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Application of Random Regression Model to Estimate Genetic Parameters for Average Daily Gains in Lori-Bakhtiari Sheep Breed of Iran

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Abstract: A random regression model was applied to estimate (co) variances, heritabilities and additive genetic correlations among average daily gains. The data was a total of 10876 records belonging to 1828 lambs (progenies of 123 sires and 743 dams) born between 1995 and 2001 in a single large size flock of Lori-Bakhtiari sheep breed in Iran. In the model, fixed environmental effects of year-season of birth, sex, birth type, age of dam and random effects of direct and maternal additive genetic and permanent environment were included. Orthogonal polynomial regression (on the Legendre scale) of third order (cubic) was utilized to model the genetic and permanent environmental (co) variance structure throughout the growth trajectory. Direct and maternal heritability estimates of average daily gains ranged from 0.011 to 0.131 and 0.008 to 0.181, respectively in which pre-weaning average daily gain (0-3 in months) had the lowest direct and highest maternal heritability estimates among the other age groups. The highest and lowest positive direct additive genetic correlations were found to be 0.993 and 0.118 between ADG (0-9) and ADG (0-12) and between ADG (0-3) and ADG (0-12), respectively. The direct additive genetic correlations between adjacent age groups were more closely than between remote age groups.

Key words: Random regression, growth, Lori-Bakhtiari sheep, Iran

INTRODUCTION

Based upon the species of farm animals, several traits such as milk yield, body weight, feed intake and longevity are used for selection of candidate animals as the genetic evaluation is practiced (Akbas *et al.*, 2004). As mentioned by Meyer (1999) growth of animals is a prime example of a trait measured repeatedly per individual along a continuous scale (time) which changes gradually and continually which can be modeled by random regression (Meyer, 2004).

In any meat producing sheep industry, lamb weight and average daily gain are considered to be important components for market lamb production (Mousa *et al.*, 1999). As mentioned by Arango and Van Vleck (2002), growth is continuous during an animal's life from zygote formation until the adult stage (mature weight) and therefore should be evaluated by growth rate or by weight and size increases during different stages of life. In order to select superior sheep for feed conversion, growth rate and feed intake at genetic level are fundamentally important (Cammack *et al.*, 2005). A number of growth models such as Brody, Von Bertalanffy, Gompertz, Richards and logistic describing weight-age relationships for growing animals have been proposed and applied in which weight of animals is regressed on time using data

across animals (Akbas *et al.*, 2004; Arango and Van Vleck, 2002; Lambe *et al.*, 2006). Often these curves have been fit to a single animal's data and the parameters analysed for genetic components rather than fitting across animals (Lewis *et al.*, 2002). Random regression models and the Associated Covariance Functions (CF) have been recently advocated for the analysis of traits measured repeatedly per animal facilitating changes in the trait under consideration over time and its (co) variance structure (Meyer, 2001). Random regression model were first proposed and developed by Henderson (1984), Laird and Ware (1982) and suggested by Schaeffer and Dekkers (1994) in dairy cattle breeding. Random regression model has been utilized to describe a linear model including appropriate covariates to model the effect of time on repeated records as fixed and random terms (Schaeffer and Dekkers, 1994). Random regression models are able to predict covariance structure at any point along a continuous scale. Using random regression models there is no need to correct towards certain landmark ages (Meyer, 2004). Random regression models will also make more efficient use of the available data for individual animals resulting in increasing the accuracy of genetic evaluation. Furthermore, in random regression models fewer parameters are needed to describe longitudinal data compared to a multivariate model. Moreover,

in comparison to a multivariate model, a random regression model estimates variances and covariances smoother and with less bias (Kirkpatrick *et al.*, 1990) particularly as it is not applied beyond the range of the data. Application of random regression models have recently concentrated on the analysis of milk test day records in dairy cows (Brotherstone *et al.*, 2000; Druet *et al.*, 2003) or weight records on growing animals (Lewis and Brotherstone, 2002; Bohmanova *et al.*, 2005; Iwaisaki *et al.*, 2005). In meat producing animals, as pointed out by Meyer (2004), genetic merit of an animal for growth recorded at different ages or ranges of ages is assessed as different traits which can be analysed by applying a random regression model.

The main objective of the present study was an attempt to determine whether heritability and correlation patterns of average daily gains change with age for Lori-Bakhtiari sheep breed of Iran with the use of a random regression model based on orthogonal Legendre polynomials.

MATERIALS AND METHODS

Lori-Bakhtiari breed is a fat-tailed Iranian sheep and it is considered a large-frame and meat type breed mostly distributed in south western part of Iran (Vatankhah and Talebi, 2002). The typical body colour of this breed is white although light and dark brown sheep are not unusual in this breed (Tavakolian, 2000). Seasonal mating is usually carried out in August and September particularly for those groups of animals kept by nomadic people although in farm flocks mate ewes are mated during all seasons (Tavakolian, 2000).

In this study, a total of 10876 average daily gain records at different range of ages starting from birth to yearling collected from 1828 Lori-Bakhtiari sheep were used. The animals with records were pedigreed half-sib and full-sib progeny from the mating of 123 sires and 743 dams and born between 1995 and 2001 in a single large size flock of Lori-Bakhtiari breed belonging to a province

(Chahar Mahal and Bakhtiari) located in western Iran. The average birth and weaning weights (at day 90) of the lambs studied in the present research were 4.873 and 27.327 kg, respectively. In this breed, the percentages of single, twin and triple births were 71.1, 27.8 and 1.1, respectively and the average litter size was 1.30 lambs. The sheep flock in this material, were housed indoors, usually in insulated buildings during the winter season. Lambing took place during spring and winter seasons.

Based on the weight records of individual lambs, average daily gains (in gram) were calculated for 10 different ranges of ages (in month) consisting of ADG(0-3), ADG(0-6), ADG(0-9), ADG(0-12), ADG(3-6), ADG(3-9), ADG(3-12), ADG(6-9), ADG(6-12) and ADG(9-12). Some descriptive statistics of the data are presented in Table 1.

Direct and maternal additive genetic as well as permanent environmental variance and covariance components for average daily gains (ADG) at different range of ages were estimated by implementing an animal random regression model of third order (cubic, K = 4) using Powel derivative-free restricted maximum likelihood (REML) algorithm with DXMRR sub-programme of the DFREML package (Meyer, 1998). The model was as follows:

$$\begin{aligned}
 y_{ij} = & F_{ij} + \sum_{m=0}^{K-1} \beta_m \phi_m(a_{ij}) + \sum_{m=0}^{K-1} \alpha_{im} \phi_m(a_{ij}) \\
 & + \sum_{m=0}^{K-1} \gamma_{im} \phi_m(a_{ij}) + \sum_{m=0}^{K-1} \delta_{im} \phi_m(a_{ij}) + \varepsilon_{ij}
 \end{aligned}
 \tag{1}$$

where, y_{ij} is the j^{th} record from the i^{th} animal, a_{ij} is the standardized (-1 to +1) range of age according to Kirkpatrick *et al.* (1994), $\phi_m(a_{ij})$ is the m^{th} Legendre polynomial of age, F_{ij} is a set of fixed effects including year-season of birth, sex, birth type and age of dam (as covariate up to quadratic order), β_m are the fixed regression coefficients to model the population mean, α_{im} , γ_{im} , δ_{im} are the random regression coefficients for direct and maternal additive genetic and permanent

Table 1: Some descriptive statistics of average daily gains (g) at different age groups

Age groups	Statistical characteristics					
	No.	Min.	Max.	Mean	SD	CV %
1 (ADG 0-3)	1804	75	407	245.27	52.93	21.58
2 (ADG 0-6)	1441	89	367	191.95	37.50	19.53
3 (ADG 0-9)	963	111	260	174.30	26.61	15.26
4 (ADG 0-12)	824	87	219	143.90	23.89	16.60
5 (ADG 3-6)	1438	-128	372	132.75	53.42	40.24
6 (ADG 3-9)	962	55	233	132.78	32.90	24.77
7 (ADG 3-12)	824	31	185	105.97	27.10	25.57
8 (ADG 6-9)	971	0	350	134.23	43.00	32.03
9 (ADG 6-12)	828	-75	199	93.07	29.88	32.10
10 (ADG 9-12)	821	-248	290	52.15	45.13	86.53
Total data	10876	-248	407	152.78	68.27	44.68

environmental effects, respectively ϵ_{ij} and ϵ is the measurement error. In matrix notation, the model can be re-written as:

$$y = Xb + Z_1\alpha + Z_2\gamma + Z_3\delta + \epsilon \quad (2)$$

The model assumptions were as follows:

$$V \begin{bmatrix} \alpha \\ \gamma \\ \delta \\ \epsilon \end{bmatrix} = \begin{bmatrix} K_A \otimes A & 0 & 0 & 0 \\ 0 & K_M \otimes A & 0 & 0 \\ 0 & 0 & K_C \otimes I & 0 \\ 0 & 0 & 0 & R \end{bmatrix} \quad (3)$$

where y is the vector of observations, b is the vector of fixed effects in the model (including F_{ij} and β_m), α is the vector of direct additive genetic random coefficients, γ is the vector of maternal additive genetic random coefficients, δ is the vector of permanent environmental random coefficients, X , Z_1 , Z_2 and Z_3 are the corresponding incidence matrices, K_A , K_M and K_C are the matrices of coefficients of the covariance function for direct and maternal additive genetic and permanent environmental effects respectively and ϵ is the vector of measurement error which were considered independently distributed with variance $R = \sigma_c^2$, so $Cov(\epsilon_{i1,i2}) = \sigma_c^2$ for $I = j$ and 0 otherwise. A is the additive genetic numerator relationship matrix to account for additive genetic covariance between animals, \otimes denotes the kronecker product and I is an identity matrix. In the model, single measurement error variance was assumed to be constant

for all age groups. Furthermore, due to problems associated with reaching to a convergence point for the estimation of (co)variance components, no attempt was made in this study to fit permanent maternal environment as an additional random effect in the model.

RESULTS

Direct and maternal heritability estimates obtained for average daily gains at different range of ages are shown in Table 2. Direct heritability estimates found in the present study ranged from 0.011 to 0.131. The highest heritability estimate was found for ADG (0-9) while the lowest heritability was revealed to be for ADG (0-3) followed by ADG (9-12). The heritability estimates of average daily gain at 3-6, 3-9 and 3-12 were approximately the same. The heritability estimates obtained for average daily gain at 6-9 was greater than that of 6-12.

Direct additive genetic, permanent environment and maternal additive genetic correlations among average daily gains at different range of ages were also calculated and presented in Fig. 1 and Table 2. As can be seen, the correlations between adjacent periods were generally more closely correlated than between remote periods. Moreover, direct additive genetic correlations (Fig. 1) were generally higher than maternal correlations. Furthermore, most of direct additive genetic correlations were positive indicating that selection for average daily gains at early age would have a positive effect on the same trait at a later age.

Table 2: Direct heritability (diagonals, top), maternal heritability (diagonals, down), permanent environment (upper diagonals) and maternal additive genetic (lower diagonals) correlations among average daily gains (ADG) at different range of ages

ADG	0-3	0-6	0-9	0-12	3-6	3-9	3-12	6-9	6-12	9-12
	0.011									
0-3	0.181	0.783	0.289	0.003	-0.132	-0.208	-0.272	-0.355	-0.420	-0.365
		0.077								
0-6	0.989	0.065	0.820	0.613	0.486	0.395	0.299	0.137	-0.150	-0.366
			0.131							
0-9	0.527	0.644	0.008	0.953	0.891	0.829	0.745	0.570	0.164	-0.252
				0.127						
0-12	-0.455	-0.328	0.506	0.016	0.985	0.953	0.893	0.738	0.317	-0.167
					0.111					
3-6	-0.583	-0.473	0.350	0.982	0.031	0.990	0.951	0.819	0.405	-0.109
						0.100				
3-9	-0.572	-0.471	0.327	0.963	0.994	0.041	0.984	0.882	0.492	-0.036
							0.100			
3-12	-0.539	-0.452	0.297	0.920	0.965	0.989	0.047	0.949	0.621	0.102
								0.107		
6-9	-0.536	-0.480	0.154	0.796	0.876	0.924	0.970	0.046	0.833	0.393
									0.099	
6-12	-0.579	-0.596	-0.269	0.424	0.572	0.652	0.742	0.878	0.041	0.834
										0.059
9-12	-0.541	-0.641	-0.776	-0.169	0.020	0.099	0.197	0.403	0.786	0.047

Table 3: Eigenvalues of coefficient matrix of the direct additive genetic covariance function for cubic model (K = 4)

Eigenvalues				Proportion of total (%)			
First	Second	Third	Fourth	First	Second	Third	Fourth
236.918	55.143	0.331E-04	3.784	80.08	18.64	1.118E-06	1.28

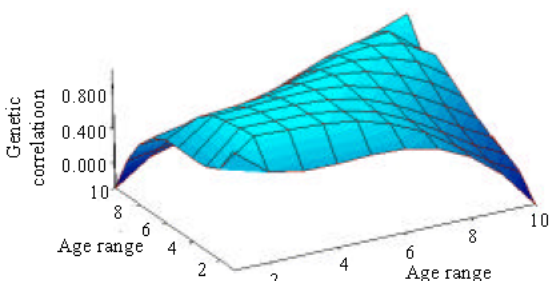


Fig. 1: 3D picture of direct additive genetic correlations between average daily gains at different range of ages

Four eigenvalues of the estimated direct additive genetic covariances function for third order (cubic, K = 4) of polynomial fit are presented in Table 3. In this table, proportion of each eigenvalue of the total eigenvalues was also given to determine their importance.

Based on the results shown in Table 3, the first, second, third and fourth eigenvalues of the coefficient matrix of the direct additive genetic covariance function were 236.918, 55.143, 0.331E-04 and 3.784, respectively. The lower value of eigenvalue for third order than that of fourth order was unclear. Akbas *et al.* (2004) used a random regression model applying Legendre polynomials of quintic order (K = 6) for genetic analysis of quail body weights and they found lower eigenvalue for the second order than the third and fourth orders. In this study, approximately 80.08% of the sum of all eigenvalues for cubic model was accounted for by the first eigenvalue of the coefficient matrix of the direct additive genetic covariance function.

DISCUSSION

As pointed out by Arango and Van Vleck (2002), genetic and non-genetic factors influence on body growth of an animal. Additive and non-additive genetic effects determine the genetic structure of the animal's growth (Arango and Van Vleck, 2002). There is an interaction between the genetic structure and environmental factors such as climate, nutrition and management sex, age (Arango and Van Vleck, 2002). Furthermore, the phenotypic expression of growth can be also affected by maternal as well as random environmental factors (Arango and Van Vleck, 2002).

The results found in the present study revealed that the direct heritability of average daily gain of Lori-Bakhtiari breed of Iran at different age intervals from birth to yearling were generally low and ranged from 0.01 to 0.131. Pre-weaning average daily gain had the lowest direct heritability while the highest direct heritability was obtained for the age range of 0-9. The direct heritability estimate of pre-weaning average daily gain found in this study was lower than that obtained by Talebi and Edriss (1998) and Vatankhah and Talebi (2002) who worked on the same breed due to different models applied for analysis of the same trait. The average direct heritability estimate of post-weaning gain obtained in this study was approximately 0.101 which is lower than that found by Mousa *et al.* (1999). Low direct heritability estimates obtained in the present study indicate that the direct additive genetic variation between individuals only contributes a low proportion of total variation in the population under consideration suggesting that non-genetic factors associated with flock management, nutrition and the other environmental effects are mostly involved in phenotypic variance of average daily gains at different range of ages. Moreover, the low direct genetic variation may also be a function of the random regression model especially when analyzing the data as rates of gain rather than as weight.

Studies of various sheep breeds have shown that both direct and maternal genetic influences are of importance for lamb growth (Janssens *et al.*, 2000; Naser *et al.*, 2000; Boujenane and Kansari, 2002; Lewis *et al.*, 2002; Ekiz *et al.*, 2004). Offspring are influenced by both sire's and dam's genes. Dam, however, has an extended effect on offspring through the maternal environment (Eriksson, 2003). Cytoplasm of the egg, uterine environment, size of the pelvic opening, strength of labour during parturition, behavior and milk production are considered as maternal influences (Eriksson, 2003). The maternal effect of the dam on the progeny may be due to her own genotype and/or her environment she provides and it decreases as the age of the progeny increases (Eriksson, 2003). Based upon the results obtained in the present study, as expected, the maternal heritabilities of average daily gains at different range of ages except 0-3 were generally lower than the corresponding direct heritabilities. As pointed out by Diop and Van Vleck (1998) this is due to the fact that after weaning age (day 90) the maternal effects are expected to

fade out because dependency of the progeny on their mother decreases. Therefore animal's growth after weaning weight, as mentioned by Diop and Van Vleck (1998), should reflect the direct genetic effects to that age with only carry-over maternal effects from before weaning.

With one exception, the direct additive genetic correlations between adjacent ranges of ages were greater than 0.90 between which average daily gain at 0-9 had the highest direct additive genetic correlation with average daily gain at 0-12. Generally, most of the direct additive genetic correlations between average daily gains at different range of ages were positive reflecting that a higher weight gain at earlier ages of an animal is genetically associated with a higher average daily gain at older ages suggesting that animals selected with a greater breeding value for pre-weaning daily gain (0-3) tend to have a greater breeding value for post-weaning daily gain except at 9-12. The phenotypic correlations between average daily gains measured at different range of ages were generally lower than the corresponding direct additive genetic correlations which are in general accordance with findings for other economic traits associated with weight or milk production in sheep or the other farm animals (Pollott *et al.*, 1998; Mousa *et al.*, 1999; Boujenane and Kansari, 2002).

Based upon the large size of the first eigenvalue for the direct additive genetic covariance function in the present study, it can be concluded that genetic selection would produce a rapid change as genetic alteration in the mean growth trajectory is favored. However, this may not be the case for the other eigenvalues because the second, third and fourth eigenvalues accounted for about 18.64%, 1.118E-06 and 1.28% of the total sum of all eigenvalues, respectively. Therefore, in contrast to the first eigenvalue, other eigenvalues only represent a small proportion of the variation in direct additive genetic variance for the trait under consideration. Due to increasing the number of variance and covariance components and computational limitations, in this study measurement error variance was assumed to be constant through the growth trajectory and was estimated as 467.3 g² for cubic random regression model. However, as high speed and capacity computers are increasing, measurement error variance may be assumed to be different at individual range of ages.

Regarding to the advantages of random regression model, which has become the method of choice (Meyer, 2004), in terms of increasing the accuracy of genetic evaluation (due to taking account of the variation of weight gain at both genetic and environmental levels over the period of time, more accurate taking account of environmental factors) and with respect to the higher heritability of average daily gain in Lori-Bakhtiari sheep

breed of Iran at age interval 0-9, it could be suggested that ADG (0-9) may be used as a selection criterion for having faster - growth lambs in next generations.

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