

GENETIC PARAMETERS FOR DIRECT AND MATERNAL EFFECTS ON DIFFERENT GROWTH RATES IN BARKI LAMBS

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SUMMARY

To investigate direct and maternal effects on growth rates taken at various intervals in Barki sheep, body weight data were obtained from the Barki sheep flock from 1994 to 2001. Records of 1169 lambs, progenies of 690 ewes and 83 sires, were used. Heritability and correlation estimates were estimated by DFREML program. Six different animal models were fitted by including or excluding maternal effects while regarding sex, year of birth and age of dam as fixed effects and animal, sire and dam as random effects. Akaike information criterion (AIC) was used to determine the most appropriate model for the studied traits. Average growth rate during pre-weaning stage was higher than that of post-weaning ones. Based on AIC, Model two is the most appropriate model for GR_{b-w} and GR_{b-6m} . Whereas Model one is the best model for GR_{w-6m} , GR_{b-9m} , GR_{w-9m} and GR_{6m-9m} low estimates of h^2_d indicate that low genetic improvement is expected for growth rates in Barki sheep. However, selection for GR_{b-w} would be more effective than other studied growth rates. The relatively higher and positive additive genetic correlations between GR_{b-w} and other post-weaning growth traits might reveal that growth rate from birth to weaning is a suitable selection criterion to improve growth performance in Barki sheep.

Keywords: Barki sheep, animal model, heritability, growth rate

INTRODUCTION

In mammalian species, growth traits are not only influenced by the genes of the individual for growth and the environment under which it is raised, but also by the maternal genetic and environment provided by the dam (Ekiz, 2005). In young animals, the milk supply of their dam and the maternal care, provide contribution to their growth (Bradford, 1972; Lewis and Beatson, 1999 and Ekiz, 2005). The genotype of the dam affects the phenotype of the young through a sample of half her direct additive genes for growth in addition to her maternal effects on growth (Meyer, 1992). The efficiency of selection in a maternally influenced trait can sometimes be reduced when direct heritability considered alone as a result of a negative correlation between direct and maternal influences, which in turn results in a lower total heritability (Snyman *et al.*, 1995). While some literatures indicated negative associations between direct and maternal genetic effects for growth traits (Yazdi *et al.*, 1997, Van Wyk *et al.*, 2003 and Ekiz 2005), other reports showed positive relationships (Maria *et al.*, 1993; Matika, 2003 and El-Wakil and Gad, 2014). There are wide discrepancies in the literatures regarding the intervals during which the growth rate is usually measured. Improving growth performance through breeding programs is an important way to increase meat output in lamb production systems. Selection for growth traits is complicated since it is determined not only by the animal's own additive genetic merit but also by maternal effects and ignoring the later would result in overestimation of direct heritability and hence a biased predicted responses to selection (Ghafouri-Kesbi and Eskandarinasab, 2008 and Barazandeh *et*

al., 2011). Therefore, both direct and maternal effects have to be considered in selection procedures (Ghafouri-Kesbi and Eskandarinasab, 2008). The objectives of the present study were, first, to determine the most appropriate model for the data set used and, secondly, to investigate the importance of maternal genetic and environmental effects on growth rates taken at various intervals in Egyptian Barki lambs.

MATERIALS AND METHODS

Data were obtained from the records of the Barki sheep flock raised at Maryout Research Station, (35 km west of Alexandria) belongs to the Desert Research Center through the period from 1994 to 2001. At birth, lambs were ear-tagged and kept with their mother's to suckle and weighed within 24 hours after birth and weaned at four months of age. Body weights were recorded at birth and biweekly intervals until weaning and monthly intervals till the animals were culled from the flock. Ewes were often first mated at approximately 16 months of age. Detailed feeding and flock management was described elsewhere (El-Wakil *et al.*, 2009). Body weight records consist of 1169 lambs, progenies of 690 ewes and 83 sires, were used, growth rate, b, w, 6m, and 9m: birth, weaning, at six month, at nine month, respectively.

Statistical analysis

Estimates of (co)variance components and log likelihood values for growth rates at different intervals were obtained using Derivative-Free Restricted Maximum Likelihood (DFREML) procedures (Boldman *et al.*, 1995). GLM procedure

(SAS, 2004) was performed on a model including fixed effects of sex, year and age of dam. All these fixed effects were significant for all traits studied and were included in the models. Also, the model included the animal, sire and dam as random effects. Six different animal models were fitted for each trait, by ignoring or including maternal genetic effect, covariance between direct-maternal effects and maternal permanent environmental effect as follows:

$$\text{Model 1: } y = Xb + Z_1a + e,$$

$$\text{Model 2: } y = Xb + Z_1a + Z_2c + e,$$

$$\text{Model 3: } y = Xb + Z_1a + Z_3m + e,$$

$$\text{Cov}(a, m) = 0$$

$$\text{Model 4: } y = Xb + Z_1a + Z_3m + e,$$

$$\text{Cov}(a, m) = A\sigma_{a,m}$$

$$\text{Model 5: } y = Xb + Z_1a + Z_2c + Z_3m + e,$$

$$\text{Cov}(a, m) = 0$$

$$\text{Model 6: } y = Xb + Z_1a + Z_2c + Z_3m + e,$$

$$\text{Cov}(a, m) = A\sigma_{a,m}$$

Where y is the vector of observations, b is the vector of fixed effects, a , m , c and e are the vectors of direct additive genetic effect, maternal genetic effect, maternal permanent environmental effect and the residual effect, respectively. X , Z_1 , Z_2 and Z_3 are incidence matrices relating individual records to b , a , c and m , respectively. The (co)variance structure for the model was:

$$V(a) = A\sigma_a^2, V(m) = A\sigma_m^2, V(c) = I_n\sigma_c^2, V(e) = I_e\sigma_e^2 \text{ and } \text{Cov}(a, m) = A\sigma_{a,m}$$

where I_n and I_e are identity matrices of order equal to the number of dams and number of records, respectively. σ_a^2 , σ_m^2 , σ_c^2 and σ_e^2 are direct additive genetic variance, maternal genetic variance, maternal permanent environmental variance, and residual variance, respectively, and $\sigma_{a,m}$ is direct-maternal genetic covariance. Analysis of animal models was used to generate variance components and estimate direct (h_d^2) and maternal heritabilities (m^2) and direct genetic, maternal and phenotypic correlations. The bivariate animal models which included the same fixed effects as univariate models were used to estimate (co) variances between each pair of traits. The models applied in two trait analyses were those fitted for each of the underlying traits in the single trait analyses. DFREML program of Boldman *et al.* (1995) was also used to estimate genetic parameters with a REML algorithm. A variance of 10^{-9} of simplex function values was chosen as the convergence criterion which gives a good accuracy of estimation. Traditionally log-likelihood ratio tests (LRT) were used to determine the most appropriate model by comparing the differences between log-likelihoods ($-2 \log L$) to a critical value from a chi-square distribution. Using LRT, only models that differ by at least one parameter are comparable, i.e., comparison of Model 2 with Model 3 is not feasible by LRT because both models include the same number of parameters. For this reason, the Akaike information criterion (AIC) of Akaike (1973) was computed to rank the models. Let p denote the number of random (co) variance parameters to be estimated and $-2 \log L$ is the maximum likelihood,

then the Akaike information criterion is defined as: $AIC = -2 \log L + 2p$. The model yielding the smallest AIC fits the data best.

RESULTS AND DISCUSSION

Different growth rates are presented for various growth phases in table (1). The average growth rate during pre-weaning period was higher than that of post-weaning ones. Even though the growth rate associated with birth weight appeared to be consistently higher than the corresponding ones started from weaning while the least growth rate was recorded for GR_{6m-9m}. That difference might be attributed to changes in feeding stuff after the suckling period.

AIC values for different models are presented in table (2). Based on AIC, Model two is the most appropriate model for GR_{b-w} and GR_{b-6m} in which maternal genetic effect was ignored, whereas Model one is the best model describing the data of other studied growth rates. For GR_{w-6m}, GR_{b-9m}, GR_{w-9m} and GR_{6m-9m}, the model including only direct additive effect (Model 1) was sufficient to explain the variation in the data. It is notable that data structure has a great impact on the accuracy of maternal effects estimation. Maniatis and Pollott (2002) indicated that a large data set and several well-linked generations of records and many relationship between relatives related to the mother were needed to accurately separated maternal genetic components and maternal permanent environmental effects from combined and direct effects.

Table (1). Estimates of growth rates (GR) at various intervals in Barki lambs

GR	No	Mean ±SE
GR _{b-w}	1169	130.90±0.96
GR _{b-6m}	978	111.20±0.74
GR _{w-6m}	978	87.24±0.71
GR _{b-9m}	791	95.61±0.67
GR _{w-9m}	791	74.42±0.72
GR _{6m-9m}	791	60.10±0.90

GR= growth rate, b, w, 6m, and 9m: birth, weaning, at 6 month, at 9 month, respectively.

Model one which ignored maternal effects resulted in generally higher estimates of h_d^2 than did the other models (Table 2). Estimates of h_d^2 ranged from 0.08 to 0.18 as indicated from table (2). Fitting maternal permanent environmental variance (c^2) in Model two generally reduced the estimates of h_d^2 compared to Model 1, while inclusion of maternal genetic effects (Models 3-6) showed further reduction in h_d^2 for which there is negligible differences in h_d^2 of the other models within each trait.

Table 2. Direct ($h^2_d \pm SE$) and maternal heritability ($m^2 \pm SE$) as well as direct ($e^2 \pm SE$), maternal permanent environmental variances ($c^2 \pm SE$) and AIC values for average growth rates at various intervals obtained from various models in Barki lambs

GR\intervals	Models	h^2_d	m^2	c^2	e^2	AIC
GR _{b-w}	1	0.17±0.06	-	-	0.83±0.06	8993.89
	2	0.14±0.06	-	0.06±0.04	0.80±0.06	8991.01
	3	0.14±0.06	0.06±0.04	-	0.80±0.06	8993.29
	4	0.13±0.06	0.02±0.14	-	0.80±0.06	8992.90
	5	0.14±0.06	0.00	0.06±0.2	0.80±0.06	8995.29
	6	0.13±0.06	0.03±0.27	0.00	0.77±0.06	8995.49
GR _{b-6m}	1	0.18±0.07	-	-	0.82±0.07	6857.74
	2	0.12±0.07	-	0.10±0.05	0.77±0.07	6856.96
	3	0.12±0.07	0.11±0.06	-	0.78±0.07	6858.70
	4	0.11±0.07	0.04±0.17	-	0.78±0.07	6858.28
	5	0.12±0.07	0.11±0.23	0.0	0.78±0.07	6860.70
	6	0.12±0.07	0.00	0.08±0.23	0.78±0.07	6860.50
GR _{w-6m}	1	0.14±0.07	-	-	0.86±0.07	6704.67
	2	0.14±0.07	-	0.19±0.05	0.67±0.07	6706.67
	3	0.14±0.07	0.00	-	0.86±0.07	6708.67
	4	0.13±0.07	0.00	-	0.85±0.07	6708.59
	5	0.14±0.07	0.00	0.00	0.86±0.07	6710.67
	6	0.14±0.07	0.00	0.02±0.29	0.79±0.07	6710.82
GR _{b-9m}	1	0.16±0.08	-	-	0.84±0.08	5179.48
	2	0.11±0.07	-	0.10±0.06	0.79±0.08	5181.47
	3	0.11±0.07	0.10±0.06	-	0.79±0.08	5181.49
	4	0.11±0.07	0.04±0.23	-	0.79±0.08	5181.22
	5	0.11±0.07	0.00	0.10±0.35	0.78±0.08	5183.04
	6	0.11±0.08	0.00	0.11±0.35	0.79±0.08	5183.07
GR _{w-9m}	1	0.15±0.08	-	-	0.85±0.08	5175.91
	2	0.14±0.08	-	0.03±0.06	0.84±0.08	5177.77
	3	0.14±0.08	0.01±0.06	-	0.84±0.08	5177.86
	4	0.14±0.08	0.03±0.25	-	0.76±0.08	5181.79
	5	0.14±0.08	0.00	0.03±0.43	0.84±0.08	5181.27
	6	0.14±0.08	0.04±0.58	0.00	0.75±0.08	5184.36
GR _{6m-9m}	1	0.09±0.07	-	-	0.91±0.07	5566.32
	2	0.08±0.07	-	0.04±0.06	0.88±0.07	5568.05
	3	0.08±0.07	0.03±0.06	-	0.88±0.08	5570.05
	4	0.12±0.08	0.21±0.27	-	0.83±0.09	5569.25
	5	0.08±0.07	0.04±0.52	0.00	0.88±0.08	5572.05
	6	0.13±0.08	0.06±0.60	0.00	0.71±0.08	5577.35

GR= growth rate, b, w, 6m, 9m: birth, weaning, at 6 month, at 9 month, respectively. The ratio of direct ($e^2 = \sigma^2_d / \sigma^2_p$) and maternal ($c^2 = \sigma^2_m / \sigma^2_p$) permanent environmental variances to the phenotypic variance (σ^2_p), AIC= Akaike information criterion (best models are in bold). $\pm SE$ =standard errors.

The present estimate of h^2_d for GR_{b-w} was found to be within the range of 0.13 to 0.26 for the corresponding values estimated from different animal models in the same Barki sheep flock as reported by El-Wakil, and Gad (2014). Moreover, the same authors found that estimates of h^2_d for the growth rate from weaning to yearling stage to be ranged from 0.08 to 0.10. Direct additive genetic effects for average growth rates obtained from the appropriate models appeared to be low to moderate values which indicate that low genetic improvement

is expected for growth traits in Barki sheep. However, selection for GR_{b-w} and GR_{b-6m} would be more effective compared with other studied growth rates.

Table (2) showed that estimates of m^2 had slight differences within each trait (Models 3-6) and ranged from 0.02 to 0.21. Estimates of m^2 for average growth rates were slightly low in the models without direct-maternal covariance, whereas the opposite trend occurred for those models with the negative covariance between direct and maternal genetic effect.

In Barki sheep of the same flock, El-Wakil, and Gad (2014) used six animal model reported that estimates of m^2 ranged from 0.10 to 0.17 for GR from birth to weaning and from 0.01 to 0.07 for growth rate from weaning to yearling. These results indicated poor maternal genetic variability compared with the direct genetic one which might reveal that selection for growth rates should be based on direct heritability rather than maternal ones in Barki sheep.

Estimates of maternal permanent environmental effects (c^2) seems to be less than direct environmental effects (e^2) which also indicate the importance of direct environmental effects compared with maternal permanent ones in controlling growth rates in Barki sheep (Table 2). In Barki sheep, El-Wakil, and Gad (2014) found that estimates of c^2 ranged from 0.05 to 0.14 for GR from birth to weaning and from 0.00 to 0.14 for growth rate from weaning to yearling. Maternal permanent environmental effects were generally low while the highest estimate obtained was 0.19 for GR_{w-6m} . These effects may be due to the effects of uterine environment and multiple births on milk production of ewes, level of nutrition at late gestation and maternal behavior (Maria *et al.*, 1993 and Snyman *et al.*, 1995).

Correlations coefficients among studied growth rates are showed in table (3). The additive genetic correlations of GR_{b-w} and GR_{w-6m} with other studied growth rates at different stages were generally higher than the corresponding maternal genetic ones. Whereas those additive genetic correlations of GR_{b-6m} with other studied growth rates were generally less than the respective maternal genetic correlations. Additive genetic correlations among studied growth rates were positive and ranged from 0.19 to 0.89. The

phenotypic correlations between studied growth rates measured at different intervals were lower than the corresponding direct additive genetic ones which agreed in general with findings obtained elsewhere (Pollott *et al.*, 1998; Mousa *et al.*, 1999; Ghafouri-Kesbi and Baneh, 2012 and El-Wakil and Gad, 2014). The relatively higher and positive additive genetic correlations between GR_{b-w} and other post-weaning growth traits, makes this trait to be a suitable selection criterion to improve growth performance of the Barki sheep.

CONCLUSION

Our results indicate the importance of direct genetic and environmental effects rather than maternal genetic and permanent environmental effects in controlling growth rates at various intervals in Barki sheep. Therefore, selection based on direct genetic effects would be more effective and using GR_{b-w} would be better than any other form of growth rates in this flock. The relatively higher and positive additive genetic correlations between GR_{b-w} and other post-weaning growth traits might reveal that growth rate from birth to weaning is a suitable selection criterion to improve growth performance in Barki sheep.

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Table 3. Correlations coefficients between studied growth rates estimated from bi-variate analysis

Trait 1	Trait 2	r_a	r_m	r_p
GR_{b-w}	GR_{b-6m}	0.89	0.69	0.46
GR_{b-w}	GR_{w-6m}	0.38	0.22	0.13
GR_{b-w}	GR_{b-9m}	0.31	0.10	0.19
GR_{b-w}	GR_{w-9m}	0.19	-0.04	0.10
GR_{b-w}	GR_{6m-9m}	0.52	0.30	-0.03
GR_{b-6m}	GR_{w-6m}	0.57	0.88	0.81
GR_{b-6m}	GR_{b-9m}	0.54	0.91	0.24
GR_{b-6m}	GR_{w-9m}	0.67	0.77	0.37
GR_{b-6m}	GR_{6m-9m}	0.72	0.82	0.33
GR_{w-6m}	GR_{b-9m}	0.77	0.66	0.29
GR_{w-6m}	GR_{w-9m}	0.42	-0.26	0.10
GR_{w-6m}	GR_{6m-9m}	0.48	0.48	0.20
GR_{b-9m}	GR_{w-9m}	0.82	0.87	0.90
GR_{b-9m}	GR_{6m-9m}	0.37	0.78	0.71
GR_{w-9m}	GR_{6m-9m}	0.30	0.87	0.83

r_a = direct additive effect genetic correlation, r_m = maternal genetic correlation, r_p = phenotypic correlation, GR= growth rate, b, w, 6m, 9m: birth, weaning, at 6 month, at 9 month, respectively.

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المعالم الوراثية للتأثيرات الأمية والمباشرة علي معدلات النمو المختلفة في الأغنام البرقي

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الهدف من هذه الدراسة هو البحث عن أهمية التأثيرات المباشرة والأمية علي معدلات النمو المأخوذة علي فترات مختلفة من عمر الأغنام البرقي. استخدمت في هذه الدراسة سجلات أوزان الجسم وسجلات النسب المتحصل عليها من قطيع الأغنام البرقي في محطة بحوث مريوط التابعة لمركز بحوث الصحراء منذ عام ١٩٩٤ إلى عام ٢٠٠١. استخدمت سجلات لعدد ١١٦٩ من الحملان أبناء لعدد ٨٣ كبش و ٦٩٠ نعجة في التحليل الإحصائي حيث تم تقدير المكافآت الوراثية المباشرة والأمية وكذلك الارتباطات الوراثية والأمية والبيئية والمظهرية باستخدام برنامج DFREML. استخدمت الدراسة ستة نماذج للحيوان في التحليل الإحصائي اختلفت فيما بينها في احتوائها أو عدم احتوائها على التأثيرات الأمية بالإضافة إلى اعتبار سنة الميلاد و عمر الأم كتأثيرات ثابتة بينما الحيوان والكباش والنعاج كتأثيرات عشوائية. كما تم استخدام Akaike information criterion (AIC) لتحديد أنسب نموذج لاستخدامه في دراسة الصفات المدروسة. تم حساب معدلات النمو من الميلاد إلي الفطام، من الميلاد إلي عمر ٦ شهور، من الفطام إلي عمر ٩ شهور، من الميلاد إلي عمر ٩ شهور، من الفطام إلي عمر ٩ شهور إلي عمر ٩ شهور. كانت معدلات النمو في مرحلة ما قبل الميلاد أعلى من مثيلاتها في مرحلة ما بعد الميلاد. بناء على AIC، كان النموذج الثاني هو الأنسب لمعدلات النمو من الميلاد وحتى الفطام، من الميلاد وحتى عمر ٦ شهور، بينما كان النموذج الأول هو الأنسب لمعدلات النمو من الفطام إلى عمر ٦ شهور، من الميلاد إلى عمر ٩ شهور، من الفطام إلى عمر ٩ شهور، من عمر ٦ شهور إلى عمر ٩ شهور. تراوحت تقديرات المكافئ الوراثي المباشر من ٠.٠٨ إلي ٠.١٨ والتي تشير إلي أنه من المتوقع أن يكون التحسين الوراثي لمعدلات النمو بطيئا في الاغنام البرقي. كما أن الانتخاب لمعدل النمو من الميلاد وحتى الفطام كان الأكثر كفاءة مقارنة بمعدلات النمو الأخرى المدروسة. أوضحت الدراسة ان تقديرات المكافئ الوراثي الأمي كانت بصفة عامة أقل من مثيلاتها المباشرة مما يشير إلى أن الانتخاب لمعدلات النمو في الأغنام البرقي يجب أن يعتمد على المكافآت الوراثية المباشرة وليست الأمية. كما كانت تقديرات التأثيرات الأمية البيئية الدائمة أقل أهمية من التأثيرات البيئية المباشرة لمعدلات النمو المدروسة. أظهرت الدراسة أن الارتباطات الوراثية المباشرة بين معدلات النمو ما بين الميلاد والفطام ومثيلاتها في مرحلة ما بعد الفطام كانت عالية وموجبة مما يوضح أن معدل النمو من الميلاد حتى الفطام قد يكون معيار انتخابي مناسب لتحسين مظاهر النمو في الأغنام البرقي.