SHORT COMMUNICATION



# Estimation of genetic parameters for lamb weight at various ages in Mehraban sheep

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## ABSTRACT

The aim of the present study was to estimate variance components and genetic parameters among growth traits of Iranian Mehraban sheep using single and two-trait animal models. Analyzed traits included, birth weight (BW), weaning weight (WW), weight at 6 months (W6), weight at 9 months (W9) and yearling weight (YW). (Co)variance components were estimated with REML for an animal model that included fixed effects of year, season, age of dam, sex and type of birth. Random effects included direct and maternal additive genetic effects, maternal permanent environmental effects with a direct-maternal genetic covariance and random residual effects. Direct heritability ( $h^2$ ) was increased from 0.19 at birth to 0.36 at yearling age. Inversely, maternal heritability ( $m^2$ ) estimates were decreased from 0.11 at birth to 0.01 at yearling age. Estimates of maternal permanent environmental variance as a proportion of phenotypic variance ( $c^2$ ) were 0.06 and 0.04 for BW and WW, respectively and they were very negligible for other traits. Direct-maternal genetic correlation ( $r_{am}$ ) was positive and it increased with age from 0.05 for BW to 0.73 for YW. For the two-trait analyses, the genetic correlations were larger among WW, W6, and W9 (0.59 to 0.82) and were small between BW, W9, and YW (<0.4). Positive genetic correlations between traits show that selection at any age is possible.

Key words: Body weight, Growth, Mehraban sheep, (Co)variance components, Heritability.

#### RIASSUNTO

#### STIMA DEI PARAMETRI GENETICI DEL PESO DI AGNELLI DI RAZZA MEHRABAN A DIVERSE ETÀ

Lo scopo del presente studio era la stima dei componenti della varianza e dei parametri genetici tra le caratteristiche di accrescimento di agnelli Iranian Mehraban per mezzo di modelli animali a una e a due vie. Le caratteristiche analizzate sono state il peso alla nascita (BW), il peso allo svezzamento (WW), il peso a 6 mesi (W6), il peso a 9 mesi (W9) e il peso a un anno di vita (YW). Le componenti della (co)varianza sono state stimate con REML per un modello animale che comprendeva gli effetti fissi anno, stagione, età della madre, sesso e tipo di nascita. Sono stati inclusi gli effetti casuali: effetti genetici additivi diretti e materni, effetti permanenti dell'ambiente materno con una covarianza genetica direttamaterna ed effetti residui. L'ereditabilità diretta (h<sup>2</sup>) è aumentata da 0,19 alla nascita a 0,36 a un anno di età. Le stime della varianza ambientale materna permanente, quali parti della varianza fenotipica (c<sup>2</sup>), sono state 0,06 per BW e 0,04 per WW, e sono risultate del tutto trascurabili per gli altri carat

teri. La correlazione genetica diretta-materna ( $r_{am}$ ) è risultata positiva ed è aumentata con l'età da 0,05 per BW a 0,73 per YW. Per le analisi a due vie, le correlazioni genetiche sono state più forti tra WW, W6 e W9 (da 0,59 a 0,82), e basse tra BW, W9 e YW (< 0,4). Le correlazioni genetiche positive tra i parametri dimostrano che la selezione è possibile a qualunque età.

Parole chiave: Peso corporeo, Crescita, Pecora Mehraban, (Co)varianza, Ereditabilità.

#### Introduction

The sheep population in Iran is composed mainly of fat tailed, carpet-wool native breeds (Farid et al., 1977). Lamb and mutton are traditional sources of protein and the consumption levels are high in comparison with meat from beef cattle and goats. Due to the fact that the supply of meat from sheep does not cover the demands, a breeding scheme is needed to increase the efficiency of sheep production by improving litter size, body conformation, lamb weight and milk vield (Yazdi et al., 1997). The Mehraban breed is one of the common native breeds in Iran adapted to mountainous areas in western parts of the country. Recently, the Mehraban breed population has increased rapidly, reaching about 1 million heads (Tavakolian, 1999). So there is an increasing interest in genetically improving this breed.

Growth is one of the traits of great economic importance in sheep production. Profitability of sheep production for meat depends to a great extent on lamb weight, so the selection objective should concentrate on this trait (Tosh and Kemp, 1994). Estimates of genetic and environmental parameters of different component traits related to growth are needed to develop a proper selection program. In addition, these parameters are necessary for prediction of the response to selection.

Studies of various sheep breeds have shown that growth traits, particularly in early ages, are not only influenced by the genes of the individual for growth and by the environment in which it is raised, but also by the maternal genetic composition and environment provided by the dam (e.g. Maria et al., 1993; Tosh and Kemp, 1994; Nasholm and Danell, 1996; Yazdi et al., 1997). The term maternal effect refers to influences of the mother on her offspring other than through the genes she transmits to them. Principally, these represent the dam's milk production and mothering ability, though effects of the uterine environment and extra-chromosomal inheritance may contribute (Meyer, 1992). Hence, to achieve optimum progress in a selection program both direct and maternal components should be taken into account, especially if an antagonistic relationship between them exists. It is generally assumed that the covariance between direct and maternal genetic effects on body weight is negative (Maria et al., 1993; Tosh and Kemp, 1994). However, a positive relationship has also been found (Nasholm and 1996; Yazdi Danell. et al., 1997). Relationships could also exist between the maternal, litter, and permanent environmental effects. They could be estimated simultaneously in data of multiparous sheep.

Information on genetic parameters for growth traits in the Mehraban breed is sparse. Therefore, the aim of the present investigation was to study the direct and maternal influence on lamb weight at different ages in this breed. The relationships between traits were also studied.

# Material and methods

## Data

Live body weight records of Mehraban lambs that were collected between 1990 and 2005 were used in this study. The data was from the RAMPLANE database of the Mehraban sheep breeding unit of the Agriculture Organization of Hamadan Province in western Iran. For the genetic improvement of Mehraban sheep and an increase in its growth performance, the RAMPLANE project was started in the spring of 1989 by the Agriculture Ministry of Iran. In this project, rams were selected at 1 year of age from some purebred flocks. Then, the rams were assigned to some of selected local flocks under supervision of Mehraban Sheep Breeding Unit. In these flocks pedigree information and other information related to growth traits were recorded carefully. This information was collected from flocks and recorded in the database of the Mehraban Sheep Breeding Unit for investigating the amount of success of the RAMPLANE project.

In the Mehraban breed, the mating period was from the end of September to the end of October. Lambing was commenced in March. During the lambing season, the ewes were indoors and carefully managed. The lambs were weighed and ear tagged within 12 h of birth. The identities of newborns and of their parents, date of birth, sex, birth type and birth weight were recorded. After lambing, the ewes and their lamb(s) were placed in separate pens and kept there for a few days, depending on the number of lambs born and the ewe's rearing ability. Then a flock composed of suckling lambs and their dams was formed. The length of the suckling period wasn't same for all lambs. During the suckling period, lambs were kept indoors and additionally fed with hay grass. Most of lambs were weaned in June. Animals are usually marketed when they are 6 months or more of age.

The analyzed traits included birth weight (BW), weaning weight (90 days of age, WW), weight at 6 months (W6), weight at 9 months (W9) and yearling weight (YW). Initially records with implausible dates or weights were eliminated. In addition, a few lambs that were born beyond 2005 were excluded from the estimation of variance components. A summary of data structure with some pedigree information for each trait is presented in Table 1.

#### Statistical analysis

To identify fixed effects to be included in the models, least square analyses were conducted using the GLM procedure (SAS, 1999). This was performed on a model including fixed effects (year - 16 classes; season - 2 classes; age of dam in years - 8 classes; sex - 2 classes; and type of birth - 3 classes). All of these fixed effects were significant (P $\leq$ 0.01) for all of the traits, and were then included in the models. The general representation of the animal model used is as follows:

$$y = Xb + Z_aa + Z_mm + Z_cc + e$$

where y is a n×1, vector of records, b denotes a vector of fixed effects in the model with association matrix X, a is the vector of direct genetic effects with association matrix  $Z_a$ , m is the vector of maternal genetic effects with association matrix  $Z_m$ , c is the vector of maternal permanent environmental effects with association matrix  $Z_c$ , and e denotes the vector of residual (temporary environment) effects. The variance-covariance structure for the model is

Item	Trait						
		BW	WW	W6	W9	YW	
N. of records		3744	2247	1965	1551	1444	
N. of progeny		2376	1473	1270	1013	914	
N. of sires with progeny		102	93	93	82	79	
N. of dams with progeny		1235	665	613	453	439	
N. of granddams with progeny		767	521	498	375	368	
N. of dams with record		964	435	392	285	271	
N. of granddams with record		324	282	244	211	216	
Mean	kg	3.89	20.05	34.00	43.64	51.20	
SD	"	0.729	2.969	3.892	4.552	5.659	
CV	%	19	15	11	10	11	

Table 1.	Pedigree info	prmation, me	ean, standard	deviation (SD	), and coefficient of
	variation (C)	<ol> <li>of live wei</li> </ol>	ght traits <sup>1</sup>		

<sup>1</sup> Live body weight at birth (BW), weaning (WW), 6 months (W6), 9 months (W9) and yearling weight (YW).

#### as follows:

$$W\begin{bmatrix}\mathbf{a}\\\mathbf{m}\\\mathbf{c}\\\mathbf{e}\end{bmatrix} = \begin{bmatrix} \mathbf{A}\boldsymbol{\sigma}_{a}^{2} & \mathbf{A}\boldsymbol{\sigma}_{am} & \mathbf{0} & \mathbf{0}\\ \mathbf{A}\boldsymbol{\sigma}_{am} & \mathbf{A}\boldsymbol{\sigma}_{m}^{2} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}_{c}\boldsymbol{\sigma}_{c}^{2} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}_{e}\boldsymbol{\sigma}_{e}^{2} \end{bmatrix}$$

Where A is the numerator relationship matrix,  $I_c$  is an identity matrix with order number of ewe, and  $I_e$ , is an identity matrix with order number of records,  $\sigma_a^2$  is direct genetic variance,  $\sigma_m^2$  is maternal genetic variance,  $\sigma_{am}$  is covariance between direct and maternal genetic effects,  $\sigma_c^2$  is variance due to maternal permanent environmental effects, and  $\sigma_e^2$  is variance due to residual (temporary environmental) effects.

Mousa *et al.* (1999) reported that in the case of bivariate growth traits analyses, maternal effects should be included in the model, unless maternal effects were shown to be unimportant from analyses of single traits. Since, in the present study the mater-

nal effects on lamb body weights were low, thus maternal effects were omitted from the bivariate analyses. On the other hand, because the maternal effects were so limited on lamb body weights, the correlations between maternal effects for underlying traits seem to have little meaning. In total ten different combinations of traits were used to analyze the pairs of traits and genetic correlations were calculated for all traits by fitting simple direct additive models.

The DFREML programs of Meyer (2001b) were used for variance component estimation by the restricted maximum likelihood for all of the analyses. Principles of derivative-free restricted maximum likelihood (DFREML) have been previously described by Meyer (1989). Convergence was assumed when the variance of likelihood values in the simplex was less than  $10^{-8}$ . In addition, a restart of each analysis was performed with different starting values to attempt to avoid convergence to local maxima.

#### **Results and discussion**

#### Single-trait analyses

Estimates of variances and covariances relative to phenotypic variances for BW, WW, W6, W9, and YW are shown in Table 2, for single-trait analyses. tability was increased with age. This is most likely caused by two reasons, increase in the expression of genes with direct additive effects on body development and decrease in variances due to maternal effects in later ages, which will result in larger direct heritability estimates for the later ages.

Table 2.	Estimates of genetic parameters from single-trait analyses for live weight traits <sup>1, 2</sup> .						
Trait	h²	m²	C <sup>2</sup>	r <sub>am</sub>	$\sigma_p^2$		
BW	$0.19(\pm 0.04)$	0.11(±0.02)	0.06(±0.02)	0.05	0.54		
WW	0.25( ± 0.05)	0.06(±0.02)	0.04(±0.02)	0.21	8.63		
W6	0.23( ± 0.05)	0.02(±0.01)	$0.01(\pm 0.01)$	0.22	14.12		
W9	$0.31(\pm 0.06)$	$0.01(\pm 0.01)$	$0.01(\pm 0.01)$	0.32	15.72		
YW	0.36( ± 0.07)	0.01(±0.01)	0.00(±0.01)	0.73	25.71		

<sup>1</sup>Live body weight at birth (BW), weaning (WW), 6 months (W6), 9 months (W9) and yearling weight (YW). <sup>2</sup>Numbers between parentheses are standard errors.

The  $h^2$  estimates here are lower than those reported by Snyman et al. (1995) who reported direct heritability estimates on Afrino sheep of 0.22, 0.33, 0.47, and 0.58 for BW, WW, W9, and YW, respectively. But, they were higher than those obtained by Nasholm and Danell (1996) on Finewool sheep of 0.07, 0.12 and 0.21 for BW, WW, and W6, respectively. However, our results are closer to those reported by Fogarty (1995), who proposed direct heritability estimates of 0.21, 0.23, 0.27, and 0.38 for BW, WW (100 days), post-weaning (200 days) and YW (350 days), respectively. Moreover, Atkins et al. (1991) reported h<sup>2</sup> estimates of 0.23, 0.21, and 0.31 for WW (100 days), post-weaning (200 days), and YW (350 days), respectively, which further supports the findings of the present study.

Results from our study and other studies (Atkins *et al.*, 1991; Snyman *et al.*, 1995; Notter and Hough, 1997; Yazdi *et al.*, 1997; Mousa *et al.*, 1999) suggest that direct heri-

The  $m^2$  estimates were 0.11, 0.06, 0.02, 0.01, and 0.01 for BW, WW, W6, W9, and YW, respectively. The larger estimate of maternal heritability for birth weight compared with the estimate for later weights supports the conclusion of Robinson (1981) that maternal genetic effects generally are important for weight at younger ages and diminishes with an increasing in age. The tendency of m<sup>2</sup> to decline from birth to later ages, as obtained here, is in agreement with other literature (Nasholm and Danell, 1996; Notter and Hough, 1997; Yazdi et al., 1997; Mousa et al., 1999). For instance, Mousa et al. (1999) reported a decrease in m<sup>2</sup> from 0.17 at birth to 0.01 at 19 months of age for a composite breed of sheep. The low maternal genetic influence on all weights (except than BW) was presumably due to poor quality of pasture, preventing the ewe's genetic ability to provide enough milk for her lamb(s). Thus, the lack of adequate pasture could be masking the expression of the maternal ability of the ewe.

Estimates of  $c^2$  were 0.06, 0.04, 0.01, 0.01, and 0.00 for BW, WW, W6, W9, and YW, respectively. Estimates of c<sup>2</sup> were high at birth, when direct effects were least important, but decreased sharply after weaning and in the highest age this effect was negligible. However, most studies reported such a decrease as time lapses post-weaning (Snyman et al., 1995; Vaez Torshizi et al., 1996). Maria et al. (1993) reported that differences in c<sup>2</sup> between pre-weaning and post-weaning ages could result from the difference that suckling lambs are still dependent on their mothers, whereas weaned lambs depend on themselves. Furthermore, the influence of the non-permanent environmental factors becomes more important after weaning. In addition, Meyer (2001a) reported that breed differences in the importance of maternal environmental effects are important and in some breeds a lower c<sup>2</sup> is due to an earlier decline of the lactation curve than in other breeds.

However, it should be remembered that estimation of maternal effects is dependent on key pedigree relationships and data structure. The impact of data structure on separating maternal genetic and maternal environmental effects from combined and direct effects has been demonstrated by Maniatis and Pollott (2003). The authors showed that the accuracy of estimation of maternal effects depends on the family structure and demonstrated that both the number of progeny per dam and the proportion of dams having their own record in the data considerably affect the variance components estimation. On the other hand, in addition to environmental conditions that influence the maternal components estimates (Ekiz, 2004), the relatively low maternal effects obtained in this study may be, to some extent, due to size and structure of data. In a study by Gut et al. (2001) on a multigenerational population of 1892 Polish Whiteheaded Mutton sheep lambs, due to a relatively small number of offspring per dam, the direct and maternal heritabilities for BW were 0.17 and 0.02, respectively, which further emphasizes the impact of data structure on estimates of the genetic parameters. So, for accurately separating maternal genetic components and maternal permanent environmental effects from combined and direct effects, a large dataset and several well-linked generations of records and many relationship between relatives related to the mother are needed (Maniatis and Pollott, 2003).

Overall maternal effects were larger in early stages of the life of Mehraban lambs. Although Meyer (2001a) showed that maternal variance tended to be higher at younger ages and in the highest ages the maternal effects are not considerable, Meyer (1992) and Maniatis and Pollott (2003), reported that maternal influence never completely disappeared after weaning. Likewise, from a genetic analysis of growth traits of Afrino sheep, Snyman et al. (1995) reported that whereas maternal effects tend to diminish with age of progeny, these effects might persist into the post-weaning growth period. Finally, the tendency that a decreasing part of the variation in lamb weight from birth to yearling age depends on maternal effects shows that the ability of Mehraban ewes to increase body weight of lambs at birth seems to be the only meaningful maternal trait to be included in the selection criterion, if any.

Correlations between direct and maternal genetic effects  $(r_{am})$  were 0.05, 0.21, 0.22, 0.32, and 0.73 for BW, WW, W6,

W9, and YW, respectively. Nasholm and Danell (1996) reported estimates of direct-maternal genetic correlation as 0.11, 0.47, and 0.64 for BW, WW, W6, respectively. Moreover, Yazdi et al. (1997) estimated correlation between direct and maternal genetic effects in another Iranian sheep breed, the Baluchi, as 0.17, 0.52, 0.32 and 0.12 for BW, WW, W6 and YW, respectively. The low direct-maternal genetic correlation observed for BW indicates that direct and maternal contributions differ during pregnancy. Nasholm and Danell (1996) concluded that, in the case of positive correlation between direct and maternal genetic effects, selection for increased weights in lambs will also improve the maternal ability of the ewes. Numerous studies have found a negative correlation between additive direct and additive maternal effects for body weight in various ages of various breeds (Maria et al., 1993; Hanford et al., 2002; Ekiz, 2004). The reasons for the negative estimates obtained could not conclusively be explained by these authors. It may be due to natural selection for an intermediate optimum (Tosh and Kemp, 1994). However, an investigation conducted by Dodenhoff et al. (1999) on several breeds of beef cattle indicates that dependencies between direct and maternal effects are determined by breed. Cundiff (1972) postulated that from an evolutionary standpoint the relationship is negative and, hence, prevents species from becoming increasingly larg-Extremely high values er. of direct-maternal genetic correlations, therefore, seem biologically unlikely.

#### Two-trait analyses

Estimates of genetic and phenotypic correlations among the traits are presented in Table 3.

The genetic correlations between WW, W6, W9, and YW, in the present study are moderately high, indicating that selection for increased WW in Mehraban sheep will also result in genetic improvement of W6, W9, and YW. The largest positive relationship was between chronologically adjacent weight traits rather than nonadjacent ones. This result is expected because an autocorrelation would exist among the genetic and environmental effects associated with the successive measurements (Mousa et al., 1999). The positive estimate of genetic correlation between BW and WW suggests that animals with above average weaning weight would tend to be above average in genetic merit for birth

	triangle) among live weight traits <sup>1, 2</sup> .						
Trait	BW	WW	W6	W9	YW		
BW	1	0.44(±0.04)	0.42(±0.04)	0.37(±0.05)	0.33(±0.05)		
WW	0.49	1	0.82(±0.06)	0.59(±0.06)	0.58(±0.07)		
W6	0.43	0.78	1	0.67(±0.07)	0.52(±0.07)		
W9	0.40	0.63	0.68	1	$0.41(\pm 0.06)$		
YW	0.32	0.60	0.58	0.40	1		

Table 3. Genetic correlations (upper triangle) and phenotypic correlations (lower

<sup>1</sup>Live body weight at birth (BW), weaning (WW), 6 months (W6), 9 months (W9) and yearling weight (YW). <sup>2</sup>Numbers between parentheses are standard errors.

weight. Correlations between BW and post-weaning weight (especially W9 and YW) were lower than corresponding values between other ages, which indicates that body weight at higher ages cannot be well predicted from body weight at birth. In general, the absence of genetic antagonisms among the various traits indicates that none of the traits should be affected adversely through correlated response.

#### Conclusions

Heritability is large enough for selection to be effective for improving any of the growth traits. The relative importance of direct and maternal effects changes with age, and maternal effects on early

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growth of lambs are noticeable, while the direct effects are important at later ages. However, results showed that in maternally influenced traits, for accurate estimates of maternal components, data structure has a key role. Moreover, in the case of poor environmental conditions, maternal effects would be compacted; therefore, more studies are recommended for environmental conditions of this breed. Genetic correlations among growth traits of Mehraban sheep were positive, indicating that selection for WW would also increase BW and other weights.

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