

Estimates of genetic parameters for different body weights and muscle and fat depths of Karayaka lambs

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Abstract: In the current paper the direct additive and maternal genetic effects on birth, weaning (at 90 days of age), and scanning (at 20 weeks of age) weights and muscle and fat depths of the ribeye area in Karayaka lambs were investigated. Analyses were carried out by the restricted maximum likelihood approach, fitting 6 animal models with various combinations of direct and maternal effects. The best model was chosen after testing for improvement in the log-likelihood values. Direct heritability (h^2_d) for all traits decreased when maternal genetic effects were included in the models. The maternal heritability (h^2_m) ranged from 0.15 to 0.22 for birth weight, from 0.04 to 0.14 for weaning weight, and from 0.08 to 0.16 for scanning weight. The effects of h^2_m on muscle depth and fat depth of the ribeye area were not considered due to their insignificance. The permanent environmental effect of the dam was significant for birth, weaning, and scanning weights. Moderate negative genetic correlations (r_{am}) between the direct and maternal genetic effects were observed, which were significant for birth (-0.179 and -0.221), weaning (-0.310 and -0.415), and scanning (-0.116 and -0.141) weights. As a result, h^2_d and h^2_m can be used as selection criteria for birth, weaning, and scanning weights in Karayaka lambs.

Key words: Lamb, Karayaka, direct heritability, maternal heritability, body weights

1. Introduction

The Karayaka sheep is a nonfat-tailed, medium-sized (40–45 kg), indigenous breed of Turkey and native to the Black Sea Region, numbering about 1.3 million (1). The color of the breed is white, with black and brown spots on the head, neck, and body (2). The Karayaka sheep is generally defined as a carpet wool breed and is mainly kept for its high quality meat. Male lambs of the breed are raised and fattened for meat production; they have high quality meat due to their mosaic distribution pattern of fat among muscle fibers (1). The breed is highly tolerant to harsh environmental conditions, but the profitability of Karayaka sheep farming is limited due to insufficient biological and socioeconomic resources.

Body weight is the primary parameter in meat production and is influenced by genetic and environmental factors. The aim of lamb producers is to improve this economically important trait (2). For the last four decades, a trend has been observed in consumer demand for leaner meat (3) that is without thick layers of fat between and

around the muscles (4). Thus, it is important to take into consideration lamb weights to build a breeding scheme. Birth weight (BW), weaning weight (WW), ultrasonic scanning weight (SW), and carcass composition (fat and muscle depths) are vital traits in the sheep industry; therefore, most selection programs include these traits and scientists and farmers try to improve them. A selective breeding program for Karayaka sheep began in 2006 and the overall objective of this program was to increase the productivity of Karayaka sheep. The traits included in the breeding program were BW, WW (at 90 day), SW (at 140 days), and scanning fat and muscle depths.

There are a limited number of studies on genetic parameters calculated by restricted maximum likelihood (REML) algorithms for weights of Karayaka lambs. The aim of the present study was to estimate the genetic parameters for different body weights and carcass composition traits of Karayaka lambs by fitting 6 animal models in an attempt to separate direct genetic, maternal genetic, and maternal permanent environmental effects.

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2. Materials and methods

The study was conducted in the sheep research farm of Gaziosmanpaşa University, Tokat, Turkey (40°31'N, 36°53'E, and 650 m above sea level). The data were collected from 2006 to 2011 to estimate (co)variance components for BW, WW, SW, and muscle depth (MD) and fat depth (FD) of the ribeye area from 1262 Karayaka lambs, some of which were twins or born in different breeding seasons of the same dam (for BW, WW, and SW 1262 lambs were used, and for MD and FD 1059 lambs were used). The Karayaka lambs were obtained from 554 ewes sired by 53 rams. The weights of all lambs at birth, at 90 days of weaning age, and at 140 days of scanning age, and calculated based on MD and FD measurements of the ribeye area, were taken with a 50 g sensitivity scale. The MD and FD of the ribeye area were recorded at the 3rd lumbar in the lambs by an ultrasonic linear prop (Falco Vet Linear prop 8.0 MHz; Pie Medical Equipment Co., Maastricht, the Netherlands)

Minitab Version 12.1 (Minitab Inc., State College, PA, USA) was used for preliminary data analyses with the general linear model. In each of the linear mixed models, the analyses included the fixed effects of birth year, sex, birth type, and dam age. Lamb age was fitted as a linear covariate. Estimates of genetic parameters and variance components were obtained by the REML approach, fitting 6 different animal models and utilizing all pedigree information using the ASREML program (5). The model included the random effects of animal, sire, and dam. The 6 different animal models used to estimate the BW, WW, and SW parameters are presented in Table 1, where Y is the vector of observations; b is the vector containing year of birth, sex, type of birth (single and multiple), and age of dam as fixed effects; a , m , c , and e are vectors of the direct additive genetic effects, the maternal genetic effects, the permanent environmental effect of the dam, and the residual, respectively; X , Z_a , Z_m , and Z_c are incidence matrices relating observations to b , a , m , and c , respectively; A is the numerator relationship matrix;

Table 1. The models used in the analyses.

Model 1	$Y = Xb + Za_a + e$	
Model 2	$Y = Xb + Za_a + e$	
Model 3	$Y = Xb + Za_a + e$	$Cov(a, m) = 0$
Model 4	$Y = Xb + Za_a + e$	$Cov(a, m) = A\Gamma_{am}$
Model 5	$Y = Xb + Za_a + e$	$Cov(a, m) = 0$
Model 6	$Y = Xb + Za_a + e$	$Cov(a, m) = A\Gamma_{am}$

and σ_{am} is the covariance between the direct and maternal genetic effects.

The (co)variance structure of the random effects in the analysis can be described by the following:

$$V(a) : A\sigma_A^2; V(m) : A\sigma_M^2; V(c) : I_d\sigma_C^2;$$

$$V(e) : I_n\sigma_E^2; Cov(a, m) : A\sigma_{AM}^2$$

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}^2 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 the identity matrices of an order equal to the number of dams and records, respectively (6).

The (co)variance components and genetic parameters were determined using model 1 for the MD and FD of the ribeye area because the other models gave insignificant results.

3. Results

Estimates of the (co)variance components and genetic parameters obtained from the 6 different models for BW are shown in Table 2. According to model 1, which took into consideration the direct additive effect and ignored the maternal genetic effect, the direct heritability (h_d^2) of BW was 0.44 ± 0.063 . When the maternal genetic effects were taken into consideration in the models, h_d^2 for BW decreased from 0.36 to 0.24. The inclusion of the maternal, genetic, and/or environmental effects into the model resulted in a direct additive variance value that varied between 0.07 and 0.08. In model 6, which took into account the genetic maternal and environmental effects, the correlation between the direct and maternal genetic effects was -0.22 , while the covariance between them was -0.05 . The values for h_m^2 ranged between 0.15 and 0.22 in the present study.

Estimates of the (co)variance components and genetic parameters obtained from the 6 different models for WW are shown in Table 3. Depending on the model being employed, the h_d^2 estimates for WW ranged between 0.40 and 0.27. For WW, model 1 provided an h_d^2 value of 0.40 ± 0.066 . The negative covariance between the direct and maternal effects in models 4 and 6 resulted in r_m estimates of -0.31 and -0.41 , respectively. For models 4 and 6, c_{am} was -0.06 . For WW, h_m^2 values within the range of 0.04–0.14 were estimated.

Estimates of the (co)variance components and genetic parameters obtained from the 6 different models for SW are shown in Table 4. For models 1, 2, 3, 4, 5, and 6, the h_d^2 estimates for SW were 0.48 ± 0.071 , 0.35 ± 0.087 , 0.29 ± 0.091 , 0.30 ± 0.122 , 0.31 ± 0.094 , and 0.34 ± 0.126 , respectively.

Estimates of the (co)variance components and genetic parameters obtained from the 6 different models for MD and FD are shown in Table 5. For model 1, the h_d^2 estimate

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

Traits	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	0.130	0.106	0.070	0.053	0.068	0.081
σ^2_M			0.044	0.082	0.047	0.064
σ^2_{AM}				-0.011		-0.016
σ^2_C		0.028			<0.01	<0.01
σ^2_E	0.161	0.153	0.171	0.163	0.170	0.161
σ^2_P	0.291	0.288	0.285	0.287	0.285	0.291
h^2_d	0.44	0.36	0.25	0.29	0.24	0.28
(s.e.)	(0.063)	(0.074)	(0.076)	(0.109)	(0.078)	(0.105)
h^2_m			0.15	0.19	0.16	0.22
(s.e.)			(0.042)	(0.072)	(0.071)	(0.109)
c^2		0.098			<0.01	<0.01
(s.e.)		(0.036)			(0.057)	(0.272)
c_{am}				-0.041		-0.055
r_{am}				-0.179		-0.221
h^2_T	0.44	0.36	0.14	0.27	0.15	0.16
-2 log L	181.836	186.000	188.100	188.199	188.083	188.064

σ^2_A = direct additive genetic variance; σ^2_M = maternal additive genetic variance; σ^2_{AM} = the covariance between direct and maternal genetic effects; σ^2_C = the variance of the permanent environmental effect of the dam (maternal environmental variance); σ^2_P = phenotypic variance; h^2_d = direct heritability; h^2_m = maternal heritability; c^2 = the permanent environmental variance due to the dam as a proportion of phenotypic variance; c_{am} = genetic variance between direct and maternal effects as a proportion of the total variance; r_{am} = genetic correlation between direct and maternal effects; h^2_T = total heritability; -2 logL = log likelihood; s.e. = standard error.

Table 3. Estimates of (co)variance components and genetic parameters for weaning weight.

Traits	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	3.127	2.522	2.087	2.604	2.252	2.886
σ^2_M			0.726	1.069	0.308	0.524
σ^2_{AM}				-0.518		-0.510
σ^2_C		0.723			0.512	0.585
σ^2_E	4.655	4.473	4.844	4.549	4.608	4.249
σ^2_P	7.783	7.719	7.658	7.706	7.683	7.735
h^2_d	0.40	0.33	0.27	0.34	0.29	0.37
(s.e.)	(0.066)	(0.075)	(0.082)	(0.119)	(0.083)	(0.124)
h^2_m			0.09	0.14	0.04	0.06
(s.e.)			(0.041)	(0.069)	(0.053)	(0.074)
c^2		0.093			0.06	0.07
(s.e.)		(0.037)			(0.051)	(0.054)
c_{am}				-0.067		-0.066
r_{am}				-0.310		-0.415
h^2_T	0.40	0.33	0.32	0.30	0.31	0.31
-2 log L	-1805.63	-1802.20	-1802.60	-1802.21	-1801.73	-1801.26

σ^2_A = direct additive genetic variance; σ^2_M = maternal additive genetic variance; σ^2_{AM} = the covariance between direct and maternal genetic effects; σ^2_C = the variance of the permanent environmental effect of the dam (maternal environmental variance); σ^2_P = phenotypic variance; h^2_d = direct heritability; h^2_m = maternal heritability; c^2 = the permanent environmental variance due to the dam as a proportion of phenotypic variance; c_{am} = genetic variance between direct and maternal effects as a proportion of the total variance; r_{am} = genetic correlation between direct and maternal effects; h^2_T = total heritability; -2 logL = log likelihood; s.e. = standard error.

Table 4. Estimates of (co)variance components and genetic parameters for scanning weight.

Traits	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	8.199	5.824	4.845	5.264	5.151	5.582
σ^2_M			2.469	2.724	1.379	1.613
σ^2_{AM}				-0.439		-0.424
σ^2_C		2.211			1.102	1.113
σ^2_E	8.680	8.450	9.198	8.902	8.808	8.546
σ^2_P	16.879	16.485	16.512	16.451	14.82	16.43
h^2_d	0.48	0.35	0.29	0.30	0.31	0.34
(s.e.)	(0.071)	(0.087)	(0.091)	(0.122)	(0.094)	(0.126)
h^2_m			0.15	0.16	0.08	0.10
(s.e.)			(0.046)	(0.071)	(0.074)	(0.093)
c^2		0.134			0.067	0.067
(s.e.)		(0.042)			(0.067)	(0.068)
c_{am}				-0.026		-0.025
r_{am}				-0.116		-0.141
h^2_T	0.48	0.48	0.36	0.36	0.39	0.35
-2 log L	-1966.63	-1960.75	-1960.49	-1960.45	-1960.08	-1960.03

σ^2_A = direct additive genetic variance; σ^2_M = maternal additive genetic variance; σ^2_{AM} = the covariance between direct and maternal genetic effects; σ^2_C = the variance of the permanent environmental effect of the dam (maternal environmental variance); σ^2_P = phenotypic variance; h^2_d = direct heritability; h^2_m = maternal heritability; c^2 = the permanent environmental variance due to the dam as a proportion of phenotypic variance; c_{am} = genetic variance between direct and maternal effects as a proportion of the total variance; r_{am} = genetic correlation between direct and maternal effects; h^2_T = total heritability; -2 logL = log likelihood; s.e. = standard error.

Table 5. Estimates of (co)variance components and genetic parameters for muscle and fat depth of the ribeye area.*

Traits	Model 1 for MD	Model 1 for FD
σ^2_A	0.653095E-02	0.253765E-04
σ^2_M		
σ^2_{AM}		
σ^2_C		
σ^2_E	0.557189E-01	0.267435E-02
σ^2_P	0.6225E-01	0.2700E-02
h^2_d (s.e.)	0.1049 (0.0616)	0.0094 (0.0369)
h^2_m		
c^2	0.1049	0.0094
c_{am}		
r_{am}		
-2 logL	893.555	2520.16

*The (co)variance components and genetic parameters were determined using model 1 for of muscle depth and fat depth weight.

σ^2_A = direct additive genetic variance; σ^2_M = maternal additive genetic variance; σ^2_{AM} = the covariance between direct and maternal genetic effects; σ^2_C = the variance of the permanent environmental effect of the dam (maternal environmental variance); σ^2_P = phenotypic variance; h^2_d = direct heritability; h^2_m = maternal heritability; c^2 = the permanent environmental variance due to the dam as a proportion of phenotypic variance; c_{am} = genetic variance between direct and maternal effects as a proportion of the total variance; r_{am} = genetic correlation between direct and maternal effects; -2 logL = log likelihood; s.e. = standard error.

for MD was 0.10 ± 0.061 . Also, the log likelihood value was 893.55. The h^2_d and the log likelihood value estimates for FD were 0.009 ± 0.0369 and 2520.16, respectively.

4. Discussion

4.1. BW

Estimates of h^2_d for BW obtained in the present study were in agreement with previously reported findings by Ulutas et al. (7) for Karayaka lambs (0.48) and by Tosh and Kemp (8) for Hampshire lambs (0.39). Moreover, our values were higher than the ones reported by Nasholm and Daniel (9) for Swedish landrace lambs (0.07), Poll Dorset lambs (0.12), and Romanov lambs (0.07), and by Ligda et al. (10) for Chios lambs. Model 1 had the highest estimations for heritability. Taking the maternal genetic effects into account in models 3, 4, 5, and 6 resulted in a decrease in h^2_d by 43.18%, 34.09%, 45.45%, and 36.36%, respectively.

Depending on the model that was used, the maternal effect consisted of environmental and genetic components. In model 6 the maternal genetic effect was 22% of the total variance, while the permanent environment of the dam was <0.01%. It can be clearly seen that the values of h^2_d and the maternal heritability (h^2_m) were significantly affected by the model used. In model 4, where the permanent environment of the dam was ignored, the maternal variance was considered as accounting for all of the total variance, which led to an overestimation of the h^2_m in comparison with that in model 6. Using a similar model, Ligda et al. (10) estimated a genetic covariance value of -0.08 between the direct and maternal effects in Chios lambs. In addition, the same authors also determined that the genetic variance between the direct and maternal effects as a ratio of the total variance (c_{am}) was -0.44. Based on the same models, the estimates calculated by Ulutas et al. (7) for h^2_m , the genetic correlation between the direct and maternal effects (r_{am}), c_{am} , and the permanent environmental variance of the dam as a ratio of phenotypic variance (c^2) in Karayaka lambs were between 0.08 and 0.19, -0.45 and -0.46, -0.15 and 0.77, and 0.0004 and 0.07, respectively. On the other hand, the estimates calculated by Rashidi et al. (11) for the maternal heritability, r_{am} , c_{am} , and c^2 of Kermani lambs were between 0.23 and 0.24, 0.11 and 0.13, 2.00 and 2.40, and 0.00 and 0.17, respectively.

Nasholm and Danell (8) reported higher h^2_m (0.30) in Swedish landrace than that in our study, as well as a positive genetic correlation between the direct and maternal genetic effects. On the other hand, Tosh and Kemp (9) calculated estimates for h^2_m and c^2 of 0.13 and 0.32 in Romanov lambs, of 0.31 and 0.27 in Polled Dorset lambs, and of 0.22 and 0.37 in Hampshire lambs, respectively. The estimates for c^2 and h^2_m were within the range reported by other researchers. Ligda et al. (10), conversely, estimated higher values for h^2_m (0.33) in Chios lambs, and identified

negative genetic correlation between the direct and maternal genetic effects. When only the maternal genetic effects were taken into consideration in the model, h^2_m for BW was 0.15. However, when the permanent environment of the dam (c^2) was considered as well, h^2_m for BW ranged between 0.16 and 0.22.

Tosh and Kemp (9) estimated negative genetic correlations for Poll Dorset, Hampshire, and Romanov lambs whose values ranged between -0.13 and -0.56. Maria et al. (12) observed even higher negative estimate values, which they considered to be associated with the small number and structure of their data. Ligda et al. (10) reported that the genetic correlation estimations for Chios lambs were negative. On the other hand, Nasholm and Danell (13) showed that estimates for Swedish fine-wool lambs were positive. Cundiff (14) previously described that, from an evolutionary standpoint, negative covariance between direct and maternal genetic effects prevents the species from becoming larger over time. The results of the current study were in disagreement with the previous findings of Nasholm and Danell (8). On the other hand, various authors have reported that a possible negative environmental covariance between offspring and dam may lead to a prejudiced estimation of genetic correlation between the direct and maternal effects (10). For the 6 different models that had the best model components, the likelihood values that were determined using the log likelihood ratio tests are provided in Table 1. Model 1, which only included the additive direct effect, was identified as the best model based on the -2 logL value. According to ASREML principles, the model with the smallest -2 logL value should be considered as the best model (7,15). This result is similar to the findings of Ulutas et al. (7). Mohammadi et al. (16), on the other hand, determined that the best model was model 3, which is the model that took into account both the direct and maternal additive genetic effects.

4.2. WW

Depending on the model being employed, h^2_d estimates for WW were higher than the ones reported for Chios lambs by Ligda et al. (10). Model 1, which did not take the maternal effects into account, estimated the highest heritability values, while models 3, 4, 5, and 6, which took the maternal effects into account, estimated h^2_d values that were lower by 32.50%, 15.00%, 27.50%, and 7.50%, respectively, as compared with model 1.

In model 3, the estimates of h^2_m for WW were lower than the estimates of h^2_m for BW. This indicated a decline in the maternal effect from the time of birth to weaning. In the present study the negative covariance between the direct and maternal effects in models 4 and 6 resulted in r_{am} and c_{am} estimates that were similar to the results of Ligda et al. (10), who also obtained negative values for r_{am} and c_{am} .

With respect to WW, the correlations between the direct and maternal effects have generally been negative, with a range of -0.1 to -0.6 (17,18). However, certain studies have also reported zero correlations (19,20) and positive correlations (21,22). Estimates of this correlation can be influenced by the model that is used, and problems relating to the precision of the estimations were previously described by Larsgard and Olesen (19). The value of the h^2_m estimate was lower than the published values. There is evidence that the estimate of WW is affected by the model that is used, and this estimate generally declines from BW to WW (8,12,17,21,23). The lower values in comparison with those for BW can possibly be explained by the fact that the maternal effects gradually decrease as the lambs grow older (24). The maternal genetic and environmental effects for BW followed the same pattern; however, the magnitude of these effects was lower. The value of h^2_m was lower (0.07) than that of h^2_d (0.16) in models 3, 4, 5, and 6.

In model 5, which took into consideration both the genetic and environmental maternal effects, the maternal genetic effects accounted for 4% of the total variance, while the permanent environment of the dam accounted for 6% of the total variance. In previous studies lower values of h^2_m and c^2 were reported for other breeds in comparison with the ones determined in the present study. For Hampshire and Poll Dorset lambs, Tosh and Kemp (9) estimated h^2_m values of 0.14 and 0.19, respectively, while the h^2_m for Romanov lambs was 0.06. The estimates of genetic correlation between the direct and maternal effects of these breeds ranged between 20.39 and 20.57. It was also observed that the permanent environment of the dam contributed to a greater extent to the total phenotypic variance, and the estimates for the 3 traits varied between 0.18 and 0.27. Maria et al. (12) reported an h^2_m of 0.25 for Romanov lambs in Spain; however, they did not observe any environmental variance due to the permanent effect of the dam.

For the 6 different models, the likelihood values with the most appropriate model components that were determined by using the log likelihood ratio tests are provided in Table 3. Model 6, which took into account both the maternal effect and permanent environmental effect due to the dam, was identified as the best model based on the $-2 \log L$ value. According to ASREML principles, the model with the smallest $-2 \log L$ value should be considered the best model (7,15). These results are in agreement with Ligda et al. (10), who indicated that model 6 (the one that took both the maternal effect and permanent environmental effect of the dam into account) was the best model. The lack of a maternal genetic effect might have resulted from the small size of the data set. Mohammadi et al. (16) previously determined in another study that the best model was model 3, which is the model that took into consideration the direct and maternal additive genetic effects.

4.3. SW

In the present study, the h^2_d estimates for scanning weight were lower than those reported by Ap Dewi et al. (25) for Welsh Mountain sheep (0.29). Gilmour et al. (26) reported a heritability value of 0.19, 0.11, and 0.37 for Poll Dorset sheep of 3 age groups, 5–9 months, 10–13 months, and 14–18 months, respectively. Fogarty et al. (27) reported an h^2_m value of 0.44 for Hyfer sheep. The h^2_m value for SW in the current study ranged between 0.8 and 0.16. This result is in agreement with the values reported for Welsh mountain sheep (0.11) by Ap Dewi et al. (25) using a similar model. Model 1, which ignored the maternal effect, estimated the highest heritability values among the different models. On the other hand, the h^2_d estimated by models that took the genetic maternal effects into account, i.e. models 3, 4, 5, and 6, were lower by 27.08%, 20.83%, 35.41%, and 29.16%, respectively.

Taking the maternal genetic effect into account in models 3, 4, 5, and 6 resulted in a decrease in the log likelihood in comparison with model 1. Model 1 provided considerably higher estimates for the direct additive genetic variance (σ^2_a) and heritability than models 2, 3, 4, 5, and 6. Models that ignored the additive maternal effects (models 1 and 2) yielded higher h^2_d values than models that included the additive maternal effects (models 3 and 4). In model 1, the h^2_d value was 0.48, while the inclusion of maternal genetic effects in models 3, 4, 5, and 6 resulted in lower h^2_d values. When the maternal genetic effects and the genetic and/or environmental effects were included into the model, the value for the direct additive genetic variance ranged between 4.84 and 5.58. Depending on the model that was used, the maternal effect consisted of environmental and genetic components.

Model 5, which removed the covariance between the direct additive and maternal effects and the genetic correlation between the direct and maternal effects, provided h^2_m estimates of relatively small values. Compared with the other models, model 1, which ignored the maternal effect, estimated the highest values for h^2_d and the direct additive genetic variance σ^2_a .

In model 2, which took into account the maternal environmental effect, both the σ^2_a and h^2_d values were lower than those in model 1. However, the σ^2_a and h^2_d values in model 2 were higher than those in the other models. In model 3, taking the additive maternal effect into account while ignoring the maternal environmental effects resulted in lower values for σ^2_a and h^2_d than the ones estimated by the other models. The covariance between the direct additive and maternal effects and the additive maternal effect were considered in model 4 while ignoring the maternal environmental effects, which resulted in higher values for σ^2_a than the one estimated by model 3. Model 4, which ignored the variance in the permanent environmental effect, estimated the highest values for h^2_m .

In model 5, maternal effects were considered while the covariance between the direct and maternal genetic effects (σ_{am}^2) was ignored. As a result of this, model 5 estimated lower values for σ_a^2 and h_d^2 than model 4. In model 6, in which both the environmental and genetic maternal effects were considered, the maternal genetic effects were 10% of the total variance, while the permanent environment of the dam accounted for 0.06% of the total variance. It was evident that the values estimated for h_d^2 and h_m^2 were considerably influenced by the model that was employed. In model 4, where the permanent environment of the dam was not taken into consideration, the maternal genetic variance accounted for all of the total variance, which led to an overestimation of h_m^2 in comparison with models 3, 5, and 6. The genetic correlation between the direct and maternal genetic effects was -0.14 , while the covariance was -0.02 .

Ap Dewi et al. (25) previously reported that for the SW, the genetic correlation between the direct and maternal genetic effects and the genetic variance between the direct and maternal effects were estimated as 0.40 and 0.12, respectively. That result was not in agreement with the findings of the present study. On the contrary, Ap Dewi et al. (25) also obtained a positive r_{am} for SW. For the 6 different models, the likelihood values that had the most appropriate model components and that were determined using the log likelihood ratio tests are provided in Table 1. Model 6, which took into account the maternal and permanent environmental effects of the dam, was identified as the best model based on its $-2 \log L$ value. According to ASREML principles, the model with the smallest $-2 \log L$ value should be considered as the best model (15). This result is similar to the findings reported by Ligda et al. (10), identifying model 6 as the best model. The lack of a maternal genetic effect might have stemmed from the small size of the data set.

4.4. MD and FD

For model 1, the h_d^2 estimates for MD and the log likelihood values were similar to those previously reported by Maxa et al. (28) for Suffolk lambs (0.16) and lower than those reported by Larsgard and Olesen (19) for Norwegian Dala lambs (0.32). In addition, Larsgard and Olesen (19) showed a major difference in h_d^2 for MD at 47 days of

preweaning age (0.05) compared with that at 144 days of weaning age (0.32). Conington et al. (23) reported a heritability value of 0.27 for MD at 119 days, while Olesen and Husabø (29) reported an MD heritability value of 0.46 in Dala and Spælsau lambs at the weaning ages of 149 and 144 days, respectively. Maniatis and Pollott (30), on the other hand, reported a relatively low estimate for MD (0.09) for Suffolk lambs. This value may be due to the fact that the animals in their study underwent ultrasonic measurements at 5 months of age. Previous studies that included an analysis of ultrasound assessments ignored the maternal genetic effects (19,23,28).

Larsgard and Olesen (19) reported higher FD estimates at weaning age (0.05), while Maxa et al. (28) reported higher estimates at the same age as in our study. The present study results differed from the findings reported by Maniatis and Pollott (30) for Suffolk lambs (0.19), which were obtained with a similar model, but a different ultrasonic measurements age (5 months). Conington et al. (23) reported higher FD estimates (0.16) and Olesen and Husabø (29) estimated that the h_d^2 value for FD was 0.26 at weaning. These researchers made use of data gathered in the field, which were analyzed using REML and a single trait sire model in order to avoid confusion with possible maternal effects.

In conclusion, the heritability values observed for body weights in the present study were within the ranges described in the literature. On the other hand, the h_d^2 values that were observed for MD and FD were somewhat lower than the values reported in the literature. This is possibly because many of the studies that analyze ultrasound measurements do not take maternal genetic effects into account. The results of the present study indicated that the best models to estimate the genetic effects were model 3 on BW and WW, and model 6 on SW. These results were similar to those of other studies that have made estimations regarding the maternal genetic effects. Favorable h_d^2 values for BW, WW, MD, and FD support the idea of using these traits as measurements in sheep breeding programs, and the estimates obtained from the present study can be effectively used in the genetic evaluation of Karayaka lambs in Turkey.

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