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Bayesian Estimates of Genetic Relationships between Growth Curve Parameters in Shall Sheep via Gibbs Sampling

Research Article

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ABSTRACT

The objective of this study was to estimate variance components and genetic parameters for growth curve parameters in Shall sheep. Studied traits were parameters of Brody growth model which included A (asymptotic mature weight), B (initial animal weight) and K (maturation rate). The data set and pedigree information used in this study were obtained from the Animal Breeding Center of Iran and comprised 4020 growth curve parameters of lambs from birth to 400 days of age during 1982 to 2012. Marginal posterior distributions of parameters and variance components were estimated using TM program. The Gibbs sampler was run 300000 rounds and the first 60000 rounds were discarded as a burn-in period. Posterior mean estimates of direct heritabilities for A, B and K were 0.13, 0.15 and 0.19, respectively. Estimates of direct genetic correlation between growth curve parameters were 0.41, -0.30 and -0.31 between A-B, A-K and B-K, respectively. Residual correlations between growth curve parameters varied from -0.57 (between A-K) to 0.62 (between A-B). Also, phenotypic correlations between growth curve parameters varied from -0.48 (between B-K) to 0.30 (between A-B). The low estimates of heritability obtained in this study implies that although genetic selection could be partially affected on the growth curve parameters, much of the improvement in these parameters could be attained by improvement of production environment rather than genetic selection in this breed of sheep.

KEY WORDS bayesian methodology, fat-tailed sheep, genetic parameter, Gibbs sampling, growth curve.

INTRODUCTION

The Shall sheep is a local sheep breed of Iran with a population of more than 600000 heads. The breed is fat-tailed, large-size, predominantly black or brown with white spots in front of head, well adapted to the harsh climate and raised mainly for its meat that is most important source of protein in Iran and sale of its surplus lambs is the main source of cash income for farmers. The data on reproductive performance were collected from 2001 to 2007 at the breeding station of Shall sheep located in Buin Zahra city, Qazvin province of Iran. Ewes were randomly exposed to the rams at the age of 18 months and lambing occurred in one season, from mid-January to mid-March. Ewes were kept in the flock up to 6 years old. Rams were kept until a male offspring was available for replacement. During the breeding season, single sire pens were used allocating 20-25 ewes per ram. Ewes usually lamb thrice every two years. Lambs remained with their dam until weaning. The flock was mainly kept on range and was fed by cereal pasture, but supplemental feed, including alfalfa and wheat straw, was provided especially around mating season (Amou Posht-e- Masari *et al.* 2013). Studies focusing on growth curves have increased in recent years due to the development of new computational methods for faster and more accurate analyses as well as the availability of new models to be tested (Souza *et al.* 2013). Growth rate is related to rate of maturing and mature weight and these latter traits have been suggested to have relationships with other lifetime productivity parameters in sheep (Bedier *et al.* 1992; Abegaz *et al.* 2010). Growth curve parameters provide potentially useful criteria for modifying the relationship between body weight and age through selection (Kachman and Gianola 1984) and an optimum growth curve can be obtained by selection for desired values of growth curve parameters (Bathaei and Leroy, 1998). Non-linear mathematical models, empirically developed by plotting body weight against age, have been suitable to describe the growth curve in different animal groups (Malhado *et al.* 2009). Accurate estimates of variance components are important in animal breeding because genetic parameters are based upon (co)variance components, which must be accurately estimated (Schaeffer, 1984). Therefore, improved methodologies for estimation of these components are constantly evolving. The Gibbs Sampling algorithm (Magnabosco *et al.* 2000) enables estimation of random samples of parameter estimates based on a given data set, by generating posterior distributions of parameter values that are proportional to the product of the parameter probabilities and the observation probabilities (Ghavi Hossein-Zadeh and Ardalan, 2010). Estimates of variance components and heritabilities for growth curve parameters in sheep are very scarce in the literature. Therefore, the objective of this study was to estimate variance components and genetic parameters for growth curve characteristics in Shall sheep using Gibbs sampling algorithm in Bayesian methodology.

MATERIALS AND METHODS

The data set and pedigree information used in this study were obtained from the Animal Breeding Center of Iran and comprised 4020 growth curve parameters of lambs from birth to 400 days of age during 1982 to 2012. Among a number of mathematical models, Brody function (Brody, 1945) has been found to be adequate for comparing individual differences in rate of maturing and mature weight (Gbangboche *et al.* 2008). Additionally this function has advantages of mathematical simplicity and biological interpretability (Abegaz *et al.* 2010). Therefore, Brody model was used to estimate parameters of the growth curve for each animal and is presented as follows:

$$y= A(1-Be^{-Kt})$$

Where:

y: represents body weight at age t (day).

A: represents asymptotic weight, which is interpreted as mature weight.

B: integration constant related to initial animal weight. The value of B is defined by the initial values for y and t.

K: maturation rate, which is interpreted as weight change in relation to mature weight to indicate how fast the animal approaches adult weight.

The data were screened several times and atypical growth curves resulting in out of range parameters were deleted. Also, lambs with incomplete records of parentage or with registration numbers lower than the numbers of their parents were left out. The characteristics of data used in this study are presented in Table 1. Also, the number of animals (in total), sires, dams, founders and non-founders in the pedigree of Shall sheep were 64964, 720, 18345, 31270 and 33694, respectively. The choice of fixed effects to be considered was made after testing whether the effects were statistically significant with a linear fixed effects model analyzed with GLM procedure of SAS (2002). Level of significance for the inclusion of effects into the model of analysis was declared at $P < 0.05$. The final model of analysis for A, B and K parameters included the fixed class effects of flock, birth year, birth month, sex, litter size and age of dam. All models of analysis included the random additive direct genetic effect of animal. The univariate animal model fitted for the genetic analysis of the growth curve parameters was as follows:

$$y= Xb + Za + e$$

Where:

y: $N \times 1$ vector of records for each growth curve parameter.

b: denotes the fixed effects in the model with association matrix X.

a: vector of direct genetic effects with the incidence matrix Z.

e: denotes the vector of residual effects.

From a Bayesian perspective, it was assumed that prior distribution for additive direct effects was multivariate normal distribution with mean 0 and variance $A\sigma^2_a$:

Where:

A: additive numerator relationship matrix.

σ^2_a: additive direct variance.

Residual effects were assumed to be multivariate normally distributed with mean 0 and variance $I_n\ \sigma^2_e$:

Where:

I_n: identity matrix with order equal to the number of individual records, respectively.

σ^2_e: residual variance.

Bivariate or pair-wise analyses were carried out for every pair of the traits. The models applied in pair-wise analyses were those fitted for each of the traits in the univariate analyses.

Table 1 Characteristics of data set

Trait	No. of records	Mean	SD
A	4020	43.20	11.00
B	4020	0.90	0.03
K	4020	0.0076	0.0037

A: represents asymptotic weight, which is interpreted as mature weight; B: integration constant related to initial animal weight. The value of B is defined by the initial values for y and t and K: maturation rate, which is interpreted as weight change in relation to mature weight to indicate how fast the animal approaches adult weight.
SD: standard deviation.

The prior distribution for the genetic and residual (co)variance matrices is assumed to be an inverted Wishart distribution. Marginal posterior distributions of parameters and variance components were estimated, using TM program (Legarra *et al.* 2011). The Gibbs sampler was run 300000 rounds, and the first 60000 rounds were discarded as a burn-in period (Legarra *et al.* 2011). A thinning interval of 100 rounds was used to retain sampled values that reduced lag correlation among thinned samples. The bayesian output analysis (BOA version 1.1.5; Smith, 2005) package was used to calculate the mean, standard deviation (SD) and 95% high posterior density (HPD) interval for all parameters from the individual marginal posteriors, under the free software R (http://www.rproject.org/). The HPD region provides the interval that includes 95% of samples and is a measure of reliability. Also, the HPD can be applied to non-symmetric distributions (Hyndman, 1996).

RESULTS AND DISCUSSION

The posterior means, medians and modes of variance components and direct heritabilities and their HPDs for growth curve parameters obtained from univariate models of analysis are presented in Table 2. Posterior mean estimates of direct heritabilities for A, B and K were 0.13, 0.15 and 0.19, respectively. The low estimates of heritabilities for A, B and K parameters could be assigned to the high phenotypic variance arising from large environmental variation. This therefore implies that much of the improvement in these growth curve parameters could be obtained by improvement of environment rather than genetic selection (Van der Westhuizen *et al.* 2001; Ghavi Hossein-Zadeh 2011).

It is important to note that the variation range of HPDs of the direct heritabilities are located at the region greater than zero. Hence, the probability of obtaining a zero estimate for these parameters was almost null. Posterior distributions of the direct estimates of heritabilities for different parameters of growth curve are shown in Figure 1.

Estimates of variance components and direct heritabilities for growth curve parameters showed no or slight differences between median, mode and mean. Therefore, a normal posterior density was assumed for direct heritabilities. Abegaz *et al.* (2010) reported the estimates of heritabilities were 0.29, 0.18 and 0.14 for A, B and K parameters in Horro sheep, respectively. Inconsistent with the current results, Bathaei and Leroy (1998), Stobart *et al.* (1986) and Stobart (1983) reported high estimates of heritability for A parameter, but Mavrogenis and Constantinou (1990) and Näsholm (1990) reported lower heritabilities for this parameter in Chios sheep and Swedish Finewool sheep, respectively. The lower heritability for mature weight is probably due to maturity at a earlier age in Shall sheep, where the influence of environmental factors becomes large. In general, several factors such as breed of the animal, genetic variation within population, management and environmental conditions, the method of estimating parameter, etc., would have affected the differences between estimations (Ghavi Hossein-Zadeh and Ardalan, 2010). The heritability and genetic relationship between traits are needed for planning an efficient breeding system and development of effective genetic evaluation. The current estimates of genetic parameters for growth curve characteristics in Shall sheep could be used for designing future selection schemes in this breed. The posterior mean, median and mode of direct genetic, residual and phenotypic correlations between growth curve parameters of Shall sheep are reported in Table 3. Estimates of direct genetic correlation between growth curve parameters were 0.41, -0.30 and -0.31 between A-B, A-K and B-K, respectively. The positive and high genetic correlation between A and B parameters are evidence for common genetic and physiological mechanism controlling these traits. Also, positive genetic correlation between these traits suggesting that selection of sheep in favour of one parameter of growth curve would also improve other parameter.

Positive genetic correlation between A-B indicated that heavy lambs at birth had greater mature weight. On the other hand, genetic correlations between A-K and B-K were negative and medium. It has been shown that a negative and high genetic correlation between direct and maternal genetic effects for a specific trait might be a product of both existing genetic antagonism and can be influenced by data structure (Maniatis and Pollott, 2003). It seems possible that the antagonism between the effects of an individual's genes for growth and those of its dam for a maternal ability might be due to natural selection for an intermediate optimum (Tosh and Kemp, 1994). Negative genetic correlation between A-K in this study was consistent with the reports of Abegaz *et al.* (2010), Bathaei and Leroy (1998) and Stobart *et al.* (1986).

Table 2 The posterior mean, median and mode of direct genetic, residual and phenotypic variances and direct heritabilities for growth curve parameters of Shall sheep [standard deviations (PSD) of marginal posterior distribution of mean estimates are in brackets]

Parameter	Item	Mean	Median	Mode	HPD
A	σ_a^2	10.23 (2.99)	9.97	11.00	4.28-15.91
	σ_e^2	66.73 (2.84)	66.85	67.84	61.14-72.14
	σ_p^2	76.96 (1.80)	76.95	76.31	73.46-80.24
	h_a^2	0.13 (0.04)	0.13	0.11	0.06-0.21
B	σ_a^2	0.70 (0.20)	0.69	0.65	0.29-1.08
	σ_e^2	3.96 (0.18)	3.96	4.05	3.61-4.32
	σ_p^2	4.66 (0.11)	4.66	4.65	4.46-4.89
	h_a^2	0.15 (0.04)	0.15	0.15	0.06-0.22
K	σ_a^2	1.94 (0.58)	1.89	1.72	0.80-3.07
	σ_e^2	8.09 (0.49)	8.10	8.06	7.15-9.06
	σ_p^2	10.03 (0.26)	10.01	9.95	9.55-10.55
	h_a^2	0.19 (0.06)	0.19	0.18	0.09-0.30

h^2_a: direct heritability; σ^2_a: direct additive genetic variance; σ^2_e: residual variance and σ^2_p: phenotype variance.

HPD: 95% high posterior density interval.

A: represents asymptotic weight, which is interpreted as mature weight; B: integration constant related to initial animal weight. The value of B is defined by the initial values for y and t and K: maturation rate, which is interpreted as weight change in relation to mature weight to indicate how fast the animal approaches adult weight.

Table 3 The posterior mean, median and mode of direct genetic and residual correlations between growth curve parameters of Shall sheep [standard deviations (PSD) of marginal posterior distribution of mean estimates are in brackets]

Correlation	Item	Traits		
		A-B	A-K	B-K
$r_{a_1a_2}$	Mean	0.41 (0.15)	-0.30 (0.18)	-0.31 (0.18)
	Median	0.43	-0.31	-0.33
	Mode	0.42	-0.36	-0.38
	HPD	0.08-0.66	-0.68-0.06	-0.65-0.08
$r_{e_1e_2}$	Mean	0.62 (0.02)	-0.57 (0.03)	-0.51 (0.03)
	Median	0.62	-0.58	-0.51
	Mode	0.61	-0.58	-0.51
	HPD	0.58-0.65	-0.63- -0.53	-0.57- -0.46
$r_{p_1p_2}$	Mean	0.30 (0.01)	-0.26 (0.02)	-0.48 (0.01)
	Median	0.30	-0.26	-0.48
	Mode	0.30	-0.26	-0.48
	HPD	0.28-0.33	-0.29- -0.22	-0.51- -0.45

r_{a1a2}: direct genetic correlation between growth curve parameters; r_{e1e2}: residual correlation between growth curve parameters and r_{p1p2}: phenotypic correlation between growth curve parameters;

HPD: highest posterior density at 95%.

A: represents asymptotic weight, which is interpreted as mature weight; B: integration constant related to initial animal weight. The value of B is defined by the initial values for y and t and K: maturation rate, which is interpreted as weight change in relation to mature weight to indicate how fast the animal approaches adult weight.

The variation range of HPDs for the direct genetic correlations of A-K and B-K include zero which indicate there was a probability of obtaining zero estimates for these correlation estimates, but the HPD interval of genetic correlation between A-B did not include zero. Posterior distribution of direct genetic correlations between growth curve parameters are shown in Figure 2. There were generally slight differences between median, mode and mean estimates of direct genetic correlations. Therefore, a normal posterior density could be assumed for direct genetic correlations.

Residual correlations between growth curve parameters varied from -0.57 (between A-K) to 0.62 (between A-B). Also, phenotypic correlations between growth curve parameters varied from -0.48 (between B-K) to 0.30 (between A-B).

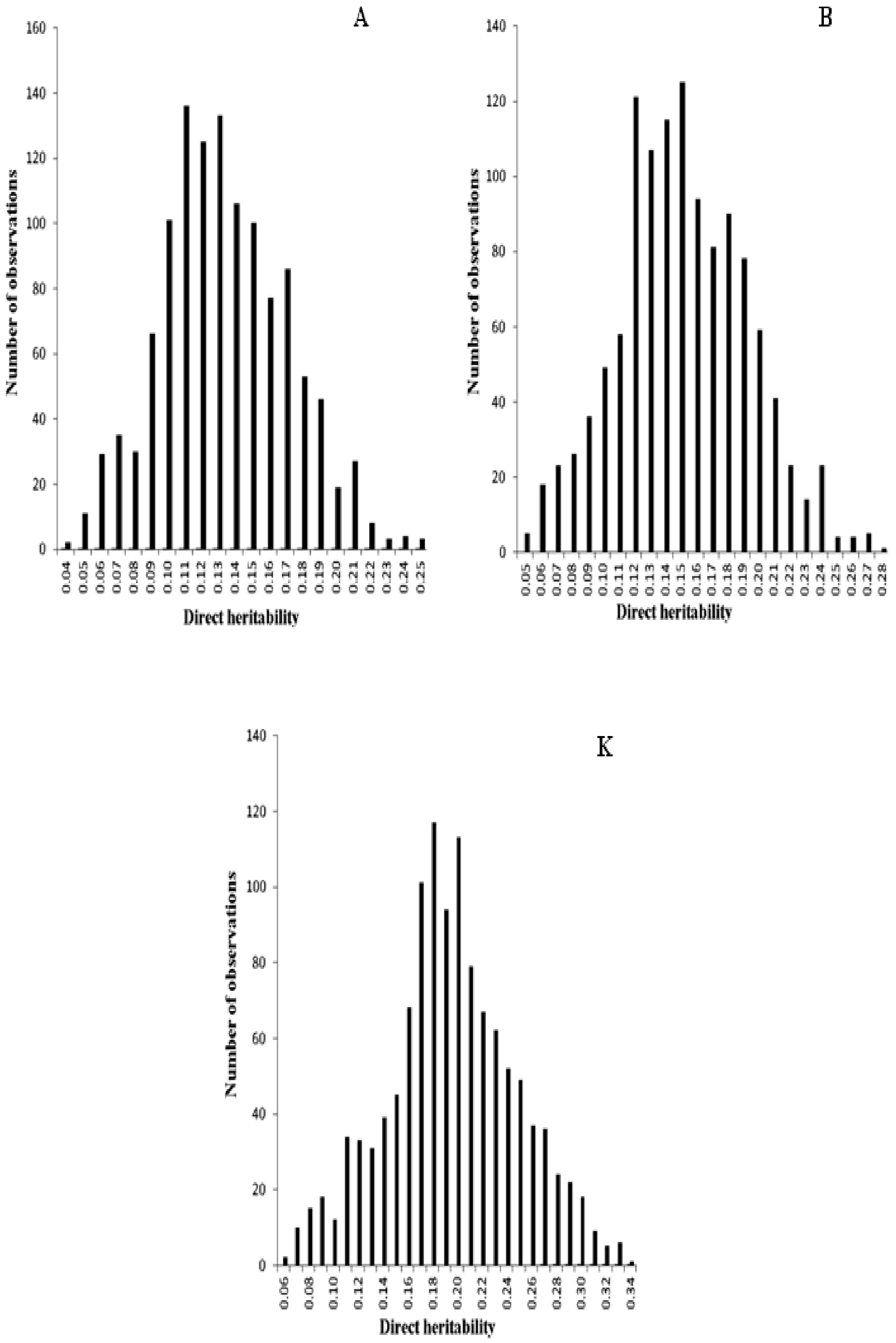

Figure 1 Posterior distribution of the direct heritabilities for growth curve parameters of A, B and K

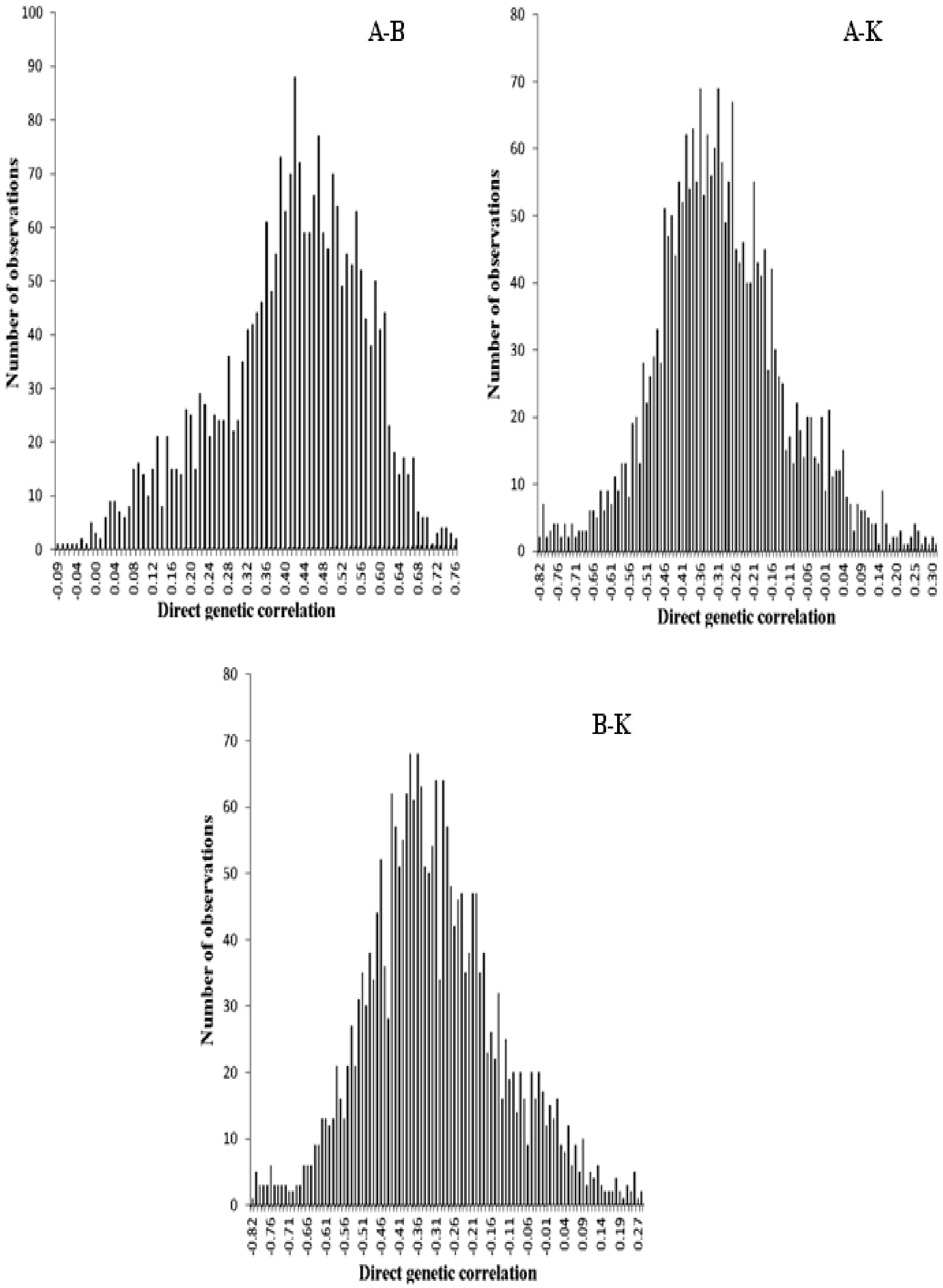

Figure 2 Posterior distribution of direct genetic correlations between growth curve parameters

In general, the HPD interval of residual and phenotypic correlations did not include zero; therefore, these correlations were assumed to be different from zero. The negative residual correlation between A-K in this study indicated the provision of appropriate environmental conditions for early maturity could not have positive effects in mature weight. This negative residual correlation could result in negative phenotypic correlation between these traits because corresponding genetic correlation was near to zero.

CONCLUSION

Current estimates of genetic parameters for growth curve characteristics in Shall sheep could be applied in designing selection program in this breed. The low estimates of heritabilities for growth curve parameters could be assigned to the high phenotypic variance arising from large environmental variation. Therefore, much of the improvement in these growth curve parameters could be obtained by improvement of environment rather than genetic selection. It is important to provide good environmental conditions along with optimal management strategies in the flock to achieve a desired shape of growth curve through changing the parameters of model.

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