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ESTIMATES OF GENETIC PARAMETERS FOR DIRECT AND MATERNAL EFFECTS WITH SIX DIFFERENT MODELS ON BIRTH WEIGHT OF BROWN SWISS CALVES

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ABSTRACT

The aim of the present study was to estimate variance components, genetic parameters and breeding values for birth weights in Brown Swiss calves. Data were collected from the Malya State Farm in Kırşehir province of Turkey from 1995 through 2006. Random effects included direct and maternal additive genetic effects, maternal permanent environmental effects with direct maternal genetic covariance and random residual effects. Variance and covariance components and genetic parameters were estimated using the WOMBAT software by fitting six single-trait animal models. Depending on the model, h_D^2 varied from 0.13 to 0.30 for birth weight. Estimates of m^2 ranged from 0.10 to 0.14 for birth weight. The maternal permanent environmental effect was significant for birth weight and ignoring maternal effects in the model caused the over estimation of direct heritability. The present study shows the importance of inclusion of maternal effects in designing appropriate breeding programs for genetic improvement in Brown Swiss calves for birth weight.

Keywords: direct heritability; maternal effects; calves, model.

INTRODUCTION

Recently, birth weight has become one of the selection criterias in a cattle population. Animals follow different growth patterns (Krejčová *et al.,* 2008) due to different environments, management restrictions, and compensation from changing environments. Animals with high growth potential are negatively affected by unfavourable environmental factors more than animals with poor growth capability (Přibyl *et al.,* 2008). Estimates of environmental and genetic parameters of different component traits related to growth are needed to develop a proper selection program. In addition, these parameters are necessary for the prediction of a response to selection. Researches of various cattle breeds have shown that growth traits, particularly at early ages, are influenced not only by the genes of the individual for growth and by the environment in which it is raised, but also by the maternal genetic composition and environment provided by the dam (Ghafouri *et al.,* 2008). Maternal effects in animals have been studied intensively in recent years both because of their economic importance in farmanimals and because of their theoretical interest (Willham, 1972). From the mother's perspective, maternal effects on progeny performance result from maternal traits controlled by her genotype and associated environmental factors. Therefore, these effects are divided into genetic and environmental components. However, in terms of the offspring, maternal effects are reflected as environmental. Hence, there are indirect genetic and environmental effects. In consequence, maternal genetic effects are defined as any influence from dam to progeny, excluding the effects of directly transmitted genes (Szwaczkowski *et al.,* 2006). To take advantage of different schemes for breed utilization, the genetic parameters for the traits of importance should be known (Boujenane and Bradford, 1991).

Approximately 50% of cattle population of Turkey is consisted of European originated cattle (Holstein, Brown Swiss, Simmental, Jersey) and their crosses. Brown Swiss has more meat producing capacity in addition to the milk yield on Anatolian highlands which gives them a special place among others.

The aim of this study was to estimate genetic parameters and breeding values for birth weights in Brown Swiss calves by fitting six animal models, attempting to separate direct genetic, maternal genetic and maternal permanent environmental effects. In addition, the genetic correlation between additive direct and additive maternal effects was estimated.

MATERIALS AND METHODS

The data used in this research study were collected from the Malya state farm in Kırşehir province of Turkey from 1995 to 2006. Data were collected from 1995 through 2006, with records on 2,889 calves (1112 female, 1677 male) progeny of 59 sires and 502 dams. On an average there were 5.75 progenies per dam. The average birth weight of calves was 38.12±0.006 kg (37.26±0.008 kg for female calves, 38.99±0.026 kg for male). There were eight age of dam groups and twelve birth year groups. The calf weights were taken at birth using a scale with 100 g sensitivity. Recording of the weights of the calves were performed within 24 hours after birth. All calves were ear tagged, and all pedigree and birth information had been recorded at the birth. The available pedigree information included in data on animal code, sire and dam; while the available birth information included the calves' date of birth, sex, birth weight, and birth type. Records related to diseased or aborted calves were not included in the data set. Six different animal models were fitted to estimate (co)variance components and corresponding genetic parameters by using the WOMBAT (Meyer, 2008) software. To identify the fixed effects to be included in the models, the GLM procedure in the SAS program (SAS Institute 2009) was used. The analysis showed that fixed effects of year of birth, sex, type of birth (single and twin) and age of dam were significant for birth weight. Consequently, these effects were included in the models. The effects of calving season on birth weight was not significant and, therefore, this factor was exluded from the models.

The random effects in used mixed models are summarized in Table 1. All models included an additive direct effect, and this was the only random factor in Model 1. Model 2 included the maternal permanent environmental effect, fitted as an additional random effect, uncorrelated with all other effects in the model. Model 3 included an additive maternal effect fitted as a second random effect. Model 4 was the same as Model 3, but allowed for a direct maternal covariance (Cov (a,m)). Model 5 and Model 6 included additive maternal and maternal permanent environmental effects, ignoring and fitting, respectively, direct maternal covariance. Allowing for and ignoring genetic covariances between direct and maternal effects yielded up to six different analyses for birth weight.

The models were as follows;

Model 1: $Y = Xb + Z_a a + e$

Model 2: $Y = Xb + Z_a a + Z_c c + e$

Model 3: $Y = Xb + Z_a a + Z_m m + e$ with Cov $(a,m) = 0$

Model 4: $Y = Xb + Z_a a + Z_m m + e$ with Cov $(a,m) = A\sigma_{am}$

Model 5: $Y = Xb + Z_a a + Z_m m + Z_c c + e$ with Cov$(a,m) = 0$

Model 6: $Y = Xb + Z_a a + Z_m m + Z_c c + e$ with Cov$(a,m) = A\sigma_{am}$

Where;

Y : vector of observations

b vector contained year of birth, sex, type of birth (single and multiple) and age of dam as fixed effects

a, m, c, e : vectors of direct additive genetic effects, maternal genetic effects, permanent environmental effect of dam and the residual, respectively

X, Za, Zm, Zc : incidence matrices relating observations to b, a, m and c, respectively

A : numerator relationship matrix

σ_{am}: covariance between direct and maternal genetic effects

The (co)variance structure of the random effects in the analysis can be described as:

$V(a) : A\sigma^2_A$; $V(m) : A\sigma^2_M$; $V(c) : I_d\sigma^2_C$; $V(e) : I_n\sigma^2_E$; Cov $(a,m) : A\sigma_{AM}$

where:

A : numerator relationship matrix

σ^2_A : direct additive genetic variance

σ^2_M : maternal additive genetic variance

σ_{AM} : direct-maternal additive genetic covariance

σ^2_C : maternal permanent environmental variance

σ^2_E : residual variance

I_d, I_n : identity matrices of an order equal to the number of dams and records, respectively (Ekiz *et al.*, 2004).

The covariance and variance structure of the model is as follows;

$$v\begin{vmatrix} a \\ m \\ c \\ e \end{vmatrix} = \begin{vmatrix} A\pm^2_A & A\pm_{\mathrm{AM}} & 0 & 0 \\ A\pm_{\mathrm{AM}} & A\pm^2_M & 0 & 0 \\ 0 & 0 & I_{\mathrm{c}}\pm^2_C & 0 \\ 0 & 0 & 0 & I_{\mathrm{n}}\pm^2_E \end{vmatrix}$$

I the identity matrix, (I_{c} : an identity matrix with order number of lambs and I_{n} : an identity matrix with order number of records), $\pm^2_A$ the direct additive genetic variance, $\pm^2_M$ the maternal genetic variance, $\pm^2_C$ the variance of the permanent environmental effect of the dam, $\pm^2_E$ is the residual variance,

Total heritability ($h^2_T = (\pm^2_A + 0.5\pm^2_M + 1.5\pm_{AM})/\pm^2_P$) is as defined by Willham (1972); The (co) variance components and genetic parameters of birth weight was estimated by means of AI-REML algorithm of the WOMBAT software (Meyer, 2008).

Convergence was assumed when the variance of likelihood values in the simplex was less than 10^{-8}. In addition, a restart of each analysis was performed with different initial values to avoid convergence to local maxima. The most appropriate model for each trait was selected according to the Akaike's information criterion (AIC) (Akaike, 1974):

$\mathrm{AIC}_i = -2 \log L_i + 2 p_i$

where $\log L_i$ represents the maximized log likelihood, and $\mathbf{p_i}$ is the number of parameters obtained for each model. The model having the lowest AIC, is the appropriate model for that trait.

Genetic trends were obtained by regressing means of predicted genetic values on year of birth for Brown Swiss calves.

RESULTS AND DISCUSSION

The average birth weights were 37.26±0.008 kg for female calves, 38.99±0.026 kg for male and 38.12±0.006 kg for all calves (female, male). Estimates of (co)variance components and genetic parameters regarding birth weights are presented in Tables 2. The effect of age of dam on birth weight and year of birth on birth weights are shown in figures 1 and 2.

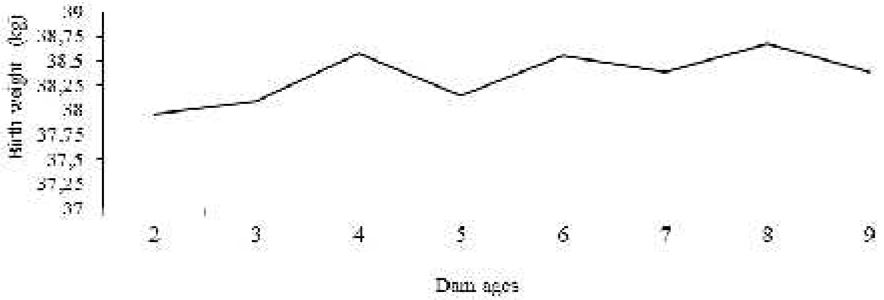

Figure 1. Mean birth weight according to dam ages

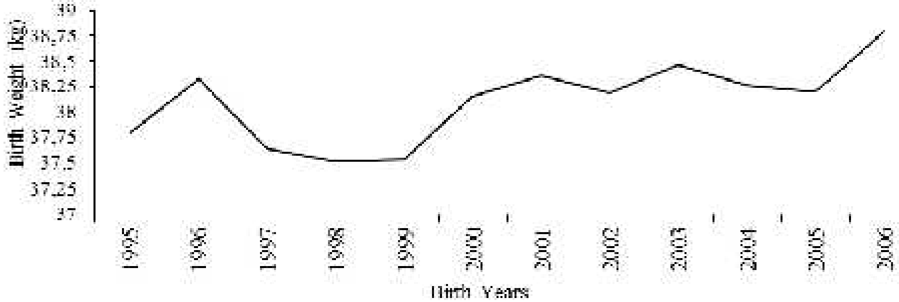

Figure 2. Birth weight according to birth years

The genetic parameters and variance components for models (model 1 to model 6) are summarized in Table 2. Model 1, which ignored maternal effects, resulted in higher estimates for $\sigma_A^2$and h^2_D than the other models did. In Model 2, the addition of the maternal environmental effect reduced both $\sigma_A^2$and h^2_D values, compared to Model 1.

Models 3 and 4, which included the additive maternal effect but not the maternal environmental effect, yielded smaller es-timates of $\sigma_A^2$and h^2_D than Models 1 and 2 did.The same result was found in previous reports which compared models for Brown Swiss calves (Tilki *et al.*, 2008). Meyer (1992) showed that models not accounting for maternal genetic ef-fects could result in substantially higher estimates of additive direct genetic variance and, therefore, higher estimates of h^2_D.

Table 1. Description of animal models fitted.

Models	**(Co)Variance components estimated**
Model$_1$	σ_A^2, σ_E^2
Model$_2$	σ_A^2, σ_C^2, σ_E^2
Model$_3$	σ_A^2, σ_M^2, σ_E^2
Model$_4$	σ_A^2, σ_M^2, σ_{AM}, σ_E^2
Model$_5$	σ_A^2, σ_M^2, σ_C^2, σ_E^2
Model$_6$	σ_A^2, σ_M^2, σ_{AM}, σ_C^2, σ_E^2

σ_A^2 : direct additive genetic variance; σ^2_M: maternal additive genetic variance; σ_{AM}: direct-maternal genetic covariance; σ_C^2 : maternal environmental variance; σ_E^2 : error variance

The impact of data structure on separating maternal genetic and maternal environmental effects from combined and direct effects was demonstrated by Maniatis and Pollott (2003). They showed that the accuracy of estimation of maternal effects depends on the family structure and demonstrated that both the number of progeny per dam and the proportion of dams having their own record in the data considerably affect the variance component estimation.

Including additive maternal effect with no maternal environmental effects in model 3 resulted in smaller σ^2_A and h^2_D compared to those estimated in models 1 and 2. However, including additive maternal effect with no maternal environmental effects in model 4 resulted in smaller σ^2_A and h^2_D compared to those estimated in models 1 and 2.

In model 5, additive maternal effects were included but σ^2_{AM} was excluded. In this case, model 5 produced lower σ^2_A and h^2_D values than model 4.

It is clear that the relative values of direct heritability and maternal heritability were greatly influenced by the model used in the analysis. Model 3 and 6 produced similar m^2 while model 3 and 5 generated the same m^2 (Table 2).

Table 2. Estimates of (co)variance components and genetic parameters for birth weight

	Model ^{1}	**Model ^{2}**	**Model ^{3}**	**Model ^{4}**	**Model ^{5}**	**Model ^{6}**
σ^2_A	4.199	2.16	1.919	1.322	1.132	1.87
σ^2_M			1.559	1.256	1.407	1.5
σ^2_{AM}				1.517		1.51
σ^2_C		0.051			1.869	0.892
σ^2_E	9.2	8.096	8.923	7.455	8.331	8.89
σ^2_P	13.40	10.26	10.84	8.78	9.46	10.76
h^2_D	0.31	0.21	0.18	0.15	0.12	0.17
S.E	0.018	0.023	0.003	0.031	0.073	0.036
M^2			0.15	0.10	0.12	0.14
S.E			0.003	0.048	0.087	0.003
C_{AM}				0.14		0.12
S.E						
r_{AM}				0.99		0.96
S.E				0.35		0.073
C^2		0.63			0.36	0.97
S.E		0.047			0.084	0.054
h^2_T	0.31	0.21	0.25	0.48	0.19	0.45
AIC	8333.553	8149.267	8115.206	8332.937	8301.007	8100.19

σ^2_{AM} in model 4 and 6 indicates that relationship between the genetic structure of the calve and genetic structure of the dam has a certain effect on the calve birth weight. Cantet *et al.* (1988) reported a negative σ^2_{AM} for birth weight of Hereford cattle, Meyer (1992) stated the positive σ^2_{AM} for the BW of Hereford and Angus cattle, which is in line with the outcomes of the present study. Depending on the model, h_D^2 ranged from 0.13 to 0.30, m^2 ranged from 0.10 to 0.14 for birth weight in this study. Although estimated h_D^2 in the present study was lower than the direct heritability (h_D^2) of birth weight for Angus (0.36) and Hereford (0.40) breeds, maternal heritability (m^2) was higher for Brown Swiss compared to both Angus (0.06) and Hereford (0.08) for BW (Meyer, 1992).

The higher estimate of maternal heritability for birth weight compared with the estimate for weaning weight supports the conclusion of Robinson (1981) that maternal genetic effects generally are important for weight at younger ages and diminish with an increasing age. The tendency of m^2 to decline from birth to later ages, as obtained here, is in agreement with previous literature (Tosh and Kemp, 1994; Ligda *et al.*, 2000).

Tilki *et al.*, (2008) reported the h_D^2 of birth weight for Brown Swiss calves, which was lower than the h^2_D of model 1 and model 6 in the corresponding study but the h^2_D obtained from model 6 was higher compared to the reported values.

The estimated h^2 of this study was also compared with the h^2 value of Brown Swiss birth weight in other research. According to this comparison, present value was higher than the value (0.08) found by Kaygısız (1998), lower than the value (0.36) found by Akbulut *et al.* (2001). Estimation of m^2 for BW in this research for Brown Swisscattle was higher compared to Rhodes cattle.Tilki *et al.,* (2008) stated the range of estimates of σ^2_{AM} from 2.16 to 2.37 for Brown Swiss calves. Also, Rodriguez-Almeida *et al.* (1995) reported the range of estimates of σ^2_{AM} from -0.16 to 0.10 for BW, which is lower than the corresponding covariance (1.51) estimated for Brown Swiss.

Maternal permanent environment variance as a proportion of phenotypic variance (C^2) ranged from 0.36 to 0.97 for birth weight. Tilki *et al.* (2008) reported estimates for c^2 of 0.001 and 0.08 for Brown Swiss calves and Dezfuli and Mashayekhi (2009) reported 0.01 and 0.07for Najdi calves using a similar models.

Correlations between direct and maternal genetic effects (r_{am}) ranged from 0.96 to 0.99 for birth weight. Numerous studies have found a negative correlation between additive direct and additive maternal effects (r_{am}) for birth and weaning weights of various breeds (Tosh and Kemp, 1994; Ligda *et al.*, 2000).

However, positive relationships have also been reported (Nasholm and Danell, 1996; Tilki *et al.,* 2008). Nasholm and Danell (1996) concluded that selection for increased weights will also improve the maternal ability in the case of a positive correlation between direct and maternal genetic effects. The reasons for the negative estimates obtained could not be explained conclusively by these au-thors. It may be due to natural selection for an intermediate optimum (Tosh and Kemp, 1994). It is generally assumed that the covariance between direct and maternal genetic effects on body weight is negative (Tosh and Kemp, 1994). However, a positive relationship was also found (Nasholm and Danell, 1996; Tilki *et al.,* 2008). In this study we found different covariances between direct and maternal genetic effects.

Szwaczkowski *et al.* (2006) showed that the negative covariance between direct and maternal genetic effects indicates different rankings of individuals when the maternal contribution is omitted in the evaluation procedure. Moreover, Swalve (1993) suggested that the negative covariance between direct and maternal genetic effects may be the result of management system.

However, an investigation conducted by Dodenhoff *et al.* (1999) on several breeds of beef cattle indicates that dependences between direct and maternal ef-fects are determined by breed. Moreover, Přibyl *et al.* (2008) showed that editing the database plays a role in estimating genetic parameters and includes a more complex pedigree as well as produces slightly different results. In the case of birth weight a posi-tive covariance between direct and maternal genetic effects was registered.

The likelihood values under six different models with the most appropriate model components determined using log likelihood ratio tests are given in Table 2. Model 6 with only the additive direct effect was chosen as the best model based AIC value. According to the principles of WOMBAT program, AIC smallest value of the model should be preferred as the best model (Meyer, 2008). This result is in agreement with the findings of Tilki *et al.* (2008) who reported that model 6 was the best model (with MTDFREML statistical program) which included both maternal and permanent environmental effect due to dam.

Breeding values for birth weight of individual animals were estimated utilizing all available pedigree and performance information. The breeding values (EBV) were estimated according to the best model (model 6). The trends in direct breeding values according to years are presented in Figure 3.

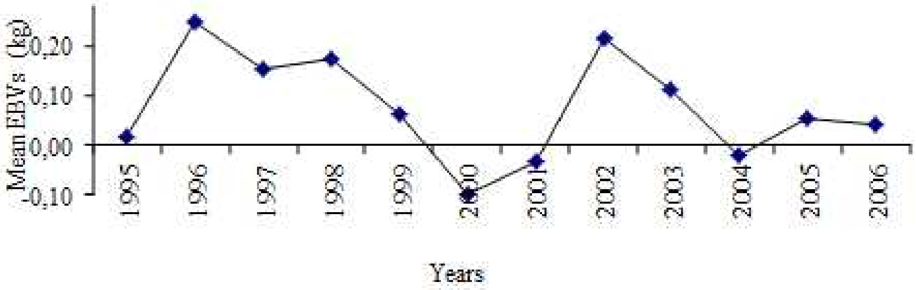

Figure 3. Mean EBVs of birth weight according to years

The genetic trend was calculated for birth weight by linear regression of average estimated breeding value (EBV) on year. There was no apparent genetic trend during the years studied. Breeding values for birth weight were negative in some years, whereas, breeding values for birth weights were positive in others.

The present research is a contribution to the model comparison and estimation of genetic parameters in Brown Swiss calves. We determined that model 6 containing both maternal and direct genetic effects could better explain the genetic variation observed in early growth traits. In conclusion, maternal effects on birth weight in Brown swiss calves were significant and ahould be taken into consideration in any selection program for this breed.

Authors' contributions: Project concept and design: ES (%60), experimental design AS (%40). All authors read and approved the final manuscript.

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