

EFFECT OF ADDITIVE AND MATERNAL GENETIC EFFECTS ON THE GENETIC PARAMETERS ESTIMATES OF BARKI SHEEP IN EGYPT

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ABSTRACT

Genetic parameters and (Co)variance component were estimated for birth weight (BW), weight at 120 day (W120d) weight at 180 day (W180d) and yearling weight (YW) for a flock of 2248 Barki sheep (1303 males and 945 females) progeny of 74 unrelated rams over a period of 23 years from 1979 to 2001. Analyses were carried out by REML, fitting an animal model and ignoring or including maternal genetic or permanent environmental effects. Four animal models were fitted for all traits studied, and the best model was chosen after testing improvement in log-likelihood values. The fixed effects in the model were year of birth, sex, type of birth and age of dam. Number of days between birth date and the date of obtaining measurement of each record was used as a covariate.

Direct heritabilities estimates were inflated substantially for BW and W120d traits when maternal effects were ignored and vice versa for W180d and YW. Based on the most appropriate fitted model, direct heritability of BW, W120d, W180d and YW were 0.24 ± 0.05 , 0.20 ± 0.03 , 0.19 ± 0.03 , and 0.18 ± 0.02 , respectively. Corresponding maternal heritabilities were 0.10 ± 0.02 , 0.07 ± 0.02 , 0.07 ± 0.02 and 0.07 ± 0.03 for above traits, respectively. Maternal genetic effects contributed 10 to 14% of the total phenotypic variance for BW, and their effect diminished further with other traits.

Estimates of the fraction of variance due to maternal permanent environmental effects were 0.07 ± 0.02 , 0.09 ± 0.03 , 0.06 ± 0.02 and 0.07 ± 0.02 , for BW, W120d, W180d and YW, respectively. These results indicate that selecting for improved maternal and for direct effects in Barki sheep would generate slow genetic progress in growth traits.

Direct and maternal genetic correlations (r_{a1a2} , r_{m1m2}) among the lamb weights varied between 0.67 and 1.00 and between 0.79 and 0.98, respectively. The results showed that the maternal influence on lamb weights decreased with advanced in age at measurement. More over, ignoring maternal effects from the model caused overestimation of direct heritability. Maternal effects are significant sources of variation for growth traits and ignoring these effects in the model would cause inaccurate genetic evaluation of lambs.

Keywords: Barki sheep, direct and maternal genetic effects, variance component, Animal model.

INTRODUCTION

Barki sheep which dominate the north western desert of Egypt with population of 470,000 heads (11% of the total Egyptian sheep population) are know to be well –adapted to the desert harsh conditions and scarce vegetation (El-Wakil, *et al.*, 2008). The basic information on their body conformation are available (Ragab and Ghoneim 1961). Major information regarding the genetics of their body weigh growth is still lacking.

Early growth traits are important factors influencing profitability in any meat producing enterprise the birth weight of an animal its early growth rate in particular until weaning are determined not only by its own genetic potential but also by the maternal environment. These maternal effects reflect mainly the dam's milk production and mothering ability, though effects of the uterine environment and extra chromosomal inheritance may also contribute. These maternal effects have three causes (Falconer 1989): those due to the dam's own genotype for milking and mothering ability (maternal additive effects); those consistent among all lambs produced by a dam but not of additive genetic origin (permanent environmental effects), and those specific to individual lambs (temporary environmental effects). The genotype of the dam therefore affects the phenotype of the young through a sample of half of her direct, additive genes for growth as well as through her genotype for maternal effects on growth. Bradford (1972) and Robison (1981) argued that traits recorded in early life are most affected by maternal ability. When some of these growth traits are included in the breeding goal, both the direct and maternal component should be taken into account to achieve optimum progress in a selection program Robison (1981) postulated that understanding of the relationship between direct and maternal effects would facilitate formulation of optimum breeding programs and improvement of selection efficiency.

The partitioning of additive direct, additive maternal, and permanent environmental maternal effects requires data on the performance of related (commonly half-sib) ewes in pedigreed matings across several lambing years the availability of restricted maximum likelihood (REML) algorithms for fitting animal models has simplified the estimation of (Co)variance components due to maternal effects (Meyer, 1997). However, meaningful partitioning of direct and maternal effects still requires an adequate underlying data structure the possible existence of genetic correlation between direct and maternal additive effect introduces additional difficulties in fitting maternal effect model (Hanrahan, 1976 and Willham, 1980). Numerous studies have reported a negative correlation between additive direct and additive maternal effects on growth traits of various sheep breeds (Maria *et al.*, 1993; Tosh and Kemp, 1994; Notter, 1998 and Ligda *et al.*, 2000). In many cases, these estimates have been too large (< -0.8) to be biologically reasonable. However, positive relationships have also been reported (Nasholm and Danell, 1996 and Yazdi *et al.*, 1997).

Estimates of (Co)variance components and genetic parameters for growth traits by REML procedures have not been reported for Barki sheep. Most reported heritabilities of growth traits for this breed are based on ratios of variance components estimated mainly by paternal half-sib method, without consideration of maternal effects. Therefore, the present study was conducted to estimate variance and covariance components due to direct genetic effects, maternal genetic effects and maternal permanent environmental effects for different pre-and post weaning growth traits in Barki sheep.

MATERIALS AND METHODS

Data

The data used in the present study were collected over 23 years started in 1979 and ended in 2001 on an experimental north western coast Barki sheep flock belonging to the desert Research center ministry of Agriculture and land Reclamation, Egypt. Records on 2248 lambs (1303 males and 945 females) descended from 1907 ewes and 74 rams were included in the analysis. Traits studied were birth weight (BW), weight at 120 day (W120d), weight at 180 day (W180d) and yearling weight (YW). The structure of data were presented in Table (1).

Management of flock

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 until weaning at 4 months of age. After weaning, lambs were fed a concentrate mixture (50% Cottonseed cake; 18% Wheat bran; 15% Yellow Maize; 11% Rice polish; 3% Molase; 2% Limestone and 1% common salt) amounting 0.5 to 1.0 kg/head/day according to physiological status ad-libitum amounts of Berseem hay (*Trifolium alexandrinum*). Fresh water was available for flock once a day.

Ewes grouped in 20-30 to mating with one ram. Lambs were weighted within 24 hours after birth and weekly thereafter until weaning. In addition, body weights were recorded just before morning feeding at bimonthly intervals starting from weaning until 16 months of age, then at yearly intervals thereafter until the animals was removed from the flock. Weight at 48 months of age was considered the mature weight as it was the last weight taken and was different significantly ($P < 0.05$) from the preceding weight.

Table (1): Phenotypic means, standard deviations (SD), coefficient variabilities (C.V%) and distributions of the data of Barki sheep.

Trait	BW	W120d	W180d	YW
Items				
Mean \pm SD, (kg)	3.23 \pm 0.33	18.84 \pm 3.11	22.71 \pm 4.01	31.91 \pm 5.59
C.V (%)	10.22	16.51	17.66	18.46
Number of records	2248	2024	1937	1084
number of sires	74	74	74	74
number of dam	1907	1817	1787	846
number of male	1303	1173	1103	640
number of female	945	851	834	444
Single	2022	1800	1713	943
Twins	226	224	224	105

Analysis

The Harvey program statistic (Harvey, 1990) and the unequal subclass analysis of variance was used to test the significance of the fixed effects of year of birth (23 levels), sex (male and female), type of birth (single and twin) and age of dam (2, 3, 4, 5 and 6 years of age or older). The analysis of

variance showed that fixed effects of year of birth, sex, and age of dam were significant for all four traits studied. Consequently these effects were included in all four models for those traits. The effect of birth type was only significant for birth weight and weight at 120 days, and were included in models for birth weight and weight at 120 days. Number of days between birth date and the date of measurement for each record was used as a covariate.

Variance and covariance components and genetic parameters were estimated using the MTDFREML program (Boldman *et al.*, 1995) by fitting four single trait animal models. Univariate analyses for each trait four different models to assess the importance of maternal affects. The models used are summarized in Table (2).

Table (2): Description of animal model fitted*

Model	(Co)variance components estimated
Model 1	$\sigma^2_a + \sigma^2_e$
Model 2	$\sigma^2_a + \sigma^2_c + \sigma^2_e$
Model 3	$\sigma^2_a + \sigma^2_m + \sigma^2_e$ [Cov (a,m) = A σ_{am}]
Model 4	$\sigma^2_a + \sigma^2_m + \sigma^2_c + \sigma^2_e$ [Cov (a,m) = A σ_{am}]

* σ^2_a = direct additive genetic variance, σ^2_m = maternal genetic variance, σ_{am} = direct maternal genetic covariance, σ^2_c = maternal permanent environmental variance and σ^2_e = residual (temporary environmental variance)

Total. heritability (h^2_t), and repeatability (r) are as defined by Willham (1972):

$$h^2_t = [(\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{dm}) / \sigma^2_p],$$

$$r = [(\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma_{dm} + \sigma^2_c) / \sigma^2_p]$$

Where σ^2_a = direct additive genetic variance, σ^2_m = maternal genetic variance, σ_{am} = direct maternal genetic covariance, σ^2_e = residual (temporary environmental variance), σ^2_c = maternal permanent environmental variance, σ^2_p = phenotypic variance, c^2 = fraction of phenotypic variance due to maternal permanent environmental effects and e^2 = fraction of phenotypic variance due to residual effects.

Estimation of (Co)variance components was carried out using the MTDFREML program. A simplex algorithm is used to search for variance components to minimize the function, $-2\log$ likelihood (L). Convergence was assumed when the variance of the function values ($-2\log L$) of the simplex was less than 10^{-8} . For all models, a restart was performed after a first convergence to verify that convergence was not at a local minimum a log likelihood ratio test was used to choose the most suitable random effects model for each trait the reduction in $-2\log l$ when a random effect was added to the model was calculated if this reduction was greater than the value of the chi-square distribution with one degree of freedom ($P < 0.05$), the additional random effect fitted was considered significant. When log likelihoods did not differ significantly ($P < 0.05$), the model that had the fewer number of parameters was selected as the most appropriate. Several two-trait analyses were carried out between the four traits studied to estimate the correlations. The full model (model 4) was used for all traits.

RESULTS AND DISCUSSION

Means, standard deviations and coefficients of variation for investigated traits are presented in Table (1). The mean values for the different traits are smaller than those of other breeds (Tosh and Kemp, 1994, Yazdi *et al.*, 1997, Ekiz *et al.*, 2004 and Behzadi *et al.*, 2007), probably due to the more extensive conditions under which the herd was maintained. Barki sheep in Egypt are adapted with the desert conditions (very low rainfall), which has a great influence on the amount of available forage. The coefficient of variation for BW is much less than that for other traits, which is an indication of the smaller effect of environment on BW than on the other traits.

Estimates of genetic parameters in single-trait analyses are presented in Table (3). Model 1, which ignored permanent environmental and maternal genetic effects, resulted in larger estimates for σ^2_a and h^2_a compared with other models. With Models 2 and 3, the addition of the maternal environmental effect (Model 2) and maternal genetic effect (Model 3) increased the log likelihood values significantly ($P < 0.05$, Table 4) and reduced the estimates of both σ^2_a and h^2_a compared with Model 1. Meyer (1992) showed that models not accounting for maternal genetic effects could result in substantially higher estimates of additive direct genetic variance and therefore, higher estimates of h^2_a . If maternal effects are present but not considered, the estimate of additive genetic variance will include at least part of the maternal variance. Therefore, estimates of direct heritability will decrease when maternal effects are included. Model 3, which included an additive maternal effect, yielded smaller estimates of σ^2_a and h^2_a than did Models 1 and 2. The additive maternal genetic effect was determined to be more important than the permanent maternal environmental influence of the dam for these traits of Barki sheep.

Heritability estimates of h^2_a and h^2_m reported by several authors were 0.04 - 0.39 and 0.09 - 0.31 for birth weight and 0.06-0.39 and 0.01-0.38 for weaning weight, depending on the model used and the breed of lamb (Snyman *et al.*, 1995; Nasholm and Danell, 1996; Yazdi *et al.*, 1997; Ekiz *et al.*, 2004 and Behzadi *et al.*, 2007).

Direct heritabilities for body weights showed a tendency to increase with age measured, because estimates of direct additive genetic variance component increased faster than the environmental variance components. Tendency for estimates of direct heritability to increase with age measured has also been reported in several studies (Mavrogenis *et al.*, 1980; Yazdi *et al.*, 1997 and Behzadi *et al.*, 2007). For all traits, estimates of maternal heritability, were as large as or larger than the estimates of direct heritability. This suggests that maternal effects need to be considered in selecting for growth in Kermani sheep. Estimates of maternal heritability tended to decline from birth to yearling weight. Maternal genetic effects expressed during gestation and lactation had been expected to have a diminishing influence on weight as lambs became older. Maternal heritability decreased with age, which confirms the proposal by Robison (1981) that maternal effects in mammals are substantial in young animals but diminish with age.

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Maternal heritability estimates of birth to yearling weights in this study were smaller than values reported by Maria *et al.* (1993); Snyman *et al.* (1995); Yazdi *et al.* (1997); Saatci *et al.* (1999); Ligda *et al.* (2000); Naser *et al.* (2001), Ekiz *et al.* (2004), Mandal *et al.* (2006) and Behzadi *et al.* (2007) for several sheep breeds.

For animals raised on pasture without any supplementary feeding the length of time from birth to yearling is probably not enough that compensatory gain could buffer completely the maternal effect existing at birth. Robison (1981) suggested that even if maternal effects tend to diminish with age, some adult traits will nevertheless contain this source of variation.

Maternal heritabilities for pre-weaning weights be-creased with age, which confirms findings of Tosh and Kemp (1994), Snyman *et al.* (1995), Nasholm and Danell (1996), Yazdi *et al.* (1997), and El Fadili *et al.* (2000) who also observed that maternal effects were substantial in young animals but diminished with age.

In general, the trend of increasing direct heritabilities and decreasing maternal heritabilities with age in Barki sheep are similar to have average trends reported for other breeds. The direct and maternal heritability estimates for lamb body weight found in the present study are within the range of those presented in literature (Notter and Hough, 1997; Matika *et al.*, 2003 and Behzadi *et al.*, 2007). The relatively low heritability estimates for growth traits in this study can be explained by the low nutritional level and poor quality of the pasture at the sheep breeding station, creating large environmental variations.

Table (4): Log-likelihood values* obtained for each trait under the four different models with the best model in bold

Trait	<i>Model 1</i>	<i>Model 2</i>	<i>Model 3</i>	<i>Model 4</i>
BW	-117.20**	-100.25**	-111.13**	-12.82
W120d	1310.58**	1306.60**	1310.85**	735.41
W180d	1443.29**	1346.31	1449.41**	1477.41**
YW	2016.01**	1801.82	2011.58**	2014.13**

*As deviations from the model with the highest value

Table (5): Estimated parameters and their standard errors from the best model for each trait*

Trait	Model	σ^2_a	σ^2_m	σ^2_c	σ^2_e	σ^2_p	h^2_a	h^2_m	c^2
BW	4	0.071	0.031	0.022	0.182	0.301	0.24 (0.05)	0.10 (0.02)	0.07 (0.02)
W120d	4	2.23	0.80	0.95	6.94	10.93	0.20 (0.04)	0.07 (0.02)	0.09 (0.03)
W180d	2	4.11	-	1.30	16.57	21.98	0.19 (0.03)	-	0.06 (0.02)
YW	2	6.50	-	2.45	27.55	36.50	0.18 (0.02)	-	0.07 (0.02)

* Figures in parentheses are standard errors of the estimate. See Table (3) for abbreviations.

Table (6): Estimates of correlations between investigated traits from two-trait analysis

Trait 1	Trait 2	r_{a1a2}	r_{m1m2}	r_{e1e2}	r_{p1p2}
BW	W120d	0.83	0.94	0.39	0.54
BW	W180d	0.89	0.79	0.34	0.43
BW	YW	0.67	0.84	0.13	0.0.38
W120d	W180	1.00	0.98	0.51	0.76
W120d	YW	0.99	0.88	0.69	0.73
W180d	YW	0.99	0.92	0.71	0.82

The correlation between the direct and maternal genetic effects (r_{am}) (Table 3) were positive and smaller for all traits, except for birth and yearling weights. The genetic correlation ranged from -0.11 to 0.17 for the various age stages. Negative estimates of r_{am} were reported by Maria *et al.*, (1993); Tosh and Kemp (1994); Jara *et al.*, (1998); Ligda *et al.*, (2000), and Ekiz *et al.*, (2004) for several sheep breeds. However, Nasholm and Danell (1996), Yazdi *et al.*, (1997), and Behzadi *et al.*, (2007) reported a positive correlation for Swedish Finewool, Baluchi lambs and Kermani sheep respectively. Maria *et al.*, (1993) found extreme direct-maternal genetic correlations (≥ 0.97) for lamb weight in Romanovs. Result for birth weight suggested that the negative correlation could be due to a negative direct influence of the dams on the maternal ability of their female offspring through overfeeding. Negative correlation (r_{am}) for yearling weight may be the result of an adaptation of the animals to the dry and hot environment where food resources are scarce. The positive direct-maternal genetic correlation suggest that selection for increased body weight of the lamb will also improve the maternal ability of the ewe. In spite of this facts, we have to be cautious with the estimates obtained in this study, and probably it would be necessary to check them again with larger data sets.

The large direct genetic correlation (0.83) between birth and W120d (Table 6) indicates that selection on W120d may lead to an increase in birth weight. The direct genetic correlations between weight at 120 days and YW (Table 6) were high (0.99), indicating that selection for increased W120d in Barki sheep will also result in genetic change for W180d, and YW. Therefore, it is reasonable to suggest that the traits to be included in the sheep recording scheme could be confined to the traits expressed early in life of the lambs, such as their birth weight and W120d in which both the direct and maternal effects are involved. In Iran, Behzadi *et al.*, (2007) came to the same conclusion on Kermani sheep. The estimate of the additive direct correlation between birth and yearling weight was (0.67) less than that between W120d and yearling weight (0.99), indicating that selection for yearling weight would quickly result in increased birth weight.

The positive maternal genetic correlations (0.79 to 0.94) of birth weight with later weights indicate that maternal influences on the later weights are partly originating from the prenatal period. The results with higher maternal heritability for birth weight than for all later weights also support this conclusion. Genetic correlations among growth traits of Barki lambs were, all

positive, indicating that selection for any of the traits should result in positive genetic change in the other traits.

Conclusions

The estimates of genetic parameters reported for the Barki lambs here are in general agreement with those reported in the literature on several breeds. This study showed that the addition of maternal effects to the model resulted in a decrease in the estimates of direct heritability for all weight traits of Barki sheep. Maternal effects remained important at first year of age in this breed of sheep. In conclusion, maternal effects on weights in different ages of Barki sheep were significant and should be taken into consideration in any selection program on this breed. The genetic parameters estimated for growth traits indicate that there is genetic variation among the animals that can be utilized for genetic change in these traits by selection in Barki sheep raised under their specific harsh desert conditions.

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Table (3): Estimates of (co)variance components and genetic parameters for birth weight (BW), weight at 120 days (W120d), weight at 180 days (W180d) and yearling weight (YW) of Barki sheep.

Traits	Models	σ^2_a	σ^2_m	σ_{am}	σ^2_c	σ^2_e	σ^2_p	c_{am}	r_{am}	h^2_a	h^2_m	h^2_t	r	c^2	e^2
BW	Model 1	0.081	-	-	-	0.229	0.310	-	-	0.26	-	0.26	-	-	0.74
	Model 2	0.074	-	-	0.021	0.205	0.300	-	-	0.25	-	0.25	0.32	0.07	0.68
	Model 3	0.071	0.045	-0.002	-	0.206	0.320	-0.006	-0.04	0.22	0.14	0.28	0.28	-	0.64
	Model 4	0.071	0.031	-0.005	0.022	0.182	0.301	-0.02	-0.11	0.24	0.10	0.31	0.38	0.07	0.60
W120d	Model 1	2.97	-	-	-	8.04	11.01	-	-	0.27	-	0.27	-	-	0.73
	Model 2	2.40	-	-	0.47	7.96	10.83	-	-	0.22	-	0.22	0.27	0.04	0.74
	Model 3	2.03	0.98	0.10	-	7.56	10.47	-0.01	0.07	0.19	0.09	0.23	0.23	-	0.72
	Model 4	2.23	0.80	0.10	0.95	6.84	10.93	-0.01	0.08	0.20	0.07	0.25	0.34	0.09	0.63
W180d	Model 1	6.56	-	-	-	15.45	22.01	-	-	0.30	-	0.30	-	-	0.70
	Model 2	4.11	-	-	1.30	16.57	21.98	-	-	0.19	-	0.19	0.25	0.06	0.75
	Model 3	5.56	1.62	0.51	-	16.05	22.72	-0.02	0.17	0.24	0.07	0.25	0.25	-	0.70
	Model 4	5.31	1.15	0.10	1.32	15.23	22.91	-0.004	0.04	0.23	0.05	0.25	0.31	0.06	0.66
YW	Model 1	11.91	-	-	-	24.49	36.40	-	-	0.33	-	0.33	-	-	0.67
	Model 2	6.50	-	-	2.45	27.55	36.50	-	-	0.18	-	0.18	0.25	0.07	0.75
	Model 3	9.21	2.60	-0.17	-	25.36	37.00	-0.005	-0.04	0.25	0.07	0.28	0.28	-	0.68
	Model 4	9.01	2.01	-0.24	2.40	23.96	37.14	-0.006	-0.06	0.24	0.05	0.26	0.33	0.06	0.65

σ^2_a = direct additive genetic variance, σ^2_m = maternal genetic variance, σ_{am} = direct maternal genetic covariance, σ^2_e = residual (temporary environmental variance), σ^2_{pe} = maternal permanent environmental variance, σ^2_p = phenotypic variance, r_{am} = direct-maternal genetic correlation, h^2_a = direct heritability and h^2_m = maternal heritability, h^2_t = total heritability $[(\sigma^2_d + 0.5\sigma^2_m + 1.5\sigma_{dm}) / \sigma^2_p]$, r = repeatability $[(\sigma^2_d + 0.5\sigma^2_m + 1.5\sigma_{dm} + \sigma^2_c) / \sigma^2_p]$, c^2 = fraction of phenotypic variance due to maternal permanent environmental effects and e^2 = fraction of phenotypic variance due to residual effects.