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Bayesian threshold-linear model for genetic evaluation of direct and maternal calving traits in Iranian primiparous Holstein cattle

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Abstract The main objective of this study was to estimate the genetic parameters for multi-trait evaluation of birth weight (BW), gestation length (GL) and calving difficulty (CD) in first-parity Iranian Holstein dairy cattle. The data included 29,950 calving records collected during 1995 to 2014 by the Animal Breeding and Improvement Center of Iran. A threshold-linear sire-maternal grandsire model was fitted. The model included the effect of sex of calf born, age at first calving and calving month (for GL and BW) as fixed effects and sire, maternal grandsire, herd-year-season of calving and residual effects as random effects. Posterior means (posterior standard deviations) of direct heritabilities were 0.12 (0.01) for BW, 0.40 (0.03) for GL and 0.07 (0.01) for CD. The maternal heritability estimates for BW, GL and CD were 0.04 (0.01), 0.07 (0.01) and 0.04 (0.01), respectively. Direct-maternal genetic correlations were -0.15 (0.04) for BW, -0.36 (0.08) for GL and -0.53 (0.14) for CD ($P<0.01$). Direct additive genetic correlations for BW-GL and BW-CD were 0.39 (0.06) and 0.43 (0.09), and the corresponding maternal additive genetic correlations were 0.58 (0.08) and 0.47 (0.13), respectively. Direct and maternal additive genetic correlations for GL-CD were non-significant. The estimated posterior means for phenotypic and environmental correlations were positive and low to medium. Non-linear phenotypic relationships were found for GL-CD and BW-CD. The existence of corresponding non-linear and also cause-and-effect (which is usually ignored in traditional genetic evaluation programs) relationships between CD-GL and CD-BW may influence the genetic evaluation of these traits under standard mixed models.

Keywords: first-parity Holsteins, dystocia, birth weight, gestation length, sire-maternal grand sire model

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Introduction

Maintaining or enhancing production efficiency of livestock enterprises requires designing appropriate breeding strategies and performing genetic selection decisions with an emphasis on the genetic merit of functional traits (Amer, 2012). Functional traits are those that enhance efficiency of production by reducing the costs of inputs, not by increased the output of products (Mark, 2004). Interest in selection for functional traits is increasing for most dairy breeds and in several counties (Luo et al., 2002; Mark, 2004). Calving performance traits, such as dystocia, are typical functional traits. Genetic selection could improve calving performance, and inclusion of calving traits in genetic evaluation programs is of great importance (Eaglen et al., 2012). Calving complications result in potential loss and/or impaired production and reproduction performance, with implications also for animal welfare which lead to increased labor and veterinary costs, and consequently decrease the farm revenue (Eaglen et al., 2012).

Calving difficulty, as a result of the incompatibility between the size of calf and pelvic area of the dam (Meijering, 1984), has a low heritability. Therefore, for its inclusion in selection programs, joint analysis of this trait with highly heritable and correlated indicator traits such as birth weight (Johanson and Berger, 2003) and gestation length (Hansen et al., 2004; Lopez de Maturana et al., 2009) has been suggested.

Traits such as birth weight of calves and gestation length can be used as correlated traits to increase the accuracy of genetic evaluation for calving difficulty (Lee et al., 2002). Methodology for joint analysis of categorical and continuous traits was developed by Janss and

Foulley (1993). The phenotypes of calving difficulty are generally scored on categorical scales, which are sensitive to subjectivity (Dekkers, 1994). Due to the categorical nature of calving difficulty, the genetic analysis of this trait under linear model is not theoretically optimal (Lee et al., 2002). Luo et al. (2001) pointed out that estimation of variance components of categorical traits under linear models may present problems such as estimation of confidence intervals and the possibility of reaching a local maximum rather than a global maximum in maximization of algorithms. Therefore, threshold models have been suggested as alternative approaches for genetic analysis of such traits (Gianola and Foulley, 1983).

The phenotypes of calving traits are affected by two main sources of genetic variations including direct additive genetic effects (originated from the contribution of the calf, which arise in terms of body size, hormonal balance and weight) and direct maternal genetic effect (originated from the contribution of the dam, stemming from pelvic area, ability to express maternal behaviors and respond to parturition signaling), and the existence of such components complicates the selection of appropriate models for statistical analysis (Willham, 1972; Eaglen et al., 2012). Therefore, the model fitted for genetic analysis of calving traits should allow the separation of direct and maternal effects. Due to attractive properties of animal models in using information from all relatives, these models are widely used for estimating variance components of traits of interest in animal breeding context (Luo et al., 2001). However, for categorical traits, because of extreme category problem, analysis under threshold animal model via the Gibbs sampling may yield biased estimates, poor or slow mixing of the chain, or even "blowing up" of the Gibbs chains (Hoeschele and Tier, 1995). When a Gibbs chain blows up, the genetic variance continues to increase and soon reaches unreasonable values so that the inverse of the genetic variance matrix is zero and Gibbs sampling stops (Luo et al., 2001). Therefore, the majority of applications of threshold models to predict genetic merit of animals for maternally influenced categorical traits are based on sire-maternal grand sire models (Berger, 1994). In a sire-maternal grand sire model, which is an extension of the sire model, the effects of sire of the calf and sire of the dam are fitted as additive direct and maternal genetic effects, respectively (Eaglen et al., 2012). The estimation of (co)variance components for calving traits under sire-maternal grand sire models have been well documented (Wiggans et al., 2003; Hansen et al., 2004; Eaglen and Bijma, 2009; Lopez de Maturana et al., 2009; Eaglen et al., 2013).

To our knowledge, there are no reliable estimates of the direct and maternal genetic relationships between calving traits in Iranian Holstein cattle. Therefore, the main objective of the present study was to separate the direct and maternal additive genetic components for calving related traits in primiparous Holstein dairy cows in Iran under a Bayesian-linear sire-maternal grand sire model, and to estimate the direct and maternal heritability and corresponding correlation estimates.

Materials and methods

Phenotypic traits and data editing

Data, collected from 1995 to 2014 by the Animal Breeding and Improvement Center of Iran, and comprising of 29,950 calving records from first-parity Iranian Holstein dairy cattle, were used for genetic analysis. Data and pedigree structure are presented in Table 1. Calving traits included the calving difficulty (CD), calf birth weight (BW), and gestation length (GL). In the initial data, CD scores were assessed subjectively on a 1 to 5 scale, with 1 (unassisted calving), 2 (slight assistance), 3 (moderate assistance), 4 (considerable force and hard pull) and 5 (extreme difficulty and cesarean). After editing the data, cows with and without calving difficulty records constituted 74.06% and 25.94 % of all records, respectively. Due to low frequency of cows with CD scores of 4 (0.35 %) and 5 (0.03 %) these categories were combined into the third category; second and third categories constituted 21.50% and 4.44% of the records, respectively. Disproportionate ratio was observed for sex of calves born with fewer male (38.66%) than female calves (61.34%).

BW was defined as the live weight within 24 h of birth, and GL was measured as the interval between the date of last insemination resulting in conception and the

Table 1. Pedigree and data structure of the first-parity cows

Item	Number
Data	
Animals	29,950
Sires	563
Average progeny per sire	53.20
Sires-service	933
Average progeny per sire-service	32.20
Dams	25,464
Pedigree	
Animals	99,765
Sires	3,060
Dams	60,952
Average progeny per sire	9.78
Animals with both parents known	80,807
Animals with both parents unknown	1,799
Animals with one parent unknown	1,7159

subsequent calving date.

The following data editing protocol was applied. First, only single records from artificial inseminations were kept and all suspect records, including records with out-of-range values or records with missing information such as missing identification, birth and calving date, herd identification, calving score and sex of calves were removed. In addition, the extreme category problem, arising often in threshold models (Moreno et al., 1997), was alleviated by classification of calving difficulty scores into three categories; fourth and fifth categories were combined with the third category. As CD is assessed subjectively by dairymen, further editing was carried on CD scores. For this, herd-year with zero standard deviation was omitted to avoid herds where all incidences of the calving had been recorded in the same category. Age at first calving was limited 20 to 38 months; BW records between 24 to 52 kg and GL records between 260 and 288 days were kept. Finally, only sires with at least 10 daughters and contemporary groups of herd-year of calving with at least 5 records were kept. Descriptive statistics of the edited records for each trait are presented in Table 2.

Models

Threshold model

The concept of threshold was introduced by Wright (1934) who postulated that an ordered categorical variable such as y_i in an individual i is the expression of an underlying unobservable continuous variable l_i, referred to as liability (Falconer, 1965). The variable y_i falls in one of C ordered and mutually exclusive categories, which are bounded by $C+1$ thresholds ($\boldsymbol{t}$). Therefore, the probability that y_i corresponds to category k, given the liability and the threshold(s), is as follow:

$$Pr\left(y_i=k \middle| l_i,\boldsymbol{t}\right) = \sum_{j=1}^{c} f\left(t_{j-1}<l_i\leq t_j\right) I\left(y_i=k\right) \tag{1}$$

where, f (.) is a probability density function, and I (.) denotes an indicator function, taking the value 1 when expression (.) is true and the value 0 otherwise.

Statistical analyses

Least squares analyses were performed for selecting non-genetic effects to be included in the final models using GLM procedure (SAS, 2004). A Bayesian approach with Gibbs sampling has been proposed by Korsgaard et al. (2003) for multi-trait modes including various categorical and Gaussian traits. Following this approach, the liability for CD and observed data for BW and GL was modeled as a trivariate Bayesian threshold-linear model:

Table 2. Descriptive statistics for the studied traits[a]

Trait	Mean	S.D.	C.V. (%)	No. of records
BW	39.77	4.22	10.61	29950
GL	276.5	4.59	1.66	29950
CD	1.31	0.56	42.75	29950

[a] BW= birth weight (kg), GL= gestation length (days), CD = calving difficulty (scores 1 to 3)

S.D.= standard deviation, C.V.= coefficient of variation

$$\mathbf{y_i} = \mathbf{X_i b} + \mathbf{Z_{i(h)} h} + \mathbf{Z_{i(s)} s} + \mathbf{Z_{i(mgs)} mgs} + \mathbf{e_i} \tag{2}$$

where $\mathbf{y_i}$ is a vector with the liability for CD and observed data for BW and GL for animal i, $\mathbf{b}$ is a vector of fixed effects including calf sex (2 levels), cow age at first calving (18 levels, 20 to 38 mo) and calving month (12 levels) for GL and BW only, $\mathbf{h}$ is a vector of herd-year-season of calving (918 levels), $\mathbf{s}$ is a vector of sire-service effects (933 levels), $\mathbf{mgs}$ is a vector of maternal grandsire effects (563 levels), and $\mathbf{e}$ is a vector of residual effects. $\mathbf{X}$, $\mathbf{Z_h}$, $\mathbf{Z_s}$ and $\mathbf{Z_{mgs}}$ are incidence matrices relating the corresponding effects to $\mathbf{y}$. Among the bulls, 406 bulls had records as both sire and maternal grandsire.

It was assumed that sires and dams were mated at random, and that the daughters of a maternal grandsire represented in the dataset were a random sample of all daughters of that maternal grandsire. To allow estimation of the correlations between sire and maternal grandsire genetic effects, a bull was regarded as both even if it had no records for one of the effects (Wiggans et al., 2003).

Treating herd-year-season of calving as a fixed effect with a threshold model may cause some statistical problems and convergence issues due to the extreme category problem (Vanderick et al., 2014), and generally fitting herd-year-season of calving effect as random overcomes this problem (Misztal et al., 1989). Even if this issue is less problematic in linear models (Vanderick et al., 2014), the effect of herd-year-season of calving for BW and GL was assumed random.

Multivariate normal distributions were assumed, a priori, for sire and maternal grandsire effects with a null mean vector and a (co)variance matrix $\mathbf{G_0} \otimes \mathbf{A}$, where $\mathbf{A}$ is the numerator relationship matrix among sires and maternal grandsires. The matrix $\mathbf{G_0}$ takes the form:

$$\mathbf{G_0}=\begin{bmatrix} \sigma^2_{s_{CD}} & \sigma_{s_{CD}\,s_{BW}} & \sigma_{s_{CD}\,s_{GL}} & \sigma_{s_{CD}\,mgs_{CD}} & \sigma_{s_{CD}\,mgs_{BW}} & \sigma_{s_{CD}\,mgs_{GL}} \\ & \sigma^2_{s_{BW}} & \sigma_{s_{BW}\,s_{GL}} & \sigma_{s_{BW}\,mgs_{CD}} & \sigma_{s_{BW}\,mgs_{BW}} & \sigma_{s_{BW}\,mgs_{GL}} \\ & & \sigma^2_{s_{GL}} & \sigma_{s_{GL}\,mgs_{CD}} & \sigma_{s_{GL}\,mgs_{BW}} & \sigma_{s_{GL}\,mgs_{GL}} \\ & & & \sigma^2_{mgs_{CD}} & \sigma_{mgs_{CD}\,mgs_{BW}} & \sigma_{mgs_{BW}\,mgs_{GL}} \\ & & & & \sigma^2_{mgs_{BW}} & \sigma_{mgs_{BW}\,mgs_{GL}} \\ \mathit{Symmetric} & & & & & \sigma^2_{mgs_{GL}} \end{bmatrix}$$

in which, for example, $\sigma^2_{s_j}$ and $\sigma^2_{mgs_j}$ denote the between-sire variance and between-maternal grandsire variance for j^{th} trait, respectively; $\sigma_{s_j\, s_k}$ implies the covariance between sire effects of traits j and k.

It was assumed that the effects of herd-year-season of calving (**h**) follow a multivariate normal distribution with null mean vector and (co)variance matrix $\mathbf{H_0} \otimes \mathbf{I_h}$, where:

$$\mathbf{H_0} = \begin{bmatrix} \sigma^2_{h_{CD}} & \sigma_{h_{CD}\, h_{BW}} & \sigma_{h_{CD}\, h_{GL}} \\ & \sigma^2_{h_{BW}} & \sigma_{h_{BW}\, h_{GL}} \\ Symmetric & & \sigma^2_{h_{GL}} \end{bmatrix}$$

with, $\sigma^2_{h_j}$ being the variance for herd-year-season effects of the jth trait, $\sigma_{hj\, hk}$ the covariance between herd-year-season of calving effects of the jth and kth traits, and $\mathbf{I_h}$ an identity matrix of order 918.

The vector of residual effects was assumed to follow a multivariate normal distribution with a null mean vector and (co)variance matrix $\mathbf{R_0} \otimes \mathbf{I_n}$, where $\mathbf{I_n}$ is an identity matrix of order 29950. The matrix $\mathbf{R_0}$ has the following structure:

$$\mathbf{R_0} = \begin{bmatrix} \sigma^2_{e_{CD}} & \sigma_{e_{CD} e_{BW}} & \sigma_{e_{CD} e_{GL}} \\ & \sigma^2_{e_{BW}} & \sigma_{e_{BW} e_{GL}} \\ Symmetric & & \sigma^2_{e_{GL}} \end{bmatrix}$$

in which, $\sigma^2_{e_j}$ and $\sigma_{e_j\, e_k}$represent the residual variance within the jth trait and the residual covariance between the jth and kth traits, respectively.

Statistical inference

The Monte Carlo Markov Chain (MCMC) implementation of the considered multi-trait threshold-linear model was as follows:

Denote $\boldsymbol{\theta} = (\mathbf{b}, \mathbf{h}, \mathbf{s}, \mathbf{mgs}, \mathbf{G_0}, \mathbf{H_0}, \mathbf{R_0}, \mathbf{t})$. For simplicity, hyperparameters were ignored in the notation. Let $\mathbf{y}_{CD}$ be a vector referring the observed categories of CD. Then, the joint posterior density of $\boldsymbol{\theta}$ and the liability to CD is presented by:

$$p\ (\mathbf{I}_{CD}, \boldsymbol{\theta} \mid y_{BW}, y_{GL}, y_{CD}) \propto p\ (\mathbf{I}_{CD}, y_{BW}, y_{GL}, y_{CD}, \boldsymbol{\theta}) = p\ (y_{CD} \mid \mathbf{I}_{CD}, \mathbf{t}_{CD})\ p\ (y_{BW}, y_{G}, \mathbf{I}_{CD} \mid \boldsymbol{\theta})\ \ p\ (\boldsymbol{\theta}) \qquad (3)$$

The second term in the above equation is the density of the sampling model for BW, GL and the liability to CD. The term "p($\boldsymbol{\theta}$)" is the joint prior density of the unknown parameters in the model, and it can be factorized as follows, under the assumption of prior independence between parameters:

$$p(\boldsymbol{\theta}) = p(\mathbf{b})\, p(\mathbf{h}|\mathbf{H_0})\, p(\mathbf{H_0})\, p(\mathbf{s},\mathbf{mgs}|\mathbf{G_0})\, p(\mathbf{G_0})\, p(\mathbf{R_0})\, p(\mathbf{t}) \quad (4)$$

To ensure identifiability of CD, the first and second thresholds categories were set to 0 and 1, respectively. Multivariate normal prior distributions were assigned to systematic fixed, herd-year-season of calving, sire and maternal grandsire effects so that their fully conditional distributions were also multivariate normal. The prior distribution of the genetic ($\mathbf{G_0}$) and herd-year-season of calving ($\mathbf{H_0}$) (co)variance matrices were assumed to be inverted Wishart distribution with 35 and 8 degrees of freedom, respectively, so that their fully conditional posterior distributions were also inverted Wishart (Sorensen and Gianola, 2002).

Implementation

Fitting simultaneously a Bayesian MCMC threshold model for CD and linear models for BW and GL was performed using THRGIBBS1F90 program (Mizstal et al., 2002), which implements Gibbs sampling to evaluate the posterior density of the parameters. The length of the chain and the burn-in period were inspected by visual examination of the trace plots related to posterior samples of parameters in several preliminary analyses. Inferences were then based on 300,000 samples obtained after discarding the first 50,000 samples as burn-in period with a thinning interval of 50. Hence, 5,000 samples were used for calculating features of the posterior distribution. Posterior analysis for estimating posterior means, posterior standard deviations and convergence checking were performed using the POST-GIBBSF190 program (Mizstal et al., 2002). Posterior samples of (co)variance components were used for calculation of posterior means and standard deviations of the genetic and non-genetic parameters according to the corresponding formulas; for example, the formula for heritability and/or any type of correlation.

Direct and maternal genetic parameters

Sire and sire-maternal grand sire variances were transformed to direct additive and maternal additive genetic (co)variances (Willham, 1972) as:

$$\begin{bmatrix} \sigma^2_d \\ \sigma_{dm} \\ \sigma^2_m \end{bmatrix} = \begin{bmatrix} 4 & 0 & 0 \\ -2 & 4 & 0 \\ 1 & -4 & 4 \end{bmatrix} \begin{bmatrix} \sigma^2_s \\ \sigma_{smgs} \\ \sigma^2_{mgs} \end{bmatrix},$$

where σ^2_d, σ^2_m, σ^2_s and σ^2_{mgs} are direct additive genetic, maternal additive genetic, sire and maternal grandsire variances, respectively; σ_{dm} and σ_{smgs} are the (co)variances between direct additive and maternal additive genetic effects and between sire and maternal grandsire effects, respectively. Additive genetic (co)variances between direct and maternal effects among each pair traits of j and k were computed according to Kriese et al. (1991):

$$\begin{bmatrix} \sigma_{d_j d_k} \\ \sigma_{d_j m_k} \\ \sigma_{m_j d_k} \\ \sigma_{m_j m_k} \end{bmatrix} = \begin{bmatrix} 4 & 0 & 0 & 0 \\ -2 & 4 & 0 & 0 \\ -2 & 0 & 4 & 0 \\ 1 & -2 & -2 & 4 \end{bmatrix} \begin{bmatrix} \sigma_{s_j s_k} \\ \sigma_{s_j mgs_k} \\ \sigma_{mgs_j s_k} \\ \sigma_{mgs_j mgs_k} \end{bmatrix}$$

where $\sigma_{d_j\, d_k}$ is the covariance between direct additive genetic effects for traits j and k, $\sigma_{m_j\, m_k}$ is the covariance between maternal additive genetic effects for traits j and k, $\sigma_{d_j\, m_k}$ is the covariance between direct additive genetic effects of trait i and maternal additive genetic effects of trait j and $\sigma_{m_j\, d_k}$ is the covariance between maternal additive genetic effects of trait j and direct additive genetic effects of trait k. For each trait, phenotypic variance(σ_p^2), direct heritability(h_d^2), maternal heritability (h_m^2) and correlation between direct and maternal additive genetic effects $(r_{d,m})$ were calculated as follow:

$$\sigma_p^2 = \sigma_s^2 + \sigma_{mgs}^2 + \sigma_h^2 + \sigma_e^2, \tag{5}$$

$$h_d^2 = \sigma_a^2 \,/\, \sigma_p^2, \tag{6}$$

$$h_m^2 = \sigma_m^2 \,/\, \sigma_p^2, \tag{7}$$

and $$r_{dm} = \sigma_{dm} \,/\, \sqrt{\sigma_d^2\, \sigma_m^2}\ . \tag{8}$$

In the case of absence of maternal effects, response to selection is a function of selection intensity, accuracy, and the square root of additive genetic variance. Also, the proportion of phenotypic variance attributable to additive genetic effects is solely related to direct additive genetic effects. But for maternally-influenced traits, there is a difference between the proportion of phenotypic variance attributable to additive genetic effects and the amount of genetic differences that can be applied to generate selection response. Due to the fact that genetic improvement is the main purpose in animal breeding programs, the magnitude of the genetic differences that can be exploited to generate response to selection is of crucial importance (Eaglen and Bijma, 2009). There are two sources of additive genetic variances for maternally-influenced traits that can respond to selection; direct additive genetic variance, which is the variance of direct breeding values, and maternal additive genetic variance, that is equivalent to the variance of maternal breeding values of individuals under random mating in the population (Eaglen et al., 2012). Therefore, the term "total additive variance" is more appropriate for maternally-influenced traits in terms of response to selection. Bijma et al. (2007) pointed out that the total breeding value of an individual (TBV_i) for maternally-influenced traits can be defined as the sum of corresponding direct (A_{di}) and maternal (A_{mi}) breeding values. Therefore, the total heritable variance (σ_{TBV}^2), that is total genetic variance available for response to selection, can be expressed as follows (Eaglen and Bijma, 2009):

$$\sigma_{TBV}^2 = \sigma_{Ad}^2 + 2\sigma_{Adm} + \sigma_{Am}^2 \tag{9}$$

The ratio of total heritable variance to phenotypic variance was defined as T^2, which expresses the total heritable variance on the scale of heritability as follows (Eaglen and Bijma, 2009):

$$T^2 = \sigma_{TBV}^2 \,/\, \sigma_p^2\ . \tag{10}$$

In this context, the total heritable variance is different from that presented by Willham (1972), which refers strictly to the response to mass selection. The presented total heritable variance shows the extent of genetic differences that can be applied to generate a response to selection, regardless of the selection method.

Results and discussion

Least squares means ± standard error of BW for male calves (40.99±0.04 kg) was ($P<0.01$) higher than that for females (38.98±0.03 kg). The corresponding value of GL for dams with male calves born was ($P<0.01$) higher than that of dams with female calves (277.26±0.04 days *vs.* 276.08±0.03 days). Least squares means for CD score in cows with male calves (1.35±0.01) was ($P<0.01$) higher than that of cows with female calves (1.27±0.04). As shown in Figure 1, there was a non-linear association between CD frequency and GL in Iranian primiparous dairy cattle. A polynomial relationship (R^2= 70.73%) appropriately described the observed non-linear relationship between GL and frequency of CD. The higher incidence of CD was associated with longer gestation length, with a non-linear relationship observed between CD and BW (Figure 2). A polynomial relationship (R^2=88.56%) appropriately described the observed non-linear relationship rather than an exponential relationship (R^2=82.65%) or a linear relationship (R^2 = 77.32%).

Direct and maternal heritability estimates

Posterior means and standard deviations for direct and maternal heritability estimates are presented in Table 3. All direct and maternal heritability estimates were significantly different from zero; 99% highest posterior density (HPD) interval did not include zero. On the average, direct heritability estimates were approximately three times as large as maternal heritabilities. Direct heritability of CD (in a liability scale) was lower than direct heritability estimates of BW and GL. Vanderick et al. (2014) estimated the direct and maternal genetic parameters for calving ease in Walloon dairy cattle under linear and threshold models; estimates of direct heritability of calving ease were approximately 0.07 under linear models and 0.12 under threshold models while the estimates of maternal heritability varied from 0.02 under linear models to 0.04 under threshold models. Generally, previous published heritability estimates for CD ranged from 0.004 (Steinbock et al., 2003) to 0.325 (Cervantes et al., 2010) for direct heritability, and from 0.012 (Ghiasi et al., 2014) to 0.14 (Johanson et al., 2011) for maternal heritability.

Calving difficulty is a trait that is affected by both direct and maternal genetic effects with low to medium direct and maternal heritabilities (Jamrozik and Miller, 2014; Vanderick et al., 2014). Therefore, genetic evaluation for CD is difficult, and the estimated breeding values for CD often suffer from low accuracy, unless the progeny groups are large enough (Jamrozik and Miller, 2014).

High direct (0.40) and low maternal (0.07) heritability estimates were obtained for GL in the present study, which agree with the published values (Hansen et al., 2004; Norman et al., 2009; Cervantes et al., 2010; Johanson et al., 2011). The results revealed that GL was mainly influenced by direct genetic effects as also reported by Hansen et al. (2004). It is generally believed that parturition is initiated by the activation of the fetal adrenal cortex , secretion of cortisol and placental production of prostaglandins (Stabenfeldt, 1992), the processes some of which are to some extent under genetic control (Hansen et al., 2004).

The direct and maternal heritability estimates for BW were 0.11 and 0.04, respectively. Hansen et al. (2004) estimated the direct and maternal heritabilities for calf size, measured on four categories, in first-parity Holsteins using a threshold model as 0.22 and 0.04, respectively. Johanson et al. (2011) reported the direct and maternal heritability estimates of 0.26 and 0.08 for BW in Holstein calves.

Table 3. Posterior means and standard deviations (PSD) of the genetic parameter estimates[a]

Trait	h_d^2 *(PSD)*	h_m^2 *(PSD)*	$r_{d,m}$ *(PSD)*	T^2*(PSD)*
BW	0.12 (0.01)	0.04 (0.01)	-0.15 (0.04)	0.14 (0.02)
GL	0.40 (0.03)	0.07 (0.01)	-0.36 (0.08)	0.35 (0.03)
CD	0.07 (0.01)	0.04 (0.01)	-0.53 (0.14)	0.05 (0.01)

[a] BW: birth weight; GL: gestation length, CD: calving difficulty; h_d^2 : direct heritability; h_m^2: maternal heritability; $r_{d,m}$: correlation between direct and maternal additive genetic effects; T^2 = ratio of total heritable variance to phenotypic variance.

The estimated values in the presented study are not directly comparable with those in the literature due to different models and methodologies (animal *vs.* sire and/or sire-maternal grandsire model, linear *vs.* threshold and univariate *vs.* multivariate analysis). However, most of the previously published estimates showed that direct heritability estimates for BW, GL and SD were greater than maternal heritability estimates (Lopez de Maturana et al., 2009; Eaglen et al., 2012; Jamrozik and Miller, 2014).

Additive direct-maternal correlation and total heritable variance

All the within-trait direct-maternal genetic correlations were significant and negative; ranging from -0.15 for BW to -0.53 for CD (Table 3). In many studies, negative correlations were found between direct and maternal genetic effects. Taking these effects simultaneously into account in a selection program is of crucial importance to achieve optimum genetic progress (Heydarpour et al., 2008). Data structure is one of the possible reasons for negative direct-maternal genetic correlation (Gerstmayr, 1992). Contrary to our results, Vanderick et al. (2014) found no significant correlations between direct and maternal additive genetic effects of calving ease in Walloon dairy cattle breed. Johanson et al. (2011) estimated a value of -0.67 for direct-maternal additive genetic correlation of calving difficulty in Holstein cows, which is comparable with our estimated value but their corresponding correlation estimates for BW and GL were not significant ($P>0.05$). Jamrozik and Miller (2014) found positive direct-maternal genetic correlations with moderate magnitude for BW, GL and calving ease in Canadian Simmentals. Negative correlation estimates between direct-maternal additive genetic effects imply an antagonistic relationship between them. Therefore, selecting solely on direct additive genetic effects for any of the studied traits may deteriorate traits in terms of maternal additive genetic effects and vice versa. It should be noted that estimated values for additive direct-maternal correlation estimates are mainly dependent on data structure and model used (Heydarpour et al., 2008), and should be interpreted with caution.

Total heritable variance provides a comprehensive measure of genetic variance affecting maternally-influenced traits, as it takes both direct and maternal sources of variation into account. The ratio of total heritable variance to phenotypic variance (T^2) with posterior standard deviation in the parenthesis for BW, GL and CD were 0.14 (0.02), 0.35 (0.03) and 0.05 (0.01), respectively. Eaglen et al. (2012) obtained values of 0.01 and

0.51 for T^2 of calving ease and GL under a sire-maternal grandsire models in Holstein-Friesian cows in UK, respectively. If selection decisions were based on maternally affected traits, the performance of the population will change in response to both the direct and maternal breeding values (Eaglen et al., 2012).

Correlation estimates

A significant ($P<0.01$) value of -0.29 was predicted for additive genetic correlation between the direct effect of BW and maternal effects of CD; implying an antagonism relationship between direct genetic ability of calves to grow during prenatal period and maternal genetic ability of dams for calf growth. Posterior means and standard deviations for direct additive and maternal additive genetic correlations between the studied traits are presented in Table 4. BW was positively correlated with GL and CD. Direct additive genetic correlations for BW-GL (0.39) and BW-CD (0.43) were moderate, and the 99 % HPD interval did not include zero. Johanson et al. (2011) obtained direct additive genetic correlations for BW-GL and BW-CD in Holstein dairy cows as 0.52 and 0.73 under an animal linear-threshold model, respectively, which are in general agreement with the estimated values in the present study.

Theoretically, sire selection for CD would help to decrease the incidence of dystocia and prenatal mortality. Nevertheless, several reports showed that the incidence of dystocia and prenatal mortality is increasing (Luo et al., 2002; Steinbock et al., 2003; Hansen et al., 2004). BW is regarded as a correlated trait with vital importance for CD in dairy cows (Johanson and Berger, 2003; Johanson et al., 2011), which has been used in beef industry for many years. Longer GL period was moderately associated with heavier BW in terms of direct additive genetic effects in the first parity Iranian Holsteins. The direct additive genetic correlation for GL-CD was not significantly different from zero (95% HPD did include zero). Lopez de Maturana et al. (2009) pointed out that there was a non-linear relationship between GL and frequency of CD in Holstein dairy cows. Such non-linear relationship was observed between GL and CD in the present study (Figure 1). Therefore, estimation of the correlation between GL and CD may be affected by the existence of such a non-linear phenotypic relationship which is ignored in standard mixed models. Eaglen et al. (2013) pointed out that in the case of existence a non-linear relationship between phenotypes, correlation estimates obtained under multiple-trait model may be obscured. Norman et al. (2009) reported that there was an optimum level of performance for a range of functional traits such as CD at intermediate levels of GL. In other words, with respect to traits such as CD very short or very long GL is unfavorable. Therefore, selecting on direct GL to improve CD appears meaningless because any gains in either lengthening or shortening GL would likely result in detrimental effects in other functional traits such as CD (Eaglen et al., 2013).

Estimates of maternal genetic correlations followed similar pattern of the direct genetic ones. BW had a positive and medium to relatively high maternal genetic correlations with CD (0.48) and GL (0.69). In line with our estimate, Jamrozik and Miller (2014) estimated a value of 0.60 for maternal genetic correlation between BW and GL in first-parity Canadian Simmentals. They estimated a value of -0.17 for maternal genetic correlation between BW and calving ease in first-parity Simmentals. The difference in sign of maternal genetic correlation between BW and CD in our study and that of Jamrozik and Miller (2014) is related to a different definition of trait as calving ease and/or calving difficulty. In the present study, a statistically non-significant maternal genetic correlation between GL and CD was found (95% HPD did include zero).

Posterior means and standard deviations (PSD) of phenotypic and environmental correlations between traits are presented in Table 5. All estimated environmental and phenotypic correlations were positive, low to relatively medium, and significantly different from zero (99% HPD did not include zero). The largest environmental (0.26) and phenotypic (0.29) correlations were found between BW and GL, while the smallest environmental (0.08) and phenotypic (0.09) were obtained

Table 4. Posterior means and standard deviations (PSD) for direct additive (above diagonal) and maternal additive (below diagonal) genetic correlations between the studied calving traits

Trait [a]	BW	GL	CD
BW	-	0.39 (0.06)	0.43 (0.09)
GL	0.58 (0.08)	-	0.07 (0.09) [b]
CD	0.47 (0.13)	-0.05 (0.14) [b]	-

[a] BW: birth weight; GL: gestation length; CD: calving difficulty
[b] HPD 95 % region included 0.

Table 5. Posterior means and standard deviations (PSD) for phenotypic (above diagonal) and environmental (below diagonal) correlations of the studied calving traits

Trait [a]	BW	GL	CD
BW	-	0.29 (0.02)	0.16 (0.02)
GL	0.26 (0.01)	-	0.09 (0.01)
CD	0.20 (0.01)	0.08 (0.01)	-

[a] BW: birth weight; GL: gestation length; CD: calving difficulty.

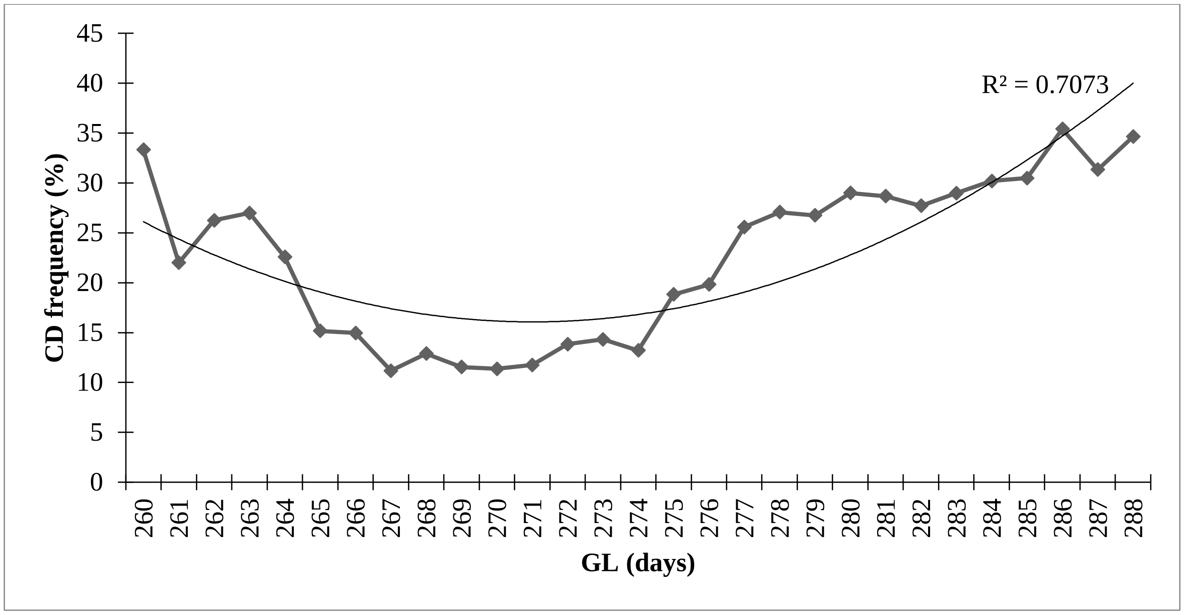

Figure 1. Phenotypic relationship between gestation length (GL) and frequency of calving difficulty (CD) in Iranian Holstein cows

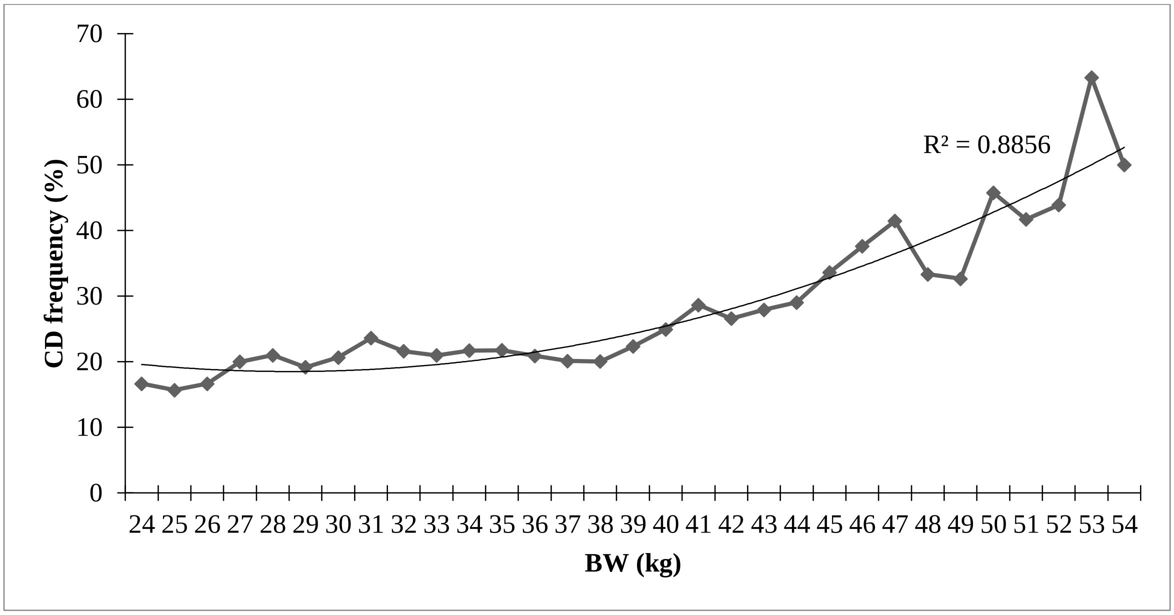

Figure 2. Phenotypic relationship between calf birth weight (BW) and frequency of calving difficulty (CD) in Iranian Holstein cows

between GL and CD.

Jamrozik et al. (2005) reported values of 0.16 and 0.06 for residual correlations of gestation length with calf size and of gestation length with calving ease in Canadian Holsteins, respectively. They also found a moderate value of 0.24 for residual correlation between calving ease and calf size. Lopez de Maturana et al. (2009) estimated environmental correlation between GL and CD in US primiparous Holsteins as 0.10, which is in line with the corresponding estimated value in the present study.

Conclusions

Direct heritability estimates for several calving traits were higher than those of maternal heritability estimates. It might implicitly denote that the expression of calving traits in first-parity Iranian Holstein dairy cows is mainly controlled by genetic effects of the calf rather than genetic effects of the cow. Furthermore, low to medium phenotypic, environmental, direct and maternal genetic correlations between calving traits emphasize that these traits are separate and thus should be regarded as such. The GL and BW showed non-linear phenotypic relationships with CD. Because such non-linear phenotypic relationships are not covered under standard mixed models, the use of GL and BW as correlated and indicator traits in a standard multi-trait model may not appropriately describe the genetic and phenotypic correlations between calving traits in the present study.

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References

Amer, P.R., 2012. Turning science on robust cattle into improved genetic selection decisions. *Animal* 6, 551-556.

Berger, P.J., 1994. Genetic prediction for calving ease in the United States: data, models, and use by the dairy industry. *Journal of Dairy Science* 77, 1146-1153.

Bijma. P., Muir, W.M., Van Arendonk, J.M., 2007. Multilevel selection 1: Quantitative genetics of inheritance and response to selection. *Genetic*s 175, 277-288.

Cervantes, I., Gutierrez, J.P., Fernandez, I., Goyache, F., 2010. Genetic relationships among calving ease, gestation length, and calf survival to weaning in the Australian de los Valles beef cattle breed. *Journal of Animal Science* 88, 96-101.

Dekkers, J.C.M., 1994. Optimal breeding strategies for calving ease. *Journal of Dairy Science* 77, 3441-3453.

Eaglen, S.A.E., Bijma, P., 2009. Genetic parameters of direct and maternal effects for calving ease in Dutch Holstein-Friesian cattle. *Journal of Dairy Science* 92, 2229-2237.

Eaglen, S.A.E., Coffey, M.P., Woolliams, J.A., Wall, E., 2012. Evaluating alternate models to estimate genetic parameters of calving traits in United Kingdom Holstein-Friesian dairy cattle. *Genetics Selection Evolution* 44, 23

Eaglen, S.A.E., Coffey, M.P., Woolliams, J.A., Wall, E., 2013. Direct and maternal genetic relationships between calving ease, gestation length, milk production, fertility, type, and lifespan of Holstein-Friesian primiparous cows. *Journal of Dairy Science* 96, 4015-4025.

Falconer, D.S., 1965. The inheritance of liability to certain disease estimated from the incidence among relatives. *Annual Human Genetics* 29, 51-76.

Gerstmayr, S., 1992. Impact of the data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. *Journal of Animal Breeding and Genetics* 109, 321-336.

Gianola, D., Foulley, J.L., 1983. Sire evaluation for ordered categorical data with a threshold model. *Genetics Selection Evolution* 15, 201-224.

Ghiasi, H., Khaldari, M., Taherkhani, R., 2014. Genetic parameters and calving ability index for direct and maternal calving difficulty and stillbirth in Iranian Holstein cows. *Livestock Science* 165, 22-26.

Hansen, M., Lund, M.S., Pedersen, J., Christensen, L.G., 2004. Gestation length in Danish Holsteins has weak genetic associations with stillbirth, calving difficulty, and calf size. *Livestock Production Science* 91, 23-33.

Heydarpour, M., Schaeffer, L.R., Yazdi, M.H., 2008. Influence of population structure on estimates of direct and maternal parameters. *Journal of Animal Breeding and Genetics* 125, 89-99.

Hoeschele, I., Tier, B., 1995. Estimation of variance components of threshold characters by marginal posterior modes and means via Gibbs sampling. *Genetics Selection Evolution* 27, 519-540.

Janss, L.L.G., Foulley, J.L., 1993. Bivariate analysis for one continuous and one threshold dichotomous trait with unequal design matrices and an application to birth weight and calving difficulty. *Livestock Production Science* 33, 183-198.

Jamrozik, J., Fatehi. J., Kistemaker, G.J., Schaeffer, L.R., 2005. Estimates of genetic parameters for Canadian Holstein female reproduction traits. *Journal of Dairy Science* 88, 2199-2208.

Jamrozik, J., Miller, S.P., 2014. Genetic evaluation of calving ease in Canadian Simmentals using birth weight and gestation length as correlated traits. *Livestock Science* 162, 42-49.

Johanson, J.M., Berger, P.J., 2003. Birth weight as a predictor of calving ease and perinatal mortality in Holstein cattle. *Journal of Dairy Science* 86, 3745-3755.

Johanson, J.M., Berger, P.J., Tsuruta, S., Misztal, I., 2011. A Bayesian threshold-linear model evaluation of perinatal mortality, dystocia, birth weight, and gestation length in a Holstein herd. *Journal of Dairy Science* 94, 450-460.

Kriese, L.A., Bertrand, J.K., Benyshek, L.L., 1991. Age adjustment factors, heritabilities, genetic correlations for scrotal circumferences, related growth traits in Hereford, Brangus bulls. *Journal of Animal Science* 69, 478-489.

Korsgaard, I.R., Lund, M.S., Sorensen, D., Gianola, D., Madsen, P., Jensen, J., 2003. Multivariate Bayesian analysis of Gaussian, right censored Gaussian, ordered categorical and binary traits using Gibbs sampling. *Genetics Selection Evolution* 35, 159-183.

Lee, D., Misztal, I., Bertrand, K., Rekaya, R., 2002. National evaluation for calving ease, gestation length and birth weight by linear and threshold model methodologies. *Journal of Applied Genetics* 43 (2), 209-216.

Lopez de Maturana, E., Wu, X-L., Gianola, D., Weigel, K.W., Rosa, G.J.M., 2009. Exploring biological relationships between calving traits in primiparous cattle with a Bayesian recursive model. *Genetic*s 181, 277-287.

Luo, M.F., Boettcher, P.J., Schaeffer, L.R., Dekkers, J.C.M., 2001. Bayesian inference for categorical traits with an application to variance component estimation. *Journal of Dairy Science* 84, 694-704.

Luo, M.F., Boettcher, P.J., Schaeffer, L.R., Dekkers, J.C.M., 2002. Estimation of genetic parameters of calving ease in first and second parities of Canadian Holsteins using Bayesian methods. *Livestock Production Science* 74, 175-184.

Mark, T., 2004. Applied genetic evaluations for production and functional traits in dairy cattle. *Journal of Dairy Science* 87, 2641-2652.

Meijering, A., 1984. Dystocia and stillbirth in cattle – A review of causes, relations and implications. *Livestock Production Science* 11, 143-177.

Misztal, I., Gianola, D., Foulley, J.L., 1989. Computing aspects of a non-linear method of sire evaluation for categorical data. *Journal of Dairy Science* 72, 1557-1568.

Misztal, I., Tsuruta, S., Strabel, T., Auvray, B., Druet, T., Lee, D., 2002. BLUPF90 and related programs (BGF90). Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, Montpellier, France.

Moreno, C., Sorensen, D., Garcia-Cortes, L.A., Varona, L., Altarriba, J., 1997. On biased inferences about variance components in the binary threshold model. *Genetics Selection Evolution* 29, 145-160.

Norman, H.D., Wright, J.R., Kuhn, M.T., Hubbard, S.M., Cole, J.B., Van Raden, P.M., 2009. Genetic and environmental factors that affect gestation length in dairy cattle. *Journal of Dairy Science* 92, 2259-2269.

Statistical Analysis System (SAS), 2004. SAS Users' Guide, Version 9.1. SAS Institute Inc., Cary, North Carolina, USA.

Sorensen, D., Gianola, D., 2002. Likelihood, Bayesian and MCMC Methods in Quantitative Genetics. Springer-Verlage, New York, USA.

Stabenfeldt, G.H., 1992. Pregnancy and parturition. In: Cunningham, J.G. (Ed.), Textbook of Veterinary Physiology. W.B. Saunders, Philadelphia, pp. 457-466.

Steinbock, L., Nasholm, A., Berglund, B., Johansson, K., Philipsson, J., 2003. Genetic effects on stillbirth and calving difficulty in Swedish Holsteins at first and second calving. *Journal of Dairy Science* 86, 2228-2235.

Vanderick, S., Torch, T., Gillon, A., Glorieux, G., Gengler, N., 2014. Genetic parameters for direct and maternal calving ease in Walloon dairy cattle based on linear and threshold models. *Journal of Animal Breeding and Genetics* 131, 513-521.

Wiggans, G.R., Misztal, I., Van Tassell, C.P., 2003. Calving ease (co)variance components for a sire-maternal grandsire threshold model. *Journal of Dairy Science* 86, 1845-1848.

Willham, R.L., 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animal breeding. *Journal of Animal Science* 35, 1288-1293.

Wright, S., 1943. An analysis of variability in number of digits in an inbred strain of Guinea pigs. *Genetics* 19, 506-536.

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ارزیابی ژنتیکی برخی صفات گوساله زایی گاوهای هلشتاین ایران در زایش اول

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چکیده هدف از این مطالعه برآورد پارامترهای ژنتیکی صفات وزن تولد، طول آبستنی و سخت زایی در اولین شکم زایش گاوهای هلشتاین ایران با استفاده از یک مدل ارزیابی چند صفتی است. داده های مورد استفاده ۲۹۹۵۰ رکورد گوساله زایی بودند که طی سال های ۱۳۷۸ تا ۱۳۹۳ توسط مرکز اصلاح دام و بهبود تولیدات دامی کشور ثبت شده بودند. از یک مدل آستانه ای-خطی مولد نر- پدر بزرگ مادری استفاده شد. در این مدل اثرات جنس گوساله، سن در زایش نخست و ماه زایش (برای وزن تولد گوساله و طول دوره آبستنی) به عنوان اثرات ثابت و اثرات مولد نر، پدر بزرگ مادری، گله- سال- فصل زایش و باقی مانده عنوان اثرات تصادفی در نظر گرفته شدند. میانگین های پسین (انحراف معیار پسین) وراثت پذیری های مستقیم وزن تولد گوساله (۰/۰۱) ۰/۱۲، طول آبستنی(۰/۰۳) ۰/۴۰، و سخت زایی (۰/۰۱) ۰/۰۷ برآورد گردیدند. میانگین های پسین (انحراف معیار پسین) وراثت پذیری های مادری وزن تولد، طول آبستنی و سخت زایی به ترتیب (۰/۰۱) ۰/۰۴، (۰/۰۱) ۰/۰۷ و (۰/۰۱) ۰/۰۴ برآورد گردیدند. همبستگی های ژنتیکی اثرات مستقیم- مادری صفات مقادیر منفی، کم تا متوسط و معنی دار (p< ۰/۰۱) بودند که برای وزن تولد گوساله (۰/۰۴) ۰/۱۵-، طول آبستنی (۰/۰۸) ۰/۳۶- و سخت زایی (۰/۱۴) ۰/۵۳- برآورد گردیدند. همبستگی های ژنتیکی افزایشی مستقیم بین وزن تولد با طول آبستنی و وزن تولد گوساله با سخت زایی به ترتیب (۰/۰۶) ۰/۳۹ و (۰/۰۹) ۰/۴۳ و همبستگی های ژنتیکی افزایشی مادری بین آن ها به ترتیب (۰/۰۸) ۰/۵۸ و (۰/۱۳) ۰/۴۷ برآورد گردیدند. همبستگی های ژنتیکی افزایشی مستقیم و مادری بین طول آبستنی و سخت زایی از لحاظ آماری معنی دار نبودند. برآورد های میانگین های پسین همبستگی های فنوتیپی و محیطی مثبت و کم تا متوسط بودند. بین طول دوره آبستنی با سخت زایی و وزن تولد با سخت زایی روابط فنوتیپی غیر خطی مشاهده شد. وجود رابطه غیر خطی و نیز یک رابط علّی و معلولی بین سخت زایی و طول دوره آبستنی و نیز بین سخت زایی و وزن تولد گوساله (که عموماً در مدل های معمول ارزیابی ژنتیکی نادیده گرفته می شود) ممکن است بر ارزیابی ژنتیکی این صفات با مدل های مختلط استاندارد تاثیر گذارد.