

RESEARCH OPINIONS IN ANIMAL & VETERINARY SCIENCES

ISSN 2221-1896 (PRINT) www.roavs.com

ISSN 2223-0343 (ONLINE)

Estimation of genetic parameters for growth traits in Moghani sheep using random regression

M. J. Najafi¹, A. Lavvaf¹, B. Hemmati¹, T.Farahvash² and R. Abdollahpoor³

¹Department of Animal Science, Karaj Branch, Islamic Azad University, Karaj, Iran ²Department of Animal Science, Shabestar Branch, Islamic Azad University, Shabestar, Iran ³Department of Animal Science, Ghaemshahr Branch, Islamic Azad University, Ghaemshahr, Iran

Abstract

The aim of this study was to estimate genetic parameters for body weight traits in Moghani sheep using random regression models. The Data were 19388 test day records collected from 6013 animals at JafarAbad plain research station located in Moghan, Ardebil province, from 1995 to 2009. The model used to analyze data included: year-season, birth year-season, sex, birth type and dam parity records as classified fixed effects and dam's age at parturition and animal's age as covariate variables. Random effects included in model were; direct additive genetic effect, maternal additive genetic effect, direct permanent environment effect and residual effect. Model 9 with 2th order of fit for genetic effects and 4th order of fit for permanent environment effect and with 21 parameters were considered as the most appropriate model. Residual effects were assumed heterogeneous between recording ages. Data analyzed by using of the DFREML software. Direct heritability for birth weight, 90, 180, 270 and 360 days of age were: 0.069, 0.002, 0.005, 0.013 and 0.021, respectively. These results showed that direct heritability reduced after birth and reached to the lowest amount in 90 days of age, but after that increased as the age increased. Maternal heritability had considerable reduction after birth and then increased as the age increased to 360. The weight of 270d and 360d had correlation which reduced as the distance between ages increased.

Keywords: Heritability, Random Regression, Genetic Parameters, Growth Traits

Introduction

One of the best models for analyzing repeated data in different ages (that is called repeated data at time), is that different means and co-variances of the animal's life involved in evaluating the genetic parameters (Aziz et al., 2005; Mrod, 2005). Schaeffer and Dekkers (1994) suggested Random Regression Model (RRM) for the analysis of test day records in dairy cattle. In this model, the co-variance between repeated traits through the whole life of animal is considered. Kirkpatrick et al. (1990) and Kirkpatrick et al. (1994) used Covariance Functions (CF) to analyze repeated records over time and described growth traits using this model. RRM allows to study changes in genetic variation over the time and to select individuals in order to alter the general patterns of response over time (Scheaffer, 2004). RRM have

advantages such as: non-require to correct records to obtain weight at specific age, possibility to allow specific environment effects proper to each age of recording in statistical analysis for estimating genetic parameters and predicting breeding value and it seems to be a better method in evaluating genetic parameters and predicting breeding value in comparison to animal models (Meyer, 1998; Dekkers, 2002; Meyer, 2002). During recent years, many studies have been done in cattle using RRM to estimate genetic parameters of body weight traits (Albuquerque and Meyer, 2001; Meyer, 2001; Meyer, 2002; Aziz et al., 2005) and sheep (Levis and Brotherstone, 2002; Fischer et al., 2004, Abbasi et al., 2004; Safaei et al., 2006; Molina et al., 2007; Nedaii et al., 2010; Oliveira et al., 2010). Prediction of breeding value at lower ages and welltimed decision-making in culling and/or selecting animals, reducing of generation interval and

Corresponding author: Abolghasem Lavvaf, Department of Animal Science, Faculty of Agriculture, Karaj Branch, Islamic Azad University, Karaj, Iran. Phon:00989126632834 increasing the accuracy of estimation of genetic parameters and prediction of breeding value makes RRM as a popular method in animal breeding (Kirkpatrick et al., 1990, Swalve, 1998). In RRM, a fixed regression is used to describe the average growth curve of all of animals and a random regression is used for each animal to calculate the deviations from the average growth curve that allows involving specific environment effect of each record in model (Levis and Brotherstone, 2002). The aim of this study was to estimate the genetic parameters of growth traits in Moghani sheep by using random regression method.

Materials and Methods

Data used in present research include test day records proper to body weight traits in Moghani sheep collected from 1995 to 2009 at JafarAbad Animal Research and Breeding Institution, Iran. Fixed effects were: sex, birth type, dam parity, year-season of record and year-season of birth as classified fixed effects and age of dam in parturition and age of lamb at the time of recording as covariant variables. The test of normality was done by using SAS software. Parameters estimated by using DFREML software with the average of information (AI- REML). Statistical model used to estimate parameters was as follows:

$$y_{ijfdkm} = YSR_{i} + YSB_{j} + S_{f} + L_{d} + P_{k} + \sum_{n=0}^{2} \dot{b}_{n} \left(Age_{ijfdkm} \right)^{n} + \sum_{m=0}^{4} \beta_{m} \phi_{m} \left(a^{*}_{ijfdkm} \right) \\ + \sum_{m=0}^{k_{0}-1} \alpha_{pm} \phi_{m} \left(a^{*}_{ijfdkm} \right) + \sum_{m=0}^{k_{m-1}} \gamma_{pm} \phi_{m} \left(a^{*}_{ijfdkm} \right) \\ + \sum_{m=0}^{k_{0}-1} \rho_{pm} \phi_{m} \left(a^{*}_{ijfdkm} \right) + \varepsilon_{ijfdkm}$$

Where; y_{ijfdkm} : test day records; YSR_i : ith yearseason of record; YSB_j : jth year-season of birth; S_f : fth sex of animal; L_d : dth birth type of animal; P_k : kth parity of dam; b_n : nth regression coefficient for age of ewe at parturition; β_m : mth fixed regression coefficient for age at record; α_{pm} , γ_{pm} and ρ_{pm} : mth order random regression coefficients for direct additive genetic, maternal additive genetic and direct permanent environmental effects, respectively; ε_{ijfdkm} : random residual effect; a^*_{ijfdkm} :standardized age (-1 to +1) at recording that obtained by this formula:

$$a^*_{ijfdkm} = -1 + \frac{2(t - t_{\min})}{t_{max} - t_{\min}}$$

Which: t: age of record; \mathbf{t}_{max} :maximum age at recording; \mathbf{t}_{min} :minimum age at recording; Age_{ijfdkm} :age of dam parturition; $\boldsymbol{\phi}_m \left(\boldsymbol{a^*}_{ijfdkm} \right)$: mth Legendre polynomial of age at recording and \boldsymbol{k}_a , \mathbf{k}_m and \mathbf{k}_q :the orders of fit for covariance functions of direct additive genetic, maternal additive genetic and direct permanent environmental, respectively. The variance (covariance) matrix of model was:

$$\operatorname{Var} \begin{vmatrix} \alpha \\ \gamma \\ \rho \\ \epsilon \end{vmatrix} = \begin{vmatrix} k_{A} \otimes A & 0 & 0 & 0 \\ 0 & k_{M} \otimes A & 0 & 0 \\ 0 & 0 & k_{Q} \otimes I & 0 \\ 0 & 0 & 0 & R \end{vmatrix}$$

where: A: numerator relationship matrix; \mathbf{k}_{A} , \mathbf{k}_{M} and \mathbf{k}_{Q} :matrices of variance (covariance) of random regression coefficients for direct additive genetic, maternal additive genetic and direct permanent environmental effects, respectively and \mathbf{R} :matrix of variance (covariance) of residual effect. The matrix form of model is:

$$\gamma_2 + Z_1 \alpha y = \beta X + Z + Z_3 \rho_+ \varepsilon$$

Where: y:vector of test day records; β :vector of fixed effects, including the fixed regression coefficients; α , γ and ρ :vectors of random regression coefficients for direct additive genetic, maternal additive genetic and direct permanent environmental effects, respectively; ϵ :vector of residual effect; X, Z₁, Z₂ and Z₃ incidence matrices for fixed regression coefficients, random regression coefficients for direct additive genetic, maternal additive genetic, maternal additive genetic and direct permanent environmental effects, respectively.

Comparison of models & selection of better model

Totally twelve models were fitted, models differ by type of available effects in model and the order of fit used for these effects. In all of models, Residual effects considered as heterogeneous. Criterion for selection of better model was having of high log likelihood and low amounts for AIC (AIC = $2\log L + 2p$ and BIC (BIC =- $2\log L + p \log(n - x)$). Where; p: number of parameters; n:number of records; x:number of fixed effects. Criterion paramount and most complete was BIC and a model that has least of BIC was better model. Number of parameters calculated by this formula (Kirkpatrick et al., 1990):

$$p = \frac{k(k+1)}{2}$$

Where; k: order of fit for Legendre polynomials for each of random effect.

Results

Number of records and mean weights at various ages are shown in figure 1. Body weight has an increasing trend with age from birth to 360 days of age, while number of records reduced during this time. Different models were fitted for data and a description of each with the corresponding Log L, AIC and BIC values are given in table 1. The variance (co-variance) matrices of RR coefficients and corresponding correlations for model 9 are listed in table 2. Figure 2 illustrates variance components for model 9 for each random component. Figure 3 illustrates the amount of direct and maternal heritability. The proportion of environmental direct permanent variance to phenotypic variance and repeatability are shown in figure 4. Table 3 shows the direct genetic and phenotypic correlations between weights at selected ages.



Fig. 1: Number of records and mean weights for various ages of Moghani sheep





Fig. 2: Estimates of direct additive genetic, maternal additive genetic, direct permanent environment, residual and phenotypic variance





Fig. 3: Estimates of direct and maternal heritability





Fig. 4: Estimates of proportion of direct permanent environmental variance to phenotypic variance and repeatability

Discussion

In first six models, available effects in model other than residual effect were including of direct additive genetic effect and direct permanent environment effect (Table 1). Increased order of fit for these effects, improved the BIC value (model 1 to 6). Adding maternal additive genetic effect to model, improved BIC value. Increasing the order of fit for direct additive genetic and maternal additive genetic effects from 2 to 3 or more, did not showed desirable results but increasing the order of fit for direct permanent environment effect from 2 to 4 seemed to be effective, but higher order of fit, increased BIC value. Finally based on the main criterion for better model (a model with the least BIC value) model 9

Model	ka	\mathbf{k}_m	\mathbf{k}_q	р	Log L	-2LL	AIC	BIC
1	2	0	2	11	-26439.8	52879.5	52901.5	52988.04
2	2	0	3	14	-25239.4	50478.8	50506.8	50616.89
3	3	0	3	17	-25221.1	50442.3	50476.3	50610.01
4	4	0	4	25	-25159.1	50318.2	50368.2	50564.84
5	4	0	5	30	-25137.9	50275.8	50335.8	50571.82
6	5	0	5	35	-25064.7	50129.4	50199.4	50474.74
7	2	2	2	14	-26356	52711.9	52739.9	52850.06
8	2	2	3	17	-25165.3	50330.5	50364.5	50498.25
9	2	2	4	21	-25111	50221.9	50263.9	50429.12
10	3	3	3	23	-25132.6	50265.3	50311.3	50492.24
11	3	3	5	32	-25068.4	50136.8	50200.8	50452.5
12	4	4	4	35	-25070.9	50141.9	50211.9	50487.22

 Table 1: Different models for fit of covariance functions and their descriptions

 k_a , k_m and k_q are the orders of fit for covariance functions of direct additive genetic, maternal additive genetic and direct permanent environmental, respectively

Table 2: Estimates of matrices of variance (covari- ance) of random regression coefficients (lower triangle) and the corresponding correlations (upper triangle) together with eigenvalues (λ) of the variance (covariance) matrices (0: intercept, 1: linear, 3: quadratic, 4: cubic)

	intercept, 1: linear, 3: quadratic, 4: cubic)						
0	1	2	3	Λ			
k _A							
0.44	0.95			0.60			
0.26	0.17			0.01			
k _M							
1.3	0.95			1.58			
0.59	0.30			0.02			
k _O							
30.40	0.62	-0.99	0.18	33.54			
5.70	2.76	-0.56	-0.65	2.17			
-7.81	-1.33	2.048	-0.27	0.03			
0.71	-0.79	-0.28	0.53	0.0007			

 k_A , k_M and k_Q are the matrices of variance (covariance) of random regression coefficients for direct additive genetic, maternal additive genetic and direct permanent environmental effects, respectively.

 Table 3: Genetic (above diagonal) and Phenotypic (below diagonal) correlations between weights at selected area (in down)

selected ages (in days)							
Age	1	90	180	270	360		
1	1	0.36	-0.01	-0.14	-0.21		
90	0.27	1	0.93	0.87	0.83		
180	0.24	0.70	1	0.99	0.98		
270	0.25	0.71	0.83	1	0.99		
360	0.20	0.51	0.63	0.80	1		

with order of fit 2 for genetic effects and 4 for direct permanent environment effect with 21 parameter, was selected as the most appropriate model. Levis and Brotherstone (2002) mentioned the effect of dam as a part of model, improved fit of model and excluding the dam effect from the model had result in increased direct genetic variance, consequently higher estimates of heritability. Ghafouri Kesbi et al. (2008) suggested that including maternal genetic effect to the model significantly increased the Log L and showed the importance of maternal genetic effect on lamb's weight.

Random regression coefficients

In all cases intercept of the polynomial regression explained the highest proportion of variation, and there were positive correlations between the linear and intercept coefficients for all effects, which is consistent with Fischer et al. (2004) and Ghafouri Kesbi et al. (2008). Correlation between the linear and quadratic coefficients was negative for direct permanent environment effect. A large eigenvalue represents considerable genetic variation for pattern and changes in the growth curve that can be improved by selection, whereas small or zero eigenvalue indicated that the change will be slow (Kirkpatrick et al., 1990). The first eigenvalue of the K matrix for K_A , K_M and K_O was the largest, indicating a large proportion of the total variance (93-98 %) can be explained by the first eigenvalue of each CF. Fischer et al. (2004) working with Poll Dorset sheep reported that 89-94 % of total variance can be explained by the first eigenfunction of each CF. Ghafouri Kesbi et al. (2008) reported amount of 95-98%. Eigenfunctions that estimated from the eigenvectors of genetic variance matrix provided an insight into the effects of selection across the growth trajectory (Kirkpatrick et al., 1990). A small portion of variation can be explained by second eigenvalues from direct additive genetic covariance function, suggesting that there is some scope to alter growth patterns genetically (Fischer et al., 2004).

Estimates of variance components

Direct additive genetic variance increased steadily over the trajectory. Levis and Brotherstone (2002), Fischer et al. (2004), Safaei et al. (2006) and Ghafouri Kesbi et al. (2008) reported a similar pattern of variation for direct additive variance. Maternal additive genetic variance fallowed an increasing trend from birth to 360 days of age. Safaei et al. (2006) reported that maternal variances tended to be higher at younger age and declines with age, particularly beyond post-weaning ages (>120 days). Ghafouri Kesbi et al. (2008) reported that maternal additive genetic variance increased after birth to a peak around 150 days and decreased thereafter. Fischer et al. (2004) concluded that maternal variance to be effectively constant throughout the trajectory, and Meyer (2001) has shown that maternal variance tends to be higher at younger ages. Direct permanent environment variance increased from birth to 270 days of age and then decreased at 360 days of age. Ghafouri Kesbi et al. (2008) reported that direct permanent environment variance increased with age and reach to a peak at 240 days of age and remained relatively constant thereafter. Fischer et al. (2004) reviewed that direct permanent environment effect increased after birth to a peak at 300 days and then decreased. Oliveira et al. (2010) reviewed that this variance was constant until 150 days of age and thereafter had increasing trend to end of age. Abbasi et al. (2004) reported decrease of this variance to 150 days and increase thereafter. Residual variance increased from birth to 180 days of age but reach to the least amount at 270 days of age, finally again reached to maximum at 360 days of age, which is different from results of studies of Abbasi et al. (2004), Ghafouri Kesbi et al. (2008) and Fischer et al. (2004). They mentioned that this variance had increasing trend to end without decrease. Phenotypic variance increased from birth to 180 days of age and a little decreased at 270 days and increased at 360 days of age. Oliveira et al. (2010) reported increasing trend for phenotypic variance without any decrease until then. Fischer et al. (2004) reported a decrease of phenotypic variance at 400 days and further increase thereafter.

Heritability

Generally the heritability measures of this study were law (0.002-0.069) which was similar to the results reported by Boujenant and Kansari (2002). They indicated that the main reason of low estimate were the extensive conditions for nurture. Range of direct heritability and maternal heritability was 0.02 to 0.07 and 0.01 to 0.08, respectively. Direct heritability decreased at 90 days of age to least amount then increased to 360 days of age. It was in consistent with results of studies such as Nedaii et al. (2010), Oliveira et al. (2010) and Rashidi et al. (2006). Oliveira et al. (2010) reported 0.24, 0.12, 0.44, 0.84 and 0.96 amounts of heritability for the weight at birth, 50 day, 150 day, 250 day and 411 day, respectively in Santa Ines sheep. Nedaii et al. (2010) also reported a decline in heritability at 90d and increase thereafter. Fischer et

al. (2004) studied Poll Dorset sheep and indicated that direct heritability increased with age. However it can be said that difference from results reported by Fischer et al. (2004), was non-consideration of birth weight. Molina et al. (2007) reported that direct heritability increased at 45day of age. Meyer (2002) studied Australian cattle from birth to 820 days and suggested that direct heritability decreased sharply after birth and increased again after about 100 days of age. Abbasi et al. (2004) reported that direct heritability increases up to 150 days of age and decreased thereafter, while at above study only two direct genetic and permanent environment effects considered and maternal effect did not considered. Fischer et al. (2004) expressed an increase for direct heritability at later ages due to decrease of the other variance components particularly maternal variances.

Maternal heritability decreased sharply after birth and then increased with low sway as the age increased. Most of studies indicated that maternal heritability decreased after weaning. Ghafouri Kesbi et al. (2008) reported that maternal heritability increased from birth up to 120 days and then decreased gradually until 270 days of age. Albuquerque and Meyer (2001) found that maternal heritability maximized near weaning, which is very important in the selection method based on maternal ability. Rasooli et al. (2010) studied Markhoz kids and reported a decrease for maternal heritability after an increase at 60 days of age. Nedaii et al. (2010) reported that maternal heritability decreased from birth to 180 days of ages.

According to the estimated amounts of heritability, it can be expressed that a set of reasons, among that contribution of genetic effects and direct permanent environment effect in creation of diversity between records (phenotypic variance) is small and more contribution of residual effects among management variations during fifty years such as, variations in nutrition system, variations in weaning age of lambs and what not harden the precise notation of records.

The proportion of direct permanent environmental variance to phenotypic variance and repeatability

Proportion of direct permanent environment variance to phenotypic variance decreased after birth but then increased until 270 days and reached to maximum at 270 days of age. After that decreased at 360 day and reached to least. Ghafouri Kesbi et al. (2008) reported that this proportion showed a gradual increase after 60 days of age until approximately 180 days of age, where it plateaus. Fischer et al. (2004) indicated that the proportion of direct permanent environmental variance to phenotypic variance increased from 50 to 200 days of age and thereafter fallowing decreasing trend until 500 days of age. According to results reported by Nedaii et al. (2010), proportion of direct permanent environmental variance to phenotypic variance gradually increased after 90 days until near 360 days of age. Abbasi et al. (2004) showed that this proportion had decreasing trend from birth to 150 days of age and then fallowing decreasing trend until 360 days of age. Aziz et al. (2005) reported that direct permanent environmental variance ratio decreased from 0.41 at birth to 0.12 at 90 day, and then increased gradually up to 0.40 at 270 day, where it oscillated around this value up to the end. Repeatability decreased after birth but thereafter increased until 270 day of age and finally reached to the least amount at 360 days of age. Aziz et al. (2005) found that repeatability of birth weight was 0.79. After birth, the values fluctuated across the age trajectory with a minimum of 0.65 at 90 day and a maximum of 0.86 at 240 day. Meyer (2001) reported an increase up to 0.82 at approximately 1 month of age, followed by a decrease to a minimum of 0.57 at approximately 4 month of age and again an increase up to 0.80 at 240 d of age.

Correlations

Direct genetic correlation between birth weight and other weights were lower than the corresponding values observed between weights at adjacent ages, suggesting that birth weight is not under the same genetic control as weights at other ages. Oliveira et al. (2010) reported negative genetic correlations between birth weight and weights at 231 and 411 day of age. Fischer et al. (2004) indicated that the correlations decreased as the age distance between weights increased. However, they concluded that genetic correlation between early (day 50) and late (day 450) weights was moderate (0.37), suggesting early weights were not under exactly the same genetic control as weights taken at an older age. In addition, they concluded that genetic correlation between weights at younger ages (50 vs. 250 days) were lower (0.46) than correlation between weights taken at older ages (300 vs. 500 days) with the same time lag (0.86). This is attributable to the influence of the part- whole relationship between weights, whereby weights at later ages depends on earlier weights, thus as time progresses the correlations between later weights increases. A similar pattern reviewed in genetic correlation between growth data taken at different ages on cattle (Meyer, 2002 and Aziz et al., 2005) and sheep (Ghafouri Kesbi et al., 2008). Genetic correlation between tow ages showed that selection for body weight at an age would have positive effect on body weight at other age. Abbasi et al. (2004) indicated that genetic correlation between near ages in Baluchi sheep was up and decreases with increase of distance between them. Abbasi et al. (2004) suggested a direct genetic correlation between weights at 90d and180d (0.92), between weights at 90d and 270d (0.86) and between weights at 90 and 360 day (0.83), showed that the correlation decreases with increase of distance between those. It was in agreement with the results of present study.

Maternal genetic correlation between birth weight and other weights also were lower than the corresponding values observed between weights at adjacent ages. Amount of this correlation decreased with increase of distance between ages. Oliveira et al. (2010) reported that maternal genetic correlation between birth weight and weights at 85d, 158d, 231d and 411 were 0.88, 0.84 and 0.96, respectively. These results were lower than the present study. Fischer et al. (2004) showed that maternal genetic correlation were very high (> 0.7) for all ages suggesting that maternal genes acting at early age are similar to those acting at later ages of the trajectory. Ghafouri Kesbi et al. (2008) reported that maternal genetic correlations between birth weight and days over 180 were lower than 0.3, suggesting that there is a very little genetic relationship between maternal genetic control of fetal growth and milk production. They also founded that maternal genetic correlations between weights from 180 to 270 days of age were higher than 0.6, indicating that maternal effects at later ages are primarily governed by the same genes. In the present study also between weights at higher ages, maternal genetic correlation was near to 1. For example, maternal genetic correlation between weights at 90 and 180 day, between weights at 180 and 270 day and between weights at 270 and 360 day were 0.98, 0.99 and 0.99, respectively. Maternal genetic correlation between weights in the present study was between 0.54 to 0.99.

Direct permanent environmental correlation was very low between birth weight and other weights (0.23-0.32), which indicated that there was weak relation between animal's permanent environment values for weights at later ages. Levis and Brotherstone (2002) reported that correlation between observations on adjacent days was approximately unity, and declined as the days apart increased, falling to around 0.28 between live weights at age 2 days and live weight at age 150 days. Aziz et al. (2005) viewed that animal permanent environment correlations between weights at birth and other weights were lower than those among weights at other ages. They were with a minimum of 0.40 between weights at birth and 356 day and a maximum approached unity between weights at 90 and 120 day, between 180 and 210 day of age. Almost one can say that for most of weights, phenotypic correlation was lower than previous correlations. Ghafouri Kesbi et al. (2008) and Levis

and Brotherstone (2002) found that this correlation decreased with increase at distance between records. Aziz et al. (2005) found that phenotypic correlation between birth weight and weights at other ages was lower than the correlations observed between other weights that upholds results of present study. In relation with each three of correlations (direct genetic, maternal genetic and direct permanent environmental correlations) maximum amount for these correlations were between weights at 270 and 360 day of age which indicated strong relation between these two weights.

Conclusions

The results of this study emphasizes on the importance of the maternal effect on estimating the parameters. Not involving this effect in the model, causes higher estimates of heritability. According to the higher amount of maternal heritability to the direct heritability, breeding value of dam should be considered in selection procedures. It is recommended to evaluate animals for other traits (such as litter size) by using RRM.

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