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Estimates of (co) variance components for direct and maternal effects on birth weight of Karacabey Merino lambs

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Abstract: The aim of the present study was to estimate (co) variance components for birth weights of Karacabey Merino lambs. The model fitted included direct genetic, maternal genetic, and direct-maternal genetic covariance and maternal permanent environmental effects. Data and pedigree information of the Karacabey Merino sheep used in this study were collected at the Marmara Animal Breeding Research Institute from 1998 to 2002. Variance components for birth weights were estimated by the MTDFREML. A direct heritability estimate of 0.08 and a maternal heritability estimate of 0.05 were obtained for birth weight. The maternal permanent environmental effect was significant. The estimate of the direct-maternal genetic correlation was found high and negative. In conclusion, maternal effects on birth weight of Karacabey Merino lambs were significant and need to be considered in any selection program undertaken in this breed.

Key Words: Karacabey Merino lambs, genetic parameters, birth weight

Karacabey Merinosu kuzuların doğum ağırlıklarına ait direkt ve anaya bağlı etkiler için kovaryans bileşenlerinin tahminleri

Özet: Bu araştırmada Karacabey Merinosu kuzuların doğum ağırlıkları için kovaryans bileşenlerinin tahmin edilmesi amaçlanmıştır. Model; direkt genetik, anaya bağlı genetik, direkt-anaya ait genetik korelasyon ve anaya bağlı kalıcı çevresel etkilerden oluşmuştur. Bu çalışmada Karacabey Merinosu koyunlarının 1998–2002 yıllarına ait kayıtları Marmara Hayvancılık Enstitüsünden alınmıştır. Doğum ağırlıklarına ait varyans bileşenleri MTDFREML ile tahmin edilmiştir. Doğum ağırlıkları için tahmini direkt ve anaya ait kalıtım derecesi sırasıyla 0,08 ve 0,05 olarak bulunmuştur. Anaya bağlı kalıcı çevre etkisi önemli bulunmuştur. Direkt ve anaya ait tahmini değerler arasındaki korelasyon yüksek ve negatiftir. Sonuç olarak Karacabey Merinosu kuzuların doğum ağırlıkları üzerine anaya ait etkiler önemlidir ve bu ırkta uygulanacak herhangi bir seleksiyon programında bu noktanın dikkate alınması gerekir.

Anahtar Sözcükler: Karacabey Merinosu, kuzu, genetik parametreler, doğum ağırlığı

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Introduction

The German Mutton Merino was brought to Turkey in the 1930s to increase live weight and fleece quality of indigenous sheep breeds. The Karacabey Merino was obtained by crossbreeding the German Mutton Merino with indigenous Kıvırcık sheep at the Karacabey State Farm and with indigenous White Karaman sheep at the Central Anatolian State Farm (1). Presently, there are approximately 0.85 million purebred Karacabey Merino sheep in Turkey (2).

Many factors affect the birth weight and preweaning growth of lambs. These factors include direct genetic effects, maternal genetic effects, and environmental factors, which affect both the lamb and its dam. Hence, to achieve the optimum genetic progress in a selection program both the direct and maternal components should be taken into account (3,4).

Birth weight has received limited consideration in sheep breeding programs, but is a trait of potential economic importance through its effect on preweaning growth and hence, the economic success of producing slaughters animals. An intermediate optimum has been shown to exist for birth weight with excessively large lambs liable to dystocia and excessively small lambs at risk of death from hypothermia, starvation, respiratory diseases, and other causes (5). Smith (6) in Suffolk, Hampshire, and Oxford lambs and Notter and Copenhaver (7) in Finnish Landrace lambs found that lamb survival was maximized at birth weight of 5.2 and 5.5 kg, respectively. Means for birth weight in the populations analyzed were 4.1 and 3.9 kg, respectively.

In mammalian species maternal effects influence growth traits, particularly pre-weaning. Maternal effects imply an impact of the mother on her offspring other than that through the genes she transmits to them and are from the mother's ability to produce sufficient milk to support the growth of her lambs as well as her general maternal behavior (8).

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. The confounding of this double contribution of the dam and the possibility of a negative correlation between direct and maternal effects has led to the investigation of the magnitude of these effects (9). Modern statistical methods for variance component estimation allow the partitioning of the genetic variance into direct and maternal variances. Furthermore, by using linear animal models direct and maternal effects can also be included in the models used for genetic evaluations (10).

The aim of this investigation was to estimate genetic parameters for direct and maternal effects on birth weight of Karacabey Merino lambs, fitting animal models, including direct and maternal genetic and environmental effects. In addition, the genetic correlation between direct and maternal effects was estimated.

Materials and Methods

Data in this study were the accumulated records over the years 1998-2002 obtained from the Marmara Animal Breeding Research Institute in Turkey. Birth weight records of 3618 lambs that were progeny of 1392 ewes and 68 sires were used to estimate genetic parameters. The studied population has a typical hierarchical structure and within each generation (in 1998-2002) each sire was mated with 20 dams. The number of inbred animals was 34 in the population. The average inbreeding coefficient of these animals was 0.125. The characteristics of the data structure are shown in Table 1.

Table 1. The characteristics of the data structure for birth weight.

Number of lamb	3618
Number of sire	68
Number of dam	1392
Average of progeny for each sire	53.2
Average of progeny for each dam	2.6
Number of animal in pedigree file	4566
Mean, kg	4.75
Standard deviation	0.852
Coefficient of Variation CV (%)	17.95
Average of inbreeding coefficient	0.125

Ewes were raised in an annual breeding cycle starting in July. No culling was performed among the dams except for infertility, old age, and health problems. During lambing and suckling periods, ewes grazed on pasture and cereal crop residues. During the mating period of about 45 days and for 5 to 10 days after lambing ewes were kept indoors, and received a ration composed of sun-flower meal, straw, hay, minerals, and vitamins. Ewes were supplemented, depending on available concentrate, pasture conditions, and physiological requirements. Lambs were kept indoors during the day and had free access to hay and to a commercial crop feed that contained about 16% crude protein, 0.8% forage units, minerals, and vitamins. All lambs were weighed within 12 h of birth.

Firstly, to identify the fixed effects to be included in the model, the GLM procedure in the SPSS 10.0 program (11) was performed on age of dam, birth year of lamb, birth type, and sex. These effects were significant for birth weight, and were included in the model.

The following 3 linear models were employed to estimate genetic parameters within the population (10).

Model I: $\boldsymbol{y = Xb + Za + e}$

where $\boldsymbol{y}$ is a vector of birth weight observation, $\boldsymbol{b}$ is a vector of fixed effects, $\boldsymbol{a}$ is an unknown random vector of additive direct genetic effects, and $\boldsymbol{e}$ is an unknown random vector of residuals. $\boldsymbol{X}$ and $\boldsymbol{Z}$ are known incidence matrices relating observations to $\boldsymbol{b}$ and $\boldsymbol{a}$, respectively.

Model II: $\boldsymbol{y = Xb + Za + Wm + e}$

where $\boldsymbol{m}$ is a vector of random maternal additive genetic effects, $\boldsymbol{W}$ is design matrix.

Model III: $\boldsymbol{y = Xb + Za + Wm + Spe + e}$

where $\boldsymbol{pe}$ is a vector of random maternal permanent environmental effects, and $\boldsymbol{S}$ is design matrix.

The variance-covariance structure of the model is as follows:

$$V\begin{vmatrix} \mathrm{a} \\ \mathrm{m} \\ \mathrm{pe} \\ \mathrm{e} \end{vmatrix} = \begin{vmatrix} A\sigma_{\mathrm{a}}^2 & A\sigma_{\mathrm{am}} & 0 & 0 \\ A\sigma_{\mathrm{am}} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I_{\mathrm{pe}}\sigma_{\mathrm{pe}}^2 & 0 \\ 0 & 0 & 0 & I_{\mathrm{n}}\sigma_{\mathrm{pe}}^2 \end{vmatrix}$$

where σ_{a}^2 is the additive direct genetic variance, σ_{am} is the additive direct and maternal genetic covariance, σ_m^2 is the additive maternal genetic variance, σ_{pe}^2 is the permanent environmental variance, σ_{e}^2 is the residual variance, $\boldsymbol{A}$ is the numerator relationship matrix, $\boldsymbol{I_{pe}}$ an identity matrix with order number of ewes, and $\boldsymbol{I_n}$ an identity matrix with order number of records.

The genetic correlation between direct and maternal genetic effects, direct heritability ($\mathrm{h}_{\mathrm{d}}^2$), maternal heritability ($\mathrm{h}_{\mathrm{m}}^2$), and total heritability ($\mathrm{h}_{\mathrm{T}}^2$) were calculated from the (co)variance components at convergence. Total heritability was calculated according to Willham (12) as:

$$\mathrm{h}_{\mathrm{T}}^2 = (\sigma_{\mathrm{a}}^2 + 0{,}5\sigma_{\mathrm{m}}^2 + 1{,}5\sigma_{\mathrm{am}})/\sigma_{\mathrm{p}}^2$$

where $\mathrm{h}_{\mathrm{d}}^2$ is the total heritability, and σ_{p}^2 is the phenotypic variance.

The computations were performed by MTDFREML software (13), which is based on the general concept of the restricted maximum likelihood algorithm. The value of 10^{-9} was used as the convergence criterion in all analyses.

To check the goodness of fit of the models, the Akaike Information Criterion, AIC (14) was used:

AIC = – *2*ln*L* + *2k*,

where k is the number of parameters, and L is the value of likelihood function.

Results

The estimates of (co)variance components and genetic parameters for birth weight are presented in Table 2.

Model 1, which ignored maternal effects, resulted in higher estimates for σ_{a}^2 and $\mathrm{h}_{\mathrm{d}}^2$ than did the other models. In Model 2, the addition of the maternal effect reduced the values of both σ_{a}^2 and $\mathrm{h}_{\mathrm{d}}^2$ compared to Model 1. Model 3, which included maternal permanent environmental effect, yielded smaller estimates of σ_{a}^2 and $\mathrm{h}_{\mathrm{d}}^2$ than did Models 1 and 2. Direct heritabilities were estimated with small standard errors (0.044-0.062) and were different from zero. When the additive maternal genetic effect was

Table 2. Estimates of (co)variance components and genetic parameters of birth weight.

		Model I	Model II	Model III
	Abbreviation			
Direct additive genetic variance	σ^2_a	0.208	0.043	0.042
Maternal genetic variance	σ^2_m	-	0.174	0.027
Direct–maternal additive genetic covariance	σ_{am}	-	-0.061	-0.028
Maternal permanent environmental variance	σ^2_{pe}	-	-	0.131
Residual variance	σ^2_e	0.329	0.353	0.336
Phenotypic variance	σ^2_p	0.537	0.509	0.508
Direct heritability	h^2_d	0.39 ± 0.062	0.09 ± 0.044	0.08 ± 0.044
Maternal heritability	h^2_m	-	0.34 ± 0.062	0.05 ± 0.079
Maternal permanent environmental variance as a proportion of the phenotypic variance (c^2)	$c^2 = \sigma^2_{pe} / \sigma^2_p$	-	-	0.26 ± 0.064
Covariance ratio (C_{am})	σ_{am} / σ^2_p	-	-0.12	-0.06
Direct-maternal genetic correlation	r_{am}	-	-0.70 ± 0.231	-0.83 ± 0.485
Total heritability	h^2_T	-	0.07	0.03
-2Log*L*		1065,75	952,55	911,26
AIC		10225,75	10114,55	10075,26

included in the models, h^2_m for birth weight was higher than h^2_d. The addition of direct-maternal covariance increased in σ^2_m and h^2_m. When the maternal, genetic and/or environmental effects were included in the model, the direct additive genetic variance ranged from 0.042 to 0.208. Depending on the model used the maternal effect was partitioned into genetic and the environmental components.

Discussion

The addition of additive maternal and maternal permanent environmental effects to the models reduced the direct heritabilities. The same result was found in previous reports that compared models for various sheep (15-17). Only one study on birth weight in Karacabey Merino could be found (15). They obtained direct heritability estimates of 0.092-0.327 and maternal heritability estimates of 0.101-0.271 when fitting a series of different models, which are substantially higher than the estimates obtained in this study.

The estimates of h^2_d reported by several authors were 0.04-0.39 for birth weight, depending on the model used and the breed of lamb (4,17-20). Direct heritability estimates in this study for birth weight were within the ranges reported. Depending on the model, h^2_m ranged from 0.05 to 0.34 for birth weight in this study. Similar maternal heritability estimates for birth weight were reported by María et al. (4), Tosh and Kemp (18), and Neser et al. (21).

Estimates of maternal heritability and c^2 were in the range reported by several authors. Tosh and Kemp (18) obtained estimates for maternal heritability and c^2 of 0.22 and 0.37 in Hampshire lambs, 0.31 and 0.27 in Polled Dorset, and 0.13 and 0.32 in Romanov lambs, respectively. The estimates reported from María et al. (4) for Romanov lambs using a similar model were 0.22 and 0.10 for h^2_m and c^2, respectively. Snyman et al. (19) reported an estimate of 0.12 for the permanent environmental effect of the uterus and the effect of multiple births. The permanent environmental effect of the dam on birth weight is mainly determined by uterine capacity, feeding level at late gestation, and the maternal behavior of dam. Estimates of c^2 in this study were in agreement with Tosh and Kemp (18).

Fitting the direct-maternal covariance in models resulted in a negative estimate of the direct maternal correlation for birth weight. The genetic correlations estimated by Tosh and Kemp (18), for Hampshire, Polled Dorset, and Romanov lambs were negative and ranged from -0.13 to -0.56, while María et al. (4) reported higher negative estimates which they attributed to the small number and the structure of the data. However Näsholm and Danell (20) and Yazdi et al. (22) found a positive direct-maternal correlation for Swedish Finewool and Baluchi lambs, respectively. It is evident that the relative values of h_d^2 and h_m^2 were greatly influenced by the model used in the analysis. As the maternal genetic effect and the permanent environment of the dam were of about the same magnitude, the common environment of the lambs born in the same litter should not be neglected from the model. The covariance between direct and maternal genetic effects was -0.061-0.028 for Model II and III and the genetic correlation between them was estimated as -0.70 and -0.83, respectively. Cundiff (23) argued that the negative covariance between direct and maternal genetic effects, explained from an evolutionary point of view, prevents species from becoming increasingly larger. The findings of Näsholm and Danell (20) were not in agreement with this assumption, but also several authors mentioned that a possible existence of a negative environmental covariance between dam and offspring could result in a biased estimation of genetic correlation between direct and maternal effects (3). However, various alternative criteria to compare the goodness of fit of the models have been reported in the literature (24). Unfortunately, a majority of them are not statistical tests with controlled significance level. Recently, 2 approaches, AIC (Akaike information criterion) and BIC (Bayesian information criterion), have been particularly recommended for finding the true genetic model. Values of the AIC are listed in Table 2. The values clearly showed that model III (including direct genetic effects as well as maternal genetic and permanent environmental effects) can be considered the best.

The results of the present study show that in Karacabey Merino sheep, ignoring the maternal effects leads to overestimation of direct heritability. Furthermore, the exclusion of the permanent environmental effect of the dam results in overestimation of the maternal heritability where the maternal genetic effect is of higher magnitude. Maternal effects, as the sum of maternal genetic effects and the permanent environment of the dam, were higher than the direct additive effects. Maternal effects on birth weight of Karacabey Merino lambs were significant and should be considered in any selection program implemented in this breed.

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