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ESTIMATION OF GENETIC PARAMETERS FOR EARLY GROWTH TRAITS IN EGYPTIAN BARKI LAMBS USING MULTITRAIT ANIMAL MODELS

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ABSTRACT

Variance components of birth weight (BW), weaning weight (WW) and pre-weaning average daily gain (ADG) in Barki lambs were estimated by Multitrait derivative free restricted maximum likelihood (MTDFREML). Six different animal models were fitted by including or excluding genetic maternal effects, maternal permanent environmental effects and covariance between direct and genetic maternal effects in order to determine the most appropriate model. Genetic maternal effects appeared to be the most important effects under the conditions of this study. The most appropriate model was that allowing for the genetic direct effects, both the genetic and permanent environmental components of the dam effects and the covariance between direct and maternal genetic effects (Model 6). From this model estimates of the heritability for genetic direct effect (h^2) were 0.29, 0.23 and 0.22 for BW, WW and ADG, while for maternal effects (m^2) were 0.05, 0.39 and 0.08 for the same traits. The genetic correlations between direct and maternal effects (r_{am}) were positive for BW and ADG (0.78 and 0.37, respectively) and negative for WW (-0.34). The genetic direct correlation between BW and WW and between BW and ADG were 0.44 and -0.40, respectively. The corresponding genetic maternal correlation estimates were 0.54 and -0.34. The genetic direct and genetic maternal correlations between WW and ADG were 0.35 and 0.05. The study concluded that maternal effects have to be accounted for when estimate genetic parameters for BW, WW and ADG. The r_{am} value obtained suggested that ADG is a good selection criterion for carrying out a joint selection on lamb's growth capacity (direct effects) and ewe's suckling ability (maternal effects).

Keywords: Direct and maternal effects, genetic parameters, early growth, Barki lambs.

INTRODUCTION

The genes of the individual, the environment provided by the dam and the other environmental effects are the main factors controlling growth of mammals (Albuquerque and Meyer, 2001). Hence, ignoring the genetic contribution of the dam to the phenotypic value of her progeny and over looking the genetic covariance between the direct and maternal effects should raise paramount problems in selection programs aiming at maximum genetic improvement of early growth (Willham, 1980).

In Barki sheep, for which some estimates of genetic and phenotypic parameters of early growth are found in the literature (e.g. Fahmy, 1967; Fahmy *et al.*, 1969; Aboul-Naga and Afifi, 1982; Abdel Aziz, 2000), the role of maternal effects on early growth traits is still to be investigated. This has been searched in other sheep breeds using extensively single trait animal models (e.g. Hagger, 1998; Maria *et al.*, 1993; Tosh and Kemp, 1994; Ligda *et al.*, 2000; Neser *et al.*, 2001 and Dugma *et al.*, 2002) and infrequently multitrait animal models (e.g. Okut *et al.*, 1999).

The aim of the present study on Barki sheep was to estimate genetic parameters for body weights at birth and weaning and pre-weaning growth rate using multitrait animal models involving the genetic maternal, maternal permanent environmental effects and genetic direct-genetic maternal covariance beside the genetic direct effects.

MATERIAL AND METHODS

Source of data. The data used in the present study were collected over 20 years started in 1963 and ended in 1995 on an Egyptian North Western coast Barki sheep experimental flock belonging to Desert Research Center, Ministry of Agriculture and Land Reclamation, Egypt.

Management. As a rule, mating season takes place around July and lambing starts around December each year. Following their birth, lambs were ear-tagged and kept with their dams to suckle their milk until weaning at 4 months of age.

Traits considered. For each lamb, the body weights at birth (BW) and weaning (WW) were recorded just before the morning suckling, and the average daily gain (ADG) between birth and weaning was calculated.

Estimation of genetic and phenotypic parameters. Multitrait animal models were fitted to BW, WW and ADG. Six different models of analyses were fitted, by ignoring or including genetic maternal effect, covariance between genetic direct and genetic maternal effects. Random effects fitted to the six models are summarized in Table 1.

Table 1: Co)variance components fitted† to models used in the analyses

Model	(Co)variances fitted‡				
	σ^2_a	σ^2_m	σ_{am}	σ^2_c	σ^2_e
1	●				●
2	●			●	●
3	●	●			●
4	●	●	●		●
5	●	●		●	●
6	●	●	●	●	●

†: components marked ● are included in the model

‡: σ^2_a : genetic direct variance, σ^2_m : genetic maternal variance, σ_{am} : genetic direct- genetic maternal covariance, σ^2_c : maternal permanent environmental variance, σ^2_e : error variance. The animal models used to estimate (co)variance components were:

Model 1	$y = Xb + Z_a a + e$	
Model 2	$y = Xb + Z_a a + Z_c c + e$	
Model 3	$y = Xb + Z_a a + Z_m m + e$	with $\sigma_{am} = 0$
Model 4	$y = Xb + Z_a a + Z_m m + e$	with $\sigma_{am} = A\,\sigma^2_{am}$
Model 5	$y = Xb + Z_a a + Z_m m + Z_c c + e$	with $\sigma_{am} = 0$
Model 6	$y = Xb + Z_a a + Z_m m + Z_c c + e$	with $\sigma_{am} = A\,\sigma^2_{am}$

where: y is the vector of observations of the three traits; b, a, m, c, e are vectors of fixed effects (year of lambing, sex of lamb, type of birth and age of dam), direct additive genetic effect, maternal genetic effect, maternal permanent environmental effect and the residual effects, respectively; X, Z_a, Z_m and Z_c are incidence matrices related to observations, b, a, m and c, respectively.

The first and the second moments of the model were assumed to be: E(y) =Xb, E(a) = E(m) = E(p) = E(e) = 0. V(a) = σ^2_a A, V(m) = σ^2_m A, V(p) = σ^2_p I_n, V(e)= σ^2_eI and cov (a,m) = Aσ_{am}. where: A is the numerator relationship matrix between animals, σ^2_a is the genetic direct variance, σ^2_m is the genetic maternal variance, σ_{am} is the genetic covariance between direct and maternal effects, σ^2_c is the maternal permanent environmental variance, σ^2_e is the residual variance, and I_d and I_r are identity matrices with order equal to number of animals and records, respectively.

The estimation was carried out for the six models with derivative-free REML (Mayer, 1990) using multiple-trait derivative free restricted maximum likelihood (MTDFREML) Program of Boldman *et al.* (1995).

The importance of the random effects were assessed by comparing the log likelihood (log L) of models 1 through 6.

RESULTS AND DISCUSSION

Phenotypic variation. Phenotypic variation of body weight at birth and weaning and pre-weaning average daily gain are presented in Table 2. Much larger amount of phenotypic variation was observed for pre-weaning growth rate (32.5 %) than for body weights at birth (15.0%) and weaning (26.7%).

Table 2: Descriptive statistics for the traits considered in the present study

Item	Birth weight	Weaning weight	Pre-weaning daily gain
Unit	kg	Kg	g/day
Mean	3.8	17.4	113.3
Coefficient of variation %	15.0	26.7	32.5

Importance of genetic maternal and maternal permanent environmental effects. This importance was judged by log L values given in Table 3. The inclusion of maternal permanent environmental effects in addition to genetic direct effects improve the log L significantly (Model 2 vs. Model 1). A further significant improvement in log L resulted by adding genetic maternal effects (Model 5 vs. Model 2). To the model already fitting only genetic direct effects (Model 1), the addition of genetic maternal effects instead of maternal permanent environmental effects resulted in significantly better log L (Model 3 vs. Model 2). Hence, genetic maternal effects appeared to be the most important effects under the conditions of this study, and the most appropriate model tested was that involving the genetic direct effects, both the genetic and permanent environmental components of the dam effects and the covariance between direct and maternal genetic effects (Model 6).

Estimates of (co)variance components and heritabilities for BW. Taking account of either or both of the total maternal effects (m^2 + c^2) in model 6 reduced genetic direct effects (a^2) and direct heritability (h^2) compared with model 1, where maternal effects were ignored. The estimate of the total maternal effects ($m^2 + c^2 + ¼ h^2 + \sqrt{h^2} * \sqrt{m^2} * r_{am}$ Notter, 1998) was 0.82, indicating that the maternal effect is more important than the direct effect.

Ignoring maternal permanent environmental effects in Model 3 resulted in higher genetic maternal variances (σ^2_m) and the corresponding m^2 estimates compared with Model 5 and 6, where c^2 were fitted. Thus failure to take account of $c^2 + m^2$ together and c^2 alone resulted in an overestimation of h^2 and m^2, respectively. The same conclusion was reported by Saatci *et al.*(1999) on Welsh Mountain lambs. The relative values of σ^2_a and σ^2_m and of h^2 and m^2 were greatly influenced by the model adopted (Model 3 through 6), but σ^2_a and h^2 were always larger than their corresponding maternal values (σ^2_m and m^2). The c^2 value was greater than m^2. A similar trend was observed using the single-trait animal models on Merino lambs by Duguma *et al.*(2002).

The moderate h^2–values obtained using the most comprehensive multitrait model (M_6) for BW of Barki (0.29, Table 3), Columbia and Rambouillet (0.33, Okut *et al.*,1999) and Targhee (0.32, Okut *et al.*, 1999) lambs were in agreement with the values obtained from single-trait analyses on Chios (0.38, Ligda *et al.*, 2000) and Hampshire (0.39, Tosh and Kemp, 1994) lambs but much higher than the values reported on Romanov (0.04, Maria *et al.*, 1993; 0.07, Tosh and Kemp, 1994), Dorper (0.11, Neser *et al.*, 2001), Polled Dorset (0.12, Tosh and Kemp, 1994) and Merino (0.19, Duguma *et al.*, 2002) breeds.

Estimates of (co)variance components and heritabilities for WW. As in BW, the proportion of direct genetic variance and consequently the direct heritability decreased when any of the maternal effects was fitted in the model. Fitting the maternal permanent environmental effects (Model 2) was associated with relatively greater reduction in h^2 than fitting the genetic maternal effect (model 3). Both the maternal permanent and the genetic maternal effects were greater than the genetic direct effects.

The low direct heritability estimate obtained from the most comprehensive multi-trait model for WW in the present study on Barki (h^2 = 0.23, Table 3) and in that of Okut at al.(1999) on Columbia (0.05), Polypay (0.25) and Targhee (0.24) were comparable to the values obtained in the literature using corresponding single-trait models by Neser *et al.*(2001) on Droper (0.20, and Tosh and Kemp (1994) on Romanov (0.14) and Polled Dorset (0.25).

Estimates of (co)variance components and heritabilities for ADG.

The estimates of the genetic direct, genetic maternal and maternal permanent environmental variances followed different pattern as compared with WW. The proportions of genetic maternal and maternal permanent environmental effects were much lower than the genetic direct effects.

The full multitrait model (M_6) estimated ADG to be lowly heritable in Barki (h^2 = 0.22, Table 3), Polypay (0.22, Okut *et al.*, 1999) and Targhee (0.20, Okut *et al.*, 1999). These values were comparable to those obtained from single-trait analysis on Merino lambs (0.27) by Duguma *et al.*(2002).

Relative importance of maternal effects on BW and WW. Genetic maternal effects had comparable influence on BW (m^2 = 0.05 to 0.38) and WW (m^2 = 0.12 to 0.39) than on ADG (m^2= 0.08 to 0.14). However, maternal permanent environmental effects influenced WW more than BW (c^2 = 40.1 vs. 30.1% in model 2; 39.6 vs. 15.1% in model 6).

Table 3: Estimates of (co)variance components, direct, maternal and total heritabilities and genetic direct-genetic maternal correlation of birth weight, weaning weight and average daily gain resulted from various model

Item	Model					
	1	2	3	4	5	6
Birth weight, BW						
Variance components:						
Direct genetic, σ^2_a	11.42	5.11	8.63	7.60	6.10	5.23
Maternal permanent environmental, σ^2_c	….	5.30	….	….	2.79	2.10
Maternal genetic, σ^2_m	…..	….	6.83	6.12	3.14	0.91
Residual, σ^2_e	6.43	7.20	2.52	2.79	6.45	8.18
Phenotypic, σ^2_p	17.85	17.61	17.98	18.54	18.48	18.13
Direct-maternal genetic covariance, σ_{am}	….	….	….	2.03	….	1.71
Heritabilities:						
Direct, h^2	0.64	0.29	0.48	0.41	0.33	0.29
Maternal, m^2	….	…..	0.38	0.33	0.17	0.05
Total, h^2_t	….	….	0.67	0.74	0.42	0.46
Direct-maternal correlation, r_{am}	….	…..	….	0.30	….	0.78
Weaning weight, WW						
Variance components:						
Direct genetic, σ^2_a	11.15	6.41	9.89	8.33	8.53	6.45
Maternal permanent environmental, σ^2_c	….	11.68	….	….	11.65	0.92
Maternal genetic, σ^2_m	….	….	10.19	7.78	3.53	10.82
Residual, σ^2_e	18.18	11.03	9.09	14.77	5.71	7.06
Phenotypic, σ^2_p	29.33	29.12	29.98	27.77	29.42	28.05
Direct-maternal genetic covariance, σ_{am}	….	….	….	-3.11	….	-2.80
Heritabilities:						
Direct, h^2	0.38	0.22	0.33	0.30	0.29	0.23
Maternal, m^2	….	….	0.34	0.28	0.12	0.39
Total, h^2_t	….	….	0.50	0.27	0.35	0.27
Direct-maternal correlation, r_{am}	….	….	….	-0.39	….	-0.34
Pre-weaning average daily gain, ADG						
Variance components:						
Direct genetic, σ^2_a	13.94	7.12	10.43	8.06	12.57	10.11
Maternal permanent environmental, σ^2_c	….	0.30	….	….	1.15	9.23
Maternal genetic, σ^2_m	….	….	6.35	4.03	6.28	3.67
Residual, σ^2_e	31.03	37.10	28.74	29.44	24.88	20.66
Phenotypic, σ^2_p	44.97	44.52	45.36	44.80	44.88	45.93
Direct-maternal genetic covariance, σ_{am}	….	….	….	3.27	….	2.26
Heritabilities:						
Direct, h^2	0.31	0.16	0.23	0.18	0.28	0.22
Maternal, m^2	….	….	0.14	0.09	0.14	0.08
Total, h^2_t	….	….	0.30	0.33	0.35	0.33
Direct-maternal correlation, r_{am}	….	….	….	0.57	….	0.37
Trivariate complex log L*	56119 (1)	56167 (2)	56224 (3)	56172 (4)	56206 (5)	56239 (6)

***: The following differences are significant (P< 0.001): (6)>(5)>(4)>(1); (3)>(2)>(1); (5)>(2).**

Relative importance of genetic maternal and maternal permanent environmental effects. In model 5 involving genetic maternal and maternal permanent environmental effects, the c^2 estimate for WW was higher than that of maternal heritability (0.40 vs. 0.12). This could be an indication of larger influence of the environment on milk production. (Ekiz, 2005).

Correlations between genetic direct and genetic maternal effects for BW, WW and ADG. Examining the estimates given in Table 3 for the concerned models, it appears that negative correlation between genetic direct and genetic maternal effects was significant for WW (r_{am} = -0.39 in Model 4 and -0.34 in Model 6) Such antagonism between the effect of a lamb'sl genes for growth and those of maternal contribution reduces the total heritability and imply that genetic improvement of WW would be difficult since an increase in one component would result in a decline in the other. Several authors derived similar trend (r_{am} =-0.41, Burfening and Kress, 1993; -0.42, Abegaz and Duguma, 2000; -0.59, Torshizi *et al.*, 1996; -0.94, Fadili *et al.*, 2000; -0.97, Maria *et al.*, 1993; -0.74, Tosh and Kemp, 1994; -0.55, Neser *et al.*, 2000; -0.58, Neser *et al.*, 2001). However, Tosh and Kemp (1994), Nasholm and Danell (1996) and Yazdi *et al.*(1997) contradicted this antagonism (r_{am} = 0.47 and 0.51, respectively). The correlations were positive for BW (0.30 in Model 4 and 0.78 in Model 6, Table 3; 0.35, Neser *et al.*, 2001; 0.18, Yazdi *et al.*, 1997; 0.11, Nasholm and Danell, 1996) and ADG (0.57 in Model 4 and 0.37 in Model 6, Table 3)

The positive correlation between direct and maternal genetic effects for birth weight indicates that selection for maternal ability of the ewe would expect to be associated with some increase in BW of her progeny. This is in disagreement with the negative values of -0.35 to -0.64 obtained in the literature (Burfening and Kress, 1993; Abegaz and Duguma, 2000; Tosh and Kemp, 1994; Ligda *et al.*, 2000 and Torshizi *et al.*, 1996).

Correlations among BW, WW and ADG at phenotypic, genetic direct, genetic maternal and permanent environmental levels. For all the models (Table 4) the relationship between BW and ADG were negative in terms of phenotypic, genetic direct effect, phenotypic, genetic maternal effect and maternal permanent environmental effects. The correlation was also negative between BW and WW at maternal environmental level.

Examining the correlation results presented in Figure 1 for the most appropriate model (Model 6), the order of magnitude differs according to the variance component considered. The positive correlation between BW and WW was highest at the genetic maternal level (0.54) followed by the values in terms of genetic direct effects (0.44) and phenotypic effects (0.20). The correlation was negative at the level of maternal permanent environmental level. The highest correlation values between BW and ADG was at the genetic direct level (-0.40) followed by that estimated at the phenotypic level (-0.35), genetic maternal (-0.34) and maternal permanent environmental (-0.08) level. The estimation of correlation coefficient between WW and ADG resulted in the highest value at the maternal permanent environmental levels (0.60) followed by that obtained in terms of genetic direct (0.35), phenotypic (0.11) then genetic maternal (0.05) effects.

Table 4: Direct genetic , maternal genetic, maternal permanent environmental, residual and phenotypic correlations among body weights at birth (BW) and weaning (WW) and preweaning growth rate (ADG) estimated using various multiple-trait animal models.

Type of correlation	Model*	Correlated traits		
		BW and WW	BW and ADG	WW and ADG
Direct genetic	1	0.85	-0.86	0.99
	2	0.98	-0.18	0.04
	3	0.03	-0.95	0.29
	4	0.17	-0.08	0.13
	5	0.90	-0.72	0.34
	6	0.44	-0.40	0.35
Maternal genetic	3	0.04	-0.99	0.15
	4	0.12	-0.23	0.26
	5	0.47	-0.93	0.14
	6	0.54	-0.34	0.05
Permanent environmental	2	-0.76	-0.85	0.47
	3	-0.91	-0.01	0.01
	5	-0.32	-0.99	0.32
	6	-0.85	-0.08	0.60
Residual	1	0.31	-0.99	0.33
	2	0.89	-0.11	0.36
	3	0.91	-0.01	0.01
	4	0.69	-0.77	0.07
	5	0.41	-0.13	0.60
	6	0.97	-0.34	0.51
Phenotypic	1	0.36	-0.44	0.53
	2	0.31	-0.13	0.29
	3	0.41	-0.30	0.03
	4	0.35	-0.44	0.01
	5	0.28	-0.11	0.32
	6	0.20	-0.35	0.11

***: See Table 1.**

Fig. 1: Genetic direct, phenotypic, genetic maternal and maternal permanent environmental correlations between birth weight, weaning weight and preweaning average daily gain (ADG) estimated from the most comprehensive model (model 6).

Conclusion. It is evident that maternal effects have to be accounted for when estimating genetic parameters for BW, WW and ADG. Overestimation of the h^2 estimates resulted from ignoring both maternal genetic and maternal environmental effects. Likewise, overestimation of m^2 resulted from exclusion of maternal permanent environmental effects. Foetal growth, measured by BW, is largely influenced by direct genetic effects, with an important foeto-maternal regulation as shown by a strong positive genetic correlation between direct and maternal effects. From a selection point of view, WW is heritable enough to allow an efficient selection for direct genetic effects at the level of the lamb. However, for this trait selection solely for direct genetic effects could result in deterioration of the maternal ability because of the negative correlation between maternal and direct genetic effects (r_{am} = -0.39). In view of the high positive value of r_{am} , the ADG would be considered a good selection criterion for carrying out a joint selection on lamb's growth capacity (direct effects) and ewe's suckling ability (maternal effects).

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تقدير المعالم الوراثية لصفات النمو المبكر فى حملان البرقى المصرية باستخدام نماذج الحيوان متعددة الصفات

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تم تقدير مكونات التباين لصفات الوزن عند الميلاد والوزن عند الفطام ومتوسط الزيادة اليومية فى الوزن من الميلاد حتى الفطام فى حملان البرقى المصرية بطريقة MTDFREML. تمت موائمة عدد ٦ نماذج حيوان مختلفة فى ضمها أو إهمالها للتأثيرات الوراثية الراجعة إلى الأم، التأثيرات البيئية الدائمة المتعلقة بالتأثير الأمي والتغاير بين التأثيرات الوراثية المباشرة والتأثيرات الأمية وذلك للوصول إلى النموذج الأكثر موائمة. وقد أوضحت هذه الدراسة أن التأثيرات الأمية الوراثية هى الأكثر أهمية تحت ظروف هذه الدراسة. وأتضح أن النموذج الأكثر موائمة هو النموذج الذى يأخذ فى الاعتبار التأثيرات الوراثية المباشرة، التأثيرات الراجعة إلى وراثة الأم والتأثيرات البيئية الدائمة وكذلك التغاير بين التأثيرات الوراثية المباشرة والتأثيرات الأمية (نموذج ٦). قيم المكافئ الوراثى المقدرة من التأثير الوراثى المباشر (h^2) باستخدام هذا النموذج كانت ٢٩.٠، ٠,٢٣، ٠,٢٢ لصفات BW ، WW ، ADG على التوالى بينما القيم المقدرة من المكونات الأمية (m^2) لنفس الصفات كانت ٠,٠٥، ٠,٣٩، ٠,٠٨. وأتضح أن الارتباط الوراثى بين التأثيرات الوراثية المباشرة والأمية (r_{am}) كان موجبا لصفتى BW وADG (٠,٧٨ و ٠,٣٧ على التوالى) وسالبا لصفة ww (-٠,٣٤). وقد بلغت قيم معاملات الارتباط الوراثية المقدرة من المكونات المباشرة ٠,٤٤ بين صفتى BW و WW و٠,٤٠- بين صفتي BW و ADG . بينما كانت القيم المقابلة لها والمحسوبة من المكونات الأمية ٠,٥٤ ، -٠,٣٤ ، على التوالى. وأن الارتباط الوراثى المقدر من مكونات التباين والتغاير المباشرة بين صفتى BW وww كان ٠,٣٥ يقابله ٠,٠٥ فى حالة التقدير المبنى على مكونات التباين والتغاير الأمية.

وقد خلصت الدراسة إلى أن التأثيرات الأمية يجب أن توضع فى الاعتبار عند تقدير المعالم الوراثية للوزن عند الميلاد وعند الفطام وكذلك لمعدل الزيادة اليومية خلال المرحلة من الميلاد حتى الفطام. وكانت القيمة المتحصل عليها لمعامل الارتباط الوراثى بين التأثيرات المباشرة (التى ترجع إلى وراثة الحمل) والتأثيرات الأمية (التى ترجع للأم) تشير إلى أن صفة ADG صفة جيدة للانتخاب لكونها ستضمن الانتخاب المشترك لكل من قدرة الحمل على النمو ومقدرة النعجة على تغذيته.