for WW-ADG. Maternal permanent environmental correlations between BW and other traits were negative, and ranged from -0.34 for BW-KR to -0.03 for BW-WW, and between other traits were positive and varied from 0.55 for WW-KR to 0.89 between WW and ADG (Table 4).

Table 4. Correlation coefficients between studied traits in Makuie sheep.

Traits		Item				
		$r_{a_{12}}$	$r_{s_{12}}$	$r_{pe_{12}}$	$r_{e_{12}}$	$r_{p_{12}}$
BW	WW	0.30	0.80	-0.03	0.06	0.12
BW	ADG	-0.03	0.56	-0.26	-0.11	-0.09
BW	KR	-0.20	0.11	-0.34	-0.23	-0.20
WW	ADG	0.89	0.84	0.89	0.95	0.91
WW	KR	0.77	0.35	0.55	0.72	0.64
ADG	KR	0.96	0.80	0.85	0.88	0.89

$r_{a_{12}}$: *Direct autosomal additive genetic correlation between traits 1 and 2;* $r_{s_{12}}$: *Direct sex-linked additive genetic correlation between traits 1 and 2;* $r_{pe_{12}}$: *Maternal permanent environmental correlation between traits 1 and 2;* $r_{e_{12}}$: *Environmental correlation between traits 1 and 2;* $r_{p_{12}}$: *Phenotypic correlation between traits 1 and 2.*

DISCUSSION

The interaction between herd and year of lambing was significant for all traits. Significant influence of herd and year of lambing could be explained by difference in management, climate conditions and feeding. These fixed effects with or without interactions were shown to be significant in previous studies (ZAMANI and MOHAMMADI, 2008; ABBASI *et al*., 2012; GHAFOURI-KESBI, 2013). Most of the traits were significantly affected by sex, birth type and age of dam. The significance of these effects is mainly due to endocrine system between two genders, limited uterine space especially in young ewes, competition for milk between the twins, or inadequate pasture and feedstuff during pregnancy. These fixed effects also were shown to be significant in previous studies, such as: ABBASI *et al*. (2012) in Baluchi sheep; BOUJENANE and DIALLO, (2017) in Sardi sheep; ESKANDARINASAB *et al*. (2010) in Afshari sheep; JAFARI and RAZZAGZADEH, (2016) in Makuie sheep.

As AIC values clearly indicated, in 2nd and 3rd Models, with the addition of the maternal environmental effect or maternal genetic effect, the AIC values and the estimates of heritabilities for both autosomal and sex-linked were decreased compared with Model 1. These results suggest that ignoring maternal effects, especially the significant ones, could lead to over estimates of heritabilities for autosomal and sex-linked.

Estimate of direct autosomal heritability for BW via the best model (0.12) was in agreement with reported by TOSH and KEMP, (1994) in Polled Dorsed sheep and ABBASI *et al*. (2012) in Baluchi sheep. MOHAMMADI *et al*. (2015), BOUJENANE and DIALLO, (2009) and JAFAROGHLI *et al*. (2010) have reported the lower values of 0.09, 0.07 and 0.07 for direct heritability of BW for Lori, Sardi and Moghani sheep. However, the reports by ESKANDARINASAB *et al*. (2010) in Afshari sheep (0.23) and GIZAW *et al*. (2007) in Menz sheep (0.46) were higher than this result present study. Direct autosomal heritability obtained from the best model for WW (0.18) was close to that reported by MIRAEI-ASHTIANI *et al*. (2007) for direct heritability in Sangsari sheep (0.17). The Lower estimates (MOHAMMADI *et al*., 2015; ABBASI *et al*., 2012; BOUJENANE and DIALLO, 2017) and higher ones (ZHANG *et al*., 2009; RASHIDI *et al*., 2008) were reported for direct heritability of WW. The estimated maternal permanent environmental effect for WW and BW was consistent with estimates of SINGH *et al*. (2016). Also, both lower (ABEGAZ *et al*., 2005) and higher estimates (BOUJENANE and DIALLO, 2017) were reported in literature. Different values reported by this study can be due to different breeds, fitted statistical models, and different environmental conditions.

Direct autosomal heritability estimate of 0.37 for ADG was similar to that reported by AGUIRRE *et al*. (2016) for Santa Ines sheep (0.38). Lower direct heritability estimates were reported by ABBASI *et al*. (2012) in Baluchi sheep, MIRAEI-ASHTIANI *et al*. (2007) in Sangsari sheep and JAFARI and RAZZAGZADEH, (2016) in Makuie sheep. The estimate of maternal permanent environmental effect for ADG (0.07) was in agreement with estimates of several researchers (JAFAROGHLI *et al*., 2010; MATIKA *et al*., 2003; OZCAN *et al*., 2005; RASHIDI *et al*., 2008). The estimate of direct autosomal heritability for kleiber ratio (0.52) was higher than those reported by GHAFOURI-KESBI, (2013) in Mehraban sheep, MOHAMMADI *et al*. (2011) in Sanjabi sheep and MOHAMMADI *et al*. (2015) in Lori sheep. The ratio of ADG to metabolic body weight as an indication of feed conversion efficiency is useful to identify animals with high growth efficiency relative to body size. Indeed, animals with higher KR require lower maintenance energy (ESKANDARINASAB *et al*., 2010). According to these results, growth rate and KR in Makuie sheep are categorized as moderate and high heritable traits, so a high genetic progress would be expected through selection programs. Also, the obtained maternal permanent environmental effect for KR was 0.09 in this research which is in agreement with those reported by MOHAMMADI *et al*. (2015) in Lori sheep and GHAFOURI-KESBI, (2013) in Mehraban sheep. In this study, results show an increased trend in direct autosomal heritability estimates from birth to later ages. Similar results were reported by BAHREINI-BEHZADI *et al*. (2007); TOSH and KEMP, (1994) and GIZAW *et al*. (2007) in Kermani, Polled Dorset and Menz sheep, respectively.

Estimated direct sex-linked heritabilities except for BW were close to the estimates of maternal permanent environmental effect. The magnitude of sex-linked variances as a proportion of phenotypic variance obtained by 2nd model were 4%, 4.5%, 3% and 5.7% for BW, WW, ADG and KR, respectively. The results showed direct sex-linked heritabilities was low for BW, which showed that sex-linked genes possibly have negligible and close to zero additive genetic effects on body weights at initial ages and more noticeable effects on body weights at higher ages. This results, agreeing with the finding presented by ZAMANI and ALMASI, (2017). Therefore, suggest that sex-linked effects need to be considered in selection of growth traits in Makuie sheep. In this study, maternal permanent environmental effects were more important for BW than other traits. EKIZ *et al*. (2004) indicated that the permanent environmental influence of the dam is more important than the additive maternal effect for birth weight in Turkish Merino Lambs. This could be an indication of the large influence of environment on milk production of the ewe (MANDAL *et al*., 2006). Estimate of maternal permanent environmental effect for BW was within the range of those reported by HANDFORD *et al*. (2002); TOSH and KEMP, (1994) in Columbia and Hampshire sheep, respectively.

With the exception of observed negative autosomal genetic correlations between BW-ADG and BW-KR, genetic correlations between other traits were all positive. Therefore, selection for any of these traits will bring out positive response to selection for others. The negative autosomal genetic correlations between BW with ADG and KR imply that the gene expression mechanism is different in these traits. The low and negative autosomal genetic correlations of BW–ADG and BW–KR in this study were consistent with the low and negative direct genetic correlations reported by SHAAT and MAKI-TANILA (2009) and MOHAMMADI *et al*. (2015).

No published results were available for sex-linked genetic correlation estimates between pre-weaning traits in sheep. The sex-linked genetic correlations among all traits were positive and of medium to high magnitude for the majority of traits except the correlation between BW and KR (0.11). The positive genetic correlations between sex-linked chromosomes can increase the response to selection in each gender. Estimates of maternal permanent environmental correlations between BW-KR and WW-ADG were similar to those reported in the literature (MOHAMMADI *et al*., 2015; ABBASI *et al*., 2012; RASHIDI *et al*., 2008). The estimates of phenotypic and environmental correlations among tested traits in this study were low to high and agreement with the range reported by several authors (ABBASI *et al*., 2012; MOHAMMADI *et al*., 2015; BOUJENANE and DIALLO, 2017; ESKANDARINASAB *et al*., 2010).

The findings of the present study showed that along with direct autosomal effects, sex-linked effects also need to be considered for genetic evaluation of pre-weaning traits in Makuie sheep. Also, ignoring maternal effects, especially the significant ones, could lead to higher estimates of direct autosomal and sex-linked heritabilities.

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PROCENA GENETIČKIH PARAMETARA AUTOSOMALNIH I POLNO-POVEZANIH SVOJSTAVA KOD MAKUIE OVCE UPOTREBOM MULTIVARIJACIONE ANALIZE

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Izvod

Cilj ovog rada je bio da se odrede genetski parametri autozomnih i polno vezanih efekata za porođajnu težinu (BV), težinu odbića (VV), prosečan dnevni prirast od rođenja do odbića (ADG) i kleiber odnos (KR) kod Makuie ovaca. Skup podataka koji se koristio u ovoj studiji prikupljen je na stanici za uzgoj ovaca Makuie u provinciji Zapadni Azerbejdžan, Iran, između 1994. i 2011. godine. Fiksni efekti su uključivali godinu rođenja, pol (muški ili ženski), tip rođenja (jedan ili blizanac) i starost (pet klasa, 2-6 godina starosti). Za analizu podataka korišćena su tri multivarijaciona modela životinja, uključujući direktne (autozomne i polne) i majčinske efekte. Drugi model (uključujući direktne aditivne genetske efekte životinjskih (autozomnih i seksualnih) i trajnih efekata na životnu sredinu), sa najnižom AIC vrednošću, smatra se najprikladnijim modelom. Na osnovu najpogodnijeg modela, direktne autozomne i polno povezane heritabilnosti BV, VV, ADG i KR bile su 0,12 ± 0,04 i 0,03 ± 0,03, 0,18 ± 0,04 i 0,05 ± 0,03, 0,37 ± 0,04 i 0,04 ± 0,03, i 0,52 ± 0.05 i 0.07 ± 0.04. Veličina varijansi koje su povezane sa polom kao udeo fenotipske varijanse dobijene najboljim modelom iznosile su 4%, 4,5%, 3% i 5,7% za BV, VV, ADG i KR. Takođe, autozomni i polno vezani hromozomi, trajne ekološke i fenotipske korelacije kod majki kretale su se u rasponu od -0,20 do 0,96, od 0,11 do 0,84, -0,34 do 0,89 i -0,20 do 0,91. Rezultati ovog rada su pokazali da hromozomi povezani sa polom imaju efekte kao materinski efekti, i da to može doprineti tačnijoj proceni direktne autozomne heritabilnosti.

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