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Research Article

Estimates of Maternal Effects for Pre- and Post- Weaning Daily Gain in Turkish Merino Lambs

Bülent EKİZ
Department of Animal Husbandry, Faculty of Veterinary Medicine, İstanbul University, 34320 Avcılar, İstanbul - TURKEY
e-mail: bekiz@istanbul.edu.tr

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Abstract: The aims of the study were to investigate the importance of maternal effects and to determine the most appropriate model of analyses for pre- and post-weaning daily gain of Turkish Merino lambs. Genetic parameters were estimated by REML procedure using DFREML program. Twelve different animal models were fitted by including or excluding maternal genetic effect, maternal permanent environmental effect, maternal temporary environmental effect and covariance between direct-maternal genetic effects. On the basis of log likelihood ratio test results, Model 2b, which included direct genetic and maternal temporary environmental effects, was determined to be the most appropriate model for both traits. The maternal temporary environmental effect was the most important source of variation for both traits. This effect contributed about 35% and 14% to the phenotypic variance for pre- and post- weaning daily gain, respectively. The maternal genetic and permanent environmental effects were important for only pre-weaning average daily gain. Depending on the model, the estimates of maternal heritability ranged from 0.005 to 0.082 and from 0.010 to 0.027 for pre- and post-weaning daily gain.

Key Words: Turkish Merino lambs, maternal effects, variance components, growth

Türk Merinosu Kuzuların Sütten Kesim Öncesi ve Sonrası Günlük Canlı Ağırlık Artışları Üzerine Anaya Bağlı Etkilerin Tahmini

Özet: Araştırmada, Türk Merinosu kuzuların sütten kesim öncesi ve sonrası günlük canlı ağırlık artışları üzerine anaya bağlı etkilerin öneminin incelenmesi ve bu özellikler için en uygun analiz modellerinin belirlenmesi amaçlanmıştır. Genetik parametreler REML prosedürleri aracılığı ile DFREML programı kullanılarak tahmin edilmiştir. Anaya bağlı genetik, sabit çevresel ve geçici çevresel etkiler ile direkt-anaya bağlı genetik etkiler arası kovaryansı içerip içermediğine göre on iki farklı bireysel hayvan modeli uyarlanmıştır. Log likelihood oran testi sonuçları doğrultusunda, direkt genetik ve anaya bağlı geçici çevresel etkileri içeren Model 2b, her iki özellik için de en uygun model olarak belirlenmiştir. Anaya bağlı geçici çevresel etki her iki özellik için de en önemli varyasyon kaynağı olarak bulunmuştur. Bu etki sütten kesim öncesi ve sonrası günlük canlı ağırlık artışı için fenotipik varyansın sırasıyla % 35 ve % 14'ünü oluşturmuştur. Anaya bağlı genetik ve sabit çevresel etkiler sadece sütten kesim öncesi günlük canlı ağırlık artışı için önemli bulunmuşlardır. Modele bağlı olarak, anaya bağlı kalıtım derecesi tahmini sütten kesim öncesi ve sonrası günlük canlı ağırlık artışları için sırasıyla 0,005 ile 0,082 ve 0,010 ile 0,027 arasında yer almıştır.

Anahtar Sözcükler: Türk Merinosu kuzular, anaya bağlı etkiler, varyans bileşenleri, büyüme

Introduction

In mammalian species, 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. In young animals, the milk supply of their dam and the maternal care she provides contribute to their growth (1,2). The genotype of the dam therefore affects the phenotype of the young through a sample of half her direct additive genes for growth as well as through her genotype for maternal effects on growth (3). On the other hand, maternal environmental influences can be derived from factors consistent between each lambing of a dam but not genetic in origin (permanent environmental effect) or from factors specific to one litter of a dam (temporary environmental effect – litter effect) (2).

The efficiency of selection in a maternally influenced trait can sometimes reduce from direct heritability estimates alone. This could be the result of a negative correlation between direct and maternal influences, which in turn result in a lower total heritability (4). It is generally concluded that the covariance between direct and maternal genetic effects for growth traits of lamb is negative (5-10). However, positive relationships have also been reported (5,11,12). The estimates of direct and maternal influences for pre- and post- weaning average daily gain have been reported for several breeds. Estimates for pre-weaning average daily gain have ranged from 0.02 to 0.16 for maternal heritability, 0.03 to 0.11 for maternal permanent environmental effect, 0.12 to 0.31 for maternal temporary environmental effect and 0.03 to 0.19 for direct heritability, depending on the model used and the breed of lamb (5-7,9,12,13). Maternal influences tend to diminish with age of progeny but might persist into the post-weaning growth period (4). Meyer (3) and Maniatis and Pollott (14) reported that maternal influence never disappeared completely after weaning. The estimates of maternal heritability, permanent environmental effect and direct heritability for post-weaning average daily gain in literatures have ranged from 0 to 0.03, 0.03 to 0.06 and 0.13 to 0.22, respectively (5,8,11,12,15).

The objectives of the present study were, firstly, to determine the most appropriate model for the data set used and, secondly, to investigate the importance of maternal genetic, maternal permanent environmental and maternal temporary environmental effects on pre- and post- weaning daily gain of Turkish Merino lambs according to the determined model.

Materials and Methods

Data and pedigree information of the Turkish Merino sheep used in this study were obtained from the Marmara Animal Breeding Research Institute. The traits analysed were average daily body weight gains from birth to weaning (ADG1) and from weaning to six months of age (ADG2). Data were collected over a period of seven years (1996-2002) for ADG1 and a period of six years (1997-2002) for ADG2. Data set used for analyses consisted of 3358 records for ADG1 and 1794 records for ADG2. The lambs were the progeny of 86 rams and 1168 ewes for ADG1 and 71 rams and 870 ewes for ADG2.

Hand mating was applied once a year between June 15th and July 30th in different years and lasted for 40-45 days in individual years. 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, birth weight were recorded. Lambs were kept with their dams in individual pens for three days after birth. Then a flock composed of suckling lambs and their dams was formed. During the suckling period, lambs were kept indoors and additionally fed with grass hay and lamb grower concentrate. The length of the suckling period was same for all lambs. Average weaning age was 91 ± 0.35 days. ADG1 was calculated as the difference in weight between weaning and birth divided by age in days at weaning. Six months age weight was recorded at an average age of 185 ± 0.61 days. ADG2 was calculated as the difference in weight between six months age and weaning divided by days between them.

Estimates of (co)variance components and log likelihood values for ADG1 and ADG2 were obtained using derivative-free restricted maximum likelihood procedures. To identify fixed effects to be included in the models, GLM procedure (16) was performed on a model including fixed effects (year, age of dam, sex and type of birth). All these fixed effects were significant for ADG1 and ADG2 and were included in the models.

Single trait animal models were fitted for ADG1 and ADG2. Twelve different models of analyses 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. Random effects fitted to twelve models used in the analyses are summarised in Table 1.

Table 1. (Co)variance components fitted to models used in the analyses.

Model	(Co)variances fitted[a]
Model 1	$\sigma_a^2 + \sigma_e^2$
Model 2a	$\sigma_a^2 + \sigma_c^2 + \sigma_e^2$
Model 2b	$\sigma_a^2 + \sigma_t^2 + \sigma_e^2$
Model 2c	$\sigma_a^2 + \sigma_c^2 + \sigma_t^2 + \sigma_e^2$
Model 3	$\sigma_a^2 + \sigma_m^2 + \sigma_e^2$
Model 4	$\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_e^2$
Model 5a	$\sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_e^2$
Model 5b	$\sigma_a^2 + \sigma_m^2 + \sigma_t^2 + \sigma_e^2$
Model 5c	$\sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_t^2 + \sigma_e^2$
Model 6a	$\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_e^2$
Model 6b	$\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_t^2 + \sigma_e^2$
Model 6c	$\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_t^2 + \sigma_e^2$

[a] σ_a^2: direct additive genetic variance, σ_m^2: maternal additive genetic variance, σ_{am}: direct-maternal additive genetic covariance, σ_c^2: maternal permanent environmental variance, σ_t^2: maternal temporary environmental variance, σ_e^2: error variance.

The animal models used to estimate variance components were:

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

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

Model 2b: $Y = X\beta + Z_a a + Z_t t + e$

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

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

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

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

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

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

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

where Y is the vector of observations; β, a, m, c, t and e are vectors of fixed effects (year, age of dam, sex, type of birth), direct additive genetic effect (animal), maternal genetic effect, maternal permanent environmental effect, maternal temporary environmental effect and the residual effect, respectively; X, Z_a, Z_m, Z_c and Z_t are incidence matrices related to observations β, a, m, c and t, respectively. The variance and (co)variance structure for the random effects were:

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

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

where A is the additive 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_t^2 is the maternal temporary environmental variance, σ_e^2 is the residual variance, and I_d, I_t, and I_n are identity matrices with order equal to number of dams, litters and records, respectively.

The DFREML 3.0 program of Meyer (17) was used to estimate genetic parameters. The search for the maximum of the likelihood was stopped if the variance of the simplex function values was less than 10^{-8}. Restarts were performed to confirm global convergence.

To test the significance of random effects and 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 –2 times the difference between the log likelihood was greater than a critical value from a chi square distribution with one degree of freedom, the additional random factor was concluded to have had a significant effect (4). When log likelihoods did not differ significantly ($P > 0.05$), the model, which had fewer parameters was chosen to be the most appropriate (10,18). The efficiency of selection based on direct heritability could reduce, when negative estimates of direct-maternal genetic correlation are present (4). As the correlation between direct and maternal genetic effects were found to be negative for ADG1 and ADG2, total heritability was taken into consideration. Total heritability was calculated according to the following equation to Willham (19).

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

Results

The likelihood ratio test statistics for maternal effects and direct-maternal genetic covariance for ADG1 and ADG2 are given in Table 2.

Results in Table 3 showed that fitting maternal genetic, maternal permanent or temporary environmental effects improved the –2 log L significantly, compared to a model fitting only direct genetic effect (Model 1) for ADG1. Therefore, maternal effects were determined to be important for ADG1. The addition of maternal genetic effect with maternal environmental effects already fitted did not increase the –2 log L value significantly for ADG1. The inclusion of maternal temporary environmental effect to models resulted in a significant increase of the –2 log L value for ADG1. The inclusion of maternal permanent environmental effect in addition to maternal temporary environmental effect in the model did not improve the –2 log L any further for ADG1. Models with maternal temporary environmental effect for ADG2 resulted in significantly better –2 log L than models that ignored this effect. The addition of maternal genetic or maternal

Table 2. Likelihood ratio test statistics for maternal effects and direct-maternal genetic covariance (one degree of freedom).

Random Factor[b]	Models	Test statistic, -2 Δlog L[a] ADG1	Test statistic, -2 Δlog L[a] ADG2
σ_m^2	Model 3 – Model 1	-8.948**	-2.254
	Model 5a – Model 2a	-0.510	-0.008
	Model 5b - Model 2b	-0.210	-0.044
	Model 5c – Model 2c	-0.108	+0.016
σ_{am}	Model 4 – Model 3	-3.254	-0.330
	Model 6a – Model 5a	-4.484*	-0.104
	Model 6b - Model 5b	-2.442	-0.022
	Model 6c – Model 5c	-2.438	-0.094
σ_c^2	Model 2a – Model 1	-12.816**	-3.168
	Model 2c – Model 2b	-0.104	-0.060
	Model 5a - Model 3	-4.378*	-0.922
	Model 5c – Model 5b	-0.002	0.000
	Model 6a – Model 4	-5.608*	-0.696
	Model 6c – Model 6b	+0.002	-0.072
σ_t^2	Model 2b – Model 1	-98.684**	-13.338**
	Model 2c – Model 2a	-85.972**	-10.230**
	Model 5b - Model 3	-89.946**	-11.128**
	Model 5c – Model 5a	-85.570**	-10.206**
	Model 6b – Model 4	-89.134**	-10.820**
	Model 6c – Model 6a	-83.524**	-10.196**

[a] -2 Δlog L: -2 (log L full model – log L reduced model)

[b] σ_m^2: maternal additive genetic variance, σ_{am}: direct-maternal additive genetic covariance, σ_c^2: maternal permanent environmental variance, σ_t^2: maternal temporary environmental variance

* $P < 0.05$, ** $P < 0.01$

permanent environmental effects to models did not increase the –2 log L for ADG2. Hence, maternal temporary environmental effect was the only maternal effect, which was determined to be important for ADG2.

Estimates of (co)variance components and genetic parameters for ADG1 from twelve single trait analyses are presented in Table 3.

Models including maternal temporary environmental effect (Models 2b, 2c, 5b, 5c, 6b and 6c) had the highest log L values and the differences between these models were not significant ($P > 0.05$). So, Model 2b, which has fewer parameters than the other litter effect models, was determined to be the most suitable model for ADG1. Estimates of maternal heritability ranged from 0.005 in Model 5b to 0.082 in Model 4. The addition of direct-maternal genetic covariance increased the values of both σ_m^2 and m^2 in Models 4, 6a, 6b and 6c compared to Models 3, 5a, 5b and 5c, respectively. The addition of maternal permanent and/or temporary environmental effects decreased the estimates of σ_m^2 and m^2. The estimates of c^2 were 0.057, 0.047 and 0.053 in Models 2a, 5a and 6a, respectively. The addition of maternal temporary environmental effect with maternal permanent environmental effect already fitted decreased the estimates of σ_c^2 and c^2. Depending on the model, maternal temporary environmental effect contributed about 35% of the phenotypic variance for ADG1.

Estimates of (co)variance components and genetic parameters for ADG2 from twelve single trait analyses are given in Table 4.

Table 3. Estimates of (co)variance components[a] (g^2), genetic parameters[b] (standard errors in parentheses) and Log L[c] values for ADG1.

	Model 1	Model 2a	Model 2b	Model 2c	Model 3	Model 4	Model 5a	Model 5b	Model 5c	Model 6a	Model 6b	Model 6c
σ_a^2	355.53	214.48	185.48	179.77	237.85	370.49	211.57	178.27	178.46	405.22	294.94	301.55
σ_m^2					136.71	285.32	40.55	17.72	20.53	176.58	110.32	113.67
σ_{am}						-193.17				-216.13	-133.47	-137.37
σ_c^2		199.08		16.70			163.24		0.11	185.38		0.01
σ_t^2			1229.72	1213.82				1213.38	1210.45		1206.23	1206.46
σ_e^2	3131.47	3055.28	2073.06	2077.09	3100.42	3023.73	3054.53	2078.14	2078.15	2939.43	2019.47	2014.64
σ_p^2	3486.99	3468.85	3488.26	3487.38	3474.99	3486.36	3469.88	3487.49	3487.69	3490.48	3497.49	3498.95
h_d^2	0.102	0.062	0.053	0.052	0.068	0.106	0.061	0.051	0.051	0.116	0.084	0.086
	(0.033)	(0.026)	(0.028)	(0.029)	(0.031)	(0.032)	(0.026)	(0.028)	(0.029)	(0.033)	(0.032)	(0.035)
m^2					0.039	0.082	0.012	0.005	0.006	0.051	0.032	0.033
					(0.015)	(0.024)	(0.017)	(0.011)	(0.011)	(0.020)	(0.015)	(0.015)
C_{am}						-0.055				-0.062	-0.038	-0.039
r_{am}						-0.594				-0.808	-0.740	-0.742
c^2		0.057		0.005			0.047		<0.001	0.053		<0.001
		(0.018)		(0.014)			(0.023)			(0.024)		
t^2			0.353	0.348				0.348	0.347		0.345	0.345
			(0.032)	(0.033)				(0.033)	(0.033)		(0.032)	(0.033)
h_T^2	0.102	0.062	0.053	0.052	0.088	0.064	0.067	0.054	0.054	0.049	0.043	0.044
Log L	- 49.342	- 42.934	0.000	+ 0.052	- 44.868	- 43.241	- 42.679	+ 0.105	+ 0.106	- 40.437	+ 1.326	+ 1.325

[a] σ_a^2: direct additive genetic variance, σ_m^2: maternal additive genetic variance, σ_{am}: direct-maternal additive genetic covariance, σ_c^2: maternal permanent environmental variance, σ_t^2: maternal temporary environmental variance, σ_e^2: error variance, σ_p^2: phenotypic variance,

[b] h_d^2: direct heritability, m^2: maternal heritability, C_{am}: direct-maternal additive genetic covariance as a proportion of the phenotypic variance, r_{am}: genetic correlation between direct and maternal effects, c^2: maternal permanent environmental variance as a proportion of the phenotypic variance, t^2: maternal temporary environmental variance as a proportion of the phenotypic variance, h_T^2: total heritability.

[c] Log L: log likelihood, expressed as deviation from Model 2b.

Table 4. Estimates of (co)variance components[a] (g^2), genetic parameters[b] (standard errors in parentheses) and Log L[c] values for ADG2.

	Model 1	Model 2a	Model 2b	Model 2c	Model 3	Model 4	Model 5a	Model 5b	Model 5c	Model 6a	Model 6b	Model 6c
σ_a^2	337.69	217.58	189.67	188.97	205.81	315.32	196.84	187.99	189.40	203.78	203.91	198.49
σ_m^2					63.78	56.42	29.75	31.61	32.95	41.91	23.41	31.40
σ_{am}						-89.40				-72.82	-49.04	-64.52
σ_c^2		129.88		21.38			120.27		0.49	82.67		<0.01
σ_t^2			354.12	333.47				342.69	340.26		334.79	323.25
σ_e^2	2044.11	2035.73	1847.56	1847.87	2112.25	2099.44	2036.32	1829.25	1828.51	2128.40	1879.17	1903.52
σ_p^2	2381.80	2383.19	2391.65	2391.68	2381.84	2381.78	2383.17	2391.53	2391.60	2383.93	2392.25	2392.14
h_d^2	0.142 (0.024)	0.091 (0.021)	0.079 (0.020)	0.079 (0.021)	0.086 (0.022)	0.132 (0.024)	0.083 (0.022)	0.079 (0.021)	0.079 (0.021)	0.085 (0.022)	0.085 (0.024)	0.083 (0.026)
m^2					0.027 (0.015)	0.024 (0.015)	0.012 (0.014)	0.013 (0.011)	0.014 (0.012)	0.018 (0.013)	0.010 (0.011)	0.013 (0.012)
C_{am}						-0.038				-0.031	-0.021	-0.027
r_{am}						-0.670				-0.788	-0.710	-0.817
c^2		0.055 (0.032)		0.009 (0.012)			0.050 (0.030)		<0.001	0.035 (0.021)		<0.001
t^2			0.148 (0.023)	0.139 (0.022)				0.143 (0.022)	0.142 (0.023)		0.140 (0.023)	0.135 (0.021)
h_T^2	0.142	0.091	0.079	0.079	0.100	0.088	0.089	0.085	0.086	0.048	0.059	0.049
Log L	- 6.669	- 5.085	0.000	+ 0.030	- 5.542	- 5.377	- 5.0081	+ 0.022	+ 0.022	- 5.029	+ 0.033	+ 0.069

[a] σ_a^2: direct additive genetic variance, σ_m^2: maternal additive genetic variance, σ_{am}: direct-maternal additive genetic covariance, σ_c^2: maternal permanent environmental variance, σ_t^2: maternal temporary environmental variance, σ_e^2: error variance, σ_p^2: phenotypic variance,

[b] h_d^2: direct heritability, m^2: maternal heritability, C_{am}: direct-maternal additive genetic covariance as a proportion of the phenotypic variance, r_{am}: genetic correlation between direct and maternal effects, c^2: maternal permanent environmental variance as a proportion of the phenotypic variance, t^2: maternal temporary environmental variance as a proportion of the phenotypic variance, h_T^2: total heritability.

[c] Log L: log likelihood, expressed as deviation from Model 2b.

As in ADG1, the highest log L values were in models that included maternal temporary environmental effect, and Model 2b was determined to be the most appropriate model. Estimates of maternal heritability ranged from 0.010 to 0.027, depending on the model used. The inclusion of maternal environmental effects decreased the estimates of σ_m^2 and m^2. Estimates of the proportion of the maternal permanent environmental variance of ADG2 ranged from 0 to 0.055, depending on the model used. The maternal temporary environmental variance formed an important source of variation with the corresponding estimate of t^2 of about 0.14 for ADG2.

Discussion

To determine the importance of maternal effects, twelve different animal models were used for ADG1 and ADG2. The models containing maternal genetic, maternal permanent or temporary environmental effects had higher -2 log likelihood values than Model 1, which ignored maternal effects, for ADG1. The importance of maternal effects on ADG1 was also reported by several authors (6,7,9,13). For ADG2, the inclusion of maternal temporary environmental effect in models resulted in a significant increase of the -2 log likelihood, in comparison with models that ignored this effect. On the other hand, the addition of maternal genetic or permanent environmental effects did not increase -2 log likelihood value for ADG2. In corresponding study, the importance of maternal effects declined after weaning but never disappeared completely, in particular for temporary environmental effect. Similar results were reported by Meyer (3), Snyman et al. (4) and Maniatis and Pollot (14). On the basis of the log likelihood ratio test results and number of parameters used in models, Model 2b, which has only maternal temporary environmental effect as maternal effect, was determined to be the most appropriate model for both ADG1 and ADG2. Hence, the temporary environmental influence of the dam was determined to be the most important maternal effect for both traits in this study.

Reported estimates of direct heritability for different sheep breeds ranged from 0.03 to 0.19 (5-7,9,12,13) for pre-weaning average daily gain and from 0.13 to 0.22 (5,8,11,12,15) for post-weaning average daily gain. Estimates of direct heritability obtained in the present study were within the range of literature for ADG1; however, they were on the low end of the range for ADG2. Snyman et al. (4) and Saatcı et al. (18) reported that if maternal effects have a significant influence, ignoring maternal effects, both maternal genetic and environmental, leads to an overestimation of the direct heritability estimates. So, when maternal genetic and/or environmental effects were added to the models, estimates of direct heritabilities decreased for both ADG1 and ADG2. Hence, selection process of Turkish Merino sheep, in particular for pre-weaning growth traits, might be based on total heritability, instead of direct heritability.

Estimates of maternal heritability in the current study were influenced by the model fitted and varied from 0.005 to 0.082 for ADG1 and from 0.010 to 0.027 for ADG2. Estimates of maternal heritability obtained in this study were within the range of literature, which varied from 0.02 to 0.16 for ADG1 (5-7,9,12,13) and from 0 to 0.03 for ADG2 (5,8,11,12,15). The highest estimates of maternal heritability for ADG1 and ADG2 were in Model 4, which included covariance between direct and maternal effects and ignored maternal environmental effects. The addition of maternal environmental effects, in particular maternal temporary environmental effect, reduced the estimates of maternal heritability for both traits. Snyman et al. (4) and Saatcı et al. (18) also indicated that the exclusion of the maternal environmental effects, if these effects have a significant influence, could cause the over estimation of maternal heritability. Fitting the direct-maternal covariance in Models 4, 6a, 6b and 6c resulted in a negative estimate of the corresponding correlation and increased estimates of the direct heritability for ADG1 and ADG2. An antagonism between direct and maternal genetic effects was reported for pre-weaning daily gain (6,7,9) and post-weaning daily gain (5,8) for several sheep breeds. However, a positive correlation has also been reported (5,11,12).

The maternal permanent environmental effect for pre-weaning growth traits could be ascribed to the milk production of the dam (1,13). In Model 5a, which had maternal genetic and permanent environmental effect, the c^2 estimate was higher than that of maternal heritability. This could be an indication of the vast influence of the environment on milk production. In models that ignored maternal temporary environmental effect the estimates of c^2 were large when compared with the estimates from other models for both ADG1 and ADG2. These results indicate that maternal permanent environmental effect was a fraction of maternal temporary environmental effect. The same findings were reported by Hagger (7) for early weight gain of lambs. Estimates of c^2 for ADG1 and ADG2 in the current study were within the ranges reported by several authors (5,7,8,11,13,15).

The maternal temporary environmental effect is the most important source of variation for ADG1 and ADG2. This effect contributed about 35% to the phenotypic variance for ADG1 and about 14% to the phenotypic variance for ADG2. The estimates of t^2 for ADG1 in the current study were in accordance with those reported by Hagger (7) for early weight gain of Black-Brown Swiss sheep and White Alpine sheep. The importance of maternal temporary environment effect was also reported by van Wyk et al. (10) for birth weight (0.281) and weaning weight (0.220) of Dormer sheep, and by Ap Dewi et al. (20) for 12-week weight (0.23) of Welsh Mountain sheep.

The results of the present study clearly show the importance of maternal effects on lamb growth, in particular for pre-weaning. Including either genetic or environmental maternal effects resulted in significant improvement in likelihood values for ADG1. The maternal temporary environmental effect never disappeared completely for ADG2, probably due to carry-over effect. The maternal temporary environmental effect, which is due to temporary health problems of a ewe (such as foot rot, mastitis or digestive disorders) that affect lambs of one particular litter only, was determined to be the most important source of variation for both ADG1 and ADG2.

The difference in estimates of genetic parameters determined in different models indicated that model choice is an important aspect for obtaining accurate estimates that are going to be used when deciding on a breeding programme. Ignoring maternal effects leads to overestimation of the direct and total heritability for ADG1 and ADG2.

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