

Estimation of Variance Components for Body Weight of Moghani Sheep Using B-Spline Random Regression Models

Research Article

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ABSTRACT

The aim of the present study was the estimation of (co) variance components and genetic parameters for body weight of Moghani sheep, using random regression models based on B-Splines functions. The data set included 9165 body weight records from 60 to 360 days of age from 2811 Moghani sheep, collected between 1994 to 2013 from Jafar-Abad Animal Research and Breeding Institute, Ardabil province, Iran. Random regression models were employed to analyze the data. Contemporary groups (year-season of birth - sex-birth type-dam age at the birth) and fixed regression of body weight on age were considered as fixed parts of the models. Random regressions of direct additive genetic, permanent environment, maternal additive genetic and maternal environment were random parts of the models. Linear and quadratic B-Spline functions with two or three coefficients were fitted for fixed and random regressions of the models. A heterogeneous structure of residual variance was considered in five age classes. Variance components were estimated by average information algorithm of restricted maximum likelihood (AI-REML). Different models were compared based on Akaike information criterion (AIC) and Schwarz Bayesian information criterion (BIC). According to both criteria, the best model was a model with quadratic B-Spline functions with 3, 3, 3, 2 and 2 coefficients for fixed regression and random regressions of direct additive genetic, permanent environmental, maternal additive genetic and maternal environmental effects, respectively. According to this model, low to moderate estimates of direct heritability (0.135 to 0.330) and moderate to high estimates of coefficient of permanent environmental effects (0.229 to 0.613) were obtained, while estimates of maternal heritability (0.05 to 0.14) and coefficient of maternal environment (less than 0.01) were low or negligible in all ages.

KEY WORDS body weight, B-Spline function, random regression model, variance components.

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). Moghani sheep is one of the most important Iranian meat type sheep and it is well known for its large size, high tolerance to climatic changes and ability to produce heavy lambs (Shodja *et al.* 2006). Random regression models (RRM) are employed for analysis of the traits with repeated records over the time. According to Meyer (2000), random regression models accommodate

repeated records for traits that gradually change over time and require no assumptions about the constancy of variances and correlations. Random regression models have been applied to sheep data from research flocks which typically contain many repeated records per animal (Lewis and Brotherstone, 2002). Functions with random coefficients in longitudinal models describe variance changes of the studied trait along a trajectory. Spline functions are defined as the curves consisting individual segments of lower-degree polynomials connected at specific points, called knots (Meyer, 2005). A particular kind of Spline curve is called B-Spline (de Boor, 2001). B-Spline functions are one of the several types of functions that can be used in random regressions models. B-Spline functions are adequate to fit random effects in mixed model analyses and efficient to estimate covariance functions (Rice and Wu, 2001). Meyer (2005) modeled the growth curve of beef cattle by random regression models, using B-Spline functions and observed no differences in genetic parameter estimates between models with equidistant and non-equidistant knots. Generally, the Spline functions need less computational requirements than the corresponding analyses with the same number of coefficients using Legendre polynomials, because the mixed models based on Spline functions have more sparse matrices (Meyer, 2005; Misztal, 2006). There are several studies on the use of random regression models based on Legendre polynomial functions for analysis of sheep growth (Fischer *et al.* 2004; Sarmiento *et al.* 2006; Kariuki *et al.* 2010), but there is not any studies applying RRM based on B-Splines functions. The objective of the present study was to estimate (co) variance components and genetic parameters for body weight of Moghani sheep using random regression models based on B-Splines functions.

MATERIALS AND METHODS

Animals and management

The Moghani sheep flock of Jafar-Abad Animal Research and Breeding Institute, Ardabil province, Iran was investigated in the present study. This flock is managed under an intensive system.

The data set included 9165 body weight records from 60 to 360 days of age from 2811 sheep. These records were collected since 1994 to 2013. The animals were fed on pasture in all seasons except winter. In general, the main feeding source was rangeland grass and agricultural residues but the breeding animals were supplemented with barley grain two weeks prior to the beginning of breeding season, during late pregnancy and early lactation. The characteristics of the data set are presented in Table 1. Distribution and average of body weight records in different ages are illustrated in Figure 1.

Data analysis

A preliminary analysis for determination of the fixed effects affecting the body weight records was performed by a general linear model analysis using GLM procedure of SAS software (SAS, 2004). Contemporary groups as composition 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 thus included as the fixed effect in the models used for estimation of variance components.

Variance components were estimated by single-trait analysis of random regression models. The models included fixed effect of contemporary group (year-season of birth - age of dam at lambing - sex - type of birth), a fixed regression to describe the average shape of growth curve and four random regressions for random direct additive genetic, permanent environmental, maternal additive genetic and maternal environmental effects. Linear and quadratic B-Spline functions with either 2 or 3 parameters were used to fit the fixed or random regression functions. A heterogeneous structure of residual variance including five classes of residual variance (in 60 to 120, 121 to 180, 181 to 240, 241 to 300 and 301 to 365 days of age) was considered for the models. The model used was as follow:

$$y_{ij} = cg_i + \sum_{m=0}^{k_f-1} \beta_m B_m(t_{ij}) + \sum_{m=0}^{k_a-1} \alpha_{pm} B_m(t_{ij}) + \sum_{m=0}^{k_m-1} \gamma_{pm} B_m(t_{ij}) + \sum_{m=0}^{k_c-1} \delta_{pm} B_m(t_{ij}) + \sum_{m=0}^{k_q-1} \rho_{pm} B_m(t_{ij}) + e_{ij}$$

Where:

y_{ij} : record.

cg_i : fixed effect for the i^{th} contemporary group.

β_m : fixed regression coefficient to fit the mean growth trajectory of the population.

α_{pm} , γ_{pm} , δ_{pm} and ρ_{pm} : p^{th} random regression coefficients for direct additive genetic, maternal additive genetic, direct permanent environmental and maternal environmental effects, respectively.

Covariables $B_m(t_{ij})$: values of the m^{th} B-Spline function, evaluated for t_{ij} .

k_f : order of fit for fixed regression (degree= k_f-1).

k_a , k_m , k_c and k_q : orders of fit for the corresponding random effects.

e_{ij} : random residual effect.

Generally, a total of 26 models with different orders and number of parameters were compared for estimation of variance components. The variance components were estimated by Average information algorithm of restricted maximum likelihood (AI-REML), using the WOMBAT software (Meyer, 2007). Convergence criterion was 10^{-8} . The models with different orders and number of parameters for different effects were compared based on Akaike's information criterion (AIC) (Akaike, 1974) and Schwarz's Bayesian information criterion (BIC) (Schwarz, 1978). The AIC and BIC were calculated as follow:

$$\text{AIC} = -2 \log L + 2p$$

$$\text{BIC} = -2 \log L + p \log(N-r)$$

Where:

p: number of parameters estimated.

N: number of records.

r: rank of incidence matrix for the fixed effects.

Log L: REML maximum log likelihood.

The model with the lowest AIC or BIC values was considered as the best model. The models were identified as:

XNf-XNa, Np, Nm and Nc

Where:

X: degree of the functions (L and Q for linear quadratic, respectively).

Nf, Na, Np, Nm and Nc: number of parameters for fixed regression, direct additive genetic (a), permanent environmental (p), maternal genetic (m) and maternal environmental (c) effects, respectively.

For example, Q2-L3,3,2,2 indicates the model fitting a quadratic B-Spline function with 2 parameters for fixed regression and linear B-Spline functions 3, 3, 2 and 2 parameters for direct additive genetic, permanent environmental, maternal genetic and environmental effect regressions, respectively. The number of parameters equals the number of segments in linear functions and the number of knots in quadratic functions.

RESULTS AND DISCUSSION

Fitting the models

The results of fitting the studied models, including log likelihood, AIC and BIC values are presented in Table 2. Generally, increased order of fit from linear (L) to quadratic (Q) and increase of number of parameters from 2 to 3 decreased the BIC and AIC values and, thus, improved the fitting ability of the models.

However, the models with 3 parameters for maternal environment regression could not be converged and, thus, were not presented in Table 2.

Total number of parameters in the models varied from 17 to 26 parameters. The model 24 (Q3-Q3,3,2,2) had the highest log L and the lowest AIC and BIC and thus it is considered as the best model. The best model had quadratic B-Spline functions with three parameters for fixed regression and quadratic B-Spline functions with 3, 3, 2 and 2 parameters for direct additive genetic, permanent environmental, maternal genetic and maternal environmental effects, respectively.

Table 1 Descriptive statistics of the data set and pedigree structure

Total no. of records	9165
Average (kg)	34.6
Standard deviation (kg)	8.11
Maximum (kg)	58
Minimum (kg)	10.5
CV (%)	23.83
No. of animals with records	2811
No. of animals with 3 records	2097
No. of animals with 4 records	698
No. of animals with 5 and more records	16
No. of animals in the pedigree	4243
No. of sires	411
No. of dams	1946

CV: coefficient(s) of variation.

Estimates of variance components and genetic parameters

Estimates of variance components for body weight at different ages are presented in Figures 2, 3 and 4. Direct additive genetic variance decreased from 5.93 (day 60) to 1.97 (day 114) and increased afterwards to 7.36 in day 365, as the last studied age (Figure 2). Direct permanent environmental variance increased gradually over the trajectory, where 3.39 in day 82 and 14.17 in day 365 were the lowest and the highest estimates of permanent environmental variance (Figure 2).

This observation denotes an important effect of permanent environmental effects on body weight in higher age for the studied population. Generally, direct additive genetic and permanent environmental variances had similar trends of estimates (Figure 2). Estimate of maternal additive genetic variance decreased from 0.92 in day 60 to 0.64 in day 91, then dramatically increased to 2.6 in day 270 and finally reduced to 1.5 in day 365 (Figure 3). Maternal environmental variance had a negligible estimate of variance ranging from 0.06 to 0.20 (Figure 3). Estimates of phenotypic variance are illustrated in Figure 4. The least and the highest phenotypic variances were estimated in days 60 and 240, respectively.

Table 2 The results of fitting different models, including number of estimated parameters (NP), log likelihood (Log L), Akaike information criterion (AIC) and Bayesian information criterion (BIC)

Model	Model	NP	Log L	AIC	BIC
1	L2-L2,2,2,2	17	-16715.023	33464.046	33584.290
2	L2-L2,3,2,2	20	-16600.662	33241.324	33382.790
3	L2-L2,2,3,2	20	-16759.304	33558.608	33700.074
4	L2-L2,3,3,2	23	-16580.867	33207.734	33370.418
5	L2-L3,2,2,2	20	-16603.668	33247.336	33388.800
6	L2-L3,3,2,2	23	-16551.666	33149.332	33312.018
7	L2-L3,2,3,2	23	-16581.846	33209.692	33372.378
8	L2-L3,3,3,2	26	-16537.602	33127.204	33311.110
9	L2-Q2,2,2,2	17	-17468.670	34971.340	35091.586
10	L2-Q2,3,2,2	20	-16565.837	33171.674	33313.140
11	L2-Q2,2,3,2	20	-16602.411	33244.822	33386.288
12	L2-Q2,3,3,2	23	-16565.110	33176.220	33338.906
13	L2-Q3,2,2,2	20	-16567.686	33175.372	33316.836
14	L2-Q3,3,2,2	23	-16551.928	33149.856	33312.540
15	L2-Q3,3,3,2	26	-16551.288	33154.576	33338.482
16	Q3-L2,3,2,2	20	-16745.515	33531.030	33672.494
17	Q3-L3,2,2,2	20	-16272.785	32585.570	32727.034
18	Q3-L3,3,2,2	23	-16199.733	32445.466	32608.148
19	Q3-Q2,2,2,2	17	-17266.705	34567.410	34687.652
20	Q3-Q2,3,2,2	20	-16223.156	32486.312	32627.774
21	Q3-Q2,2,3,2	20	-16257.121	32554.242	32695.704
22	Q3-Q2,3,3,2	23	-16205.428	32456.856	32619.538
23	Q3-Q3,2,2,2	20	-16212.249	32464.498	32605.960
24	Q3-Q3,3,2,2	23	-16190.020	32426.040	32588.722
25	Q3-Q3,2,3,2	23	-16211.891	32469.782	32632.464
26	Q3-Q3,3,3,2	26	-16189.903	32431.806	32615.708

The models are identified as: XNF-XNa, Np, Nm, Nc
Where:

X: degree of the functions (L and Q for linear quadratic, respectively).

Nf, Na, Np, Nm and Nc: number of parameters for fixed regression, direct additive genetic, permanent environmental, maternal genetic and maternal environmental effects, respectively.

The best model (Q3-Q3,3,2,2), according to AIC and BIC is presented by bold font.

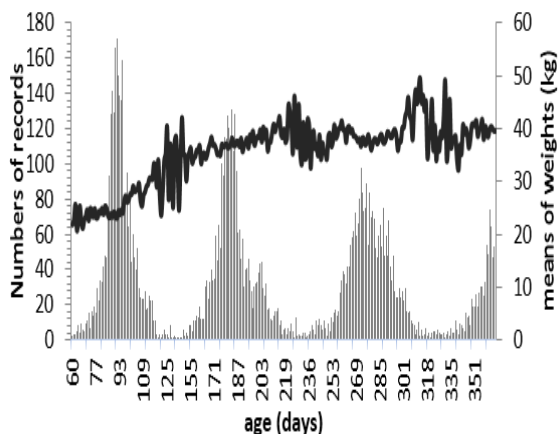


Figure 1 Numbers of records (■) and means of observed weights (—)

A distinct trend of phenotypic variance (Figure 4) is due to distinct estimation of residual variance in five classes. Estimates of direct heritability and coefficient of permanent environment as proportion of permanent environmental to phenotypic variances are presented in Figure 5.

Estimates of direct heritability declined from 0.351 in day 60 to 0.135 in day 120 then gradually increased throughout the trajectory. However, the highest estimate of heritability for post-weaning body weight (0.330) was observed in 225 d of age. Estimate of coefficient of permanent environment increased continuously with increase of age, where the lowest and the highest coefficients of permanent environment (0.229 and 0.613, respectively) were estimated in days 60 and 365, respectively. The coefficient of permanent environment had high estimates in most of growth trajectory which indicates an important role of permanent environment in phenotypic variation. Estimated values of direct heritability and coefficient of permanent environment (Figure 5) indicates that the direct additive genetic and permanent environmental effects are main sources of phenotypic variation of body weight in different ages. Maternal heritability had low estimates ranging from 0.05 in days 72-96 to 0.14 in day 225 (Figure 6), which was noticeably lower than the estimates of direct heritability (Figure 5). Coefficient of maternal environment as the proportion of maternal environmental to phenotypic variances had negligible estimates up to 0.01 in all ages (Figure 6).

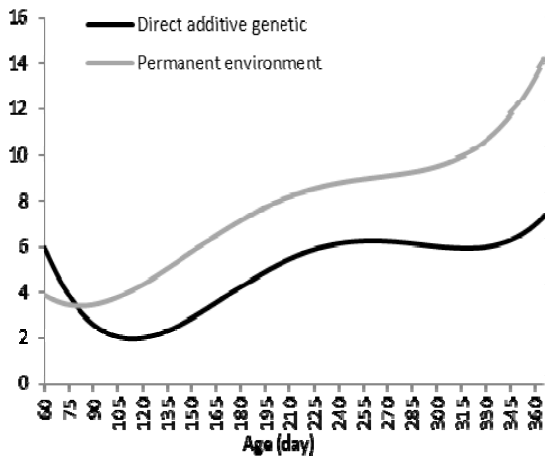


Figure 2 Estimates of direct additive genetic and permanent environmental variances by the best model (Q3-Q3,3,2,2)

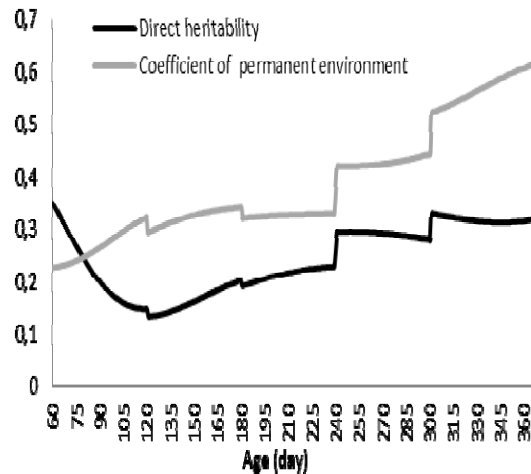


Figure 5 Estimates of direct heritability and coefficient of permanent environment by the best model (Q3-Q3,3,2,2)

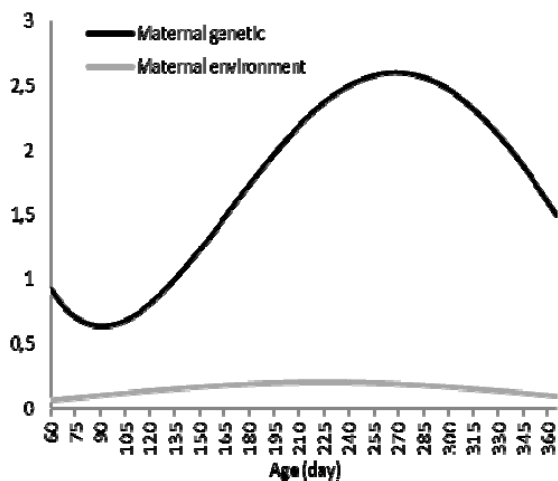


Figure 3 Estimates of maternal genetic and maternal environmental variances by the best model (Q3-Q3,3,2,2)

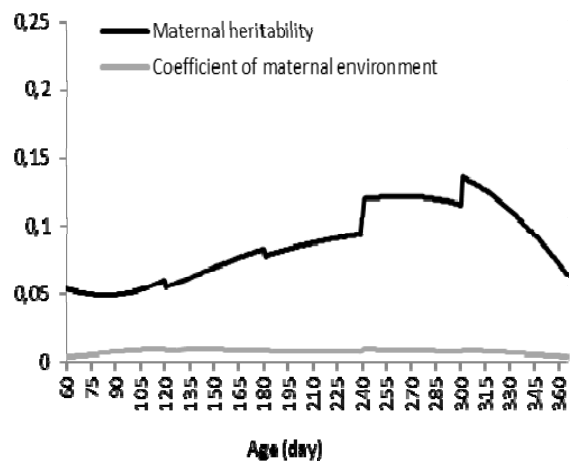


Figure 6 Estimates of maternal heritability and coefficient of maternal environment by the best model (Q3-Q3,3,2,2)

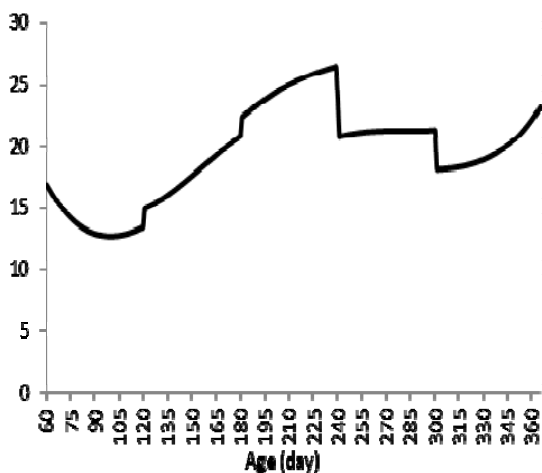


Figure 4 Estimates of phenotypic variance by the best model (Q3-Q3,3,2,2)

Estimates of direct additive genetic and phenotypic correlations between body weights at some selected ages are presented in Table 3. The estimates of additive genetic and phenotypic correlations were in ranges of -0.64 to 0.90 and -0.20 to 0.71, respectively. Generally, direct additive genetic and phenotypic correlations decreased in higher age intervals. In the present study, the model fitted by quadratic B-Spline functions with 3, 3, 3, 2 and 2 coefficients for fixed regression and random regressions of direct additive genetic, permanent environmental, maternal additive genetic and maternal environmental effects, respectively was the best model for estimation of variance components for body weight in Moghani sheep. Random regression models based on Legendre polynomial functions have been frequently used for analysis of sheep growth (Fischer *et al.* 2004; Sarmiento *et al.* 2006; Kariuki *et al.* 2010), but no study applying B-Spline RRM was found in the literature.

The pattern of direct additive genetic variance (Figure 2) was to some extent in agreement with results of a previous study in Mehraban sheep (Ghafouri Kesbi *et al.* 2008).

Table 3 Estimates of direct additive genetic and phenotypic correlations (above and below diagonal, respectively) for body weights from 60 to 365 days of age estimated by the best model (Q3-Q3,3,2,2)

Age	60	142	217	291	365
60	-	0.028	-0.512	-0.649	-0.414
142	0.156	-	0.825	0.550	-0.079
217	-0.096	0.534	-	0.901	0.318
291	-0.204	0.474	0.681	-	0.689
365	-0.156	0.153	0.379	0.715	-

Likelihoods, Kariuki *et al.* (2010) reported a similar pattern for direct additive variance in Dorper sheep. Increase of direct additive genetic variance with age has been also observed by Sarmiento *et al.* (2006), Molina *et al.* (2007) and Najafi *et al.* (2011) in Santa Ines sheep, Spanish Merino and Moghani sheep, respectively. In the study of Najafi *et al.* (2011) on body weight of Moghani sheep from birth to 365 days of age, a random regression model, based on Legendre polynomials with orders 2, 2 and 4 for direct additive genetic, maternal additive genetic and permanent environment effects, respectively, was the best model. Increase of direct additive genetic variances with age, is also reported in other studies involving random regression models based on Legendre polynomials (Lewis and Brotherstone, 2002; Fischer *et al.* 2004).

Increase of permanent environmental variance of body weight (Figure 2) is in accordance with findings of Kariuki *et al.* (2010) in Dorper sheep and Molina *et al.* (2007) in Merino sheep. Ghafouri-Kesbi *et al.* (2008) reported that the permanent environmental variance of body weight in Mehraban sheep increases with age and reach to a peak at 240 days of age and remain relatively constant thereafter. Najafi *et al.* (2011) reported that permanent environmental variance increased from birth to 270 days of age and then decreased at 360 days of age in Moghani sheep. Fischer *et al.* (2004) stated that permanent environment effect increase after birth to a peak at 300 days and then decrease.

The increasing trend observed for maternal additive genetic variance up to around 270 days of age and decreasing afterward was correspond to the result reported by Molina *et al.* (2007) and Ghafouri Kesbi *et al.* (2008) in Mehraban sheep. However, Molina *et al.* (2007) studied random regression of growth during the first three months of age. The results of the present study is also in agreement with those of Kariuki *et al.* (2010) and Najafi *et al.* (2011) who reported increase of maternal additive genetic variance over the growth trajectory.

Negligible estimates of maternal environmental variance in the present study (Figure 3) represent a low effect of maternal environment on phenotypic variance of body

weight. Ghafouri-Kesbi *et al.* (2008) reported that maternal environmental variance was considerably lower in later ages. In contrast, Wolca *et al.* (2011) reported an increase of maternal environmental variance with age. Meyer (2005), Baldi *et al.* (2010) and Boligon *et al.* (2011) used B-Spline functions in random regression models to investigate growth curve of cattle. They found that the maternal environmental and additive genetic variance increase up to a peak and then decline. Safaei *et al.* (2006) reported that the maternal variances tend to be higher at younger age and decline with age, particularly afar post-weaning ages (more than 120 days).

General trend of phenotypic variance estimated in the present study is in agreement with previous studies. Najafi *et al.* (2011) observed increasing trend of phenotypic variance with a decline at 270 days of age. Fischer *et al.* (2004) reported an increase of phenotypic variance from 50 to 300 days of age. In another study, estimation of phenotypic variance increased throughout the growth trajectory (Kariuki *et al.* 2010). Likewise, in study of Vatankhah (2012) phenotypic variance of ewe body weight increased as ewe age increased.

General trend of direct heritability estimates which declined from day 60 to day 120 then gradually increased throughout the trajectory (Figure 5) was to some extent in agreement with reports of Lewis and Brotherstone (2002) in Suffolk lambs and Kariuki *et al.* (2010) in Dorper sheep. Lewis and Brotherstone (2002) reported 0.27, 0.23, 0.26, 0.30, 0.35 and 0.39 amounts of heritability for the weight at 15 day, 30 day, 45 day, 60 day, 90 day, 120 day and 150 days, respectively. In the study of Kariuki *et al.* (2010), direct genetic heritability estimates declined sharply from 0.13 at 20 days to 0.07 at 80 days of age after which estimates were fairly constant. Najafi *et al.* (2011) obtained low values of direct heritability (0.002-0.069) for body weight of Moghani sheep, but general trend of direct heritability in their study agrees with the results of the present study.

In the present study, the coefficient of permanent environment as proportion of permanent environmental to phenotypic variances was tended to gradually increase in higher ages (Figure 5). This finding is in agreement with the report of Ghafouri-Kesbi *et al.* (2008). However, there are some different reports such as Najafi *et al.* (2011) who indicated that coefficient of permanent environmental effects increase after birth to a peak at 270 days and then decrease. Likewise, Fischer *et al.* (2004) reported that coefficient of permanent environment show an increase from 50 to 200 days of age and a decrease thereafter until 500 days of age. These differences could be attributed to many factors such as some differences in the studied populations, managements, climates, models used for analysis and so on.

Low estimates of maternal heritability in the present study are in agreement with previous studies such as Fischer *et al.* (2004), Ghafouri-Kesbi *et al.* (2008) and Najafi *et al.* (2011). Coefficient of maternal environment as proportion of maternal to phenotypic variances had negligible estimates in the present study which is similar to the results of Kariuki *et al.* (2010). However, estimates of coefficient of maternal environment in the present study are different from the reports of Fischer *et al.* (2004) and Ghafouri-Kesbi *et al.* (2008) which estimated moderate values in early ages followed by a continuous decline with age. This difference could be attributed to many factors including different populations, environments and models used for analysis.

According to the estimated values of various parameters in the present study, it could be concluded that most of phenotypic variation of body weight of Moghani sheep during 60 to 365 days of age are due to direct genetic and permanent environmental effects, while maternal (either genetic or environmental) effects have a low contributions.

In the present study, genetic and phenotypic correlations decreased with increasing interval between the weights (Table 3). This result was in agreement with the findings of Fischer *et al.* (2004) and Kariuki *et al.* (2010). Low genetic correlations between body weights at first age (day 60) and last ages (days 142 to 365) indicate that early body weights are not under same genetic control as body weight at last ages. Fischer *et al.* (2004) concluded that genetic correlation between body weights at first ages (50 and 250 days) were lower (0.46) than the correlation between body weights at adult ages (300 and 500 days) within the same period (0.86). A similar pattern of genetic correlation between different ages was reported in Meraban sheep (Ghafouri Kesbi *et al.* 2008).

CONCLUSION

According to results of the present study, the best model for estimation of variance components for body weight of Moghani sheep was a model with quadratic B-Spline functions having three parameters for fixed regression and quadratic B-Spline functions with 3, 3, 2 and 2 parameters for direct additive genetic, permanent environmental, maternal genetic and maternal environmental effects, respectively. Low to moderate estimates of direct heritability (0.135-0.330) and moderate to high estimates of coefficient of permanent environmental effects (0.229 to 0.613) were obtained, while estimates of maternal heritability (0.05 to 0.14) and coefficient of maternal environment (less than 0.01) were low or negligible in all ages. The results of the present study indicates that most of the phenotypic variation of body weight of Moghani sheep during 60 to 365 days of age are due to direct genetic and permanent envi-

ronmental effects, while maternal (either genetic or environmental) effect have low contributions.

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