Comparison of models for estimating genetic parameters and predicting breeding values for birth weight and calving ease in Czech Charolais cattle

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ABSTRACT: The most appropriate model for genetic parameters estimation for calving ease and birth weight in beef cattle was selected. A total of 27,402 field records were available from the Czech Charolais breed. For estimation of genetic parameters for calving ease and body weight, three bivariate models were tested: a linear-linear animal model (L-LM) with calving ease classified into four categories (1 – easy; 2–4 – most difficult), a linear-linear animal model (SC-LM) in which calving ease scores were transformed into Snell scores (Snell 1964) and expressed as percentage of assisted calving (ranging 0–100%), and a bivariate threshold-linear animal model (T-LM) with calving ease classified into four categories (1 – easy, 2–4 – most difficult). All tested models included fixed effects for contemporary group (herd × year × season), age of dam, sex and breed of a calf. Random effects included direct and maternal genetic effects, maternal permanent environmental effect, and residual error. Direct heritability estimates for calving ease and birth weight were, with the use of L-LM, SC-LM, and T-LM, from 0.096 ± 0.013 to 0.226 ± 0.024 and from 0.210 ± 0.024 to 0.225 ± 0.026, respectively. Maternal heritability estimates for calving ease and birth weight were, with the use of L-LM, SC-LM, and T-LM, from 0.060 ± 0.031 to 0.104 ± 0.125 and from 0.074 ± 0.041 to 0.075 ± 0.040, respectively. Genetic correlations of direct calving ease with direct birth weight ranged from 0.46 ± 0.06 to 0.50 ± 0.06 for all tested models; whereas maternal genetic correlations between these two traits ranged from 0.24 ± 0.17 to 0.25 ± 0.53. Correlations between direct and maternal genetic effects within-trait were negative and substantial for all tested models (ranging from −0.574 ± 0.125 to −0.680 ± 0.141 for calving ease and from −0.553 ± 0.122 to −0.558 ± 0.118 for birth weight, respectively), illustrating the importance of including this parameter in calving ease evaluations. Results indicate that any of the tested models could be used to reliably estimate genetic parameters for calving ease for beef cattle in the Czech Republic. However, because of advantages in computation time and practical considerations, genetic analysis using SC-LM (transformed data) is recommended.

Keywords: beef cattle; dystocia; data transformation; threshold model; Snell score

INTRODUCTION

Calf survival is a complex trait that is influenced by a number of genetic (maternal and direct) and non-genetic factors. The majority of calf losses occur in the first days after calving, so attention should be paid to this period in particular. Parturition itself is the first critical moment. Its length and course critically influence subsequent calf survival (Fries and Ruvinsky 1999). Difficult calving may result in brain injury to the foetus due to oxygen deprivation that interferes with the onset of post-partum reflexes of calves, often resulting in death. In beef cattle, up to 10% of cows experiencing a
difficult calving die (Ruvuna et al. 1992). Phocas and Laloe (2003) reported that 8% of parturitions in the Charolais breed required mechanical assistance or a caesarean section. Difficult calving is associated not only with higher calf losses. It also negatively impacts animal welfare, increases demands on husbandry and veterinary care, and may restrict future productivity of cows and calves. From the economical point of view, the calving ease is one of the most important trait for beef cattle (Wolfova et al. 2005). From a biological perspective, calving ease is influenced by direct effects of the foetus (calf weight, head width, occurrence of deformations, ability to assume a normal calving position, etc.) and by maternal effects of the dam, particularly pelvic dimensions (Fries and Ruvinsky 1999). Most experiments (Varona et al. 1999a; Carnier et al. 2000 and others) that estimated genetic parameters for both direct and maternal effects on calving ease document adequate genetic variance in these traits to allow practical and effective selection. Genetic improvement in calving ease may, however, be restricted by its high genetic correlation with birth weight of the calf (Koots et al. 1994). However, if sires with low predicted breeding values for birth weight were used, it would result in lower growth potential as well as lower birth weight of the offspring.

Typically, calving ease is recorded and analyzed as a discrete variable. Gianola (1982), however, stated that the evaluation of threshold traits using a linear model is not suitable. The estimation of genetic parameters by threshold models was studied e.g. by Varona et al. (1999a, b), Ramirez-Valverde et al. (2001), and Hansen et al. (2004). Eriksson et al. (2004) and Jamrozik et al. (2005) are among many who used linear models for the estimation of genetic parameters for calving ease. Tong et al. (1977) and Mujibi and Crews (2009) estimated genetic parameters for calving ease using a linear model with logistic transformation by means of Snell scores (Snell 1964).

Developing a statistical model for a maternally affected trait requires a careful balance between sufficient predictive ability and computational feasibility, which in turn is affected by the size of the dataset and potential biases in data recording (Eaglen et al. 2012).

The objective of the present paper was to compare a model with Snell score transformation with linear and threshold models for estimation of genetic parameters and prediction of breeding values for calving ease in Czech beef cattle.

MATERIAL AND METHODS

Data. The Czech Beef Breeders Association (www.cschms.cz) provided birth weight and calving ease data from a Charolais progeny test program. Included were records from animals with 88–100% genes of Charolais ancestry in the years 1990–2012. Average live weight at birth was 42.2 ± 6.39 kg for bull calves and 39.22 ± 5.40 kg for heifers. Animals with birth weights three times exceeding the standard deviation above or below the mean were discarded from the data set for estimation of genetic parameters. Calving ease records were scored as: easy calving – spontaneous calving without any help from a breeder (1), assisted calving – calving with help from one or two breeders (2), difficult calving – calving requiring help from three or more people or help from a vet (3), and caesarean section or dystocia requiring postpartum treatment from a vet (4). Only those animals with records for both traits were included in the analysis. The input database was adjusted so that components of variance among all considered effects would be estimable for all traits. After adjustment the data set included: sires who had at least 5 offspring with tested performance, sires who had offspring in at least two herd × year × season classes, herd × year × season classes that had offspring of at least two sires, herd × year × season classes that had at least 5 individuals, and dams that had at least two offspring and at least one half-sister (Vostry et al. 2007) (n = 27 402). The pedigree file for estimation of genetic parameters comprised three generations of ancestors (n = 39 546 animals). The effects of gestation length and weight of cows could not be included in the analysis because reliable data were not available for those traits.

Statistical analysis. Variance components and genetic parameters for calving ease were estimated by a two-trait BLUP animal model based upon the BLUP animal model currently used for breeding value estimation for the Czech national progeny test (Pribyl et al. 2003).

\[
y_{ijklmno} = \mu + HYS_j + AgeD_k + Sex_l + a_m + m_n + p_e + e_{ijklmno}
\]

where:

- \(y_{ijklmno}\) = \(i\)-th trait (calving ease or birth weight – 27 402 records)
- \(\mu\) = general mean
- \(HYS_j\) = fixed effect of \(j\)-th herd × year × season (\(j = 1, \ldots, 1457\))
Two-trait linear-linear model (L-LM) – calving ease and birth weight are modelled as linear traits – calving ease is expressed by recorded phenotypic value (1–4);

Two-trait threshold-linear model (T-LM) – calving ease is modelled as a threshold trait and birth weight is modelled as a linear trait – calving ease is expressed by recorded phenotypic value (1–4);

Two-trait linear-linear model with data transformation (SC-LM) – calving ease is modelled as a linear trait transformed by means of the Snell score and birth weight is modelled as a linear trait – calving ease is expressed as percentage of assisted calving, ranging 0–100% (least to greatest) (Snell 1964).

**Snell score.** The basic assumption of the Snell score (Snell 1964) is that for a categorical trait such as calving ease there exists a latent discrete distribution for which the Snell score represents the middle of the interval. It is computed by an approximation procedure from Snell (1964). In this procedure, a logistic model is applied to compute the score that may be generalized for normal distribution. An approximate solution to a pair of boundary points is estimated by substituting the observed proportions as the theoretical proportions into the derivatives of the log likelihood. In general, if we consider i = 1, 2, …, m groups of observations and j = 1, 2, …, k categories (e.g. calving ease), the following estimation equations have been derived (for details see Snell 1964):

\[ 0 = \frac{N_j}{(e^{x_{j-1}} - 1) + N_j} + \sum_{i=1}^{m} (n_{ij} + n_{i,j+1})p_{ij} \]

\[ 0 = \frac{N_{k-1}}{(e^{x_{k-1}} - 1) + N_{k-1}} + \sum_{i=1}^{m} (n_{i,k-1} + n_{i,k})p_{i,k-1} \]

where:
- \( x_{j} \) = estimated boundary points such as the score for category j
- \( p_{ij} \) = observed probability of group i in category j
- \( n_{ij} \) = frequency of scale values in group i and category j
- \( N_{j} \) = \( \sum_{j=1}^{m} n_{ij} \)

These two equations provide estimates for the intervals \((x_2 - x_1), (x_3 - x_2), \ldots, (x_{k-1} - x_{k-2})\). One set = 0 to obtain estimates for all individual boundary points is taken as the scores. For the two extreme categories, scores are derived from the corresponding expected values under the two tails of the distribution. The scores for the first and last
Table 1. Structure of data used for estimation of genetic parameters for birth weight, calving ease, and Snell score

<table>
<thead>
<tr>
<th>Structure of data</th>
<th>Birth weight (kg)</th>
<th>Calving ease</th>
<th>Snell score (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sires (n)</td>
<td>470</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dams (n)</td>
<td>6,605</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average n of animals per sire</td>
<td>58.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average n of animals per dam</td>
<td>18.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average n of contemporary groups per sire</td>
<td>14.46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average n of contemporary groups per sire</td>
<td>3.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average n of farms per sire</td>
<td>3.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Animals with records</td>
<td>27,402</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Animals in total</td>
<td>39,546</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>40.81</td>
<td>1.13*</td>
<td>9.49</td>
</tr>
<tr>
<td>SD</td>
<td>6.12</td>
<td>0.43*</td>
<td>21.26</td>
</tr>
</tbody>
</table>

*expressed by recorded phenotype values; calving ease = Snell score expressed as percentage of assisted calving

category are given by \( \hat{x}_y = (\log P_1/Q_1) \) and \( \hat{x}_{k-1} = \log P_{k-1}/Q_{k-1} \), where \( P_1 \) is the probability of a value greater than \( x_1 \) and \( Q_1 = 1 - P_1 \), and \( P_{k-1} \) = probability of a value less than \( x_{k-1} \) and \( Q_{k-1} = 1 - P_{k-1} \) (Tong et al. 1977).

The Snell score was transformed to a 0–100 range (percentage calving ease: score 1 = 0.1%, score 2 = 31%, score 3 = 51.8%, score 4 = 100%).

**Selection of a model.** The suitability of the various models for genetic parameters estimation and breeding values prediction for calving ease was tested on the basis of splitting or cross-validation (Shao 1993). Here the data splitting technique involved duplicating the data set, randomly discarding one-half of the calving difficulty records in one subset with the remaining calving difficulty records discarded in the other subset. Thus, each calving difficulty phenotype was present in only one of the two subsets. Solutions for each of the three models were obtained from both subsets and the correlations between individual predicted breeding values from the two subsets were calculated. Repeated samples were created according to the above criteria, and reported correlations were the average of 10 replicates. For each model, these correlation coefficients provide an informative comparative assessment of model predictive performance, useful for ranking the tested models (Ramirez-Valverde et al. 2001). These authors showed that higher correlations between complementary subsets implied a higher reliability of the model for predicting breeding value solutions in deleted animals.

Only linear models were compared on the basis of the ratio of residual error variance to total phenotypic variance (\( \text{er}^2 \)) (Jamrozik et al. 2005). Because measurement scales differ between threshold and linear models (liability vs observed value, respectively), it is not possible to use the ratio of residual error variance to total phenotypic variance for comparison between them (Gianola and Norton 1981).

For the estimation of variance and covariance components for the full data set, the AIReMLF90 programme (Misztal et al. 2002) was used for the linear-linear models and the THRIGIBBS1F90 programme (Misztal et al. 2002), which applies the Bayesian approach by means of the Gibbs sampling algorithm, was used for the threshold-linear model. According to a graphical representation, the first 100,000 samples were excluded as the burn-in. A total of 50,000 samples were then used to estimate the posterior mean and SD of the variance components. The following population parameters were derived from the estimated variance-covariance components: \( \sigma^2_y = \text{phenotype variance} \) (\( \sigma^2_y = \sigma^2_a + \sigma^2_m + \sigma^2_{am} + \sigma^2_{hm} + \sigma^2_{hm} + \sigma^2_{em} + \sigma^2_{em} \)) (Willham 1972), \( h^2_y \) = direct heritability coefficient (\( h^2_y = \sigma^2_a/\sigma^2_y \)), \( h^2_m \) = maternal heritability coefficient (\( h^2_m = \sigma^2_m/\sigma^2_y \)), \( r_{am} \) = genetic correlation of direct and maternal effects (\( r_{am} = \sigma_{am}/(\sigma_a \times \sigma_m) \)), where \( \sigma^2_a \) = additive genetic variance of direct effect, \( \sigma_{am} \) = genetic covariance of direct and maternal effect, \( \sigma^2_m \) = additive genetic variance of maternal effect, \( \sigma^2_{hm} \) = variance of the effect of the herd × year × season, \( \sigma^2_{pe} \) = variance of maternal permanent environmental effects, \( \sigma^2_e \) = variance of the effect of residual error. The pedigree set for estimation of genetic parameters comprised three generations of ancestors. Errors of the estimated heritability coefficient were approximated according to the method of Klei and Tsuruta (2008). Breeding values were predicted using the BLUPF90 and CBLUP90THR computer programmes (Misztal et al. 2002).

**RESULTS AND DISCUSSION**

**Estimation of genetic parameters.** Estimated genetic parameters for birth weight were identical for all of the tested models (Table 2). For this reason, subsequent discussion will be directed only at the calving ease trait.
Heritability estimates for direct effects on calving ease were low, ranging 0.096–0.210 (Table 2). The heritability estimate from the T-LM model was twice as large as estimates from the other models, and its standard errors also were doubled. Higher heritability estimates from threshold compared to linear models were also reported by Hansen et al. (2004); and threshold models have resulted in higher genetic parameter estimates than linear models for body conformation (Vesela et al. 2011) and health status traits (Silvestre et al. 2007; Vostry et al. 2012a, b). However, estimated heritability in the present work may not be a realistic heritability. The substantial negative direct-maternal correlation fixed a phenotypic variance, and consequently direct and maternal heritability may be overestimated. The SC-LM model had slightly higher values of direct heritability compared to the L-LM model. Maternal heritability was half as large as direct heritability in all tested models. Our estimated values of heritability for direct and maternal effects had slightly lower values from linear models (L-LM and SC-LM) than those published by Luo et al. (2001), Eriksson et al. (2004), and Mujibi and Crews (2009). On the contrary, our heritability estimates from T-LM were identical to those in Varona et al. (1999b) and Lee (2002) in cows.

Correlations between direct and maternal genetic effects within traits were negative and intermediate. The largest negative value for calving ease was from the threshold model in comparison with SC and LM (−0.680 vs −0.606 vs −0.574, respectively). These substantial direct/maternal effect correlations and maternal effect heritabilities reinforce the importance of including maternal effects in the genetic evaluation of calving ease. Estimations of the direct genetic correlation between calving ease and birth weight of calf showed that the threshold model provided the lowest value of correlation in comparison with SC and LM. Estimations of the maternal genetic correlation between calving ease and birth weight of calf were obtained for all of the tested models. The positive values of direct genetic correlation between traits were in agreement with Varona et al. (1999a) and Eriksson et al. (2004). These authors estimated slightly higher correlations (0.79 and 0.62). Koots et al. (1994)

<table>
<thead>
<tr>
<th>L-LM</th>
<th>SC-LM</th>
<th>T-LM</th>
</tr>
</thead>
<tbody>
<tr>
<td>CE</td>
<td>BW</td>
<td>CE</td>
</tr>
<tr>
<td>σ²ₘ</td>
<td>0.01 (0.00)*</td>
<td>3.20 (0.24)</td>
</tr>
<tr>
<td>σ²ₑ</td>
<td>0.01 (0.00)</td>
<td>1.05 (0.13)</td>
</tr>
<tr>
<td>σ²ₑ</td>
<td>0.01 (0.00)</td>
<td>0.59 (0.07)</td>
</tr>
<tr>
<td>σ²ₑ</td>
<td>0.13 (0.00)</td>
<td>10.38 (0.14)</td>
</tr>
<tr>
<td>σ²ₑ</td>
<td>0.15</td>
<td>14.20</td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.10 (0.01)</td>
<td>0.23 (0.02)</td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.06 (0.03)</td>
<td>0.07 (0.04)</td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.03 (0.01)</td>
<td>0.04 (0.01)</td>
</tr>
<tr>
<td>h²ₐ</td>
<td>0.853</td>
<td>0.73</td>
</tr>
<tr>
<td>rₑₑ</td>
<td>−0.57 (0.12)</td>
<td>−0.56 (0.12)</td>
</tr>
<tr>
<td>rₑₑ</td>
<td>0.50 (0.06)</td>
<td>0.47 (0.05)</td>
</tr>
<tr>
<td>rₑₑ</td>
<td>0.25 (0.35)</td>
<td>0.24 (0.17)</td>
</tr>
<tr>
<td>rₑₑ</td>
<td>0.24</td>
<td>0.23</td>
</tr>
</tbody>
</table>

σ²ₘ = variance of additive direct genetic effect, σ²ₑₘ = variance of additive maternal genetic effect, σ²ₑₚₑ = variance of maternal permanent environmental effect, σ²ₑₚₑ = variance of temporary environmental effects (residual error), σ²ₑ = phenotypic variance, h²ₐ = coefficient of direct heritability, h²ₑₘ = coefficient of maternal heritability, c² = proportion of the maternal permanent environmental variance in the total phenotypic variance, e² = proportion of the residual variance in the total phenotypic variance, rₑₑ = correlation between direct and maternal effect, rₑₑ = direct genetic correlation between traits, rₑₑ = maternal genetic correlation between traits, rₑₑ = residual correlation between traits

*standard error (posterior standard deviation from Bayesian methods) in brackets
reported the average correlation of 0.58 between calving ease and birth weight. High negative correlations between calving ease and birth weight significantly constrain possibilities for efficient breeding for birth weight because calving ease is a very important trait from the economic aspect. Based on this genetic correlation, single trait selection for calving ease would result in reduced birth weight, and vice versa.

Ratios of maternal permanent environmental to total phenotypic variance ($c^2$) were identical in results from all linear models (L-LM and SC-LM) – 3% for calving ease and 4% for live weight at birth. In T-LM, this ratio was 12.5%. Eriksson et al. (2004) published similar values of $c^2$ for Swedish Charolais and Hereford (3–5%). Nujiby and Crews (2009), however, reported $c^2$ values of 35% for Canadian Charolais. These differences may have been caused by data structure and different recording system. Mujibi and Crews (2009) included only first parity records from heifers in analysis, used a different scoring system for calving ease, and used a three-trait animal BLUP model (birth weight, calving ease, and gestation length).

Selection of a model. Both linear models (L-LM and SC-LM) yielded identical values for the ratio of residual error variance to total phenotypic variance ($e^2 = 0.85$). Thus, both models explained the same proportion of total variability.

When evaluated with the technique of data splitting, T-LM was the most suitable because it achieved 1.2 times and 1.8 times higher average correlation among predicted breeding values for calving ease than the SC-LM and L-LM models, respectively (Table 3). However, unlike for the ratio of residual variance to total phenotypic variance, SC-LM showed 1.5 times higher values than L-LM when data splitting was used. Ramirez-Valverde et al. (2001) stated that models producing higher values for the correlation among breeding values estimated from complementary subsets are more suitable for estimating breeding values of individual animals. Hence, L-LM provided the least reliability in breeding value estimation while T-LM provided the highest one. This also implies variability in correlations of breeding values during 10 replications when models T-LM and SC-LM showed the same values of standard deviations and the highest value of standard deviations was calculated for L-LM (SD = 0.27). Based on selection criteria (on the basis of data splitting), the highest reliability for the estimation of genetic parameters and subsequent predictions of breeding value was found in T-LM. These lower correlations of breeding values during 10 replications were probably caused by data structure with a smaller number of animals in groups of herd mates and limited use of artificial insemination in beef breeds in the Czech Republic.

The implementation of threshold models often requires complicated computations, substantially more time demanding than when using a linear model (Misztal et al. 1989; Kadarmideen et al. 2000). Up to several days of additional time to solve threshold models was also shown in our study. Furthermore, the threshold model has limitations in variance component estimation and breeding value prediction when the number of fixed effect classes is high (Misztal et al. 1989). This limitation can partially be solved by high information content for fixed effects and by inclusion of the effect of herd as the random effect (Varona et al. 1999b). Luo et al. (2001) also stated that convergence is problematic in threshold models and that it can result in overestimations of genetic parameters. Ramirez-Valverde et al. (2001) reported that conversion of a single-trait to a multi-trait model increases the reliability of genetic parameter estimation to a greater extent than conversion of a linear to a threshold model. In addition, linear models are routinely used for the estimation of genetic parameters and prediction of breeding values of categorical traits by animal model. Considering the above arguments and in spite of higher suitability, it is not necessary to use a threshold model for genetic analysis of categorical traits. Jamrozik et al. (2005) stated that the introduction of the Snell score technique did not significantly improve or markedly change results in comparison with a linear model. This, however, was not confirmed in the present study. Based on results from data-splitting analyses,

<table>
<thead>
<tr>
<th>Model</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>L-LM</td>
<td>0.41</td>
<td>0.27</td>
<td>0.02</td>
<td>0.73</td>
</tr>
<tr>
<td>SC-LM</td>
<td>0.63</td>
<td>0.06</td>
<td>0.57</td>
<td>0.74</td>
</tr>
<tr>
<td>T-LM</td>
<td>0.75</td>
<td>0.05</td>
<td>0.70</td>
<td>0.84</td>
</tr>
</tbody>
</table>

L-LM = linear-linear model, SC-LM = linear model with calving ease transformed by the Snell score, T-LM = threshold model.
transformation of the categorical trait of calving ease using Snell scores (SC-LM) achieved better outcomes than the linear-linear model.

Abdel-Azim and Berger (1999) reported that L-LM and T-LM models provide comparable values only if the categorical traits have 10 or more observed scores, which would allow data to be closer to normally distributed. They further concluded that for categorical data with smaller numbers of classes and for those skewed from a normal distribution, it is more advantageous to use a threshold model than data transformation or creation of a new variable to be analyzed with a linear model. In contrast, SC-LM and TM models in our experiment led to similar results and conclusions. We therefore conclude that, in spite of the lower values of tested criteria, the model with data transformation using Snell score (SC-LM) would be more suitable for the routine genetic evaluation of calving ease given its advantage in computation time and its approximation to the threshold model.

CONCLUSION

Any of the models tested in our experiment could be used to estimate genetic parameters and predict breeding values for calving ease in the Czech Charolais cattle population. Based, however, on the testing criteria and for practical considerations, threshold-linear and linear-linear models with transformation of calving ease score by means of the Snell score would achieve the highest reliability for routine genetic parameter estimation and breeding value prediction. Threshold-linear models, however, are significantly less suitable for practical application of breeding value prediction. Therefore, linear-linear models with transformation of calving ease by means of the Snell score are deemed most suitable for the genetic parameter estimation and breeding value prediction for calving ease for beef cattle breeds under management and environmental conditions in the Czech Republic.

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