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The application of six different models to estimate the genetic parameters, variance components and breeding values for birth weight of Holstein calves

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ABSTRACT

This research was conducted to determine variance component, genetic parameters and breeding values (EBV) for the birth weight (BW) of Holstein calves. In this context, the direct genetic (σ_a^2) , maternal genetic (σ_m^2) and maternal permanent environmental effects, which affect BW, were separately assessed. The multi-trait, derivative-free restricted maximum likelihood programme was used for determining the effect of the genetic parameters by using models that either included or excluded the maternal genetic and/or permanent maternal environmental effects. The estimation of the BW of Holstein calves was optimized by evaluating six different models. The best model was chosen according to the log-likelihood ratio tests. Within the context of the study, a total of 4443 calves were investigated between 1987 and 2006. Among the six different models, model 4 was selected as the best model, since it had the lowest value for the likelihood ratio. The range of the values for direct heritability $(h_{\rm d}^2)$ and maternal heritability (m^2) were between 0.07–0.13 and 0.04–0.09, respectively. In conclusion, an estimation of the genetic parameters for BW can be used as a selection criteria for Holstein calves.

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KEYWORDS

Variance component; genetic parameters; breeding value; direct genetic; maternal genetic

1. Introduction

The Holstein is a breed of cattle commonly reared across Turkey, and the calves of this breed are often raised for their meat and milk. The birth weight (BW) of calves is a vital feature of cattle breeding that significantly affects meat and milk production (Bakır et al. 2004) as well as the animal's growth performance. For this reason, BW is a parameter that is generally included in the selection criteria. The BW provides cues regarding a calf's prenatal development, while also serving as an indicator about its growth following birth. BW is controlled by a multitude of genetic, maternal and environmental factors. Such factors may be associated with the genes of the calf, the genes of the dam or with environmental factors that affect the calf and/or the dam. The overall BW is a polygenic feature that is also influenced by environmental factors. Consequently, efforts to improve live weight through selection requires a consideration of both maternal and direct components (Meyer 1992, 1993). The number of studies evaluating σ_m^2 in the BW of Holstein calves as well as the r_{am} by employing restricted maximum likelihood (REML) is limited. The purpose of the present research was to examine the significance of maternal effects on BW of Holstein calves, applying six animal models including both environmental and genetic effects. Furthermore, the six models were also used to estimate the EBV and the relationships between direct genetic effects and maternal genetic effects.

2. Materials and methods

2.1. Data collection and preparation

The records for a 20-year period (1987–2006) were obtained from the Tahirova Official Farm in Turkey with data on a total of 4433 calves (2152 females and 2281 males) descending from 940 dams and 223 sires. There were on average 3.72 off-spring for each dam.

The BW was measured utilizing a scale with 150 g sensitivity within 24 hours after birth. Abnormal records were removed from the data set.

2.2. A preliminary analysis

The fixed effects were determined by using the Minitab (1998) software (version 12.1). Analyses were performed in each one of the models, by taking into account the effects associated with the year of birth, the sex of the calf and the type of calving. Dam age was considered as a linear covariate. Effects determined as non-significant were excluded from the models by using backwards elimination.

2.3. Estimation of variance component, genetic parameters and breeding values

Variance components and genetic parameters were estimated by multi- trait, derivative- free restricted maximum likelihood



Table 1. Estimates of heritabilities and log-likelihood values.

	Direct heritability		Maternal heritability		Total heritabilities	Log likelihood values		
Models	h_d^2	S.E.	m ²	S.E.	h _T ²	−2Log L		
Model ¹	0.11	0.015	-	_	0.11	14749.53		
Model ²	0.083	0.020	_	_	0.09	14746.01		
Model ³	0.085	0.020	0.04	0.019	0.10	14748.01		
Model ⁴	0.10	0.025	0.09	0.039	0.26	14732.54		
Model⁵	0.07	0.019	0.040	0.018	0.09	14743.24		
Model ⁶	0.10	0.024	0.05	0.038	0.22	14744.01		

Notes: h_T^2 : total heritability ($h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$ Willham 1972), S.E. Standard error. σ_a^2 : direct additive genetic variance, σ_m^2 : maternal additive genetic variance, σ_{am}^2 : the covariance between direct and maternal genetic effects, σ_c^2 : the variance of the permanent environmental effect of the dam (maternal environmental variance), σ_p^2 : phenotypic variance, c^2 : the permanent environmental variance due to the dam as a proportion of phenotypic variance, cam: genetic variance between direct and maternal effects as a proportion of the total variance, r_{am} : genetic correlation between direct and maternal effects, -2log L: log likelihood.

(MTDFREML) software package (Boldman et al. 1995). Six different models were used for each analysis. In all analyses a convergence criteria was used to the value of 10⁻⁹. Each analysis was also re-started to avoid a local maximum until reaching the global one. Dam age was considered as a covariate. Random effects associated with the calf, sire and dam were also considered. The parameters estimated by using the six animal models are provided in Table 1.

The analysis was repeated with the estimates at earlier apparent convergence as the starting values until a global minimum of $-2 \log L$ was detected, when $-2 \log L$ values remained constant to the fifth denary after successive repetition (Lee and Taper 2002; Tilki et al. 2008). The parameters listed in Table 1 were estimated using the six different animal models. In the models applied, the animal was considered as a random factor. The σ_c^2 was added in the models as a random effect, with no correlation with the other effects in the models (Ap Dewi et al. 2002). The σ_m^2 was employed as a second random effect for animals with similar covariance as the direct effect. The models used in the analysis are summarized below.

Model 1: $Y_{ijklm} = F_{ijk} + a_1 + e_{ijklm}$

Model 2: $Y_{ijklmn} = F_{ijk} + a_1 + P_m + e_{ijklmn}$

Model 3: $Y_{ijklmn} = F_{ijk} + a_1 + m_m + e_{ijklmn}$ with $\sigma_{AM}A = 0$

Model 4: $Y_{ijklmn} = F_{ijk} + a_1 + m_m + e_{jiklmn}$ with $\sigma_{AM}A \neq 0$

Model 5: $Y_{ijklmn} = F_{ijk} + a_1 + m_m + p_m + e_{ijklmn}$ with $\sigma_{AM}A = 0$

Model 6: $Y_{ijklmn} = F_{ijk} + a_1 + m_m + p_m + e_{ijkmn}$ with $\sigma_{AM}A \neq 0$

In these equations;

 Y_{ijklmn} : standardized weights with dam and fixed effect composition.

 a_i : σ_a^2 , p_m : σ_c^2 , m_m : σ_m^2 , e_{ijklmn} : random error

 F_{iikl} : fixed effects $b_{mi} + s_i + b_{vk} + bt_l + \theta(X_{iikl} - Y)$

 b_{mi} : the effect of the birth season,

s_i: the effect of the calf sex,

 b_{yk} : the effect of the birth year,

 bt_1 : the effect of the birth type,

 θ : the regression coefficiency of detected weights on dam

X_{iikl}: dam age, Y: mean dam age,

 h_T^2 was determined using the next formula (Willham 1972): $h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$

The best equality was determined with the likelihood ratio test (Saatcı et al. 1999). This test involved comparing a value from the chi square distribution with the -2 Log L, and determining the difference between the two. EBV for BW was determined using the best model. For the EBV, genetic trends were calculated according to the years of birth.

3. Results and discussion

The σ_a^2 were higher than the level of σ_m^2 for all traits. Six different model analysis results are summarized in Table 1 and Table 2. In general, the σ_a^2 was higher than the σ_a^2 leading to lower estimates of m^2 compared to h_d^2 .

3.1. Heritabilities

Model 1, fitting animal as the only random effect, produced considerably higher estimates for σ_a^2 and h_d^2 than other models. Likewise, higher heritability estimates for BW from model one have been informed for different cattle breeds (Abera et al. 2011: Sahin et al. 2012).

Observed σ_a^2 and h_d^2 (0.11) in model 1 were higher than those in the other models. Except for models 1, 2 and 3, estimated σ_a^2 and h_d^2 were close to each other.

In model 1, where σ_m^2 were disregarded, h_d^2 was 0.11, while the inclusion of σ_m^2 in models 3, 4, 5 and model 6 decreased the h_d^2 . When the σ_m^2 was added in the model, σ_a^2 ranged from 0.882 to 1.142.

According to models, the maternal effects were separated into two units, as environment and genetic. In model 2 σ_c^2 decrease has been observed in both σ_a^2 and h_d^2 compared to that in model 1. Including σ_a^2 with no σ_a^2 in model 3 resulted in lowest σ_a^2 and h_d^2 compared to those estimated in models 4

But, inserting σ_m^2 with no σ_c^2 in model 4 resulted in higher σ_a^2 and h_d^2 compared to those estimated in models 2, 3 and 5.

Model 4 (σ_c^2 removed) generated the highest h_d^2 and σ_a^2 than models 2 and 5. Also, adding σ_{am}^2 in model 4 gave rise to the highest σ_a^2 and h_d^2 than models 2 and 5. When the σ_c^2 was disregarded (model 4), the σ_p^2 was attributed to the σ_m^2 , emerging in overestimation of the m^2 compared to model 3.

In model 5, σ_m^2 was added but σ_{am} was removed. Consequently model 5 created lower σ_a^2 and h_d^2 than the other models

In model 6, when σ_m^2 and σ_c^2 were included, 5% of the σ_p^2 was attributed to the σ_m^2 and 4.3% to the c^2 .

It was apparent that the model used for analysis considerably affected the relative values for maternal and direct heritability. In general, σ_m^2 is lower than $\sigma_{a'}^2$ which leads to higher estimates of h_d^2 compared to m^2 . In the current study, the h_T^2 for BW varied between 0.09 and 0.26. Higher total heritability estimates varying between 0.37 and 0.62 were reported by Abera et al. (2011) for Zebu and their crosses Jersey and Holstein cattle. Furthermore, Tilki et al. (2008) and Sahin et al. (2012) also determined higher h_T^2 for Brown Swiss cattle.

Estimates of total heritability represent a useful mean for estimating response to selection based on the phenotypic value. Estimates can be influenced by the breeds, models and data size that are used (Solomon and Gemeda 2002).

In this research, according to chosen model, h_d^2 varied from 0.07 to 0.11 and m^2 ranged from 0.04 to 0.09. Karabulut et al. (2012) reported that estimates for h_d^2 ranged from 0.02 to

Table 2. Estimates of parameters and correlations.

	Parameters and correlations										
Models	σ_a^2	σ_m^2	σ_{am}^2	σ_c^2	$\sigma_{\rm e}^2$	σ_p^2	C _{am}	r _{am}	S.E.	c ²	S.E.
Model ¹	1.249	_	_		9.876	11.124	_	_	_	_	_
Model ²	0.938	_	_	0.471	9.782	10.720	_	_	_	0.042	0.019
Model ³	0.882	0.472	_	_	9.683	10.565	_	_	_	_	_
Model ⁴	1.097	1.026	-0.808	_	9.743	10.840	0.075	-0.760	0.027	_	_
Model⁵	0.829	0.497	_	0.023	10.757	11.585	_	_	_	0.002	0.000
Model ⁶	1.142	0.632	0.657	0.470	9.792	10.934	0.060	-0.670	0.115	0.043	0.017

Notes: h_T^2 : total heritability ($h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$ Willham 1972), S.E. Standard error. σ_a^2 : direct additive genetic variance, σ_m^2 : the covariance between direct and maternal genetic effects, σ_c^2 : the variance of the permanent environmental effect of the dam (maternal environmental variance) σ_p^2 : phenotypic variance, c_a^2 : the permanent environmental variance due to the dam as a proportion of phenotypic variance, c_a^2 : genetic covariance between direct and maternal effects as a proportion of the total variance, r_{am} : genetic correlation between direct and maternal effects, -2 log L: log likelihood.

0.48, m^2 from 0.12 to 0.45, c_{am} from -0.09 to -0.14, c^2 from 0.01 to 0.24 and $r_{\rm am}$ was -1.00 for Holstein calves, respectively. But then Tilki et al. (2008) informed estimates of h_d^2 from 0.15 to 0.37, m^2 from 0.06 to 0.15, $r_{\rm am}$ from 0.73 to 0.92, $c_{\rm am}$ from 0.085 to 0.090, c2 from 0.001 to 0.083 for Brown Swiss calves, respectively. By the preferred model, m^2 ranged from 0.04 to 0.09 for BW. Based on model 4 (the best model), the estimates of m^2 for BW were 0.09 ± 0.039 . In the study of Demeke and Neser Schoeman (2003), a small (yet non-zero) estimate was also reported for maternal heritability for BW. This finding was similar to those in the study of Sahin et al. (2012). Pico (2004) and Plasse et al. (2002a, 2002b) previously informed m^2 for BW values of 0.11, 0.08 and 0.07 in Brahman cattle; these values are lower than the ones identified in the current study. Furthermore, Aynalem (2006) reported that m^2 estimates in Boran and their crosses were 0.25 ± 0.05 and 0.18 ± 0.05 , which are closer to the estimates of the current study. Low levels or the complete lack of maternal effects on growth traits indicates that improvement in these traits can be achieved more efficiently through selection based on the direct genetic potential of the animal. In general, maternal effects at birth result from the cytoplasmic effect and prenatal maternal environment (Wasike et al. 2006). On the other hand, Wasike et al. (2006) reported a lack of maternal influence on BW in Boran breeds. But then Karabulut et al. (2012) determined higher m^2 (0.12–0.45) in Holstein calves and also a negative r_{am} . However, Tilki et al. (2008) estimated higher m^2 (0.06– 0.15) for Brown Swiss calves and a positive r_{am} .

Meyer (1992) previously demonstrated that models excluding σ_m^2 could provide considerably higher estimates for the σ_a^2 , and, hence, higher estimates for h_d^2 as well. In case maternal effects are not taken into account, part of the maternal variance will be included in the estimate of additive genetic variance. Thus, including σ_m^2 will have the effect of decreasing the estimates of h_d^2 .

It was observed that the permanent maternal environmental effects (or maternal environmental variance) varied between 0.023 and 0.472 for BW. Gemeda et al. (2003) attributed the σ_c^2 in BW to the dam's uterine conditions. The same researchers also noted that the σ_c^2 was associated with the dam's uterine capacity, maternal behaviour and feeding during late gestation. It is likely that maternal behaviour reflects the rearing ability of a dam. Maniatis and Pollott (2003) previously showed the influence of record in separating maternal environmental and maternal genetic effects from the integrated direct effects. These authors indicated that the accuracy of maternal effect

estimates is dependent on the pedigree information, and that the number of progeny per dam as well as the ratio of dams having their own record in the data is significantly affected by the estimation of the variance component.

3.2. Genetic correlations and covariances

The $r_{\rm am}$ was negative and high for models 4 (-0.76 ± 0.027) and 6 (-0.67 ± 0.115). Similarly, genetic correlations estimated by Sahin et al. (2012) for Brown Swiss calves, Karabulut et al. (2012) for Holstein calves were negative and ranged from -0.58 to -1.00. However, compared to the results of the current study, lower $r_{\rm am}$ estimates (-0.35 to -0.37) have been informed for Brahman cattle (Plasse et al. 2002a; Pico 2004), while similar estimates have been noticed for Nellore cattle (-0.72, Eler et al. 1995) and Boran cattle (-0.55, Haile-Mariam & Kassa-Mersha 1995).

The negative correlation observed between the $r_{\rm am}$ effects is possibly a symptom of genetic conflict between genes; hence, taking this correlation into consideration during selection programmes is important. Meyer (1992) and Swalve (1993) previously proposed that environmental covariances between offspring and dam that are not taken into account may lead to bias in the $r_{\rm am}$. For beef cattle, Robinson (1996) noted that negative $r_{\rm am}$ could be the result of other effects in the data rather than an actual negative genetic relationship.

On the other hand, contrary to the results of the present investigation, Demeke and Neser Schoeman (2003) suggested that a large and positive correlation (0.48) between the σ_a^2 and σ_m^2 could be associated with bias due to the breed additive effect and the dam's additive effects not being taken into account. Numerous studies conducted on different breeds have reported a negative association between $r_{\rm am}$ for BW and weaning weight (Maria et al. 1993; Tosh & Kemp 1994; Ligda et al. 2000). But, a number of studies have also reported a positive relationship (Nasholm & Danell 1996; Yazdi et al. 1997). Nasholm and Danell (1996) described that, in this instance of a positive relationship between r_{am} , selection for augmented weights will also lead to an improvement in the maternal ability. These authors did not provide a conclusive explanation for these negative estimates. They might be associated with natural selection for an intermediate optimal (Tosh & Kemp 1994). It is generally assumed that, for body weight, the σ_{am}^2 is usually negative (Maria et al. 1993; Tosh & Kemp 1994); however, certain studies have also identified a positive relationship (Nasholm & Danell 1996; Yazdi et al. 1997).



The $c_{\rm am}$ ranged from 0.060 to 0.073. Cundiff (1972) stated that the negative σ_{am}^2 explained from an evolutionary point of view prevents species from becoming increasingly larger. In this study, σ_{am}^2 were determined as positive. The findings of the present research were in agreement with those of Meyer (1992) and Tilki et al. (2008). But, this result was not supported by Karabulut et al. (2012). Moreover, some researchers informed that a possible existence of a negative environmental covariance between offspring and dam could result in a biased estimation of $r_{\rm am}$ (Meyer 1992; Ligda et al. 2000).

Low σ_c^2 in model 5 reflects that σ_c^2 is not considerable for BW as mentioned by Rodriguez-Almeida et al. (1995) for Mac Nay and Rhodes calves. In this study, σ_{am}^2 was estimated as positive. Meyer (1992) reported the positive σ_{am}^2 for the BW of different calves, which is in line with the conclusions of the current research; nevertheless, Cantet et al. (1988) informed a negative σ_{am}^2 for BW of Hereford calves. Szwaczkowski et al. (2006) previously demonstrated that, when the maternal contribution is omitted during evaluation, the negative σ_{am}^2 serves as an indication of the different rankings of individuals. In addition, Swalve (1993) described that the negative σ_{am}^2 might be associated with the managing scheme. On the other hand, a study directed by Dodenhoff et al. (1999) on various strains of beef steers indicated that breed determines the dependence and r_{am}. Furthermore, Přibyl et al. (2008a, 2008b) demonstrated that correcting the records plays a role in determining the genetic parameters, and that it also contains a more complice pedigree and harvests considerably diverse conclusions.

3.3. The likelihood test

The results are shown in Table 2. According to the theories of the MTDFREML software package, model 4 with the lowest likelihood ratio is selected as the best model (Van Vleck 1993; Ulutas 1998; Lee & Taper 2002; Ulutas et al. 2002). This conclusion is in contradiction with the results of Tilki et al. (2008) who described that model 6 was the best model.

3.4. Breeding values

EBV breeding value has been estimated using the best model (model 4). According to birth year, changes of the breeding values are shown in Figure 1. The genetic trend was estimated to the regression of EBV according to birth year. It was positive, 0.0085 kg/year, and important. A significant trend was not observed in the research period. The genetic trend was determined as non-zero. According to birth year, uneven fluctuations were observed in breeding values. The genetic trend (0.0085 kg/

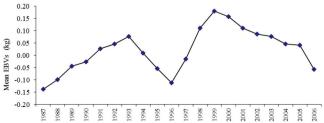


Figure 1. Mean EBVs of birth weight according to years.

year) calculated in the current research was lower than the results of Intaratham et al. (2008). However, Tilki et al. (2008) stated that no positive and negative EBV for BW was determined.

4. Conclusions

The estimates of genetic parameters for Holstein calves were consistent with previous research results. This research revealed that the addition of only maternal effect to a model caused a reduction in estimates of h_d^2 for BW of Holstein calves. Consequently, maternal effect on BW in diverse ages of Holstein cattle was important and should be considered in any selection scheme for these calves.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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