

GENETIC EVALUATION AND GENETIC TREND OF GROWTH IN MAKOOEI SHEEP VIA RANDOM REGRESSION

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ABSTRACT

The aim of this study was to estimate covariance functions for additive genetic, direct and maternal permanent environmental effects on the growth from 1 to 270 days of age using random regression models on Legendre polynomials (LPs). For this aim, 8733 body weight records of 1973 lambs from 110 sires and 550 dams were collected between 1990 and 2014 from the rearing and breeding station of Makooei sheep in Makoo (36°, 35'S and 48°, 22'E) of West Azerbaijan province. Contemporary groups (age of dam, sex of lamb, type of birth and year-season of birth) and fixed regression of body weight on age were considered as fixed parts of the models. Random regressions of direct additive genetic, maternal and direct permanent environmental were random parts of the models. The assumptions about the distribution of the residual variance were compared. The variances increased along the trajectory from 0.25 to 2.03, 0.11 to 14.85 and 0.08 to 2.26 for direct additive genetic, direct and maternal permanent environmental effect, respectively. Low to high estimates of direct heritability (0.10-0.42) and moderate to high estimates of coefficient of permanent environmental effects (0.18 to 0.77) were obtained, while estimates of maternal environmental effect (c^2) (0.06 to 0.21) was low and moderate in all ages. This finding indicated distinct environments a trait is influenced by sets of different genes and these genes are expressed at variable intensities according to the degree of similarity or difference within and between environments. Despite low, positive genetic trends were found for growth traits and genetic trend estimates for growth performance revealed that selection decisions made during the breeding program effectively improved the body weight traits.

Keywords: Makooei Sheep, Body Weight, Random Regression Model, Variance Components, Legendre Polynomial.

INTRODUCTION

Estimation of variance components and genetic parameters for main economic traits play an important role to design effective strategies of animal selection. In meat type sheep, body weight is considered as a main trait. Meat production of sheep is one of the most important goals of Iranian livestock industry. Approximately, 50 million sheep from more than 20 breeds and sub-breeds are reared in Iran (Vatankhah *et al.*, 2004). Lamb and mutton are traditional sources of protein in Iran and the consumption levels are high in comparison with cattle and goats. The sheep population in Iran is mainly composed of fat-tailed carpet-wool native breeds. They are mostly adapted to the poor range conditions of the country. A high percentage of the sheep population is managed under a migratory system, utilizing the range as the major source of feed (Ghafouri Kesbi *et al.*, 2008). More than 20 indigenous sheep breeds are reared in Iran. Makooei sheep is one of the famous breeds of the country which is reared in Azerbaijan province with an approximate population size of 2.7 million heads (Abbasi and Ghafouri, 2011). Makooei is a multipurpose sheep whose main products are meat, milk and wool. The Makooei sheep is one of the most popular breeds for milk production and is well

adapted to different conditions and can be successfully reared in different regions of the world (Akbari nejad *et al.*, 2014). Random regression models (RRM) have been suggested as an alternative methodology for the analysis of longitudinal data or repeated measures records (Schaeffer and Jamrozik, 2008). Although this technology has been used in dairy production studies for the genetic analysis of test day models (Legarra *et al.*, 2004; Yilmaz *et al.*, 2011), The RRM allow getting breeding values for milk yield at any day of lactation in a continuous manner or for functions of lactation curve, instead of finite dimensional models that only give punctual predictions of breeding values. Moreover, RRM provide estimates of breeding values with higher accuracies than the conventional finite dimensional models because all records from lactation and short length lactation records can be used in the genetic evaluation (Jamrozik *et al.*, 2000; Schaeffer *et al.*, 2000). The majority of random regression analyses fitted polynomials of time or age at recording as basic functions. Random regression models have been applied to sheep data from research flocks which typically contain many repeated records per animal (Lewis and Brotherstone, 2002). These models use polynomials in time to describe mean profiles with random coefficients to generate a correlation among the repeated observations

on each individual (Robert-Granié *et al.*, 2002). This approach has the advantage of studying change and increases statistical power. This is due to units serving as their own control and due to the possibility of estimating (co)variance components at any point on the trajectory of time. Additional advantages include the use of weight measurements without any need to correct for age and the reduction in the number of parameters to be estimated as compared to multivariate analysis. Lower approximate standard error estimates for parameters as compared to estimates from univariate analysis (Fischer *et al.*, 2004) are also additional advantages of the random regression analysis. In this study different random regression models were applied in the analysis of weight data taken from birth to 270 days of age with the objective of identifying the appropriate model, obtaining more accurate estimates and estimates of genetic changes.

MATERIALS AND METHODS

Geographical location and herd management: The present data were collected from the flock of Makooei sheep during the period 1990–2014 at the rearing and breeding station of Makooei sheep placed in Makoo (36°, 35'S and 48°, 22'E) of West Azerbaijan province. Because of the Makooei sheep's value in Azerbaijan area economy, in 1986, Makooei Sheep Breeding Station (MSBS) was initiated in the city of Makoo, Western Azerbaijan, in Iran. The chief goals of MSBS were preservation and development of this sheep breed. MSBS rearing structure consists mainly of extensive-migration on natural pastures in spring and summer (April to September) and semi-intensive in station rearing with barn feeding during autumn and winter (October to March). Alfalfa, barley, corn silage, concentrates, and grass are used to feed the animal during the semi-intensive rearing phase. The breeding season begins in late summer and lasts until early autumn. Estrus synchronization is carried out in the herd with a progesterone-releasing intra-vaginal device (CIDR). Ewes are bred either via artificial insemination in the first cycle of estrus or with guarded rams in the second or third cycle of estrus. Two programs are practical to enhance litter size: flushing (feeding ewes with a high-energy diet 2-3 weeks before breeding season) and equine chorionic gonadotropin (ECG) injection upon CIDR deletion. Ewes are kept in the herd for a maximum of 7 parities and rams stay in the herd for 5 breeding seasons. Lambing occurs once a year, and lambing season begins in January.

Data: The data involved of weight records from birth to 270 days of age. Animals that had four records in the particular age range were comprised in the analysis. Sums of 8733 records of 1973 animals with a mean weight of 20.32 kg were finally available. Animals with

records were descendants of 110 sires and 550 dams and the pedigree comprised 2163 animals. The features of data set are given in Table 1.

Number of records and mean weights for different ages are shown in Figure 1. Body weights increased evenly linear with increasing in age from 1 to 270 days of age so was the standard deviation. Therefore, the coefficient of variation remained at the relatively constant across ages.

Statistical analysis: An initially analysis for discovery of the fixed effects affecting the body weight records was performed by a general linear model analysis via GLM procedure of SAS software (SAS, 2004). Contemporary groups (CGs) were defined according to the effects of year-season of birth, age of dam at lambing (2 to 9 yr), sex (male or female) and type of birth (single, twin or triplet) had a significant effect on body weight and then included the fixed effect in the models used for evaluation of variance components. All of the fixed effects were significant ($P \leq 0.05$) and comprised in the model. Weight as a function of age in days at weighing was comprised as a fixed regression of orthogonal polynomial. This fixed regression depicts the average growth curve of all animals with records (Abegaz *et al.*, 2010). Random regression coefficients fitted to the data were three sets. These comprised direct genetic effect and direct and maternal permanent environmental effects. The form in matrix notation is:

$$Y = X + Z_1a + Z_2p + Z_3p + e$$

where y is the vector of observations, \mathbf{b} is the vector of fixed effects (including fixed effects and fixed regression), \mathbf{a} is the vector of random coefficients for additive direct effects, \mathbf{pm} is the vector of random coefficients for maternal permanent environment effects, \mathbf{pe} is the vector of random coefficients for animal permanent environment effects, \mathbf{e} is the vector of residual effects and \mathbf{X} , Z_1 , Z_2 and Z_3 are the matching incidence matrices. The model is based on the following assumptions:

$$\begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{pe} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} K_a \otimes A & 0 & 0 & 0 \\ 0 & K_m \otimes I & 0 & 0 \\ 0 & 0 & K_{pe} \otimes I & 0 \\ 0 & 0 & 0 & R \end{bmatrix}$$

Where K_a , K_{pm} and K_{pe} are (co)variance matrices between random regression coefficients for direct additive, maternal and animal permanent environmental effects, respectively. A is the relationship matrix, I is an identity matrix, \otimes is the Kronecker product between matrices and R is a block diagonal matrix containing residual variances. Correlations between random regression coefficients for different effects were put to zero.

Changes in size error variance over time were modeled as a step function with seven various classes depending on age (1–40, 41–80... 241–270) and the

theory were compared about the distribution of the residual variance (homogenous or heterogeneous).

Covariance functions and breeding value calculations:

Random regression analyses produce K matrices containing (co)variance between random regression coefficients, especially for each random effect (direct genetic, maternal and direct permanent environmental effects). Following the proposal of Kariuki *et al.* (2010), the (co)variance functions (\hat{G}_0) are estimated by pre and post multiplying K using a matrix containing Legendre polynomials (Φ) pertaining to a set of specific ages shown in matrix notation as:

$$\hat{G}_0 = \Phi \hat{\Phi}$$

Covariances between RR coefficients pertaining to different random effects were supposed to be zero. The genetic analyses were performed via WOMBAT software (Meyer, 2007) with residual maximum likelihood (REML) method for assessment of (co)variance components. Solutions for the random regression coefficients for all animals can be used to approximate breeding values (BV) for any point in the age curve between 1 and 270 d. For example, BV for the animal *i* at 150 d of age will be:

$$B_{i,150} = q_{150} \times \alpha_i$$

Where α_i display solution for animal *i*, and q_{150} is the vector of coefficients of the Legendre polynomial matching to 150d of age.

Model selection: Let *p* represent the number of parameters approximated and log L is the REML maximum log likelihood. The information criteria are then known as:

$$A = -2l + 2p$$

and

Estimate of LRT for models *i* and *j* was obtained with principle:

$$L_i = 2 \times (l_i - l_j)$$

Different models were compared by the Restricted Maximum Likelihood (REML) form of the Akaike information criterion (AIC) (Akaike, 1974), by inspecting the variance component and genetic parameter estimates. A model with the maximum significant ($P \leq 0.05$) log-likelihood ratio test (LRT) and with the least AIC was considered to be the most suitable model.

RESULTS

Log likelihoods and information criteria: A review of the random regression model fit is given in Table 2. The greatest fitting RRM according to AIC and LRT was the model to a polynomial of fourth order for fixed effect, fifth order for direct genetic effect, fifth order for direct permanent environmental and fourth order for maternal permanent environmental effects (model 14).

Orders of Legendre polynomials fit higher than quartic not measured because they were unnecessary high. Very high order polynomials may not be used here because of they didn't provide accurate approximations.

Variance component and genetic parameters: Direct additive genetic, maternal and direct permanent environmental variance estimates are presented in Table 3.

Direct additive genetic variance improved from 0.25 at birth day to 2.59 at 240 days of age and then gradually reduced to 2.03 at 270 days of age. Maternal permanent environmental variance amplified from 0.08 at birth day to 2.79 at 210 and then reduced during the path from 2.74 to 2.26. The pattern approximated for permanent environmental variance and phenotypic variance were regular and improved gradually during the path.

The estimates of direct heritabilities, maternal and direct permanent environmental variances as proportions of phenotypic variance for certain ages are shown in Table 3. Estimates of direct heritability reduced from 0.42 at birth day to 0.10 at 270 days of age. Heritability estimates for direct (h^2) and maternal permanent environmental variance (c^2) as proportions of phenotypic effect demonstrated opposite responses. Relative value of c^2 decreases until 30 d, whereas h^2 increases throughout the similar period. In general, permanent environmental variances as proportions of phenotypic variance improved along the path. Estimated error variance throughout the path that modelled in seven classes (1–40, 41–80... 241–270) were 0.16, 0.19, 0.29, 0.33, 0.63, 0.65 and 0.05, respectively.

Analyses using random regression models create estimates of covariance functions which can be considered to give estimates of genetic and environmental (co)variance components for each age on test. For shorten contribution, results shown for selected days only (Figure 2). Generally, the additive genetic correlations between weights improved with lessening interval between weighting; and moreover correlations between weight at earlier ages and at other ages were little.

Maternal and direct permanent environmental correlations between weights at selected ages are offered in Table 4. Maternal permanent environmental correlations among different days were positive and ranged from 0.11 between 1 and 60 days of age to 0.99 between 60 and 120, 180 and 240 and 240 and 270 days of age. The guess estimate of permanent environmental correlations ranged from 0.65 to 0.97. In general, permanent environmental correlations reduced in superior age intervals.

Genetic trend: The genetic trends of birth weight, 150-d weight and 270-d weight shown in Figure 3. To birth weight, the genetic changes from 1993 to 1997 show to

be parallel and then decreased until 1999. In general, the genetic trend for birth weights was different than those of the other selected body weight traits. The genetic changes of birth weight decreased from 2005 to 2009; but for the

other selected weights, plots of the mean predicted breeding values on year of birth revealed an increase over time.

Table 1.Characteristics of the data.

Number of records	8733
Means (kg)	20.32
Standard deviation (kg)	12.05
No. of animal with records	1973
No. of animal with 4 records	1024
No. of animals with 5 and more records	812
No. of animals in the analysis	2163
No. of sires	101
No. of dams	550
No. of sires with records and progeny in the data	67
No. of dams with records and progeny in the data	394

Table 2.Order of fit for the polynomial used in the different models and information criterion (best model in bold).

Model	k ^a	No. of error measures	P	Log L	AIC ^b	LRT
1	2222	1 ^c	10	-16471.81	32963.62	0.00
2	2222	7 ^d	16	-26186.15	52404.30	19428.68
3	3222	7	16	-26204.19	52440.38	19464.76
4	4222	7	16	-26216.59	52465.18	19489.56
5	3333	1	19	-5578.17	11194.34	21787.30
6	3333	7	25	-5433.55	10917.10	22076.50
7	4333	7	25	-5414.30	10878.60	22115
8	4433	7	29	-5291.74	10641.48	22360.10
9	4443	7	33	-5272.77	10611.54	22398.10
10	4444	1	31	-5437.57	10937.14	22068.50
11	4444	7	37	-14178.40	28430.80	4586.82
12	3544	7	42	-5209.64	10503.28	22524.30
13	4544	7	42	-5206.54	10497.08	22530.50
14	4554	7	47	-5200.37	10494.74	22542.90

^aOrders of fit for fixed, direct additive genetic, maternal permanent and direct permanent environmental polynomials, respectively.

^bAkaike Information Criterion (AIC \pm 15,000).

^cFor homogenous error variances.

^dFor heterogeneous error variances of seven various classes depending on age (1–40, 41–80... 241–270).

Table 3.Estimates of phenotypic (σ^2_p), direct additive genetic (σ^2_a), maternal (σ^2_c) and direct permanent (σ^2_{pe}) environmental variances and direct heritability (h^2), maternal (c^2) and direct (pe^2) permanent environmental effects as a proportion of phenotypic variance for weight at selected ages.

Age (days)	1	30	60	90	120	150	180	210	240	270
σ^2_p	0.60	1.66	3.1	4.71	6.65	8.98	12.24	15.61	18.24	19.20
σ^2_a	0.25	0.67	1.0	1.24	1.45	1.67	2.01	2.43	2.59	2.03
σ^2_c	0.08	0.11	0.43	0.86	1.41	1.96	2.47	2.79	2.74	2.26
σ^2_{pe}	0.11	0.72	1.48	2.31	3.49	5.01	7.13	9.73	12.25	14.85
h^2	0.42	0.40	0.32	0.26	0.21	0.18	0.16	0.15	0.14	0.10
c^2	0.13	0.06	0.13	0.18	0.21	0.21	0.20	0.17	0.15	0.11
pe^2	0.18	0.43	0.47	0.49	0.52	0.55	0.58	0.62	0.67	0.77

Table 4. Maternal (above diagonal) and direct permanent environmental correlations (below diagonal) among weights at selected ages

Age	1	60	120	180	240	270
1		0.11	0.27	0.36	0.41	0.45
60	0.74		0.99	0.98	0.85	0.80
120	0.70	0.92		0.98	0.95	0.90
180	0.76	0.82	0.95		0.99	0.98
240	0.76	0.78	0.90	0.97		0.99
270	0.65	0.76	0.86	0.91	0.97	

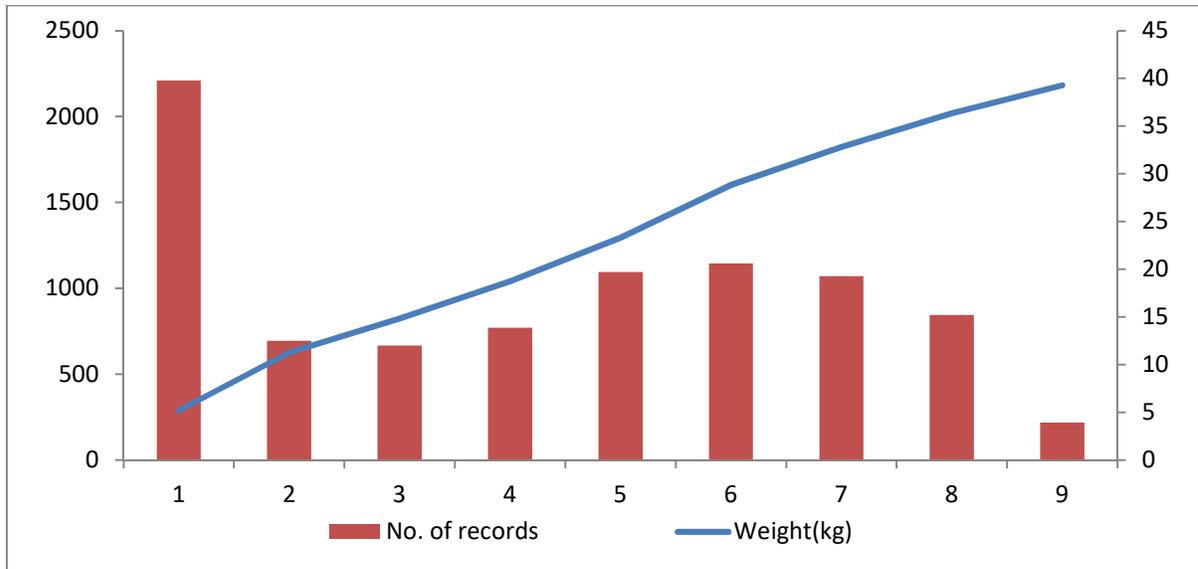


Figure 1. Number of records (bars) and test-day milk yield (lines) for each month of age.

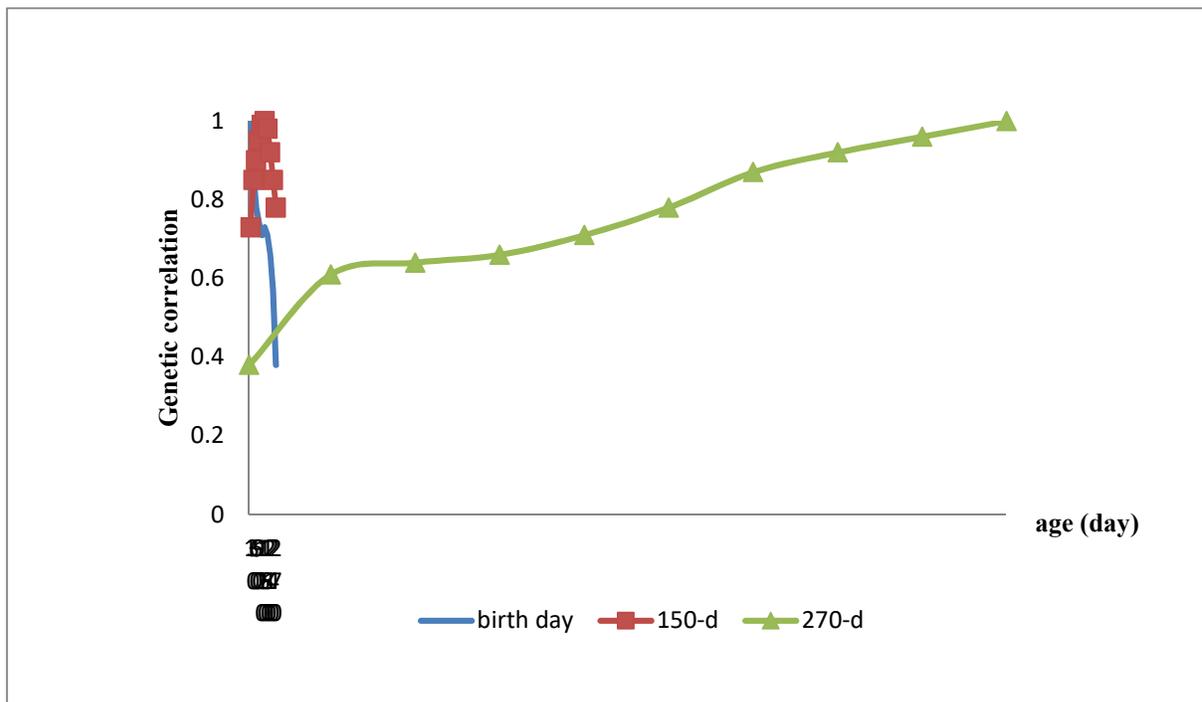


Figure 2. Genetic correlations of birth day, 150-d or 270-d with other days.

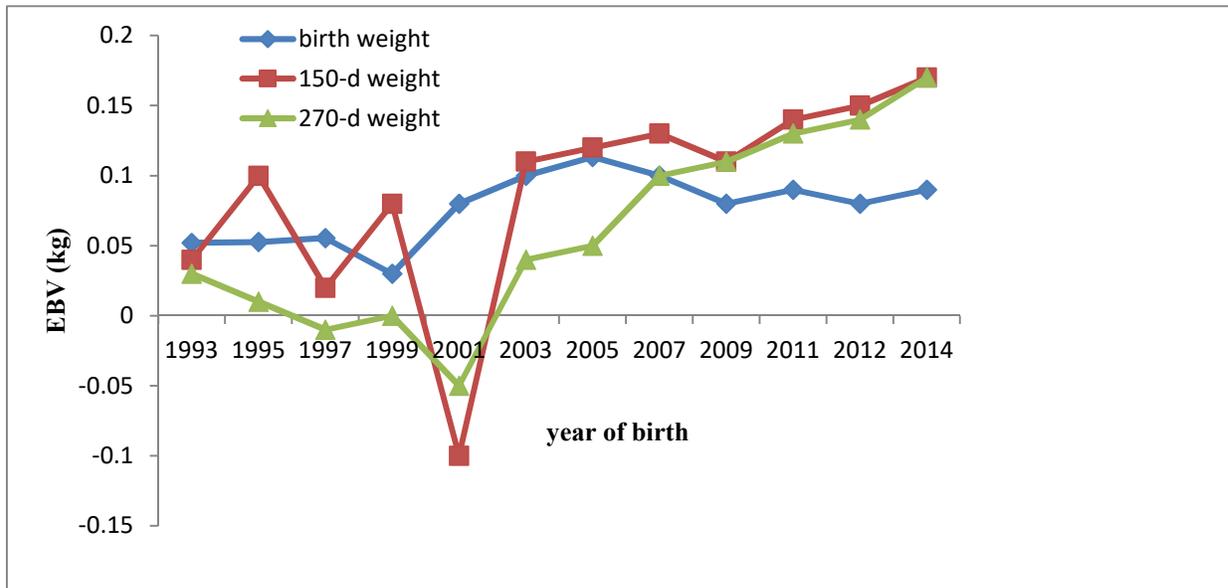


Figure 3. Mean of predicted breeding value of birth weight, 150-d and 270-d weights in each year of birth with genetic trend.

DISCUSSION

Log likelihoods and information criteria: The order of fit for the random effects was kept constant to describe the best variance formation to representation the residual variances. The results of log L and AIC demonstrated a significant improvement in the rank of fit when the heterogeneous residual variance was comprised in the model, in compared to homogeneous residual variance (Abegaz *et al.*, 2010) and model fit improved with increasing polynomial regression order. These demonstrated that residual variances had various behaviour during the age. The AIC and LRT results reflected that a step function with 7 classes was the best appropriate to apply the residual variances. The AIC results indicated that 14 models was the best proper one to explain the covariance formation of data.

Variance component and genetic parameters: The direct additive genetic variance was peak at the later ages in the growth path (Table 3). Despite of the effect of selection on additive genetic variance (Bulmer effect), the rising trend of additive genetic variance in elder ewes indicates that it is possible that a number of genes with additive effects were activated in elder ewes. This sample of changes in additive genetic variance shown that body weight of Makooei ewes are various traits at near the beginning, middle and elder ages. This rising sample of additive genetic variance as animals aged was approved with Nephawe (2004). Other studies modelling growth in sheep using random regression models have offered direct genetic variances that improved with time (Lewis and Brotherston, 2002; Fischer *et al.*, 2004; Kariuki *et al.*, 2010). The increasing trend was obtained for maternal

permanent environmental variance to 210 days, which was match to the results offered by Barazandeh *et al.* (2012) and was different from the results of Fischer *et al.* (2004) and Kariuki *et al.* (2010). Fischer *et al.* (2004) offered direct permanent environmental variances that were significantly smaller in the later ages that were different to this study. The relatively low maternal permanent environmental variances estimates found in this study can be explained by the poor quality of the pasture at the stations where sheep were raised, which resulted in lack of enough milk production available for lambs before weaning. Because the permanent environmental variance is related to non-additive genetic and non-genetic permanent environmental effects, the pattern changes in permanent environmental variance part indicated that there might be genes with non-additive genetic effect that are activated in the earlier ages, and (or) there might be non-genetic permanent effects that attach to this part in this ages. Mandal *et al.* (2006), partitioning of the total maternal effect into additive and permanent environmental components is difficult, even with the substantial numbers of repeated ewe records found in the current data. This study indicates an essential effect of permanent environmental effects on body weight in higher age for the studied population. In general, direct additive genetic and permanent environmental variances had similar trends of estimates.

Direct genetic heritability approximated in this study were upper for earlier ages, and but common trend of direct heritability in this study match to study of Kariuki *et al.* (2010) that shown estimates that declined with age. On the other hand, there are some various information that Direct genetic heritability approximated in their studies lesser for earlier ages (Lewis and

Brotherston, 2002; Fischer *et al.*, 2004; Barazandeh *et al.*, 2012). In general, estimates of direct heritability tended to reduce with age. Direct genetic heritability for earlier ages could be credited to little residual variance ratios in this range of ages due to culling surplus kids and lesser number of records compared with other ages. On the other hand, direct heritability was slighter for post-weaning weight than pre-weaning weight. These findings were in diverse with other studies (Mugambi *et al.*, 2007; Safari *et al.*, 2005; Zhang *et al.*, 2009). In this study, maternal permanent environmental effect (c^2) had modest estimates between 120 and 180 days of age and then declined during the path. Moreover, maternal permanent environmental effect had little estimates in this study which is alike to the findings of Kariuki *et al.* (2010). However, estimates of coefficient of maternal environment in this study are dissimilar from the findings of Fischer *et al.* (2004) and Ghafouri-Kesbi *et al.* (2008) which approximated modest values in near the beginning ages followed by a continuous decrease to age. This variation could be credited to a lot of factors including diverse populations, environments and models applied for analysis. The common scarcity of literature estimates for maternal effects in sheep more than a range of ages make judgment complex, however, most findings describe that maternal permanent environmental effect reduce as time lapses post-weaning (Fischer *et al.*, 2004). This connote that the dam's influence on the efficiency of their progeny was mainly affected by the environment equipped to the dam. For improved growth efficiency, it is essential that dams are equipped with a best environment (Kariuki *et al.*, 2010). According to the approximated values of different parameters in this study, it could be concluded that most of phenotypic variation of body weight of Makooei sheep during birth day to 270 days of age are related to direct genetic and permanent environmental effects, while maternal environmental effect have a little portions. In compare to the study of Kariuki *et al.* (2010) in Dorper sheep and Fischer *et al.* (2004) in Poll Dorset sheep and agreement to the findings of Ghafouri Kesbi *et al.* (2008) in Mehrabani sheep, pe^2 improved with age (Table 3), which shown environmental effects are necessary for last parts of age in Makoueisheep. The decrease in genetic correlations between weights (Figure 2) with increasing time interval between measures is fact that various weights throughout the growth curve of an individual are affected by various genes and should be considered as various correlated traits (Kariuki *et al.*, 2010). The sample of maternal permanent environmental correlations between various ages (Table 4) is similar so that correlations reduced as the age distance and this reduction is less than direct permanent environmental correlations in earlier ages. The slight direct permanent environmental correlations between earlier and later ages are an sign that the efficiency of individuals is extremely related to the ability

of the individual to endure the production conditions, i.e., produce under the harsh environment.

Genetic trend: In general, the genetic trends for birth weights were very different than those of the other body weight traits. Based on Figure 3, the genetic changes of birth weight from 1993 to 1997 show to be flat and improved in this years and then from 1997 to 1999 genetic trend declined that was probably related to the genetic trend provided by the use of negative and lowly predicted transmitting ability (PTA) rams. This trend almost was in agreement with the findings of Mokhtari and Rashidi (2010) in Kerman sheep and Bohlouli *et al.* (2013) in Zandi sheep. Selection based on birth weight was least in contrast to other body weight traits (Mohammadi *et al.*, 2011). Generally for the other weight traits (150-d and 270-d weights), there were unexpected reduces in yearly mean predicted breeding values of animals mainly in 2001. In general, Genetic trends indicated a yearly grow and were constantly positive but slight. Although the average yearly grow is a trait of economic value for beef production systems, it is not so mainly necessary for milk production systems because of selection for average yearly grow would result in improved nutritional needs near the beginning in life, with larger costs for protection of dairy ewes (Lobo *et al.*, 2000).

Conclusions: The present study showed that random regression model of 4 orders for fixed effect, 5 orders for direct genetic effect, 4 orders for direct permanent environmental and 5 order for maternal permanent environmental effects with heterogeneous residual variances, was the greatest for modelling the growth curve in adult Makooei ewes. However, there is the need to develop data set to improve accuracy of parameter estimates and let extra broad evaluations. The findings of this study shows that the majority phenotypic variation of body weight of Makooei sheep along birth day to 270 days of age are related to direct genetic and permanent environmental effects, whereas maternal environmental effect have little portions. Estimates of genetic trends showed that there was positive genetic development in all considered traits and showed that selection would be useful for the enhancement of body weight traits of Makooei sheep.

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Conflict of interest: The authors declare that they have no conflict of interest.

Ethical statement: The manuscript does not contain clinical studies or patient data.

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