

Genetic analysis of ewe body weight in Lori-Bakhtiari sheep using random regression models

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Abstract (Co)variance components and genetic parameters for test day ewe body weight of Lori-Bakhtiari sheep were estimated using a random regression model (RRM). The data consisted of 22153 individual body weight records, obtained from 1994 ewes (progeny of 205 sires and 1010 dams) between 371 and 3416 days of age, collected from the flock stud of Lori-Bakhtiari Sheep Breeding Station in Shahrekord, Iran during 1989 to 2008, with a total of 2225 animals in the pedigree. The model included the fixed effects (year of production, litter size and stage of production cycle) and random additive genetic, permanent environmental and residual effects. Random regression models were fitted with order 1 to 5 ($k = 2$ to 6) for additive genetic and permanent environmental effects. The residual variance in each model was assumed to be homogeneous or heterogeneous with 9 age classes. Results indicated that the 5th order ($k = 6$) with heterogeneous residual variance was more appropriate than others. Based on selected RRM, the additive genetic variance, permanent environmental variance and phenotypic variance increased with the ewe age. The heritability estimates were 0.38 ± 0.04 , 0.44 ± 0.04 , 0.42 ± 0.04 , 0.38 ± 0.04 , 0.37 ± 0.05 , 0.42 ± 0.06 , 0.48 ± 0.10 and 0.50 ± 0.14 for the ewe body weights at 1.5, 2.5, 3.5, 4.5, 5.5, 6.5, 7.5 and 8 years of age, respectively. The proportion of permanent environmental variance to phenotypic variance ranged from 0.16 ± 0.04 to 0.39 ± 0.05 . Genetic and phenotypic correlations of ewe body weight between consecutive test days were high, but decreased when the interval between body weight measurements increased, ranging from 0.45 ± 0.08 to 0.99 ± 0.09 and 0.37 ± 0.05 to 0.73 ± 0.01 , respectively. Thus, due to moderate genetic correlations between ewe body weight at early and older ages, genetic analysis using RRM may be recommended for improvement of ewe body weight in Lori-Bakhtiari sheep.

Keywords: heritability, genetic correlation, random regression model, Lori-Bakhtiari sheep

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Introduction

Ewe body weight has a direct relationship to feed requirements and productivity. Maintenance requirements are a function of metabolic body weight, representing up to 80% of total feed requirements in sheep (Bedier et al., 1992). Earlier studies showed that the relative economic value of ewe body weight in sheep production systems was low and in some cases negative (Gallivan, 1996; Vatankhah, 2005). Genetic correlations between ewe weight and lamb weight presented in the literature are positive, ranging from moderate to high (Fogarty, 1995; Safari et al., 2005). Therefore, selection for higher lamb weights would be expected to increase the ewe adult weight. However, this is not advantageous because on the one hand heavier ewes, due to their greater requirements for space and food, are more expensive to maintain, and on the hand, their lower productivity is lower compared with medium-

sized ewes (Vatankhah and Salehi, 2010). They are also harder to handle at shearing, at lambing, and on many other occasions (Näsholm and Danell, 1996). Selection to reduce or limit mature ewe body weight requires good estimates of genetic parameters of ewe body weights at different ages. The literature shows that the growth of an animal to a mature age is a longitudinal process whereby an animal increases in size or weight continuously over time until reaching a plateau at maturity. Such a process can be represented by a set of size-age points describing a typical trajectory process and resulting in a set of many highly correlated measures (Meyer, 1998). From an animal breeding point of view, interest lies in those genetic parameters that describe changes in these traits in time. Kirkpatrick et al. (1990) showed that phenotypic changes with age can be represented as a function of time. Tradition-

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ally, traits that are measured in time are analyzed with a multi-trait model, defining the phenotypic values at distinct ages as different traits. One advantage of random regression models over multivariate models is that by using random regression models it is possible to calculate (co)variances between or at every age or time point. Compared with a multivariate model, a random regression model estimates (co)variances more smoothly and with less bias (Kirkpatrick et al., 1990). Heritability of ewe body weight estimated from single or multivariate models were medium to high in different breeds of sheep (Fogarty, 1995; Safari et al., 2005). The Lori-Bakhtiari sheep is one of the most prominent native sheep breeds in southwestern Iran (the Zagros Mountains), with a population of more than 1.7 million heads. However, there is not much information on the genetic parameters of ewe body weight for Iranian native sheep breeds, including the Lori-Bakhtiari. The main aim of the present research was to estimate (co)variance components and genetic parameter estimates for mature ewe body weight in Lori-Bakhtiari sheep using the random regression model.

Materials and methods

Data and flock management

The data set consisted of 22153 records of individual ewe body weight, measured up to four times per year on 1994 ewes at 371 and 3416 days of age. The progeny of 205 rams and 1010 ewes were raised in the flock stud (Lori-Bakhtiari Sheep Breeding Station in Shahrekord, Iran) during 1989 to 2008, with a total of 2225 animals in the pedigree. The flock is managed under semi-migratory or village system (Vatankhah and Talebi, 2009). The flock was kept on the station from December to May, during which time the animals were fed with alfalfa hay, barley and wheat stubble indoors. At other times, the sheep grazed on the nearby ranges and pasture. The breeding period extended from late August to late October (20-25 ewes were assigned randomly to one ram), and lambing started in late January. Lambs were allowed to suckle their dams, and from 15 days of age, they had access to a creep feed *ad-libitum*. Lambs were weaned at an average age of 90 ± 5 days. The flock was subjected to different selection criteria, generally related to increased weaning weight (growth traits, total weaning weight per ewe exposed, or Kleiber ratio) during this period.

Statistical analysis

The trait considered in this investigation was the ewe body weight in kilograms. Ewe weight was recorded

at mating, and at lambing, weaning and shearing. A univariate procedure (SAS, 2000) was used to edit the data and check for normality. The GLM procedure (SAS, 2000) was used to identify important fixed effects influencing the ewe body weight. The statistical model included fixed effects of year of production (1989-2007), litter size (0, 1, and 2) and stage of production cycle (mating, parturition, shearing and weaning). All effects were significant ($P < 0.05$) and hence were included in the final model. The (co)variance components and genetic parameters of ewe body weight were estimated using the restricted maximum likelihood method by WOMBAT software (Meyer, 2006). Ewe body weight at different stages of production (at mating, lambing, weaning and shearing) and in various years was considered a longitudinal trait. Data were analyzed with a random regression model as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \sum_{j=0}^{k-1} \mathbf{Z}_{1j}\mathbf{a}_j + \sum_{j=0}^{k-1} \mathbf{Z}_{2j}\mathbf{p}_j + \mathbf{e} \quad (1)$$

in which, \mathbf{y} , \mathbf{b} , \mathbf{a} , \mathbf{p} and \mathbf{e} are the vectors of observations, fixed effects (year of production, litter size and stage of production cycle), direct additive genetic effects with order of fit k , permanent environmental effects due to repeated records with order of fit k and residual random effects, respectively. Incidence matrices \mathbf{X} , \mathbf{Z}_1 and \mathbf{Z}_2 connected the observations of trait to the respective fixed effects, additive genetic effects and permanent environmental effects, respectively.

The average information REML algorithm was used to maximize the likelihood (convergence criterion was 10^{-8}), and additional restarts were performed until no further improvement in log likelihood occurred. A total of 10 models with order of 2 to 6, including one and nine measurements error classes, were compared. The best model was selected using the likelihood ratio test, contrasting the differences between 2 models with a X^2 distribution at $\alpha = 0.05$, and the degree of freedom equal to difference between number of parameters in two models. When differences between log likelihoods were not significant, the model with the fewest order of fit was chosen as the best model.

Results

The description of the ewe body weight at different ages are set out in Table 1. The mean live weight of ewes 51 kg in 1.5-year old, to 65.19 kg in 5.5-year-old ewes, and then decreased in older ewes. The standard deviation of ewe body weight increased with age up to 3.5 years, decreased up to 5.5 years of age, due to culling some animals, and then increased slightly as age

Table 1. Description of ewe body weight at different ages in Lori-Bakhtiari sheep.

Ewe age (yr)	No. of ewes	Mean of body weight (kg)	S.D. of body weight (kg)
1.5	2803	53.51	7.94
2.5	5407	57.73	8.09
3.5	4643	63.05	8.18
4.5	3804	64.86	8.02
5.5	2746	65.19	7.86
6.5	1781	65.05	8.02
7.5	744	63.95	8.18
8	225	62.21	8.10
Overall mean	22153	61.30	9.06

increased.

Estimated log likelihood values showed a significant improvement in the level of fit when the heterogeneous residual variance was included in the model in comparison to homogeneous residual variance (Table 2). Since changes in likelihood value among models from simple linear ($k = 2$) to quintic model ($k = 6$) were significant ($P < 0.05$).

The estimates of variance components of ewe body weight are shown in Figure 1. Phenotypic variance component of ewe body weight increased as ewe age increased (Figure 1). Additive genetic variance component increased with age to 2.5 years of old, remained constant approximately to 5.5 years of age and then increased with increasing age, while permanent environment variance component increased up to 4.5 years of age and then remained approximately constant. The additive genetic and permanent environment variance components were equal from 4.5 to 5.5 years of age and then additive genetic variance increased as ewe

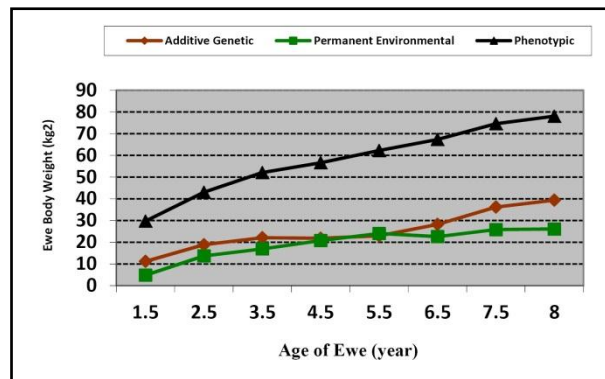


Figure 1. Estimates of variance components of Lori-Bakhtiari ewe body weight at different ages.

age increased, while permanent environment remains constant.

Estimates of heritability (h^2) and proportion of permanent environmental variance to phenotypic variance (c^2) are shown in Figure 2. The heritability values increased up to 2.5 years of age, decreased steadily up to 5.5 years and then increased with increase in ewe age. The estimates of c^2 increased between 1.5 to 4.5 years of age, remained constant up to 5.5 years, decreased to 6.5 years, and remained constant in older ewes. In general, the estimates of h^2 were larger than c^2 , but the value of c^2 from 4.5 to 5.5 years of age was equal or slightly higher than h^2 . Repeatability of mature ewe body weight in Lori-Bakhtiari sheep is a high, as indicated by the magnitude of total animal variance as a proportion of the total phenotypic variance. The estimate of repeatability ($h^2 + c^2$) of ewe body weight showed that the correlation between consecutive records of ewe body weight was high. Estimates of genetic and phenotypic correlations between ewe body weights at different ages are shown in Table 3.

Table 2. Maximum log likelihood values for different orders of fit with one and nine measurements error classes.

Order of regression model	No. measurements error classes	Number of parameters	Log likelihood	Changes in Log likelihood	Degree of freedom	Chi-squared
Linear ($k = 2$)	1	7	-44859.61	-	-	-
	9	15	-44760.30	99.31*	8	15.51
Quadratic ($k = 3$)	1	13	44643.00	117.3*	2	5.99
	9	21	-44573.07	69.93*	8	15.51
Cubic ($k = 4$)	1	21	-44488.86	84.21*	0	-
	9	29	-44416.40	72.46*	8	15.51
Quartic ($k = 5$)	1	31	-44367.19	49.21*	2	5.99
	9	39	-44288.10	79.09*	8	15.51
Quintic ($k = 6$)	1	43	-44262.29	25.81*	4	9.49
	9	51	-44240.11	22.18*	8	15.51

*Significant change ($P < 0.05$).

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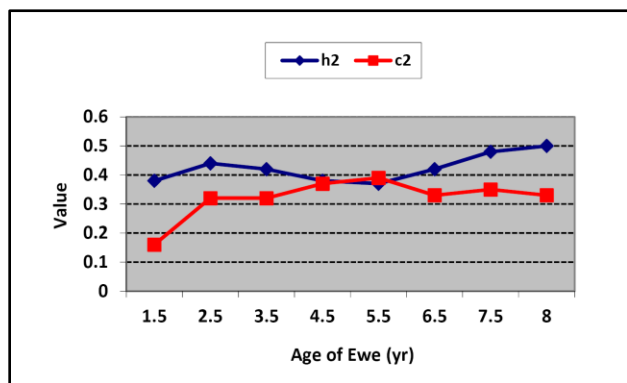


Figure 2. Heritability (h²) and proportion of permanent environmental variance to phenotypic variance (c²) of Lori-Bakhtiari ewe body weight at different ages.

The estimate of genetic and phenotypic correlations were positive for any pair of ages considered and ranged from 0.45 to 0.99 and 0.37 to 0.73, respectively. The pattern of changes in genetic and phenotypic correlations was similar in that the correlations decreased as the age distance between weights increased. In particular, the genetic correlation between subsequent ages approached unity; however, the genetic correlation between early (year 1.5) and late (year 8) weights was moderate (0.45), suggesting that early weights are not under exactly the same genetic control as weights recorded at an older age.

Discussion

One of the main objectives of the present study was to determine the change patterns in the mean and variance components of ewe body weight at different ages in Lori-Bakhtiari sheep. In contrast to mean ewe body weight which followed from the quadratic curve (Table 1), orthogonal polynomial regression of order 6 was chosen as a suitable model to fit the additive genetic and environmental with heterogeneous residual variances (Table 2). Fischer et al. (2004) modeled the weight of Poll Dorset sheep from 50 to 500 days of age

and concluded that the model with order 3, 2, 3 and 3 for direct additive genetic, maternal additive genetic, permanent environment and residual effects respectively, was the best model. Although in agreement with the results of this study, weight record of Brazilian Nelore cattle from birth to 630 d, and from birth to 730 d of age, showed that the log likelihood function increased with order (k) of the polynomial (from 3 to 9), but order of 6 were adequate to fit the variation in the data (Albuquerque and Meyer, 2001).

Despite of the availability of fewer records after 5.5 years of age, due to oldness and low production, and the effect of selection on additive genetic variance (Bulmer effect), the increasing trend of additive genetic variance in older ewes shows that it is likely that several genes with additive effects were activated in older ewes. This pattern of changes in additive genetic variance indicated that body weight of Lori-Bakhtiari ewes are different traits at early, mid and older ages. This increasing pattern of additive genetic variance as animals aged is in agreement with Nephawe (2004). Because the permanent environmental variance is due to non-additive genetic and non-genetic permanent environmental effects, the pattern changes in permanent environmental variance component showed that there may not be any genes with non-additive genetic effect that are activated after 4.5 years of age, and (or) there may not be any non-genetic permanent effects that add to this component after this age.

In general, the values obtained for heritability in this study were with the ranges reported in the literature (Fogarty, 1995; Safari et al., 2005), but the trend in heritability changes at different ages was not consistent with the values in the literature using current animal models. Fogarty (1995) and Safari et al. (2005), reviewing the literature, reported that the value of heritability increased with the age of the animal. The decrease in h² from 2.5 to 5.5 years of age could have been the result of fewer number of records in the data

Table 3. Estimates of genetic correlation (below diagonal), phenotypic correlation (above diagonal) and heritability (diagonal) of Lori-Bakhtiari ewe body weight at different ages.

Ewe Age (yr)	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8
1.5	0.38 ± 0.04	0.57 ± 0.02	0.53 ± 0.03	0.50 ± 0.04	0.48 ± 0.05	0.45 ± 0.05	0.41 ± 0.05	0.37 ± 0.05
2.5	0.86 ± 0.04	0.44 ± 0.04	0.72 ± 0.01	0.62 ± 0.01	0.53 ± 0.02	0.48 ± 0.02	0.47 ± 0.03	0.46 ± 0.04
3.5	0.81 ± 0.04	0.98 ± 0.01	0.42 ± 0.04	0.71 ± 0.01	0.69 ± 0.01	0.59 ± 0.02	0.50 ± 0.03	0.50 ± 0.04
4.5	0.73 ± 0.04	0.93 ± 0.03	0.98 ± 0.02	0.38 ± 0.04	0.71 ± 0.01	0.68 ± 0.01	0.60 ± 0.03	0.50 ± 0.04
5.5	0.68 ± 0.05	0.81 ± 0.05	0.93 ± 0.02	0.98 ± 0.02	0.37 ± 0.05	0.73 ± 0.01	0.71 ± 0.02	0.69 ± 0.03
6.5	0.60 ± 0.06	0.66 ± 0.07	0.81 ± 0.05	0.94 ± 0.02	0.98 ± 0.01	0.42 ± 0.06	0.71 ± 0.02	0.70 ± 0.02
7.5	0.50 ± 0.07	0.58 ± 0.09	0.73 ± 0.09	0.82 ± 0.05	0.95 ± 0.01	0.97 ± 0.05	0.48 ± 0.10	0.71 ± 0.03
8	0.45 ± 0.12	0.58 ± 0.12	0.73 ± 0.12	0.74 ± 0.08	0.90 ± 0.02	0.95 ± 0.06	0.99 ± 0.09	0.50 ± 0.12

set, due to culling of older ewes and to low production. The estimate of h^2 appears to increase sharply towards the end of the trajectory, accompanied by a declining trend of variance for the other effects at later ages. Similar behavior of covariance function estimates for ages where the least data is present has been shown, i.e. at the edge of the trajectory (Meyer, 2002; Fischer et al., 2004). In general, estimates of moderate heritability for ewe body weight in Lori-Bakhtiari sheep over 1.5 to 8 years of age, indicated that selection for this trait could be effective.

The values of genetic correlations among ewe body weight at different ages obtained in this study implied that if animals are selected on the weights, an animal can be below average weight at younger ages, but can be above average weight at older ages; however, this has implications for potential to select on the shape of the growth curve of animal. In addition, genetic and phenotypic correlations between weights at younger ages (1.5 vs. 2.5 years) were lower (0.86 and 0.57) than correlations between weights taken at older ages (6.5 vs. 7.5 years) with the same time lag (0.97 and 0.71). This may be attributed to influence of the part-whole relationship between weights, whereby weights at later ages depend on earlier weights, thus as time advances, the correlations between later weight increase as they are more dependent on the previous weight measures (Fischer et al., 2004). A similar pattern in correlations between weights measured at different ages was reported in sheep (Lewis and Brotherstone, 2002; Fischer et al., 2004) and cattle (Meyer, 2002).

Random regression models allow differences between animals to be accounted for and hence are a useful tool in analyzing the variations in growth curve pattern. This methodology offers a powerful means to evaluate the repeated live weight data and determine the genetic merit (Fischer et al., 2004). The genetic parameter estimates in this study, using RRM, were in agreement with estimates in the literature at specific ages (Vatankhah, 2005; Safari et al., 2005). However, heritability at ages with the least records was considered too high, in particular after 6.5 years of age. Similar estimates were reported for ages with the least data using polynomials (Meyer, 2002); however, this remains an unresolved problem for this type of modeling. The results of the present study showed that considerable genetic variation existed in the growth curve of ewe in Lori-Bakhtiari sheep. Mature weight early in life is genetically a different trait to mature weight later in life, and lower correlations have implications for potential to select on the shape of the growth curve.

Conclusions

The present study indicated that random regression model of order 6, for fitting the additive genetic and environmental with heterogeneous residual variances, was the best for modeling the growth curve in mature Lori-Bakhtiari ewes. There was a good potential for selection for reduced mature ewe body weight, due to moderate heritability. Thus, due to moderate genetic correlations between the ewe body weight at early and older ages, genetic analysis using RRM is recommended for improvement of the ewe body weight in Lori-Bakhtiari sheep.

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