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Original Article

Genetic analysis of growth curve of Afshari lambs by legendre polynomials-based random regression models

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Abstract

The aim of this study was to apply Simple Repeatability Model (SRM) and Random Regression Models (RRMs) to describe growth curve of Afshari lambs. Results revealed the inadequacy of SRM to model variation in growth curve of Afshari lambs. A RRM with orders 3, 2, 3, and 2 for direct genetic, direct permanent environment, maternal genetic and maternal permanent environmental effects was selected as the parsimonious model. Direct heritability (h^2) and maternal permanent environmental effect (c^2) were maximal at 98 days of age, and decreased with age until the end of growth trajectory. Direct permanent environmental effect (p^2) and maternal heritability (m^2) were minimal at 98 days of age, but increased thereafter to a peak at 525 days of age. In conclusion, results revealed substantial genetic potential for selection responses in early growth of Afshari lambs and that this genetic potential can be exploited by breeders to improve growth performance of Afshari lambs.

Keywords: sheep, body weight, heritability, genetic correlation

1. Introduction

Body weight is one of the most important economic traits in sheep breeding throughout the world. Especially in countries where the sale price is based on weight, live weight has a direct effect on the profitability of the production system. Body weight can be measured at different points of growth trajectory. Collecting body weights at different ages makes it a typical example of *so-called* longitudinal data (Meyer & Hill, 1997). Analysis of such repeated records require efficient statistical techniques. Different approaches and models applied to longitudinal data are reviewed extensively by Lindsey (1993). Among them, Simple Repeatability Model (SRM), Multi Trait Model (MTM), and Random Regression Model have been used to genetic analysis of repeated records. A common result which comes from these papers is the superiority of RRM (see for example Meyer, 2004; Oh, See, Long & Galvin, 2006). Due to this superiority, over the last decade, RR model has been applied for analysis of repeated records from animal breeding schemes, such as test day milk yield (Schaeffer & Dekkers, 1994), growth (Rafat *et al.*, 2011), feed intake (Schenkel, Devitt, Wilton, Miller, & Jamrozik, 2002), egg number (Wolc *et al.*, 2013), fat and mussel depth (Fischer, Van der Werf, Banks, Ball, & Gilmour, 2006) and total sperm production (Oh *et al.*, 2006).

The Afshari sheep is one of the heaviest breeds of sheep in Iran and is widely distributed in the Zanjan province. Their population is about 1 million head and mainly farmed for meat production. This breed is known with appropriate growth characteristics which make them to be an appropriate breed for selection programs aimed at increasing the efficiency of meat production (Eskandarinasab, Ghafouri-Kesbi, & Abbasi, 2010). In spite of reports indicating increase in the accuracy of genetic evaluation of growth by applying RRM (Meyer, 2004) little efforts have been made to analysis growth

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curve of sheep by RRM (Fischer, Van der Werf, Banks, & Ball, 2004; Ghafouri-Kesbi, Eskandarinasab & Shahir, 2008; Lewis & Brotherstone, 2002). In the current study, therefore, weight records of Afshari sheep from 98 to 525 days of age were analyzed using SRM and RRM to estimate genetic and non-genetic components of body weight in this breed.

2. Materials and Methods

2.1. Data

Body weight records and pedigree information on Afshari lambs were obtained from Afshari sheep flock at the department of Animal Science of the Zanjan University, Iran. Data recorded between 1998 and 2005. Each year natural service is started from September and continued for 51 days. Each group of 10 ewes is allocated to a fertile ram for 2 or 3 days. This mating system allows the identification of sire and dam of each lamb. Lambing commences in February. At birth, lambs are weighed and identified to their parents. Lambs are weaned from their mothers at an average age of 120 days. Animals are kept indoors from November to March and hand-fed according to NRC (1985). Rams are kept in the flock for a maximum of three years and ewes are usually culled after five lambing.

Data was monitored several times and incorrect records were removed. Meyer (2001) showed that the order of polynomial fit require increased when birth weight included in the data. Also, occurrence of “end effect of polynomials” or “Runge’s phenomenon” is highly expected by inclusion of birth weight (Meyer, 2005). Therefore, according to Fischer *et al.* (2004) suggestion, birth weights were removed from the analyses.

2.2. Statistical analysis

To determine significant fixed effects (year of birth, sex of lambs, birth type and age of dam at lambing), least square analyses using the GLM procedure of SAS (2004) was fitted on the data. All these effects were found to be significant ($p<0.05$) and therefore included in the model of analysis. Simple Repeatability Model (SRM) and Random Regression Model (RRM) were applied to estimate genetic parameters.

2.2.1. Simple Repeatability Model (SRM)

This model is the simplest model proposed for analyzing repeated records. The assumption of SRM is that measurements at different ages a realization of the same trait. It assumes that genetic and phenotypic correlations are of the same magnitude and equal to 1.00 (Meyer & Hill, 1997).

2.2.2. Random Regression Model (RRM)

In RRM, an animal’s breeding value is modeled as a function of a covariate which may be age in studies of growth trajectory (Meyer, 2005). The RR model for repeated body weight (including both direct and maternal additive genetic and permanent environmental effects) could be represented as follows (Kirkpatrick *et al.,* 1990):

$$y_{ij} = F_{ij} + \sum_{m=0}^{3} \beta_m \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{A-1}} \alpha_{im} \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{M-1}} \gamma_{im} \phi_m(t_{ij}^*) + \sum_{m=0}^{k_{C-1}} \rho_{im} \phi_m(t_{ij}^*) + \varepsilon_{ij}$$

where y_{ij} is the j^{th} record of i^{th} animal; $\phi_m(t_{ij}^*)$ is the m^{th} Legendre polynomials of age; t_{ij}^* is the standardized age at recording (between -1 to 1); F_{ij} is the fixed part of the model; β_m are the fixed regression coefficients for modeling the population mean; α_{im}, γ_{im}, δ_{im} and ρ_{im} are the random regression coefficients for direct additive genetic, maternal additive genetic, direct permanent environmental and maternal permanent environmental effects, respectively; k_{A-1}, k_{M-1}, k_{P-1} and k_{C-1} are the corresponding order of polynomial for each effect and ε_{ij} denotes the residual effect. Several RRM analyses considering different orders of fit for the four random effects were carried out to find the most parsimonious model describing the data best. To study the importance of maternal effects, these effects were excluded from the most parsimonious model and change in LogL was monitored. Residual variance was modeled with two distinct strategies. In the first strategy, the homogeneity (constancy) of residual variance was assumed from 98 to 525 days of age and in the second strategy, residual variance was assumed to be heterogeneous with 14 age classes (one month each).

The WOMBAT program (Meyer, 2007) was used to analysis the data. Models with different orders of fit were compared using Akaike’s Information Criterion (Akaike, 1974). Estimates of variance components were used to calculate coefficient of variations as: $CV = 100 \times \sqrt{Variance}/mean$ (Houle, 1992).

3. Results and Discussion

Figure 1 shows number of records and unadjusted weights by age (day). A total of 85 ages, ranging from 98 to 525 d, was represented. As shown with an almost linear trend, body weight tended to increase with age from 27 kg at 98 d to 60.8 kg at 525 d. Mean weights and SD for the whole period was 39.59 kg and 10.49 kg, respectively. Characteristics of data and pedigree structures are shown in Table 1. Pedigree included 1593 pedigreed animals of which 1,401 individual had recorded body weight.

Several analyses with different orders of fit were tried to find a parsimonious model that described the data adequately (Table 2). A model fitting Legendre polynomials to order k = 3 for all four random effects and fourteen measurement residual variance classes with a total of 38 parameters to be estimated, was the most complex model fitted in the current study. The order of fit was not increased beyond 3 as most of animals (34%) had three records. The SRM was among inefficient models (Model 1). Regarding estimates of residual variances for fourteen growth phases, SRM resulted in significantly higher residual variances which showed the inadequacy of this model (Table 3). Similar results

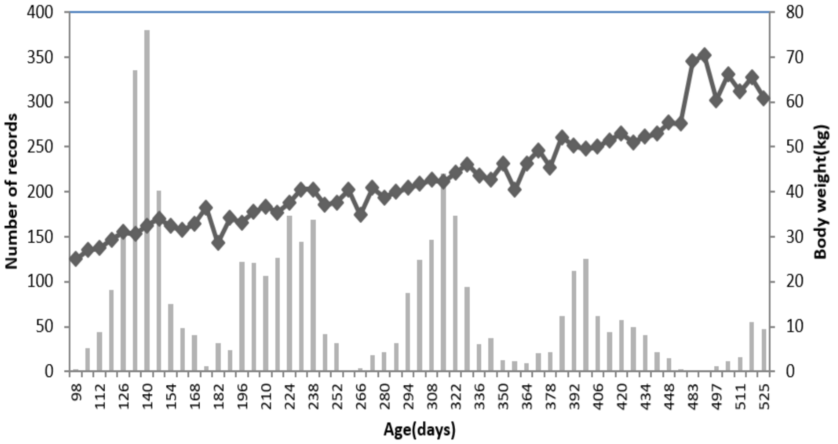


Figure 1. Numbers of records (grey bars) and mean weights (black points) for individual ages

Table 2. Order of fit for direct (K_A) and maternal (K_M) genetic, animal (K_P) and maternal permanent (K_C) environmental effects

Model	K_A	K_P	K_M	K_C	Np^{b}	LogL^{c}	AIC^{d}
1	1	1	1	1	18	-7847.33	15722.66
2	2	2	2	2	26	-7712.54	15477.08
3	2	2	3	3	32	-7705.31	15474.62
4	2	3	2	3	32	-7668.66	15401.32
5	3	2	3	2	32	-7646.05	15356.10
6	3	2	-	-	23	-7693.250	15432.50
7	3	2	3	2	19	-7857.270	15752.54
8	3	3	2	2	32	-7972.628	16009.26
9	3	3	3	3	38	-8022.51	16121.02

Np: Number of parameters, LogL: Log likelihood function, AIC: Akaike's information criterion

Table 3. Estimates of error variances for 14 growth phases for Simple Repeatability Model (Model 1), the parsimonious model (Model 5) and the model with assumption of homogeneity of error variance (Model 7)^{a}

Model	E1	E2	E3	E4	E5	E6	E7	E8	E9	E10	E11	E12	E13	E14
1	9.30	7.42	7.85	1.18	0.50	7.96	9.30	8.29	8.47	19.07	23.08	23.19	55.97	10.39
5	2.18	2.01	4.55	2.28	1.60	5.32	4.48	3.80	2.57	11.73	12.30	15.26	9.99	9.79
7	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61	4.61

^{a}E1-E14: Estimates for error variances for 14 growth phases

Table 1. Summary of pedigree and data structures of the Afshari sheep

	N
No. of Animals in the pedigree file	1,593
No. of Animals with progeny	575
No. of Animals without progeny	1,158
No. of Sires with progeny	47
No. of Sires with progeny and record	29
No. of Dams with progeny	478
No. of Dams with progeny and record	304
No. of Grand sire	32
No. of Grand dam	210

have been reported by Arango *et al.* (2004). Genetic and environmental components of phenotypic variance are frequently reported to vary over growth trajectory (Boligon, Mercadante, Lobo, Baldi, & Albuquerque, 2012; Fischer *et al.*, 2004; Ghafouri-Kesbi *et al.*, 2008) which show the erroneous of the assumption of SRM which emphasizes on constancy of phenotypic variance and its constituent components over growth trajectory.

According to logL and AIC values, Model 5 (3,2,3,2) which was able to describe the covariance structure adequately was selected as the parsimonious model. Estimates of (co)variances and correlations between RR coefficients for Model 5 are presented in Table 4. The first eigenvalue of covariance functions, *i.e.*, the matrix of covariance among RR coefficient, dominated throughout and accounted for 79, 100, 90, and 100% of the total variation for additive, maternal genetic, individual permanent environmental and maternal permanent environmental effects, respectively. In the study by Ghafouri-Kesbi *et al.* (2008), the first eigenvalue accounted for more than 90% of the total variation for direct and

Table 4. Estimates of variances (diagonal), covariance (below diagonal), and correlations (above diagonal) between random regression coefficients and eigenvalues of coefficient matrix for additive genetic (A), maternal genetic (M), animal permanent environmental (P) and maternal permanent environmental (C) effects

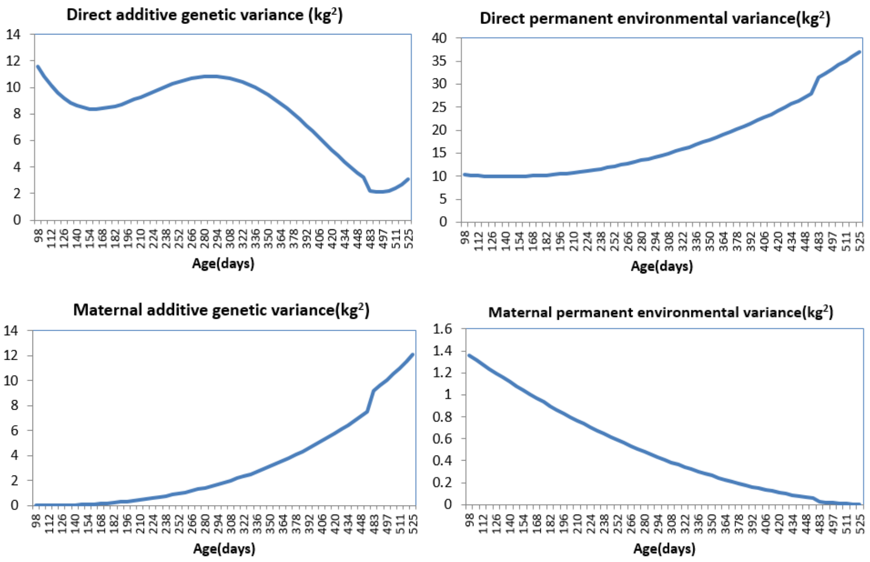
0	1	2	Eigenvalue
A			
10.515	-0.0510	-0.4201	12.21 (79%)
-2.1765	2.5522	-0.6895	2.62 (17%)
-3.4652	-0.1261	2.4018	0.64 (4%)
M			
4.7060	0.9554	0.9997	6.77 (100%)
3.1048	2.0498	0.9477	0.00 (0.00%)
0.2544	0.1693	0.0153	0.00 (0.00%)
P			
30.464	0.5877		32.67 (90%)
7.7120	5.6528		3.45 (10%)
C			
0.7515	-0.9991		0.96 (100%)
-0.3913	0.2041		0.00 (0.00%)

maternal covariance functions. Eigenvalues and corresponding eigenfunctions of a covariance function summarize both the variance and the correlation structure (Kirkpatrick, Hill & Thompson, 1990) and can be used to predict the effect of selection on the shape of growth curve. Large eigenvalues reflect large genetic variation in growth curve and the opportunity for changing the shape of growth curve genetically.

Considering homogeneity of residual variance instead of heterogeneity of residual variance significantly increased AIC (15752.54 vs. 15356.10). Residual variance results from environmental effects on phenotype and includes all the unknown effects affecting phenotype including important non-additive genetic sources. As animals aged they may experience different environmental conditions and therefore residual variance might also vary with age (Ghafouri-Kesbi *et al.*, 2008; Huisman, Veerkamp, & Van Arendonk, 2005; Meyer, 2001).

The results of logL and AIC showed an improvement in the level of fit when maternal effects included in the model, in comparison to the model in which maternal effects ignored (Model 6), in agreement with many reports including Albuquerque and Meyer (2001), Lewis and Brotherstone (2002) and Ghafouri-Kesbi *et al.* (2008). As a result, in selection programs aimed at improving growth performance of Afshari sheep, maternal effects need to be included in the model to prevent bias in prediction of breeding values.

Estimates of variance components for the ages in the data are shown in Figure 2. Corresponding estimates of genetic parameters and coefficients of variation are given in Figures 3 and 4, respectively. Direct additive genetic variance was maximal at 98 d, but decreased to around 150 d of age and then increased to 300 d of age when it started to decrease until end of growth trajectory. Direct permanent environmental variance and maternal genetic variance were minimal at 98 d of age and then increased gradually and reached the highest value at 525 d of age. Maternal permanent environmental variance showed a decreasing pattern in the whole period in a way that for higher ages it was almost zero. The observed patterns for genetic parameters were almost similar to corresponding variance components, though the trends were not as smooth as those of variances. Heritability was highest at the beginning, subsequently decreased but yet was higher than 0.3 until 365 d when it started a sharp decrease afterward. The observed trend for ***h^2*** was in agreement with Samadi, Hatami, Lavaph, Saadi, and Mohamadi (2013), though it contradicted Lewis and Brotherstone (2002) and Fisher *et al.* (2004) who reported an increase in heritability of body weight with age. However, selection in sheep usually done on early growth traits such as weaning weight which in Afshari sheep is around 98 to 120 days of age with 0.45 to 0.40 heritability. Likewise, with a maximum value at 98 d of age, CV_A had a similar general pattern with ***h^2***. It measures additive genetic variability or "capability to change" in body weight at different ages. CV_A can be high in traits with low heritabilities if



Direct additive genetic variance (kg^2)

Direct permanent environmental variance(kg^2)

Maternal additive genetic variance(kg^2)

Maternal permanent environmental variance(kg^2)

Figure 2. Estimates of variance components

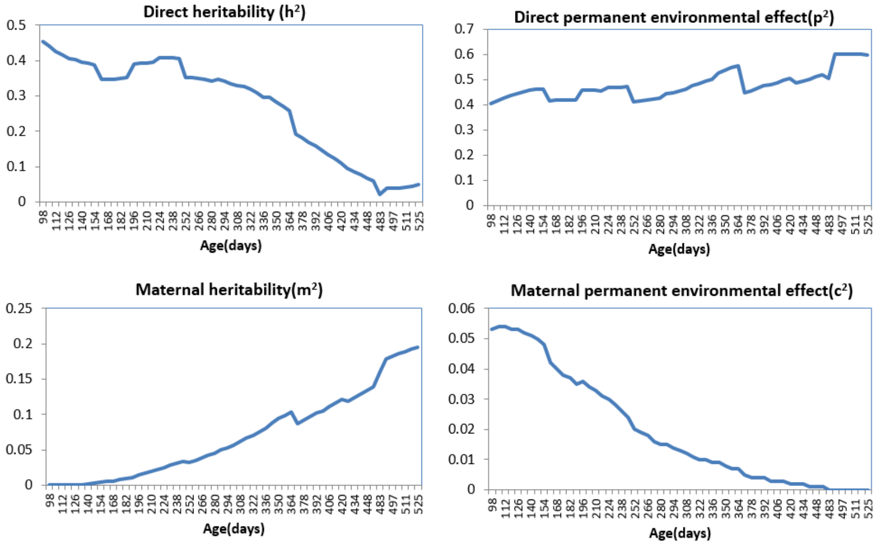


Figure 3. Estimates of direct and maternal heritability and direct and maternal permanent environmental effects

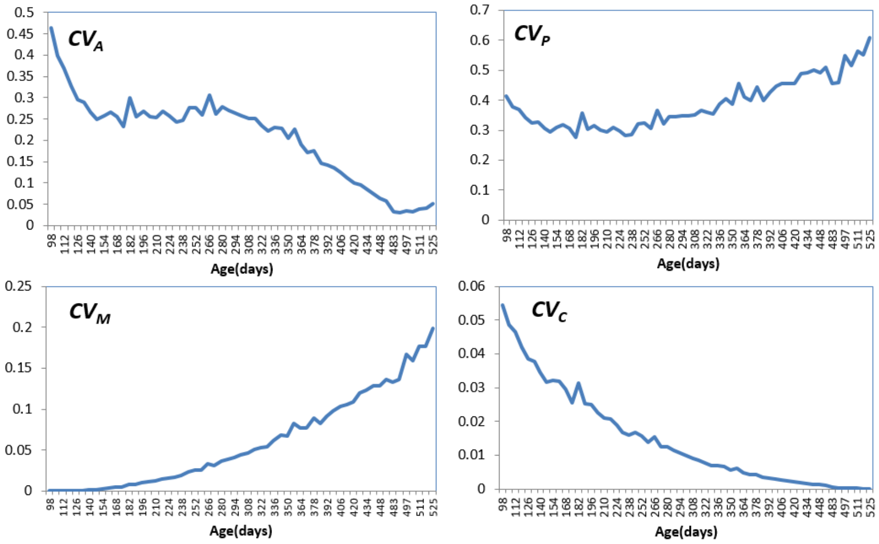


Figure 4. Estimates of direct genetic (CV_A), direct permanent (CV_P), maternal genetic (CV_M) and maternal permanent environmental coefficient of variation (CV_C)

contribution of the residual variance to the phenotypic variance is high (Houle, 1992) and *vice versa*. Both CV_A and $\boldsymbol{h^2}$ guarantee maximum response to selection in early growth of Afshari lambs. With some fluctuations, direct permanent environmental effect ($\boldsymbol{p^2}$) and corresponding CV_P increased with age throughout the period studied in consistent with other reports (Samadi *et al.*, 2013). Maternal heritability ($\boldsymbol{m^2}$) and maternal additive genetic coefficient of variation (CV_M) increased with age. In most of examined papers, a diminishing trend for $\boldsymbol{m^2}$ after birth or after weaning has been reported (Fisher *et al.*, 2004; Safaei *et al.*, 2010). Notable $\boldsymbol{m^2}$ beyond weaning may be due to carry-over effects from weaning weight (Bradford, 1972; Snyman, Erasmus, van Wyk, & Olovier, 1995). The trends for maternal permanent environmental effect ($\boldsymbol{c^2}$) and CV_C were decreasing throughout the trajectory and were below 0.05 in the whole period studied. As a result this component of maternal effects can be ignored from the genetic evaluation procedure.

Different correlations between body weighs at 98, 189, 294, 399, and 525 d of age are shown in Table 5. All the correlations decreased steadily with increasing lag in age with a minimum between body weight at 98 and 525 days of age, a result which has been frequently reported (Ghafouri-Kesbi *et al.*, 2008; Safaei *et al.*, 2010; Samadi *et al.*, 2013). The genetic correlation between 98 d body weight and body weights up to 399 d of age are positive. As a consequence, selection on body weights around weaning age will change body weight in the period between 98 to 399 d of age in the same direction. Maternal genetic correlations between 98-day body weight and body weights taken at higher ages are negative which indicates that the genes of dams which contribute in milk production have some unfavorable effect on post-weaning body weights.

Table 5. Correlations between body weights at different ages[a]

Age2	r_a	r_p	r_m	r_c	r_{ph}
189	0.663	0.926	-0.848	1.000	0.689
294	0.232	0.718	-0.843	1.000	0.423
399	0.027	0.516	-0.831	0.999	0.246
525	-0.053	0.345	-0.818	0.924	0.161
294	0.880	0.928	1.000	1.000	0.754
399	0.736	0.802	0.999	0.999	0.57
525	-0.287	0.674	0.997	0.926	0.347
399	0.957	0.967	1.000	1.000	0.744
525	-0.271	0.901	0.998	0.931	0.534
399	1.000	1.000	1.000	1.000	1.000
525	-0.06	0.982	1.000	0.94	0.664

[a] r_a, Direct additive genetic correlation; r_p, Direct permanent environmental correlation r_m, Maternal additive genetic correlation, r_c Maternal permanent environmental correlation, r_{ph} Phenotypic correlation

4. Conclusions

In conclusion, results obtained here showed the presence of notable genetic variation in growth curve of Afshari lambs up to 365 d of age that can be exploited for improving growth performance of Afshari lambs. Simple repeatability model did not show an acceptable performance in analyzing repeated body weight records. Accordingly, SRM is not recommended for analyzing repeated records of livestock. Body weight around weaning would be appropriate selection criteria as they are measured early in life, show considerable genetic variation and have positive genetic correlation with other body weights.

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