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ESTIMATES OF VARIANCE COMPONENTS AND HERITABILITIES OF PRE-WEANING GROWTH TRAITS OF BARKI AND RAHMANI LAMBS

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SUMMARY

Data representing 594 Barki and 582 Rahmani lambs raised at Alexandria University Experimental Station between 1991-2011 were utilized in this study to estimate variance components and heritability of birth weight (BW), weaning weight (WW) and average daily gain (ADG) from birth to weaning of lambs. Also, the effects of season and year of lambing, sex of lamb, type of lambing and parity on the previous traits were studied.

The analysis indicated that fixed effects on all studied traits were generally significant (P<0.01or P<0.05) except for effects of season and year of lambing on BW of Barki lambs and effects of parity on ADG of both breeds. Variance components and heritability for the studied traits were estimated using the Wombat programme fitting four univariate animal models. Estimates of the direct heritability (h^2_a) and maternal heritability (h^2_m) were ranged from 0.161-0.353 and 0.145-0.147 , from 0.100-0.171 and 0.124-0.124 and from 0.014-0.172 and 0.119-0.121 for BW, WW and ADG of Barki lambs, respectively, the corresponding values for Rahmani lambs ranged from 0.204-0.519 and 0.094-0.215, from 0.139-0.168 and 0-0.021 and from 0.125-0.144 and0-0.001, respectively. Ignoring maternal effects from the model resulted in an over estimation of direct heritability of all traits of both breeds. Estimates of the total heritability (h^2_t) were moderate to high for BW and low for WW and ADG of both breeds. Estimates of the total maternal effect (t_m) were considerable for all studied traits of both breeds. The results in general showed that maternal effects were significant source of variation for early growth traits of Barki and Rahmani lambs. Therefore, these effects should be considered when carrying out genetic evaluations of early growth traits of Barki and Rahmani lambs in this flock.

Keywords: Variance components, heritability, maternal effect, pre-weaning growth, Barki, Rahmani, lambs

INTRODUCTION

The total number of sheep population in Egypt was 5450000 heads in 2013, and they contribute about 6 % of the national total red meat (FAOSTAT, 2015). Barki and Rahmani sheep are considered as two of the three major sheep breeds in the country.

Early growth traits of lamb are important factors influencing profitability in any sheep producing enterprise (Mokhatri *et al*., 2012, Javed *et al*., 2013, Mohammadi *et al*., 2013 and Jannoune *et al*., 2015). Growth traits of lambs are determined not only by lamb's genetic potential for growth but also by maternal genetic and permanent and temporary environmental effects (Mandal *et al*., 2006, Behzadi *et al*., 2007, Rashidi*et al*., 2008, Baneh *et al*., 2010, Bayeriya *et al*., 2011, and Javed *et al*., 2013). Studies of various sheep breeds have shown that both direct and maternal genetic influences are of importance for lamb growth (Rashidi *et al*., 2008,Baneh *et al*., 2010, Gowane *et al*., 2010, Mokhatri *et al*., 2012, Javed *et al*., 2013 and Akthar *et al*., 2014). Knowledge of variance components and heritability is necessary for the determination of an optimal breeding strategy seeking the genetic improvement of the lambs' growth traits (Baneh *et al*., 2010, Tosh and Kemp, 2011, Jafari *et al*., 2012, Javed *et al*., 2013, Mohammadi *et al*., 2013, Roshanfek *et al*., 2015 and Lalit *et al*., 2016).

This investigation was carried out to estimate variance components and heritabilities of birth weight, weaning weight and pre-weaning average daily gain of Barki and Rahmani lambs in Egypt.

MATERIALS AND METHODS

Data:

Data for this study were from the records of the sheep flock of the Experimental Station, Faculty of Agriculture, Alexandria University. The records covered the period from 1991 to 2011 and were relevant to 594 and 582 Barki and Rahmani lambs presenting17 and 16 rams, 181 and 190 ewes, respectively.

Animals were housed in semi closed pens, fed on berseem (*Trifolium alexandrinum*) during winter and spring and on stubble and berseem hay and/ or fodder sorghum (*Sorghum bicolor*) during summer and autumn. Supplementary concentrate ration of about 0.25 kg / head were offered daily along the year. The structures of data are presented in Table (1).

The flock was managed for all year round lambing. Females were first mated at about 18 months of age. Rams and ewes were selected as yearlings on the basis of visual appraisal for type and size rather than on a pre-set intensive selection program. Once the ewe entered the breeding flock, there is no chance for culling until the end of its productive life.

Table 1. Means, standard deviations (SD), coefficient of variation (CV%) and distributions of the data for birth weight (BW), weaning weights (WW) and average daily gain (ADG) of Barki and Rahmani lambs

Items	Barki			Rahmani		
	BW	WW	ADG, gm.	BW	WW	ADG,gm.
Mean , (kg)	3.70	20.90	143.09	3.52	20.71	142.62
SD, (kg)	0.60	4.64	37.00	0.59	4.27	33.82
C.V (%)	16.25	22.18	25.86	16.74	20.63	23.71
No. of records	594	532	532	582	500	500
No. of sires	17	17	17	16	16	16
No. of dams	181	172	172	190	174	174
No. of ram lambs	312	282	282	289	246	246
No. of ewe lambs	282	250	250	293	254	254
No, single lambs	534	476	476	390	336	336
No, twin lambs	60	56	56	192	164	164

Statistical procedures:

Least squares of GLM procedure (SAS 2008) were utilize to test the significance of the fixed effects of season of lambing (4 seasons), year of lambing (7 periods), sex (male and female), type of lambing (single and twin) and parity (8 parities) on birth weight (BW), weaning weight (WW) and average daily gain (ADG) from birth to weaning of lambs. Lambing was classified by season into autumn lambing between September and November, winter lambing between December and February, spring lambing between March and May and summer lambing between June and August.Each breed data were analyzed separately. The statistical model fitted was:

$Y_{ijklmn} = \mu + A_i + {}_{Bj} + C_k + D_l + P_m + e_{ijklmn}$ where,

Y_{ijklmn}: either BW, WW or ADG;μ: an underlying constant specific to each trait; A_i: the fixed effect of i^{th} season of lambing; B_j: the fixed effect of j^{th}year of lambing; C_k: the fixed effect of k^{th} sex; D_l: the fixed effect of l^{th}type of lambing; P_m: the fixed effect of m^{th}parity and e_{ijklmn}: random residual assumed to be independent normally distributed with mean zero and variance σ_e^2 .

Univariate animal models were fitted to estimate (co)variance components for each trait using Wombat program (Meyer, 2006). The following four models were used:

$y = Xb + Z_a a + e,$ (1)

$y = Xb + Z_a a + Z_c c + e,$ (2)

$y = Xb + Z_a a + Z_m m + e$ (3)

$y = Xb + Z_a a + Z_m m + Z_c c + e$ (4)

where y is a n × 1 vector of observations for each trait; b, a, m, c and e are vectors of fixed effects (birth year, season of birth, parity of dam, sex and birth status of lambs), direct additive genetic effects, maternal additive genetic effects, permanent environmental effects of dam and the residual effects, respectively; X, Z_a, Z_m, Z_c are the incidence matrices of fixed effects, direct additive genetic effects, maternal genetic effects and permanent environmental effect of the dam; A is the numerator relationship matrix between animals; and σam is the covariance between additive direct and maternal genetic effects. The (co) variance structure for the model was:

$V(a) = A\sigma_a^2$,

$V(m) = A\sigma_m^2$,

$V(c) = Ip\sigma_c^2$,

$V(e) = IR\sigma_c^2$

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

where I_P and I_R are identity matrices with orders equal to the number of dams and the number of lambs, respectively and σ_a^2, σ_m^2, σ_c^2, and σ_e^2 are direct additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, and residual variance, respectively. Estimates of heritability (h^2_a), maternal heritability (h^2_m) and permanent maternal environmental effects (c^2) were calculated as ratios of estimates of σ^2_a, σ^2_m, and σ^2_c, respectively, to the phenotypic variance (σ^2_p). The direct-maternal correlation (r_{am}) was computed as the ratio of the estimates of direct-maternal covariance (σ_{am}) to the product of the square roots of estimates of σ^2_a and σ^2_m. The total heritability for each trait was estimated (Willham, 1972) as $h^2_t = h^2_a + 0.5\ h^2_m + 1.5\ mr_{am}h$, which predicts the expected response to phenotypic selection. The total maternal effect, $t_m = 1/4h_a^2 + h_m^2 + c^2 mr_{am}h$ was calculated to estimate repeatability of ewe performance (Gowane *et al*., 2010).

RESULTS AND DISCUSSION

The means, standard deviation (SD) and coefficient of variation (CV %) of the studied traits are presented in Table (1). The overall means of BW, WW and ADG of Barki lambs were 3.70 kg, 20.90 kg and 143.09 g, respectively, the corresponding values for Rahmani lambs were 3.52 kg, 20.71 kg and 142.62g, respectively. Means were higher than those of BW and WW of Barki lambs reported by Gad and El-Wakil (2013), being 3.56 kg 19.29 kg and 131.02 g, respectively and those of Rahmani lambs, being 3.42 kg, 19.49 kg and 135.00 g as reported by Abbas *et al*. (2010) on other experimental flocks of sheep in Egypt.

Fixed effects:

The results of analysis of variance for fixed effects on all studied traits are illustrated in Table 2. Fixed effects on all studied traits were generally significant (P<0.01or P<0.05) except for effects of season and year of lambing on BW of Barki lambs and effects of parity on ADG of both breeds. Significant effects of fixed effects on pre-weaning growth traits of lambs of different sheep breeds have been well documented in the literature (Matika *et al.* 2003, Abegaz *et al.* 2005, Rashidi *et al.* 2008,Abbas *et al.*, 2010, Baneh *et al.*, 2010, Jafaroghli *et al.*, 2011; Sofla *et al.*, 2011, Hammoud and Salem, 2012 and Tohidi *et al.*, 2016).

Table 2. Effects of season and year of lambing, sex of lamb, type of lambing and parity on birth weight (BW), weaning weight (WW) and pre-weaning average daily gain (ADG) of Barki and Rahmani lambs

Source of variation	Barki				Rahmani			
	df*	BW	WW	ADG	df*	BW	WW	ADG
Season of lambing	3	NS	**	**	3	*	**	**
Year of lambing	6	NS	**	**	6	**	**	**
Sex of lamb	1	**	**	**	1	**	**	**
Type of lambing	1	**	**	**	1	**	**	**
Parity	7	**	**	NS	7	**	*	NS
Error		(575)	(513)	(513)		(563)	(481)	(481)

NS: Not significant (P>0.05); * : Significant (P< 0.05); ** : Highly significant
Figures within parentheses are the degree of freedom (df) for error. df of BW of both Barki and Rahmani breeds were the same for WW and ADG except for error.

Variance components and heritabilities:

Estimates of variance components (σ^2_a, σ^2_m, σ^2_c, σ^2_e and σ^2_p), heritabilities (h^2_a, h^2_m and h^2_t), fraction of variance due to maternal permanent environmental effects (c^2), total maternal effect (t_m) and log-likelihood (Log L) for BW, WW and ADG of Barki and Rahmani lambs are presented in Table (3).

Model 1, which ignored the permanent environmental and additive maternal effects, had the lowest Log Likelihood values (Log L) for all studied traits of both Barki and Rahamani lambs. Model 3 that included direct and maternal genetic effects was the most appropriate model for BW, WW and ADG of Barki lamb. Although, the Log L of model 3 and 4 were equal for the two traits, model 3 was considered to be better than model 4, because the permanent maternal environmental effects in model 4 were equal to zero. Hence the maternal additive effect was determined to be more important than the maternal permanent environmental effect for WW and ADG of Barki lambs. For Rahmani, model 4 that included direct and maternal genetic and permanent maternal environmental effects was the most appropriate model for BW, and model 2 that included direct genetic and permanent maternal environmental effects was the most appropriate model for WW and ADG. However, the log-likelihood of model 2 and 4 were equal for the two traits. Model 2 was considered to be better than model 4 because the maternal effects in model 4 were equal to zero. Hence the permanent environmental effect was determined to be more important than maternal additive effect for WW and ADG of Rahmani lambs.

Model 1, which ignored maternal effects, had the highest estimates of σ^2_a and h^2_a for BW, WW and ADG of both breeds. The addition of the maternal effects in the models reduced the values of both σ^2a and h^2_a compared to model 1for all studied traits in both breeds. Duguma *et al.* (2002) pointed out that if maternal effects constitute a sizable part of genetic variation ignoring these effects results in upward biased estimates of h2a.

The present estimates of h^2_a and h^2_m ranged between 0.161-0.353 and 0.145-0.147, from 0.100-0.171 and 0.124-0.124 and from 0.014-0.172 and 0.119-0.121 for BW, WW and ADG of Barki lambs, respectively, the corresponding values for Rahmani lambs ranged between 0.204-0.519 and 0.094-0.215, from 0.139-0.168 and 0-0.021 and from 0.125-0.144 and0-0.001, respectively. The relatively low to moderate h^2_a estimates obtained for growth traits in this study except in model 1 for BW of both breeds indicated that direct genetic effects constitute a little portion of the phenotypic variances for the early growth traits of the two breeds. Hence, slow genetic progress would be expected through direct selection for these traits. This can be attributed to the low nutritional level and the differences in managing practices at the sheep breeding station, creating large environmental variations. The estimates of h^2_a and h2min the literature were varied from 0.03 to 0.53 and from 0.02 to 0.45 for BW and from 0.04 to 0.39 and from 0.01 to 0.038 for WW and from 0.010 to 0.20 and from 0.07 to 0.16 for ADG, respectively depending on the model used and the breed of lamb (Matika *et al.*, 2003, Ekiz *et al.*, 2004, Mandal *et al.*, 2006, Behzadi *et al.*, 2007, Mohammadi and Edriss, 2007, Rashidi *et al.*, 2008, Baneh *et al.*, 2010, Gowane *et al.*, 2010, Mohammedi *et al.*, 2010, Jafaroghli *et al.*, 2011, Mohammedi *et al.*, 2011, Shokrollahi and Baneh, 2012 and Mokhtari *et al.*, 2012). Hence, the present estimates of h^2_a and h^2_m for all studied traits are generally in agreement with those reported in the literature on several breeds of sheep.

The model in bold and gray shadow represents the most appropriate model. Values in parentheses are standard error estimates.

Estimates of h^2_a and h^2_m for body weights showed a tendency to decrease with advance in ages. This tendency has also been reported in several studies (Behzadi *et al*., 2007 and El-Awady, 2011).The present estimates of h^2_a and h^2_m for WW and ADG were relatively similar for both breeds. Estimates of h2mfor BW were relatively higher than for WW for Barki lambs and were very lower for Rahmani lambs. Hence, maternal additive effects constitute an important part of variation for BW of both breeds. This probably reflected differences in the uterine capacity for growth of the fetus (Gowane *et al*., 2010). The estimates of h^2_m for WW and ADG were larger than h^2_a in Barki lambs, but were very lower in Rahmani lambs. Ozcan *et al*. (2005) in Turkish Merino sheep reported low estimates of h^2_m for WW and ADG of lambs. Several studies showed that including of the maternal effects in the models resulted in more accurate estimation of (co) variance and genetic parameters of growth traits of lambs (Zamani and Mohammadi, 2008; Moktari *et al*., 2012and Mohammadi *et al*., 2013).

Estimates of c^2 for Barki lambs were relatively important for all studied traits for model 2 only, but were negligible for model 4. However, estimates of c^2 for Rahmani lambs were relatively important for BW in Models 2 and 4, but were different from zero for WW and ADG. Differences in estimates of $c^2$for BW of lambs were attributed to uterine capacity and the effect of multiple births. Relatively low c^2 for WW and ADG are most likely reflected in differences in rearing abilities of ewes that might be influenced by environmental fluctuations between (parities) years of her births (Duguma *et al*., 2002).

Estimates of the fraction of variance due to maternal permanent environmental effects (c^2) were ranged from 0.002-0.74, 0-0.084 and 0-0.076 for BW, WW and ADG of Barki lambs, respectively. The corresponding values for Rahmani lambs ranged between 0.089-0.136, 0.054-0.054 and 0.042-0.042, respectively. These results are in agreement with those reported by Duguma *et al*. (2002) and Mohammadi and Edriss (2007). They attributed this value to the influence of the uterus and the effect of multiple births. Relatively large c^2estimate for BW most likely reflected differences in rearing abilities of dams that might be influenced by environmental fluctuations between years or her birth status. The present estimates of c^2 for BW, WW and ADG were generally in agreement with those of Abbasi *et al*. (2012) and Moktari *et al.* (2012) in Iranian Blauchi and Arman sheep, respectively.

Estimates of the total heritability (h^2_t) were varied between 0.234-0.353, 0.073-0.171 and 0.072-0.172 for BW, WW and ADG of Bark lambs, respectively, the corresponding values for Rahmani lambs were varied between 0.311-0.519, 0.139-0.168 and 0.125-0.144, respectively. When maternal effects are important in the expression of a trait h^2_t is of crucial importance in terms breeding and is useful in selection response based on phenotypic values (Abegaz *et al*., 2005). The h^2_t estimates are model sensitive (Gowane *et al*., 2010). The obtained estimates of h^2_t for BW were in general in agreement with estimated values reported by Gowane *et al*. (2010) in Malpura sheep and Moktari *et al*. (2012) in Arman sheep in Iran.

Estimates of the total maternal effect (t_m) were ranged between 0.088-0.187, 0.042-0.127 and 0.043-0.123 for BW, WW and ADG of Barki lambs, respectively. The corresponding values for Rahmani lambs ranged between 0.129-0.252, 0.042-0.088 and 0.036-0.073, respectively. These results indicated that maternal effects were a significant source of variation for early growth traits of Barki and Rahmani lambs. The present estimates of tm were generally in agreement with those reported by Gowane *et al*. (2010), Moktari *et al*. (2012) in Malpura and Arman sheep in Iran.

CONCLUSIONS

The low to moderate genetic variations in WW and ADG of Barki and Rahmani lambs confirmed that selection for improving any of these traits would result in slow genetic progress. The results showed that including of the maternal effects in the models caused more accurate estimation of variance component and genetic parameters for growth traits of both breeds. Therefore, these effects should be considered when carrying out genetic evaluations of early growth traits of Barki and Rahmani lambs in this flock.

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تقديرات مكونات التباين والمكافيء الوراثي لصفات النمو قبل الفطام للحملان البرقى والرحمانى

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أجرى هذا البحث على بيانات السجلات الخاصة بقطيع الأغنام البرقي والرحماني بمحطة بحوث كلية الزراعة جامعة الإسكندرية. وقد استخدمت البيانات الخاصة بعدد ٥٩٤ حمل برقى و٥٨٢ حمل رحماني وهى مولودة خلال الفترة من ١٩٩١-٢٠١١. وذلك بهدف تقدير مكونات التباين، المكافيئ الوراثي لصفات وزن الميلاد، وزن الفطام ومعدل النمو اليومي من الميلاد حتي الفطام للحملان في كل من السلالاتين.وأيضاً دراسة تأثير كل من موسم الولادة، سنة الولادة، الجنس، نوع الولادة وترتيب موسم الولادة علي الصفات موضع الدراسة.

تم تحليل البيانات إحصائياً بطريقة الحد الأدنى للمربعات باستخدام برنامج الـ SAS. وأوضحت النتائج أن تأثيرات موسم الولادة، سنة الولادة، الجنس، نوع الولادة وترتيب موسم الولادة كانت معنوية (P< 0.05 أو P<0.01) علي الصفات موضع الدراسة فيما عدا أن موسم الولادة ليس له تأثيراً معنوياً على وزن الميلاد للحملان البرقي وترتيب موسم الولادة لم يكن له تأثيراً معنوياً علي معدل النمو اليومي في كل من السلالاتين.

تم تحليل البيانات المتاحة بواسطة نموذج الحيوان Univariate Animal Model بإستخدام برنامج Wombat.وذلك باستخدام أربعة نماذج تختلف فيما بينها في احتوائها أو عدم احتوائها علي التأثير الوراثي الأمي والتاثير الأمي البيئي المستديم كما تضمنت هذه النماذج تأثيرات العوامل الثابتة موضع الدراسة. تراوحت تقديرات المكافيء الوراثي االمباشر والأمي بين ٠.١٦١-٠.٣٥٣ و ٠.١٤٥-٠.١٤٧، ٠.١٠٠-٠.١٧١ و ٠.١٢٤-٠.١٢٤ وبين ٠.٠١٤-٠.١٧٢ و ٠.١١٩-٠.١٢١ لوزن الميلاد، وزن اللفطام ومعدل النمو اليومي علي الترتيب للحملان البرقي وتراوحت بين ٠.٢٠٤-٠.٥١٩ و ٠.٠٩٤-٠.٢١٥ و ٠-٠.٠٢١ و٠.١٣٩-٠.١٦٨ وبين ٠.١٢٥-٠.١٤٤ و ٠-٠.٠٠١ لنفس الصفات بالترتيب للحملان الرحماني.

إن عدم وجود التاثيرات الأمية في نموذج التحليل الاحصائي أدي إلي زيادة تقديرات المكافيء الوراثي المباشر لكل الصفات في السلالاتين. وكانت تقديرات المكافيء الوراثي الكلي متوسطة إلي مرتفعة بالنسية لوزن الميلاد ومنخفضة بالنسبة لصفتي وزن اللفطام ومعدل النمو اليومي في السلالاتين. وأوضحت النتائج أن التأثير الأمي الكلي هام بالنسبة للصفات موضع الدراسة في السلالاتين.

أظهرت النتائج بصفة عامة أن التأثيرات الأمية تعتبر من مصادر التباين الهامة بالنسبة لصفات النمو قبل الفطام في السلالاتين. لذا بنبغي وجود هذه التأثيرات في نموذج التحليل الاحصائي عند إجراء التقييم الوراثي لصفات النمو قبل القطام للحملان البرقي والرحماني في القطيع موضع الدراسة.

Table 3 Estimates of (co)variance components and genetic parameters for birth weight (BW), weaning weights (WW), and average daily gain (ADG) of Barki (B) and Rahmani (R) lambs

Breed	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	h^2_t	t_m	Log-l
		M1	0.149	-	-	0.274	0.424	0.353 (0.099)	-	-	0.353	0.088	-51.20
		M2	0.120	-	0.031	0.268	0.420	0.282 (0.110)	-	0.074 (0.046)	0.282	0.144	-49.70
	BW	M3	0.070	0.061	-	0.287	0.415	0.161 (0.112)	0.147 (0.063)	-	0.234	0.187	-47.90
		M4	0.070	0.060	0.001	0.287	0.415	0.162 (0.114)	0.145 (0.089)	0.002 (0.059)	0.234	0.187	-47.94
		M1	9.519	-	-	46.181	55.701	0.171(0.091)	-	-	0.171	0.042	-1452.2
B		M2	5.254	-	4.624	44.982	54.861	0.100 (0.084)	-	0.084 (0.046)	0.100	0.109	-1450.2
	WW	M3	0.630	6.790	-	47.277	54.690	0.012 (0.060)	0.124 (0.051)	-	0.074	0.127	-1448.1
		M4	0.617	6.800	0.001	47.283	54.700	0.011 (0.060)	0.124 (0.073)	0.0 (0.060)	0.073	0.126	-1448.1
		M1	491. 98	-	-	2371.0	2863.0	0.172(0.091)	-	-	0.172	0.043	-2566.9
		M2	288.170	-	215.330	2317.8	2821.3	0.102 (0.085)	-	0.076 (0.045)	0.102	0.102	-2565.28
	ADC	M3	38.925	334.800	-	2432.4	2806.2	0.014 (0.062)	0.119 (0.050)	-	0.072	0.123	-2562.9
		M4	38.419	340.860	0.083	2433.6	2813.0	0.014 (0.062)	0.121(0.072)	0.0 (0.059)	0.075	0.123	-2562.9
		M1	0.203	-	-	0.219	0.422	0.519 (0.097)	-	-	0.519	0.129	-33.16
		M2	0.156	-	0.056	0.201	0.414	0.878 (0.121)	-	0.136 (0.049)	0.378	0.230	-26.98
	BW	M3	0.084	0.088	-	0.240	0.413	0.204(0.125)	0.215 (0.068)	-	0.311	0.266	-27.45
		M4	0.112	0.040	0.040	0.221	0.408	0.276 (0.140)	0.094 (0.091)	0.089 (0.091)	0.323	0.252	-26.36
		M1	10.396	-	-	51.420	61.780	0.168(0.091)	-	-	0.168	0.042	-1456.87
R		M2	8.557	-	3.301	49.740	61.600	0.139(0.090)	-	0.054 (0.045)	0.139	0.088	-1456.1
	WW	M3	9.205	1.308	-	51.27	61.785	0.149 (0.101)	0.021 (0.047)	-	0.159	0.058	-1456.8
		M4	8.561	0.100	3.305	49.73	61.600	0.139 (0.097)	0 (0.050)	0.054 (0.055)	0.139	0.088	-1456.1
		M1	445. 01	-	-	2655.7	3100.7	0.144(0.086)	-	-	0.144	0.036	-2547.68
	AD	M2	388.190	-	129.170	2579.6	3096.9	0.125 (0.086)	-	0.042 (0.043)	0.125	0.073	-2547.18
		M3	444.980	1.654	-	2654.4	3101.3	0.143 (0.098)	0.001 (0.041)	-	0.144	0.036	-2547.68
		M4	38.300	0.006	129.024	2579.5	3097.0	0.125 (0.092)	0 (0.053)	0.42 (0.052)	0.125	0.073	-2547.18

σ^2_a: direct additive genetic variance, σ^2_m: maternal genetic variance, σ^2_e: residual (temporary environmental variance), σ^2_p: phenotypic variance, h^2_a: direct heritability and h^2_m: maternal heritability, c^2: fraction of phenotypic variance due to maternal permanent environmental effects.h^2_t: total heritability (h^2_t= h^2_a+ 0.5 h^2_m + 1.5 $mr_{am}h$), t_m: total maternal effect (t_m= ¼ h^2_a + h^2_m + c^2+ $mr_{am}h$), and log-l: log- likelihood value