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# Bayesian Analysis of Birth Weight and Litter Size in Baluchi Sheep Using Gibbs Sampling<sup>1</sup>

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**ABSTRACT:** Variance and covariance components for birth weight (BWT), as a lamb trait, and litter size measured on ewes in the first, second, and third parities (LS1 through LS3) were estimated using a Bayesian application of the Gibbs sampler. Data came from Baluchi sheep born between 1966 and 1989 at the Abbasabad sheep breeding station, located north-east of Mashhad, Iran. There were 10,406 records of BWT recorded for all ewe lambs and for ram lambs that later became sires or maternal grandsires. All lambs that later became dams had records of LS1 through LS3. Separate bivariate analyses were done for each combination of BWT and one of the three variables LS1 through LS3. The Gibbs sampler with data augmentation was used to draw samples from the marginal posterior distribution for sire, maternal grandsire, and residual variances and the covariance between the sire and maternal grandsire for BWT, variances for the sire and residual variances for the litter size traits, and the covariances between sire effects for different trait combinations, sire and maternal grandsire effects for different combinations

of BWT and LS1 through LS3, and the residual covariations between traits. Although most of the densities of estimates were slightly skewed, they seemed to fit the normal distribution well, because the mean, mode, and median were similar. Direct and maternal heritabilities for BWT were relatively high with marginal posterior modes of .14 and .13, respectively. The average of the three direct-maternal genetic correlation estimates for BWT was low, .10, but had a high standard deviation. Heritability increased from LS1 to LS3 and was relatively high, .29 to .37. Direct genetic correlations between BWT and LS1 and between BWT and LS3 were negative,  $-.32$  and  $-.43$ , respectively. Otherwise, the same correlation between BWT and LS2 was positive and low, .06. Genetic correlations between maternal effects for BWT and direct effects for LS1 through LS3 were all highly negative and consistent for all parities, circa  $-.75$ . Environmental correlations between BWT and LS1 through LS3 were relatively low and ranged from .18 to .29 and had high standard errors.

Key Words: Baluchi Sheep, Bayesian Theory, Birth Weight, Litter Size, Threshold Models

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## Introduction

Litter size (LS) at birth is a clearly defined and easily recorded trait, and it is a major determinant of successful reproduction in ewes. It is also a complex trait that involves several subtraits, such as ovulation rate, embryo survival, and uterine capacity. Hall et al. (1994) found that Polled Dorset ewes that gave birth to more than one lamb weaned .72 more lambs and 16.2 kg more lamb weight than ewes that gave birth

to only one lamb. Similarly, increasing litter size by one additional lamb was found to be 16.4 times as profitable as increasing average lamb weights by 1.0 kg in a Swedish production situation (Danell, 1986). Dickerson (1970) and Olesen et al. (1993) concluded that improving reproductive performance will have a large impact on the economic efficiency of most animal enterprises. Consequently, increasing litter size is one of the major goals for Iranian sheep breeders (Yazdi et al., 1997a).

Clarke (1972) and Turner (1978) reported that even though selection for litter size has generally been successful for several sheep breeds, only small improvements have actually been made. Some of the reason for this is certainly because the trait is only observed for ewes that give birth. Including information from correlated traits in the selection process could improve selection accuracy. Traits measured

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relatively early in a ewe's life are of special interest. A general relationship between body size and litter size, mediated by several hormones associated with the pituitary gland, has been postulated for litter-bearing mammals such as mice and sheep (Brien, 1986). However, reported correlations between body weight at different ages and litter size have been positive and negative (e.g., Davis and Kinghorn, 1986; Atkins, 1986; Eikje, 1975; Fogarty, 1994). The aim of this study was to examine the relationship between birth weight (**BWT**), modeled as a continuous trait, and litter size, modeled as a categorical trait on the liability scale, in Baluchi sheep.

## Materials and Methods

### Data

Data were collected from two separate research flocks of Baluchi sheep kept at the Abbasabad Sheep Breeding Station, located northeast of Mashhad, Iran. Full details of the Abbasabad breeding program are given in Yazdi et al. (1997a). Rams were selected on an index that gave equal weights to body conformation scored visually on a scale from 0 to 100 when the ram was 1 yr old, and three twinning scores. The first twinning score assigned a value of zero to single-born rams and a score of 100 to twin-born rams; the second twinning score assigned values of zero if neither the ram's sire nor dam was a twin, a value of 50 if at least one parent was twin-born, and a value of 100 if both parents were twin-born; and the third twinning score assigned values of zero if none of the ram's grandparents was twin-born, a value of 25 if only one grandparent was twin-born, a value of 50 if two grandparents were twin-born, a value of 75 if three grandparents were twin-born, and a value of 100 if all grandparents were twin-born. Similar indices were created for the ewes, but the actual selection practiced tended to put more emphasis on the conformation scores.

Ewes were first exposed to rams at 18 mo of age and kept in the flock until they died from natural causes. The only ewes that left the flock before their

natural deaths were either those that were barren (i.e., not pregnant) after only one lambing season or those that could not raise their own lambs. The majority of ewes culled were barren. The mating season started in late summer (August) or early autumn (September) and included at most three estrous cycles (51 d). Lambing started in early February and ended in late March.

The incidence of triplets was so low (< .3%) that records from lambs born in triplet litters were discarded. Although BWT was recorded for all lambs born between 1966 and 1989, the data set included BWT for all ewe lambs and for ram lambs that later became either sires or maternal grandsires. Litter size in parity 1 through parity 3 (**LS1** through **LS3**) was recorded as a trait of the dam. Number of observations, means and standard deviations, and coefficients of variation for lamb birth weights and litter size of ewe at parities 1 through 3 are presented in Table 1.

### Statistical Methods

*Model.* Genetic and environmental (co)variance components were estimated with three separate bivariate models, one for each combination of BWT as a trait of the lamb and LS1, LS2, or LS3 of the ewe. The BWT is a continuous variable, whereas LS1 through LS3 are discrete variables, with observations falling in one of two categories. Gianola (1982) has given theoretical reasons for modeling categorical variables with the nonlinear threshold model approach of Gianola and Foulley (1983) and Harville and Mee (1984). The suitability of the threshold model for analyzing litter size in sheep has been demonstrated by Urioste and Danell (1987) and Matos et al. (1997), who found litter size to be more heritable than previously thought. In order to estimate the (co)variance parameters in a bivariate analysis that included a linear model for the continuous trait and a threshold model for the categorical trait, a Bayesian approach was taken and inferences were, therefore, based on the marginal posterior distributions of relevant parameters. Posterior distributions were sampled using the multivariate Gibbs sampler program package, GIBBQB (Jensen, 1994).

Table 1. Number of observations, means, standard deviations, coefficient of variations, number of grandsires ( $n_{mgs}$ ), and number of sires ( $n_s$ ) for birth weight and litter size at the various parities

Trait <sup>a</sup>	n	Mean	SD	CV, %	$n_{mgs}$	$n_s$
BWT	10,406	4.24	.67	15.80	232	193
LS1	5,480	1.07	.26	24.30	193	166
LS2	4,150	1.15	.35	30.43	187	163
LS3	2,991	1.21	.41	33.88	175	147

<sup>a</sup>BWT = birth weight; LS1 = litter size at parity 1; LS2 = litter size at parity 2; LS3 = litter size at parity 3.

Liability values for LS were created by data augmentation, as described by Sorensen (1996); the original data values were replaced by values drawn from a normal distribution conditional on all elements included in the model except for LS. Therefore, standard linear methodology for the Gibbs sampler could be applied for both traits (Sorensen et al., 1995). We assume that there is an unobservable random variable, the liability ( $\mathbf{U}_{LS}$ ),  $\mathbf{U}_{LS} | \theta \sim N(\mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{a}, \mathbf{1})$  associated with two categories of litter size (single and twin) and with one ( $t = 1$ ) threshold.

The following model was used for BWT and LS:

$$\begin{bmatrix} \mathbf{y}_{BWT} \\ \mathbf{U}_{LS} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{BWT} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_{LS} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{BWT} \\ \mathbf{b}_{LS} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{mgs_{BWT}} & \mathbf{Z}_{s_{BWT}} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{s_{LS}} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{mgs_{BWT}} \\ \mathbf{a}_{s_{BWT}} \\ \mathbf{a}_{s_{LS}} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{BWT} \\ \mathbf{e}_{LS} \end{bmatrix}$$

where

- $\mathbf{y}_{BWT}$  ( $\mathbf{U}_{LS}$ ) = vector of BWT records (LS liabilities),
- $\mathbf{X}_{BWT}$  ( $\mathbf{X}_{LS}$ ) = known incidence matrix relating BWT records (LS liabilities) to fixed effects,
- $\mathbf{b}_{BWT}$  ( $\mathbf{b}_{LS}$ ) = vector of fixed effects affecting BWT records (LS liabilities),
- $\mathbf{Z}_{mgs_{BWT}}$  = known incidence matrix relating BWT records to random maternal grandsire additive effects,
- $\mathbf{Z}_{s_{BWT}}$  ( $\mathbf{Z}_{s_{LS}}$ ) = known incidence matrix relating BWT records (LS liabilities), to random sire additive effects,
- $\mathbf{a}_{mgs_{BWT}}$  = vector of random maternal grandsire additive effects affecting BWT records,
- $\mathbf{a}_{s_{BWT}}$  ( $\mathbf{a}_{s_{LS}}$ ) = vector of random sire additive effects affecting BWT records (LS liabilities),
- $\mathbf{e}_{BWT}$  ( $\mathbf{e}_{LS}$ ) = vector of random environmental effects particular to each BWT records (LS liabilities),

and  $\mathbf{a} | \mathbf{A}, \mathbf{G}_0 \sim N(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A})$  is the vector of sires' and maternal grandsires' additive genetic values,  $\mathbf{A}$  is the numerator relationship matrix among sires and maternal grandsires, and

$$\mathbf{G}_0 = \begin{bmatrix} \sigma^2_{mgs_{BWT}} & \sigma_{mgs_{BWT}s_{BWT}} & \sigma_{mgs_{BWT}s_{LS}} \\ \sigma_{mgs_{BWT}s_{BWT}} & \sigma^2_{s_{BWT}} & \sigma_{s_{BWT}s_{LS}} \\ \sigma_{mgs_{BWT}s_{LS}} & \sigma_{s_{BWT}s_{LS}} & \sigma^2_{s_{LS}} \end{bmatrix}$$

All (co)variances due to dominance and epistatic deviations were assumed to be zero.

The conditional distribution of the complete data set (i.e., observed and missing records) for BWT and LS,  $\mathbf{y}' = (\mathbf{y}'_{BWT}, \mathbf{U}'_{LS})$ , was:

$$\mathbf{y} | \mathbf{b}, \mathbf{a}, \mathbf{R}_e \sim N$$

$$\left[ \begin{bmatrix} \mathbf{X}_{BWT}\mathbf{b}_{BWT} + \mathbf{Z}_{mgs_{BWT}}\mathbf{a}_{mgs_{BWT}} + \mathbf{Z}_{s_{BWT}}\mathbf{a}_{s_{BWT}} \\ \mathbf{X}_{LS}\mathbf{b}_{LS} + \mathbf{Z}_{s_{LS}}\mathbf{a}_{s_{LS}} \end{bmatrix} \mathbf{R}_e \otimes \mathbf{I}_n \right]$$

The complete vector of the residuals is  $\mathbf{e}' = (\mathbf{e}'_{BWT}, \mathbf{e}'_{LS})$  with  $\mathbf{e} \sim N(\mathbf{0}, \mathbf{R}_e)$  where

$$\mathbf{R}_e = \begin{bmatrix} \sigma^2_{e_{BWT}} & \sigma_{e_{BWT}e_{LS}} \\ \sigma_{e_{BWT}e_{LS}} & \sigma^2_{e_{LS}} \end{bmatrix}$$

The fixed part of the model included the effects of flock (two classes) and year (1966 to 1989) for both traits and additional fixed effects of sex (two classes) and parity of dam (seven classes; 1 to 6 and  $\geq 7$ ) for BWT.

*Prior, Joint, and Full Conditional Posterior Distributions.* Due to lack of prior knowledge about the vector of fixed effects an improper flat prior of uniform distribution was assigned to  $\mathbf{b}$ :  $P(\mathbf{b}) \sim \text{constant}$ . Further,  $\mathbf{a} | \mathbf{G}_0 \sim N_q(\mathbf{0}, \mathbf{G}_0)$ , where  $q$  is the number of sires and maternal grandsires and  $\mathbf{a}$  is assumed to be *a priori* independent of  $\mathbf{b}$ .

It was also assumed that the additive genetic ( $\mathbf{G}_0$ ) and residual ( $\mathbf{R}_e$ ) covariance matrices followed *a priori* an independent scaled inverted Wishart distribution (Sorensen, 1996). Previous estimates of the sire and maternal grandsire additive genetic matrix ( $\mathbf{G}_0$ ) and residual covariance matrix ( $\mathbf{R}_e$ ) were used as priors for these analyses and weighted with one degree of belief to get proper posterior distributions, as proposed by Berger and Bernardo (1992).

The extension of the bivariate mixed-model equations and derivation of full conditional posterior distributions were the same as given by Sorensen (1996).

*Implementation of Gibbs Sampler.* The Gibbs sampler was used to generate random samples from the marginal posterior distribution by sampling successively from the full conditional distributions of the elements in the model: the liability of the observed and missing LS1 through LS3 observations, fixed effects, breeding values, and genetic and residual variance components. Residual variance for LS1 through LS3 was scaled to 1 in each sampling round, as suggested by Sorensen (1996). Each combination of BWT with LS1 through LS3 was run as a long-chain scheme for 337,000 sampling rounds. The first 10,000 samples in each chain were considered to belong to the "burn-in" period and discarded.

*Post-Gibbs Analysis and Density Estimations.* A post-Gibbs analysis of the autocorrelations between

the samples was performed using the time-series methods of Geyer (1992), as applied by Sorensen et al. (1995). Additive genetic, maternal genetic, environmental, and phenotypic variances for BWT and LS1 through LS3, as well as the direct-maternal genetic covariance between BWT and LS1 through LS3, were calculated for each sample of the statistical model's (co)variance components using the expectations given by Kriese et al. (1991). In order to evaluate densities of functions of the statistical (co)variance components, graphs of the marginal posterior distributions were generated with the SAS (1990) statistical package using all samples.

## Results and Discussion

As seen in Table 1, mean BWT was 4.24 kg, and the coefficient of variation was 15.8%. Average litter size increased from 1.07 lambs for LS1 to 1.21 lambs for LS3. At the same time the coefficient of variation for litter size increased from 24.3% for LS1 to 33.9% for LS3.

### Post-Gibbs Analysis

Lag correlations indicate the degree of autocorrelation between samples generated by the Markov chain. Among the nine (co)variance components sampled in each analysis sampled, values for the covariance between the maternal grandsire effect for BWT and the sire effect for litter size were consistently those with the highest autocorrelation; variation between consecutive "batches" for this parameter became nonsignificant first at lag number 120 and did not become negative until lag number 140. Corresponding values for samples of the remaining (co)variance components were in the range between 30 and 120, which is slower than similar statistics from Sorensen et al. (1995). Liu et al. (1994) and Sorensen et al. (1995) have both indicated that the Markov chain has slow mixing properties when used with augmentation techniques. Even though the ratio between the effective number of independent samples and the absolute sample size for the "worst" parameter was so small, the total number of samples saved (32,700 out of 337,000) was still judged to be large enough to draw inferences on the (co)variance parameters of interest with reasonable accuracy.

### Heritabilities

Marginal posterior distributions for BWT heritability obtained in the three bivariate analyses were very similar. Although somewhat skewed, histograms seemed to fit normal distributions satisfactorily and the mean, mode, and median were close to each other. A representative histogram of the marginal posterior distribution of BWT obtained from the bivariate

analysis of BWT and LS3 is plotted in Figure 1. Direct and maternal heritabilities for BWT were relatively low (marginal posterior modes were .14 and .13, respectively) with 95% credibility intervals of .09 to .23 and .08 to .22, respectively.

The average modal value of .14 for the direct heritability of BWT is in the middle of the range of estimates (.02 to .45) reported in the literature by Fogarty (1995). Further, direct heritability estimates were very close to the average of .15 reported by Yazdi et al. (1997a,b). Those studies analyzed BWT in a more complete version of the same data used in the present study that included observations from all lambs of both sexes. Those studies also used multiple-trait REML techniques with an animal model that included an effect of maternal permanent environment.

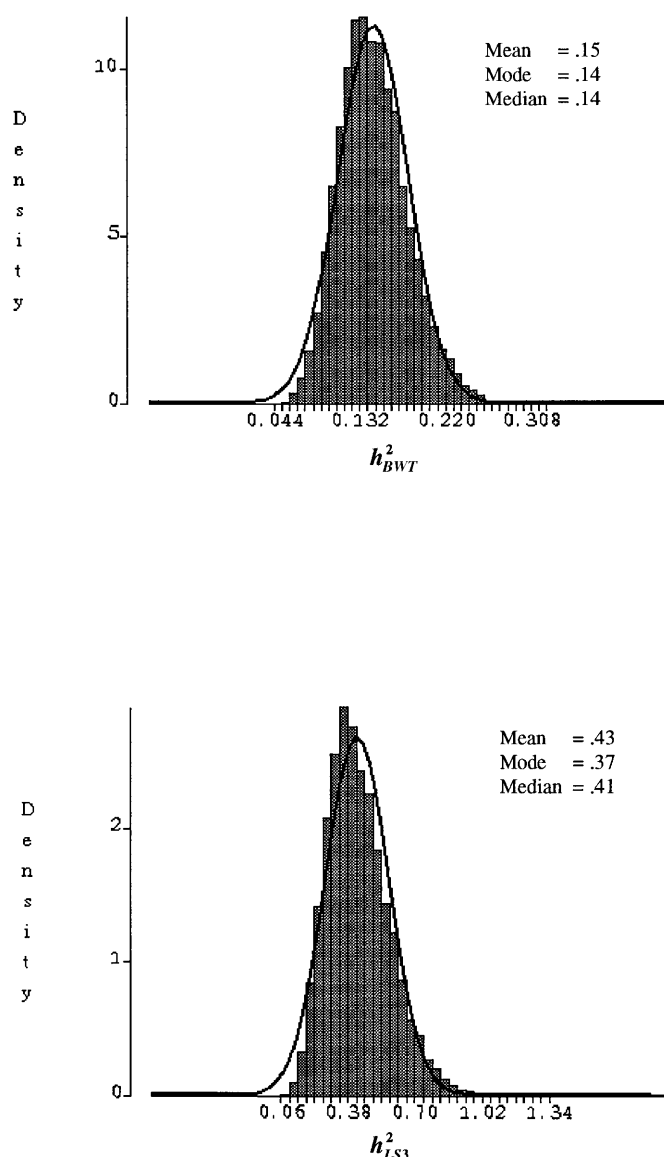


Figure 1. Distribution of heritabilities of birth weight (BWT) and litter size in parity 3 (LS3).

The maternal heritability estimates for BWT in the present study were higher, however. Estimates of the combined permanent environment associated with the dam and common environment associated with individual litters as a proportion of phenotypic variance in Yazdi et al. (1997a) were small ( $\sim .08$ ). The average number of litters per ewe in the present data set was also small (2.1) and, due to a combination of expected low variation and inaccuracy of estimation, neither the permanent environment nor the common environment effect was modeled in the present study. Snyman et al. (1995) concluded that exclusion of maternal permanent environmental effects in animal models for BWT could bias estimates of maternal heritabilities upward. Still, our analysis used a sire-maternal grandsire model for BWT and any eventual bias due to ignoring permanent maternal environment would be expected to affect the residual rather than maternal variance estimates.

The marginal posterior distribution of heritability for LS1 was more skewed than for the two other parities, probably due to low occurrence of twins (about 7%) in this parity. Moreover, it did not fit the normal distribution well. A histogram of the marginal posterior distribution of heritability for LS3 is shown in Figure 1. Litter size heritabilities increased from about .3 for LS1 to about .4 for LS3. The increase in

heritability of LS from the first to third parity (Table 2) might be attributed to increasing maturity of the ewe. Coefficients of variation from the first to third parity also increased. Because the environmental variance component was scaled to 1 in each parity the additive genetic variance components could not be compared between parities in absolute measures.

The trend of increasing heritability with parity found in this study is in agreement with results of Atkins (1986) on Scottish Blackface sheep between parities 1 to 4. However, the increasing trend in the present study is in contrast to the decrease in heritability with advancing ewe age reported by Gates and Urioste (1995). Environmental variance for fitness traits such as litter size in sheep (Gates and Urioste, 1995), number of offspring in *Drosophila* (Engström et al., 1992a), or egg production in laying hens (Liljedahl et al., 1984; Engström et al., 1992b) has been seen to increase with age, but the influence of the harsh environment of northeastern Iran makes comparison with the present study difficult.

As reported by Fogarty (1995), there is a wide range of heritability estimates for litter size at birth in the literature, from about 0 to .44 for different breeds and statistical models. Literature estimates of heritability for litter size obtained with a sire threshold model tend to be larger and range from .08 to .62 for

Table 2. Estimated phenotypic variances, heritabilities, and correlations between birth weight (BWT) and litter size (LS1 through 3) in parities 1 to 3

Component	Mean	Mode	Median	SD	Range <sup>a</sup>		MC sd <sup>b</sup>	N <sub>E</sub> <sup>c</sup>
Phenotypic variances								
BWT	.44	.44	.44	.01	.42	.46	.06	23,014
LS1	1.10	1.08	1.09	.04	1.03	1.20	.78	3,015
LS2	1.10	1.08	1.09	.04	1.04	1.19	.55	4,787
LS3	1.12	1.10	1.12	.05	1.05	1.24	.73	4,343
Heritabilities								
BWT (direct)	.15	.14	.14	.04	.09	.23	.30	14,573
BWT (maternal)	.14	.13	.14	.04	.08	.22	.35	11,822
LS1	.34	.29	.33	.14	.12	.66	2.55	2,963
LS2	.36	.31	.34	.12	.16	.63	1.80	4,695
LS3	.43	.37	.41	.15	.19	.77	2.28	4,235
Correlations								
Direct-maternal								
BWT-BWT	.10	.10	.10	.20	-.28	.50	2.17	8,814
LS1-BWT	-.56	-.64	-.58	.19	-.85	-.13	2.41	5,961
LS2-BWT	-.75	-.81	-.77	.12	-.92	-.46	1.45	6,764
LS3-BWT	-.73	-.79	-.76	.13	-.91	-.42	1.64	6,134
Direct-direct								
BWT-LS1	-.39	-.43	-.41	.22	-.77	.10	3.04	5,477
BWT-LS2	.05	.06	.05	.24	-.42	.49	3.24	5,278
BWT-LS3	-.29	-.32	-.30	.30	-.71	.21	3.37	4,917
Environmental								
BWT-LS1	.30	.27	.28	.16	.09	.63	2.03	6,018
BWT-LS2	.21	.18	.19	.12	.02	.47	1.33	7,703
BWT-LS3	.34	.29	.30	.22	.09	.78	2.45	8,210

<sup>a</sup>Range = 2.5 to 97.5%.

<sup>b</sup>Monte Carlo standard error multiplied by 1,000.

<sup>c</sup>Effective number of independent observations.

different breeds (Jorgensen, 1994; Olesen et al., 1994; Gates and Urioste, 1995; Matos et al., 1997). Estimates in the present study are comparable to these.

### Correlations

Histograms of the marginal posterior distributions of direct-maternal and direct-direct genetic correlations between BWT and LS3 are plotted in Figure 2. Estimates of genetic correlations usually suffer from poor precision, indicated by large standard errors, especially when data sets are small. Although data sets used in the present study were relatively large, there was a wide range of estimates for the correlations, which might partly be attributed to skewness of the marginal posterior distribution of the correlations.

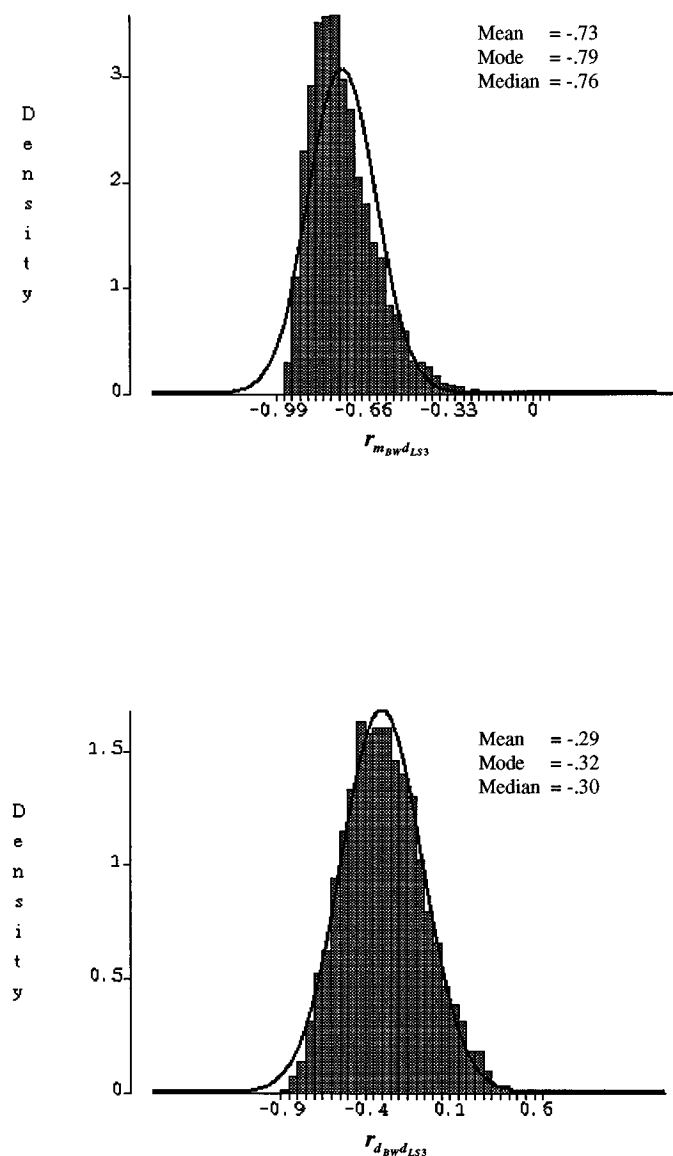


Figure 2. Distributions of direct and maternal genetic correlations between birth weight (BWT) and litter size in parity 3 (LS3).

The distribution of the direct-maternal genetic correlation was more skewed than any of the correlations between direct genetic effects.

The direct-maternal genetic correlations for BWT was low (.10 as an average of the three estimates), and the 95% credibility intervals included positive and negative values. In the literature, positive and negative correlations are reported for this trait (e.g., Robison, 1981; Maria et al., 1993; Näsholm and Danell, 1996). Because prenatal growth for ewe lambs occurs so much earlier than their eventual opportunities to provide a uterine environment to their own lambs, the genetic correlations are not expected to be large.

Results from preliminary analyses, when including type of birth for BWT into the model, showed that BWT was adjusted completely for litter size. Thus, the direct-maternal genetic correlation between LS and BWT was close to zero. When the effect of type of birth for BWT was excluded in the model, this correlation became relatively large and consistently negative across parities (-0.64 to -0.81) with the 95% credibility intervals containing only negative values.

Correlations between direct genetic effects for BWT and litter size (Table 2) were negative in the first and third parities (-0.32 to -0.43) but close to zero in the second parity (.06). The 95% credibility intervals covered a wide range, from strongly negative to small positive correlations in parities 1 and 3, and was centered about zero in parity 2.

Environmental correlations were low and positive between BWT and litter sizes in all three parities. The 95% credibility intervals contained only positive values.

From an evolutionary point of view, natural selection will force mean levels of fitness traits toward their optimum (Robertson, 1955; Beilharz and Mitpaboon, 1994) and might favor animals that are able to balance birth weight of lambs against number of lambs born. Thus, ewes with large litters give birth to lambs with low birth weights because uterine capacity and supply of essential nutrients are limited. This effect is genetic with regard to the ewe but environmental to the lamb(s). Thus, an increase in litter size will reduce the phenotypic level of birth weight in the population, which in turn leads to higher mortality of lambs (i.e., reduced fitness for low lamb birth weight). It is probable that the population will reach an equilibrium where the marginal increase in fitness caused by the increase of litter size is outweighed by the marginal decrease in fitness caused by the increase of mortality. In particular, this equilibrium should be important under the prevailing harsh environmental conditions for Baluchi sheep. Therefore, the negative direct-maternal and direct-direct genetic correlations between LS and BWT can be consequences of this equilibrium between litter size and birth weight. This evidence was explicitly

pronounced when the type of birth was excluded from the model for BWT. These results indicate that there is strong relationship between BWT and litter size that should be taken into account in the breeding program for the improvement of either one or both of these traits. However, due to the large confidence interval of our estimates, it is likely that the fluctuation observed here for direct-direct genetic correlation is caused by chance.

The negative value of direct-direct genetic correlations may also be the result of selection in the data set. In this experiment and at the time of reproduction, young ewes were selected according to a crude index (Yazdi et al., 1997a). In this way, the available information on BWT is biased toward more contribution from ewes with a high index value for LS. Therefore, the proportion of BWT records from twin births (26%) was markedly larger than the biological frequency of twin births (7%), so this to some extent might be responsible for the direct-direct genetic correlations between the birth weight and litter size. In this context, we should remember that selection operates on records that are only partly present in the analyses because we analyzed one parity at a time. In other words, the available information on BWT is a biased sample of the possible set of information.

In studies of postnatal growth in sheep, the genetic correlation between growth rate and litter size was found to be positive (Dyrmundsson, 1973; Brien, 1986). During the postnatal period, effects of dam's litter size on growth rate of the progeny are assumed to have gradually leveled off (i.e., the retarding effects of being born together with a twin are compensated for later on; Yazdi et al., 1998). This is consistent with results from several investigations in which a positive direct-direct genetic correlation has been found between body weight, especially at the yearling stage, and number of lambs born per ewe mated and per ewe lambing (e.g., Shelton and Menzies, 1968; Eikje, 1975; Atkins, 1986). In a review of genetic and physiological relationships between growth and reproduction in mammals, Brien (1986) stated that the phenotypic association between growth rate and reproductive performance is a reflection of a positive genetic relationship, particularly of growth rate with ovulation rate. In addition, this author pointed out that age of the ewe does not seem to influence the magnitude of the genetic correlation to any appreciable extent. Our results, however, point out that the relationship between prenatal growth and litter size is different from that between postnatal growth and litter size, and, therefore, prenatal growth period (i.e., birth weight) should be treated differently. Moreover, Hill (1985) argued that relationships between body size and reproductive performance in mammals may not be the same across breeds as those within, because in the evolution of distinct populations (breeds being as example) natural and artificial selection, or both, have probably been involved.

## Implications

Estimates of genetic parameters obtained from a threshold model for litter size indicate a potential for economically important increases in reproductive traits from selection in Baluchi sheep. The negative correlation between genetic effects of birth weight and litter size indicates that improvements in one of these traits hinders performance in the other and decreases the overall rate of progress for total weight of lamb. Therefore, by incorporating the maternal and direct genetic effects of birth weight and direct genetic effects of litter size into the breeding program, we would avoid the negative effects on birth weight. This, however, may lead to a predisposition for a higher rate of mortality and slower early postnatal growth rate caused by larger litter size.

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