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Estimates of Genetic Parameters for Direct and Maternal Effects with Six Different Models on Birth and Weaning Weights of Turkish Merino Lambs

Bülent EKİZ, Mustafa ÖZCAN, Alper YILMAZ
Department of Animal Husbandry, Faculty of Veterinary Medicine, İstanbul University, 34851 Avcılar, İstanbul - TURKEY
Ayhan CEYHAN
Marmara Animal Breeding Research Institute, Bandırma, Balıkesir - TURKEY

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Abstract: The aim was to estimate the genetic parameters for birth and weaning weights of Turkish Merino lambs by separating direct genetic, maternal genetic and maternal permanent environmental effects. Data and pedigree information of the Turkish Merino sheep used in this study were collected at the Marmara Animal Breeding Research Institute from 1995 to 2001. Variance components for birth and weaning weights were estimated by the REML technique. Six different animal models were fitted by including or excluding maternal effects. Depending on the model, h_d^2 varied from 0.092 to 0.327 for birth weight and from 0.057 to 0.120 for weaning weight. Estimates of m^2 ranged from 0.101 to 0.271 for birth weight and from 0 to 0.083 for weaning weight. The maternal permanent environmental effect was significant for both traits. When fitted in models, estimates of r_{am} were high and negative for birth and weaning weights. In conclusion, maternal effects on birth and weaning weights of Turkish Merino lambs were significant and may be taken into consideration in any selection program on this breed.

Key Words: Turkish Merino lambs, genetic parameters, maternal effects, birth and weaning weights.

Türk Merinosu Kuzuların Doğum ve Sütten Kesim Ağırlıklarına ait Direkt ve Anaya Bağlı Etkiler için Altı Farklı Model ile Genetik Parametre Tahminleri

Özet: Bu araştırmada, Türk Merinosu kuzuların doğum ve sütten kesim ağırlıkları için genetik parametrelerin direkt genetik, anaya bağlı genetik ve anaya bağlı kalıcı çevresel etki şeklinde unsurlara ayrılarak tahmin edilmesi amaçlanmıştır. Bu araştırmada kullanılan Türk Merinosu koyunlara ait veri ve pedigri bilgileri 1995-2001 yılları arasında Marmara Hayvancılık Araştırma Enstitüsü'nde toplanmıştır. Doğum ve sütten kesim ağırlıkları için varyans unsurları REML tekniği ile tahmin edilmiştir. Anaya bağlı etkileri içerip içermemesine göre altı değişik model uyarlanmıştır. Modele bağlı olarak h_d^2, doğum ağırlığı için 0,092 ile 0,327; sütten kesim ağırlığı için 0,057 ile 0,120 arasında değişmiştir. m^2 tahmini ise doğum ağırlığı için 0,101 ile 0,271; sütten kesim ağırlığı için 0 ile 0,083 arasında yer almıştır. Anaya bağlı kalıcı çevresel etki her iki özellik için de önemli bulunmuştur. Modele uyarlandığında, r_{am} doğum ve sütten kesim ağırlığı için yüksek ve negatif olarak tahmin edilmiştir. Sonuç olarak, maternal etkilerin Türk Merinosu kuzuların doğum ve sütten kesim ağırlıkları üzerinde etkisi önemli bulunmuş ve bu ırk için yapılacak seleksiyon programlarında maternal etkilerin de dikkate alınması tavsiye edilmiştir.

Anahtar Sözcükler: Türk Merinosu kuzular, genetik parametreler, anaya bağlı etkiler, doğum ve sütten kesim ağırlıkları.

Introduction

The German Mutton Merino was brought to Turkey in the 1930 s to improve the body performance and fleece quality of indigenous sheep breeds. The Turkish 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). At present, there are approximately 0.85 million purebred Turkish Merino sheep in Turkey (2).

Preweaning growth of lambs is important to increase the economic success of producing slaughter lambs. 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 optimum genetic progress in a selection program both the direct and maternal components should be taken into account (3,4).

Since direct and maternal effects are generally confused, there are some difficulties in the estimation of maternal effects and their covariance components. Recently, the availability of restricted maximum likelihood (REML) algorithms for analyses fitting an animal model has simplified the estimation of (co)variance components due to maternal effects (5).

Numerous studies have found a negative correlation between additive direct and additive maternal effects (r_{am}) for birth and weaning weights of various sheep breeds (4,6-8). However, positive relationships have also been reported (9,10). Results from earlier studies concerning direct and maternal genetic effects on the birth and weaning weights of lambs are summarized in Table 1.

There are no reports on maternal effects and correlation between additive direct and additive maternal effects calculated using REML algorithms for birth and weaning weights of Turkish Merino lambs. The aim of this study was to estimate genetic parameters for birth and weaning weights of Turkish Merino lambs by fitting 6 animal models, attempting to separate direct genetic, maternal genetic and maternal permanent environmental effects. In addition, the genetic correlation between additive direct and additive maternal effects was estimated.

Materials and Methods

Data and pedigree information of the Turkish Merino sheep used in this study were collected at the Marmara Animal Breeding Research Institute from 1995 to 2001. The traits analyzed were birth and weaning weights. The characteristics of the data structure are shown in Table 2.

Table 2. The characteristics of the data structure for birth and weaning weights.

	Birth Weight	Weaning Weight
Number of records	3681	2546
Number of animals	4385	3286
Number of sires	107	88
Number of dams	1148	1010
Mean, kg	4.277	29.211
Standard deviation, kg	0.921	6.612
Coefficient of variation, %	18.6	18.7

The mating period was from June 15 to the end of July. Lambings were in November and December. All lambs were weighed and ear tagged within 12 h of birth. The identities of newborns and of their parents, date of birth, sex, birth type and birth weight were recorded. The lambs were kept together with their dams in individual

Table 1. Reported estimates of genetic parameters[a] for direct and maternal effects on birth and weaning weights in different breeds of sheep.

Author	Breed	Birth Weight				Weaning Weight			
		h_d^2	m^2	c^2	r_{am}	h_d^2	m^2	c^2	r_{am}
Tosh and Kemp, 1994 (6)	Hampshire	0.39	0.22	0.37	-0.56	0.39	0.19	0.20	-0.74
Tosh and Kemp, 1994 (6)	Polled Dorset	0.12	0.31	0.27	-0.35	0.25	0.08	0.19	-0.31
Tosh and Kemp, 1994 (6)	Romanov	0.07	0.13	0.32	-0.13	0.14	0.02	0.12	+0.43
Nasholm and Danell, 1996 (9)	Swedish Finewool	0.07	0.30	-	+0.11	0.12	0.13	-	+0.47
Maria et al., 1993 (4)	Romanov	0.04	0.22	0.10	-0.99	0.09	0.01	0.07	-0.98
Snyman et al., 1995 (11)	Afrino	0.22	0.09	0.12	-	0.33	0.17	-	-
Neser et al., 2001 (12)	Dorper	0.11	0.10	0.12	+0.35	0.20	0.10	0.08	-0.58
Ligda et al., 2000 (8)	Chios	0.18	0.19	0.17	-0.44	0.17	0.07	0.08	-0.26
Saatci et al., 1999 (13)	Welsh Mountain	-	-	-	-	0.20	0.09	0.09	+0.06

[a] h_d^2: direct heritability, m^2: maternal heritability, c^2: permanent environmental variance as a proportion of phenotypic variance, r_{am}: direct-maternal genetic correlation

boxes for the first 3 days after birth. Then a flock composed of suckling lambs and their dams was formed. The suckling program of the lambs lasted for 90 days on average. During this program, grass hay and lamb grower feed were given to the lambs. Individual weaning weight was adjusted to 90 days of age, using individual birth weight and average daily gain from birth to weaning.

Variance components for direct and maternal effects were estimated with the REML technique by using a derivative free algorithm and fitting 6 different animal models. To identify the fixed effects to be included in the models, the GLM procedure in the SPSS 10.0 program (14) was performed on year, age of dam, birth type and sex. These effects were significant for birth and weaning weights, and were included in the models.

All models included an additive direct effect, and this was the only random factor in Model 1. Model 2 included the maternal permanent environmental effect, fitted as an additional random effect, uncorrelated with all other effects in the model. Model 3 included an additive maternal effect fitted as a second random effect. Model 4 was the same as Model 3, but allowed for a direct-maternal covariance (Cov (a,m)). Model 5 and Model 6 included both additive maternal and maternal permanent environmental effects, ignoring and fitting, respectively, direct-maternal covariance. The models were as follows:

Model 1: $Y = X\beta + Z_a a + e$

Model 2: $Y = X\beta + Z_a a + Z_c c + e$

Model 3: $Y = X\beta + Z_a a + Z_m m + e$ with Cov (a,m) = 0

Model 4: $Y = X\beta + Z_a a + Z_m m + e$ with Cov (a,m) $= A\sigma_{am}$

Model 5: $Y = X\beta + Z_a a + Z_m m + Z_c c + e$ with Cov (a,m) = 0

Model 6: $Y = X\beta + Z_a a + Z_m m + Z_c c + e$ with Cov (a,m) $= A\sigma_{am}$

where Y is the vector of observations. The vector β contained year, age of dam, birth type and sex as fixed effects. a, m, c, and e are the vectors of direct additive genetic effects, maternal genetic effects, permanent environmental effect of dam and the residual, respectively. X, Z_a, Z_m and Z_c are the incidence matrices relating observations to β, a, m and c, respectively. A is the numerator relationship matrix. σ_{am} is the covariance between direct and maternal genetic effects. The (co)variance structure of the random effects in the analysis can be described as

$$V(a) = A\sigma_a^2,\ V(m) = A\sigma_m^2,\ V(c) = I_d\sigma_c^2,$$

$$V(e) = I_n\sigma_e^2,\ Cov\ (a, m) = A\sigma_{am}$$

where A is the numerator relationship matrix, σ_a^2 is the direct additive genetic variance, σ_m^2 is the maternal additive genetic variance, σ_{am} is the direct-maternal additive genetic covariance, σ_c^2 is the maternal permanent environmental variance, σ_e^2 is the residual variance, and I_d and I_n are identity matrices of on order equal to the number of dams and records, respectively.

Meyer's (15) DFREML 3.0 program was used to estimate genetic parameters for birth and weaning weights. Estimates of additive direct (h_d^2), additive maternal (m^2) and permanent environmental (c^2) heritabilities were calculated as ratios of estimates of additive direct (σ_a^2), additive maternal (σ_m^2) and permanent environmental maternal (σ_c^2) variances to the phenotypic variance (σ_p^2), respectively. The genetic correlation between direct and maternal genetic effects (r_{am}) was estimated as the ratio of the estimates of the σ_{am} to the product of the square roots of the estimates of σ_a^2 and σ_m^2. Total heritability was calculated according to the following equation (16):

$$h_T^2 = (\sigma_a^2 + 0.5\ \sigma_m^2 + 1.5\ \sigma_{am}) / \sigma_p^2$$

To determine the most appropriate model, likelihood ratio tests were used for each trait. An effect was considered to have a significant influence when its addition caused a significant increase in log likelihood, in comparison with the model in which it was ignored. When log likelihoods did not differ significantly ($P > 0.05$), the model that had fewer parameters was selected as the most appropriate. Parameters were considered to be different from zero when the estimate divided by its standard error was greater than the corresponding values of the standard normal distribution (6).

Results

a. Birth Weight

Estimates of (co)variance components, genetic parameters and log likelihood values for each model for birth weight are given in Table 3.

Table 3. Estimates of (co)variance components and genetic parameters for birth weight (standard errors in parentheses).

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	0.207	0.107	0.059	0.090	0.056	0.065
σ_m^2			0.109	0.168	0.061	0.068
σ_{am}				-0.068		-0.032
σ_c^2		0.116			0.115	0.122
σ_e^2	0.426	0.385	0.451	0.431	0.376	0.388
σ_p^2	0.633	0.608	0.618	0.622	0.608	0.610
h_d^2	0.327	0.175	0.095	0.145	0.092	0.106
	(0.042)	(0.027)	(0.029)	(0.032)	(0.036)	(0.030)
m^2			0.176	0.271	0.101	0.111
			(0.024)	(0.031)	(0.027)	(0.023)
C_{am}				-0.109		-0.052
				(0.029)		(0.027)
r_{am}				-0.550		-0.477
c^2		0.191			0.189	0.199
		(0.021)			(0.023)	(0.021)
h_T^2	0.327	0.175	0.183	0.117	0.143	0.084
Log L	-54.044	0	-18.603	-16.024	+0.004	+1.913

σ_a^2: direct additive genetic variance, σ_m^2: maternal additive genetic variance,
σ_{am}: direct-maternal genetic covariance, σ_c^2: maternal environmental variance,
σ_e^2: error variance, σ_P^2: phenotypic variance, h_d^2: direct heritability, m^2: maternal heritability, C_{am}: σ_{am}/σ_p^2, r_{am}: genetic correlation between direct and maternal effects, c^2: σ_c^2/σ_p^2, h_T^2: total heritability, Log L: log likelihood, expressed as deviation from Model 2.

The results in Table 3 showed that fitting either an additive or a permanent environmental maternal effect in models increased the log likelihood values significantly ($P < 0.05$) in comparison with Model 1. Models 2, 5 and 6 had the highest log likelihood values and the differences between these models were not significant ($P > 0.05$). On the basis of log likelihood values, Models 2, 5 and 6 were significantly better ($P < 0.05$) than Models 3 and 4, which ignored the maternal permanent environmental effect. Hence the permanent environmental influence of the dam was determined to be more important than the additive maternal effect for birth weight.

Model 1, which ignored maternal effects, resulted in higher estimates for σ_a^2 and h_d^2 than did other models. In Model 2, the addition of the maternal environmental effect reduced the values of both σ_a^2 and h_d^2 compared to Model 1. Models 3 and 4, which included an additive maternal effect but not the maternal environmental effect, yielded smaller estimates of σ_a^2 and h_d^2 than did Models 1 and 2. The addition of direct-maternal covariance in Models 4 and 6 increased σ_a^2 and h_d^2 compared to Models 3 and 5, respectively. Direct heritabilities were estimated with small standard errors (0.027-0.042) and were different from zero ($P < 0.05$) in all models.

When the additive maternal effect was included in the models, m^2 for birth weight was higher than h_d^2. The addition of direct-maternal covariance increased σ_m^2 and m^2. Fitting direct-maternal covariance in models resulted in negative estimates of the corresponding correlation. c^2 was estimated with small standard errors (0.021-0.023) and was different from zero ($P < 0.05$) in all the models tested.

b. Weaning Weight

Estimates of (co)variance components and genetic parameters regarding weaning weight are presented in Table 4. The inclusion of the permanent environmental maternal effect in Models 2, 5 and 6 resulted in a significant increase in the log likelihood in comparison

Table 4. Estimates of (co)variance components and genetic parameters for weaning weight (standard errors in parentheses).

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	3.593	1.701	1.993	2.473	1.706	1.986
σ_m^2			1.459	2.456	<0.001	0.812
σ_{am}				-1.073		-0.739
σ_c^2		2.368			2.366	2.489
σ_e^2	26.282	25.558	26.235	25.880	25.556	25.065
σ_p^2	29.874	29.627	29.686	29.736	29.628	29.612
h_d^2	0.120	0.057	0.067	0.083	0.058	0.067
	(0.042)	(0.029)	(0.033)	(0.039)	(0.031)	(0.038)
m^2			0.049	0.083	<0.001	0.027
			(0.021)	(0.033)		(0.022)
C_{am}				-0.036		-0.025
				(0.023)		(0.009)
r_{am}				-0.436		-0.582
c^2		0.080			0.080	0.084
		(0.021)			(0.033)	(0.032)
h_T^2	0.120	0.057	0.092	0.070	0.058	0.043
Log L	-18.080	0	-4.994	-4.778	0	+0.221

σ_a^2: direct additive genetic variance, σ_m^2: maternal additive genetic variance,
σ_{am}: direct-maternal genetic covariance, σ_c^2: maternal environmental variance,
σ_e^2: error variance, σ_P^2: phenotypic variance, h_d^2: direct heritability, m^2: maternal heritability, C_{am}: σ_{am}/σ_p^2, r_{am}: genetic correlation between direct and maternal effects, c^2: σ_c^2/σ_p^2, h_T^2: total heritability, Log L: log likelihood, expressed as deviation from Model 2.

with Models 1, 3 and 4 ($P < 0.05$). Consequently, the permanent environmental maternal effect was more important than the additive maternal effect in the weaning weight of Turkish Merino lambs. Differences among Models 2, 5 and 6 in terms of log likelihood values were not significant ($P > 0.05$).

As with birth weight, the highest estimates for σ_a^2 and h_d^2 were in Model 1. The inclusion of maternal effects in the models led to a decrease in σ_a^2 and h_d^2. Fitting the direct-maternal covariance in Models 3 and 5 resulted in increases in σ_a^2 and h_d^2. The standard errors of direct heritabilities were different from zero for Models 1, 3 and 4 ($P < 0.05$). The addition of the permanent maternal environmental effect with the additive maternal effect already fitted reduced σ_m^2 and m^2 for weaning weight. When the permanent environmental maternal effect was included in the models, approximately 8% of the total variances was attributed to this effect (Models 2, 5 and 6). This effect was significant in all models tested ($P < 0.05$).

Discussion

Six models were examined by fitting various combinations of the direct additive effect, additive maternal effect and maternal permanent environmental effect. On the basis of the log likelihood ratio test results and number of parameters used, Model 2 was determined as the most appropriate model for the birth weight of Turkish Merino lambs. Snyman et al. (11) reported that Model 5, which included both additive maternal and maternal permanent environmental effects but not direct-maternal covariance, was the most appropriate model for the birth weight of Afrino sheep. Ligda et al. (8) found that Model 6, which included direct-maternal covariance in addition to Model 5, was the most suitable model for the birth weight of Chios lambs. In the present study, the differences among Models 2, 5 and 6 were not significant in terms of birth weight ($P > 0.05$).

Log likelihood values of Models 2, 5 and 6 for weaning weight did not differ significantly ($P > 0.05$). Model 2, which had fewer parameters than did Models 5 and 6, was determined to be the most suitable model for the weaning weight of Turkish Merino lambs. As Model 2 was better than Models 3 and 4, the maternal permanent environmental effect was considered to be more important than the additive maternal effect for weaning weight.

The addition of additive maternal and/or maternal permanent environmental effects to the models reduced the direct heritabilities for birth and weaning weights. The same result was found in previous reports, which compared models for various sheep breeds (8,13).

The estimates of h_d^2 reported by several authors were 0.04-0.39 for birth weight and 0.09-0.39 for weaning weight, depending on the model used and the breed of lamb (4,6,8,9,11-13). Direct heritability estimates in this study for birth weight were within the ranges reported. On the other hand, direct heritability estimates of weaning weight were lower than those of some authors for various breeds (6,8,11-13).

Depending on the model, m^2 ranged from 0.101 to 0.271 for birth weight and from 0 to 0.083 for weaning weight in this study. Similar maternal heritability estimates for birth weight were reported by Maria et al. (4), Tosh and Kemp (6) and Neser et al. (12). Maternal heritability estimates of weaning weight in this study were in accordance with the results for Polled Dorset and Romanov lambs (6), Romanov lambs (4) and Chios lambs (8). The estimates of m^2 for weaning weight were lower than values reported by Tosh and Kemp (6) for Hampshire lambs, by Nasholm and Danell (9) for Swedish Finewool lambs and by Snyman et al. (11) for Afrino lambs.

Fitting the direct-maternal covariance in models resulted in a negative and high estimate of the direct-maternal correlation for birth and weaning weights. The same result was also reported by Tosh and Kemp (6), Maria et al. (4), Notter (7) and Ligda et al. (8) for several sheep breeds. However, Nasholm and Danell (9) and Yazdi et al. (10) found a positive direct-maternal correlation for Swedish Finewool and Baluchi lambs, respectively. The high estimates of r_{am} in the present study were probably due to the structure of the data set (i.e. the number of generations, for animals which were measured directly and as dams, was limited).

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 the dam. Estimates of c^2 in this study for birth weight were in agreement with the reports given in Table 1.

The estimates of c^2 for weaning weight were in accordance with reported estimates for Romanov lambs (4,6), Dorper lambs (12), Chios lambs (8) and Welsh Mountain lambs (13), but lower than the estimates of Tosh and Kemp (6) for Hampshire and Polled Dorset lambs. The maternal permanent environmental effect on weaning weight is mainly determined by the milk production of the dam. In this study, the c^2 estimates were higher than those of m^2 for weaning weight. This could be evidence of the high influence of the environment on milk production.

This study showed that the addition of maternal effects resulted in a decrease in the direct and total heritabilities for the birth and weaning weights of Turkish Merino lambs. Estimates of c^2 were higher than the direct and maternal heritability values. Estimates of the correlation between direct and maternal genetic effects were high and negative.

In conclusion, maternal effects on birth and weaning weights of Turkish Merino lambs were significant and may be taken into consideration in any selection program on this breed.

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