Journal of Livestock Science and Technologies, 2017, 5 (1): 59-65 http://lst.uk.ac.ir

DOI: 10.22103/jlst.2017.10533.1199

Short communication

Estimation of genetic parameters of litter size in Moghani sheep using threshold model via Bayesian approach

M. Latifi[1], A. Mohammadi*[2], M. Bohlouli[3] and S. Alijani[4]

[1]Ph.D. Student of Genetics and Animal Breeding, Department of Animal Science, Faculty of Agriculture, University of Kordestan, Kordestan, Iran.
[2]Young Researchers and Elite Club, Hamedan Branch, Islamic Azad University, Hamedan, Iran.
[3]Young Researchers and Elite Club, Tabriz Branch, Islamic Azad University, Tabriz, Iran.
[4]Department of Animal Science, Faculty of Agriculture, University of Tabriz, Tabriz, Iran.
* Corresponding author, E-mail address: alimohammadi36@tabrizu.ac.ir

Abstract This study was conducted to estimate the genetic parameters of litter size (LS) in Moghani sheep using threshold model via Bayesian approach. The data originated from the Jafar-Abad Station of Ardabil province, Iran, and included 9698 lactation records of 4977 ewes with lambings from 1995 until 2010. The pedigree file consisted of data on animals born from 1987 to 2010. The significance of fixed effects was examined using the Logistic procedure. Six different animal models were fitted by considering direct genetic effect, including and excluding maternal effect (with and without covariance between maternal and direct genetic effects) as well as permanent environmental effect via Bayesian approach. The genetic parameters were estimated using the THRGIBBS1F90 program. The most appropriate model for LS was determined based on the Deviance Information Criterion (DIC). Based on the obtained results, the second model that included the direct genetic and permanent environmental effects of the ewe was chosen as the best model. Using the second model, the estimates of direct heritability, permanent environmental effect of the ewe and repeatability were 0.041, 0.027 and 0.068, respectively. The low estimates of genetic parameters obtained in the current study for LS in Moghani sheep indicated that selection based on the ewe's own performance may result in slow genetic improvement.

Keywords: deviance information criterion, genetic parameters, sheep, threshold model

Received: 01 Mar. 2017, *accepted:* 02 Jun. 2017, *published online:* 08 June. 2017

Introduction

Accurate prediction of animals breeding values is one of the best tools available to maximize the response to a selection program. Development of effective genetic evaluation and improvement programs requires knowledge of the genetic parameters for these economically important production traits (Safari et al., 2005).

Moghani sheep, numbering about 5.5 million, is one of the most important meat breeds in Iran (Ghavi Hossein-Zadeh, 2013). They are well-known for their large size, tolerance to climatic changes and their capability to produce heavy lambs (Shodja et al., 2006). Both sexes of Moghani breed are polled and reared in a traditional migratory system, during the summer in the mountainous areas and winter in the plain regions (Ghavi Hossein-Zadeh, 2013).

Litter size (LS) in sheep, number of lambs born per ewe per, is component of reproductive efficiency (Olesen (Olesen et al., 1994), and also an important economical trait in meat production (Janssens et al., 2004). There are two important approaches to be considered in the genetic analysis of LS. One approach suggests that LS in different parities is controlled by different genes, and therefore should be treated as different traits (Noguera et al., 2002; Roehe and Kennedy, 1995; Mekkawy et al., 2010). In the second approach, for each parity the LS has categorical characteristics observed on a discontinuous scale as a threshold or quasi-continuous trait. Also, analysis of LS by linear models, without considering the categorical nature, is not accounted for non-normal distribution (Mekkawy et al., 2010).

In many studies, LS is analyzed by linear models, and the variance components are obtained by REML methods. Compared to linear models, non-linear models have disadvantages in goodness of fit or predictive ability and they are time consuming in computation, which might be prohibitive for routine calculations (Hagger, 2000).

A handful of studies on sheep with different genetic backgrounds (Mokhtari et al., 2010; Yazdi et al., 2012; Latifi et al., 2014) were conducted aimed at estimating the genetic parameters of LS; some investigations were carried out in Moghani sheep concerning the estimation of genetic parameters of weight traits (Ghavi Hossein-Zadeh and Ardalan, 2010; Ghavi Hossein-Zadeh, 2012). There is no report regarding estimation of the genetic parameters of LS in Moghani shepp using the Bayesian method with different models. Therefore, this study was carried out to estimate the genetic parameters of LS in Moghani sheep by different models using the threshold model via Bayesian approach.

Materials and methods

The data set used in this study contained records of LS on 4977 ewes collected from 1995 to 2010 at the Moghani Sheep Breeding Center in Jafar-Abad, Ardabil province, Iran. The pedigree file consisted of the information on animals born between 1987 and 2010. The final model included the fixed effects of age (6 levels, from 2 to 7), herd (31 levels) and years of lambing (17 levels).The significance of fixed effects was examined using the Logistic procedure (SAS, 2003) software. The response of LS was modeled using the following distribution:

$$f(y_{ls}|I_{ls}) = \Pi_{i=1,nd} f(y_{i_{ls}}|I_{i_{ls}}) = \Pi_{i=1,nd} 1(I_{ls} < t)\, 1(y_{i_{ls}} = 1) + 1(t < Ils)\, 1(y_{i_{ls}} = 2) \qquad (1)$$

where, t is the threshold defining the two categories of responses; nd is the total number of data points, and I_{ls} is the underlying distribution of the LS. Genetic parameters for LS were estimated via Bayesian approach using THRGIBBS1F90 program (Misztal et al., 2002). The Gibbs sampler was run for 300,000 rounds, and the first 30,000 rounds were discarded as a burning period. A thinning interval of 100 rounds was used to retain sampled values which reduced lag correlation among thinned samples. Thus, 2700 samples were kept to compute the highest posterior density in 95% region for variance component.

Statistical Analysis

The six animal models fitted for the genetic analysis were used as following: (2)

Model 1: $\boldsymbol{y = Xb + Z_1a + e}$

Model 2: $\boldsymbol{y = Xb + Z_1a + Z_3c} + e$

Model 3: $\boldsymbol{y = Xb + Z_1a + Z_2m + e}$ $\qquad$ $\boldsymbol{Cov\ (a, m) = 0}$

Model 4: $\boldsymbol{y = Xb + Z_1a + Z_2m + e}$ $\qquad$ $\boldsymbol{Cov\ (a, m) = A\sigma_{am}}$

Model 5: $\boldsymbol{y = Xb + Z_1a + Z_2m + Z_3c + e}$ $\qquad$ $\boldsymbol{Cov\ (a, m) = 0}$

Model 6: $\boldsymbol{y = Xb + Z_1a + Z_2m + Z_3c + e}$ $\qquad$ $\boldsymbol{Cov\ (a, m) = A\sigma_{am}}$

where, $\boldsymbol{y}$ is the vector of observations; $\boldsymbol{b}$ is the vector of fixed effects; $\boldsymbol{a}$ and $\boldsymbol{m}$ are the vectors of random direct and maternal additive genetic effects, respectively; $\boldsymbol{c}$ is the vector of permanent environmental effect of the ewe and $\boldsymbol{e}$ is the vector of residuals. $\boldsymbol{X}$, $\boldsymbol{Z_1}$, $\boldsymbol{Z_2}$ and $\boldsymbol{Z_3}$ are incidence matrices for $\boldsymbol{b}$, $\boldsymbol{a}$, $\boldsymbol{m}$ and $\boldsymbol{c}$, respectively. Also, $\boldsymbol{A}$ is the additive relationship matrix and $\boldsymbol{A\sigma_{am}}$ is covariance between direct and maternal genetics effects. For (co)variance matrix of the random effects, the following assumptions were considered:

$$V_a = A\sigma_a^2;\ V_m = A\sigma_m^2;\ V_{pe} = I\sigma_{pe}^2;\ V_e = I\sigma_e^2;\ Cov_{a,m} = A\sigma_{am} \qquad (3)$$

where, σ_a^2 is the direct genetic variance; σ_m^2 is the maternal genetic variance; σ_{pe}^2 is the permanent environmental variance; σ_e^2 is the residual variance and I is identity matrices. Repeatability (r) was calculated using the following formula:

$$r = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_p^2} \qquad (4)$$

The model Goodness of fit was examined using the Deviance Information Criterion (DIC):

$$D(\theta) = -2\log\left(p(\mathbf{y}|\theta)\right) + C \qquad (5)$$

where, $\boldsymbol{y}$ is a vector of observations; θ is unknown parameter; $p(\boldsymbol{y}|\theta)$ is likelihood function, the conditional joint probability density function of the observations given the unknown parameters; C is a constant which cancels out in all calculations that compare different models, and need not to be known. The Bayesian measure of model fit is defined as the posterior expectation of the deviance:

$$\bar{D} = E_{\theta|y}[D(\theta)] = E_{\theta|y}[-2\ln f(y|\theta)] \qquad (6)$$

where, $\bar{D}$; which is defined as -2log-likelihood and therefore, attains smaller values for better models. Also, the effective number of parameters, PD, is defined as the difference between the posterior mean of the deviance and the deviance evaluated at posterior mean of the deviance and the deviance evaluated at the posterior mean $\bar{\theta}$ of the parameters:

$$PD = \bar{D} - D\left(\bar{\theta}\right) = E_{\theta|y}[D(\theta)] - D(E_{\theta|y}[\theta]) \qquad (7)$$

where, $\bar{\theta}$ is the expectation of θ. The deviance information criterion is calculated as follows:

Table 1. Descriptive statistics of the data sets for different parities in Moghani sheep

Parity	Observation	Mean	SD	Type of birth		CV
				single	twin	
First	4977	1.10	0.29	4498	479	26.9
Second	2503	1.14	0.33	2178	325	29.7
Third	1436	1.18	0.39	1168	268	32.8
Fourth	782	1.23	0.42	597	185	34.4
Total	9698	1.16	0.33	8441	1257	29.73

$$DIC=PD+\bar{D}, \quad (8)$$

The model giving the lowest DIC value was chosen as the best approximating model.

Results

The number of records, mean, standard deviation (SD), coefficient of variation (CV) and type of birth (single and twin) are summarized in Table 1. The mean LS was 1.16. The estimates of variance components and genetic parameters are shown in Table 2. The second model (that included direct genetic and permanent environmental effect of the ewe), with the lowest DIC value, was chosen as the best approximating model for LS. The estimated direct heritability, permanent environmental effect of the ewe and repeatability with most appropriate model were 0.041, 0.027 and 0.068, respectively. The maternal heritabilities were between 0.020 and 0.029 (for model 3 to 6). The maternal heritability estimates were lower than direct heritability estimates. The highest posterior density reflects the accuracy of the variance components estimates and, thus can be used as confidence intervals (Figure 1 and 2). Computation of highest posterior density (HPD) in 95% region for variance component is given in Table 3.

Discussion

Mean LS ranged from 1.36 to 1.55 for Danish Texel, Shropshire, Oxford Down and Suffolk (Maxa et al., 2007); amounted to 1.33 for Rambouillet breed (Hanfo-

Table 2. Estimates of genetic parameters for litter size in Moghani sheep

trait	Model	σ^2_a	σ^2_m	σ^2_e	σ^2_p	σ^2_{pe}	h^2_a	h^2_m	σ_{am}	c^2	r	DIC
Litter size	1	0.006	-	0.101	0.107	-	0.057	-	-	-	-	5840.23
	2	**0.004**	**-**	**0.100**	**0.108**	**0.003**	**0.041**	**-**	**-**	**0.027**	**0.068**	**5832.16**
	3	0.004	0.003	0.101	0.109	-	0.038	0.029	-	-	-	5842.52
	4	0.004	0.003	0.102	0.109	-	0.039	0.027	0.0001	-	-	5845.31
	5	0.003	0.003	0.100	0.109	0.003	0.027	0.024	-	0.025	0.052	5834.04
	6	0.002	0.002	0.100	0.108	0.003	0.022	0.020	0.001	0.031	0.050	5833.50

σ^2_a; additive genetic variance, σ^2_m; maternal genetic variance, σ^2_e; residual variance, σ^2_p; phenotypic variance, σ^2_{pe}; permanent environmental variance, h^2_a; direct heritability, h^2_m; maternal heritability, c^2; permanent environmental effect of the ewe, r; repeatability , DIC; Deviance information criterion.

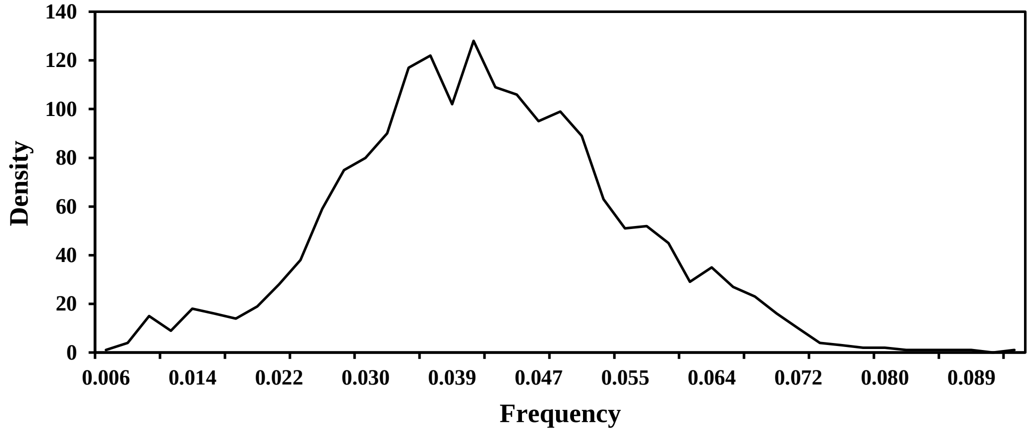

Figure 1. Marginal posterior distribution of direct heritability effect in Moghani sheep

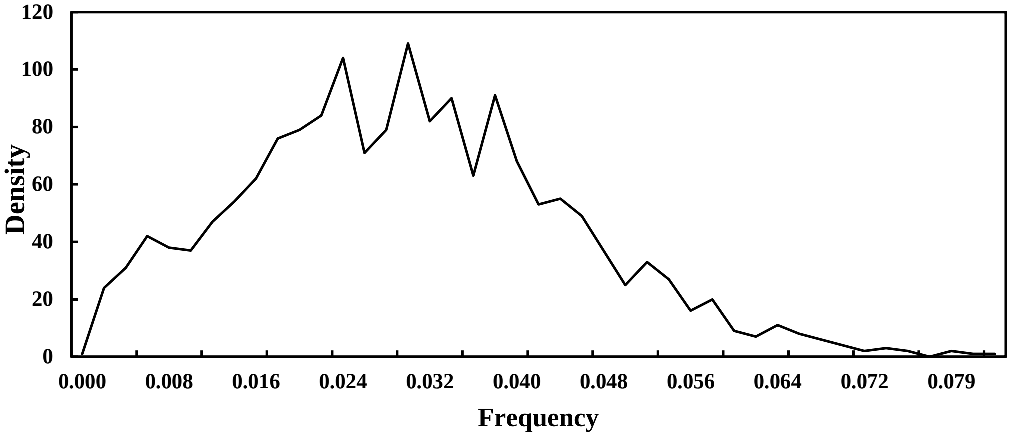

Figure 2. Marginal posterior distribution of permanent environmental effect of the Moghani ewes

Table 3. Computation of highest posterior density in 95% region for variance components in Moghani sheep

Trait	Model	σ^2_a	σ^2_m	σ^2_e	σ^2_{pe}	σ^2_p	h^2_a	h^2_m	c^2
Litter size	1	0.004-0.007	-	0.09-0.10	-	0.10-0.11	0.04-0.07	-	-
	2	0.001-0.007	-	0.09-0.10	0-0.005	0.10-0.11	0.01-0.06	-	0.027
	3	0.001-0.006	0-0.005	0.09-0.10	-	0.10-0.11	0.01-0.06	0.004-0.048	-
	4	0.001-0.007	0-0.005	0.09-0.10	-	0.10-0.11	0.01-0.06	0.002-0.046	-
	5	0-005	0-0.004	0.09-0.10	0-0.005	0.10-0.11	0.006-0.047	0.005-0.044	0.025
	6	0-004	0-004	0.09-0.10	0-0.006	0.09-0.11	0.003-0.034	0.004-0.038	0.031

σ^2_a; additive genetic variance,σ^2_m; maternal genetic variance, σ^2_e; residual variance, σ^2_p; phenotypic variance,σ^2_{pe}; permanent environmental variance,h^2_a; direct heritability,h^2_m; maternal heritability,c^2; permanent environmental effect of the ewe.

rd et al., 2005) and for Mehrabani sheep (Latifi et al., 2014) of 1.13, was in consistence with mean LS of this study.

The estimate of direct heritability (in Moghani breed) based on the best model (0.041) was close to direct heritability (0.053) in Turkish Merino (Eklz, et al., 2005) and estimates (from 0.04 to 0.06) for Danish Texel, Shropshire, Oxford Down and Suffolk (Maxa et al., 2007). The lowest and highest direct heritabilities were obtained using models 1 and 6, respectively. Direct heritability estimates of LS trait from univariate analyses varied between 0.07 to 0.09, 0.12 to 0.16 and 0.08 to 0.11 in Romanov (Maria, 1995), Chios (Ligda et al., 2000) and Rambouillet (Hanfordet et al., 2005), respectively. The estimates ranged from 0.09 to 0.11 for Targhee, Suffolk, Polypay (Rao and Notter, 2000) and 0.05 to 0.1 for Lori-Bakhtiari sheep (Poortahmaseb et al., 2007). For Rasa Aragonesa (Altariba et al., 1998), Ripollesa (Casellas et al., 2007) and Mehrabani (Latifi et al., 2014) sheep, the estimated heritabilities were 0.077, 0.13 and 0.04, respectively. In Baluchi sheep, the heritabilities in different parities were between 0.37 and 0.29 (Yazdi et al., 1999).

Inconsistencies between models and heritability values may be due to the effect of factors such as environmental effects, number of records, pedigree structure and capability of the method. The maternal heritabilities were lower than the estimates reported in other sheep breeds. The estimate of maternal heritabilities were 0.06 to 0.07 in Boutsiko mountain breed (Kominakis et al., 1998); 0.08 in Segurena (Analla et al., 1998) and Romanov (Mariya, 1995), and 0.11 in the Mehrabani sheep (Latifi et al., 2014).

Estimates of permanent environmental effect of the ewe were in agreement with those obtained in Turkish Merino (0.025) by Ekiz et al. (2005) and Chios sheep (0.028) by Ligda et al. (2000). The permanent environmental effect was equal to 0.05 in the Rambouillet (Hanford et al., 2005) and ranged between 0.08 and 0.47 in the Lori-Bakhtiari sheep (Poortahmaseb et al., 2007) and 0.07 for Kermani sheep (Mokhtari et al., 2010). Although a good agreement was found with most studies (Ligda et al., 2000; Mokhtari et al., 2010), the discrepancy between results obtained in this study and the literature could be attributed to the rate of twinning in different sheep breeds.

The estimates of repeatability for LS trait obtained in the current study ranged from 0.05 to 0.07, and were close to estimates in the Kermani sheep (0.08) by Mokhtari et al. (2010) and in Turkish Merino sheep (0.078) by Ekiz et al. (2005). The results showed low repeatability, low correlation between different records of LS and removal of ewes based on a record with low accuracy.

Conclusions

The estimates of genetic parameters obtained from a threshold model for LS indicated the likelihood of improvement in reproductive efficiency through selection in Moghani sheep. The low heritability and repeatability estimates imply that selection based on these traits may result in slow genetic improvement in reproductive efficiency. Therefore, improvement of non-genetic factors in the flocks such as the ewe nutrition before mating and during pregnancy can lead to improvement of these characteristics.

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برآورد پارامترهای ژنتیکی چند قلوزایی در گوسفند مغانی با استفاده از مدل آستانه‌ای به روش بیزی

م. لطیفی[۱]، ع. محمدی*[۲]، م. بهلولی[۳] و ص. علیجانی[۴]

[۱]دانشجوی دکتری ژنتیک و اصلاح دام، گروه علوم دامی، دانشکده کشاورزی، دانشگاه کردستان، کردستان، ایران.

[۲]دانشگاه آزاد اسلامی، واحد همدان، باشگاه پژوهشگران جوان و نخبگان، همدان، ایران.

[۳]باشگاه پژوهشگران جوان و نخبگان ، واحد تبریز، دانشگاه آزاد اسلامی، تبریز، ایران.

[۴]گروه علوم دامی، دانشکده کشاورزی، دانشگاه تبریز، تبریز، ایران.

***نویسنده مسئول، پست الکترونیک:** alimohammadi36@tabrizu.ac.ir

چکیده این مطالعه برای برآورد پارامترهای ژنتیکی صفت چند قلوزایی در گوسفند مغانی با استفاده از مدل آستانه‌ای به روش بیزی انجام گردید. اطلاعات مورد نیاز از مرکز جعفرآباد استان اردبیل شامل ۹۶۹۸ رکورد از ۴۹۷۷ راس میش بین سال‌های ۱۳۷۷ تا ۱۳۹۲ جمع‌آوری شد. فایل شجره شامل اطلاعات حیواناتی بود که بین سال‌های ۱۳۶۶ تا ۱۳۹۲ متولد شده بودند. معنی‌دار بودن اثرات ثابت با استفاده از رویه لجستیک تعیین شدند. مدل‌های حیوانی مختلف شامل اثرات ژنتیکی مستقیم برازش شده بود، شامل اثرات مادری (با و بدون کواریانس بین اثرات ژنتیکی مستقیم و مادری)، اثرات محیط دائمی به روش بیزی برازش شدند. پارامترهای ژنتیکی با استفاده از برنامه Thrgibbs1f90 برآورد گردید. مدل مناسب برای چند قلوزایی بر اساس DIC تعیین شد. بر اساس نتایج به‌دست آمده، مدل دوم که شامل اثرات ژنتیکی مستقیم و محیط دائمی میش‌ها بود به‌عنوان بهترین مدل انتخاب شد. با استفاده از این مدل، برآوردهای وراثت‌پذیری مستقیم، اثرات محیط دائمی میش‌ها و تکرارپذیری به ترتیب ۰/۰۴۱، ۰/۰۲۷ و ۰/۰۶۸ به‌دست آمدند. برآوردهای پائین پارامترهای ژنتیکی به‌دست آمده در این مطالعه برای چند قلوزایی در گوسفند مغانی نشان داد که انتخاب بر اساس عملکرد خود میش‌ها ممکن است منتج به بهبود پائین ژنتیکی شود.