Estimation of direct and maternal genetic parameters for weaning weight in Hungarian Simmental cattle

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SUMMARY

The aim of the current research was to estimate variance components and genetic parameters of weaning weight in Hungarian Simmental cattle. Weaning weight records were obtained from the Association of Hungarian Simmental Breeders. The dataset comprised of 44,278 animals born from 1975 to 2020. The data was analyzed using the restricted maximum likelihood methodology of the Wombat software. We fitted a total of six models to the weaning weight data of Hungarian Simmental cattle. Models ranged from a simple model with animals as the only random effect to a model that had maternal environmental effects as additional random effects as well as direct maternal genetic covariance. Fixed effects in the model comprised of herd, birth year, calving order and sex. Likelihood ratio test was used to determine the best fit model for the data. Results indicated that allowing for direct-maternal genetic covariance increases the direct and maternal effect dramatically. The best fit model had direct and maternal genetic effects as the only random effect with non-zero direct-maternal genetic correlation. Direct heritability, maternal heritability and direct maternal correlation of the best fit model was 0.57, 0.16 and -0.78 respectively. The result indicates that problem of (co-)sampling variation occurs when attempting to partition additive genetic variance into direct and maternal components.

Keywords: Variance components; genetic parameters; Hungarian Simmental cattle

INTRODUCTION

Weaning weight is an economically important trait in cattle breeding, as the selection for higher weight at young ages can increase the mature weight due to genetic correlations from medium to high magnitudes between weights in different ages (Silva et al., 2000; Boligon et al., 2009; Meyer, 1992). In other words, they are good indicators of animal growth potentials at older ages (Bald et al., 2010). The weaning weight (WW) is often used as a correlated trait in genetic evaluation programs and is used for decision-making on culling or selection (Guidolin et al., 2012). Weaning weight is easy to obtain (Boligon et al., 2009) and has a medium heritability which results in a high selection response (Szabo et al., 2002). The weaning weight is not only a function of the offspring genotype but also the maternal environment. This can be referred to as direct and maternal effect respectively. Any influences from dam to progeny, excluding the effects of directly transmitted genes are referred to as maternal genetic effects (Szwaczkowski et al., 2006; Legates, 1972). From the perspective of the offspring, maternal effects are purely environmental (Gholizadeh et al., 2010; Eaglen & Bijma, 2008). Maternal effects play a role in the growth of an offspring until they are weaned (Koch and Clark, 1955). Not accounting for maternal effects in genetic evaluation model results in an upward bias estimate of genetic parameters for weaning weight (Khombe et al., 1995; Robinson, 1996a) which can hamper efficiency of selection. Both direct and maternal effects should be taken into consideration to realize the optimum genetic improvement in selection programs (Robison, 1981). The Hungarian Simmental cattle is a major cattle breed in Hungary with about 65,000 individuals (Anton et al., 2018). It is a dual-purpose breed i.e. it is breed for both meat and milk (Anton et al., 2018). There are few reports about genetic parameters accounting for the maternal effect, hence, this research aims to estimate the direct and maternal genetic effect on weaning weight of Hungarian Simmental cattle.

MATERIALS AND METHODS

Weaning weight of Hungarian Simmental animals born between 1975 and 2020 were obtained from the Association of Hungarian Simmental Breeders. The dataset comprised of 44,278 Hungarian Simmental animals. The mean, standard deviation and coefficient of variation of the weaning weight was 213.08 kg, 46.77 and 22.25%, respectively. The pedigree file consisted of 56,406 animals with 879 sires and 14811 dams and average inbreeding coefficient is 0.41%.

Statistical Analysis

In order to decide on which fixed effects to be included in the model, preliminary test was performed using the analysis of variance command of the R package (R Core Team, 2021). Effects not significant were eliminated from the model. Finally, the fixed effects used in the model were herd (92 level), birth year (46), calving order (15) and sex (2) as they had a significant effect (P<0.05) on the weaning weights. The models used in matrix notation were:

\[ y = Xb + Za + e \]  \hspace{1cm} (1)
\[ y = Xb + Za + Spe + e \]  \hspace{1cm} (2)
\[ y = Xb + Za + Wm + e, \text{ with } \sigma(a, m) = 0 \]  \hspace{1cm} (3)
\[ y = Xb + Za + Wm + e \]
\[ y = Xb + Za + Wm + Spe + e \text{, with } \sigma (a, m) = 0 \]
\[ y = Xb + Za + Wm + Spe + e \]

Where \( y \) is a vector of observation, \( b \) is a vector of fixed effects, \( a \) is a vector of random animal effects, \( m \) is a vector of maternal effects, \( pe \) is a vector of permanent environmental effects. \( X, Z, W, S \) are incidence matrices relating records to fixed, animal, maternal and permanent environmental effects, respectively.

The (co)variance structure of the analysis is

\[
\begin{align*}
\text{Var}(a) &= A \sigma_a^2 \\
\text{Var}(m) &= A \sigma_m^2 \\
\text{Var}(pe) &= I \sigma_{pe} \\
\text{Var}(e) &= I \sigma_e^2 \\
\text{Cov}(a, m) &= A \sigma_{AM}
\end{align*}
\]

Where \( A \) is the numerator relationship matrix and \( I \) is an identity matrix. \( \sigma_a \) is the additive/direct genetic variance, \( \sigma_m \) is the maternal genetic variance, \( \sigma_{pe} \) is maternal permanent environmental variance, \( \sigma_e \) is the residual variance and \( \sigma_{AM} \) is covariance between direct and maternal effects.

The Restricted Maximum Likelihood method of the Wombat software (Meyer, 2007) was used to estimate these (co)variance components. At convergence restarts were initiated to ensure that it is global minimum.

Likelihood test was conducted to determine which effect was significant and consequently warrants inclusion in the model.

Total heritability was estimated as defined by Willham (1972) as

\[ h_r = (\sigma_a^2 + 0.5 \times \sigma_m^2 + 1.5 \times \sigma_{am}) / \sigma_e^2. \]

where the phenotypic variance \( (\sigma_y^2) \) was:

\[ \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_e^2 \]

**RESULTS AND DISCUSSION**

The mean weight of the Hungarian Simmental beef calves obtained in this study (213.08 kg) was similar what was reported by Kebede & Komlosi (2015) in a similar Hungarian Simmental population who reported a weaning weight of 211 kg. Conversely, Bene et al. (2010) and Szabo et al. (2012) reported a value of 217 kg and 236 kg respectively in a smaller sized population of Hungarian Simmental cattle. Though the estimates are somewhat close, the difference could be as a result of sampling variance. The coefficient of variation found in this study was in agreement with earlier findings by Bene et al. (2010) and Kebede & Komlosi (2015) in Hungarian Simmental beef calves. Contrarily, Szabo et al. (2012) reported a lower value.

Estimate of the (co)variance, genetic parameters are presented in Table 1. As shown in the log likelihood estimate the best model i.e. Model 4 included only the direct and maternal effects and allowed for their covariance. From the best model (Model 4) it can be implied that the permanent environmental effect of the dam is not important for the weaning weights of the Hungarian Simmental cattle. The direct heritability estimates from this model revealed that a considerable amount of the variation in weaning weight can be attributed to the additive genetic variance which indicates that genetic improvement through selection can be achieved.

The direct heritability estimate of the best model (Model 4) is somewhat higher than what is generally found in the literature 0.37 (Szabo et al., 2012), 0.27 (Intaratham et al., 2008), 0.25 (Ndofor-Foleng et al., 2012), 0.19 (Van Niekerk & Nesper, 2006) and 0.30 (Tramonte et al., 2019) in Hungarian Simmental, Northwestern Thai indigenous, Guadai, South African Limousin, and Guzera cattle respectively. Nevertheless, the estimate reported in this study agreed with an earlier conclusion by Wasike et al. (2006) in Kenyan Boran cattle (0.6) and Szabo et al. (2007) in Charolais cattle population (0.6) in Hungary. Wasike et al. (2006) attributed the high direct heritability estimate they obtained to be a result of the high genetic variability in the population examined. Skrypzeck et al. (2000) while commenting on the high direct heritability observed in their study noted that multibreed composition of the herd and consequently the non-inclusion of the dominance effect in the model could be a reason for the high estimates. Maternal environment comprises mainly of dam’s milk yield, lactation length and mothering ability. Maternal heritability estimate (0.16) was moderate suggesting a slow response when used as a selection criterion. Similar estimate was reported by Campelo et al. (2004), Sarmiento & Garcia (2007), Herrera-Ojeda et al. (2019) and Lopez et al. (2020) in Tabapua, Romsinuano, Charolais and Hanwoo cattle respectively. The heritability of the maternal effect was lower than the direct effect, this corroborates the findings of Skrypzeck et al. (2000), Szabo et al. (2007), Nesper et al. (2012) and Brito et al. (2020) who noted an estimate of 0.21, 0.32, 0.11, 0.05 in multi composite breed, Charolais, Brangus and
Guzera cattle respectively. This suggests that a calf’s genotype is more important than the maternal environment which consist mainly of the dam milk yield in the determination of its weaning weight. Although the maternal heritability is lower than the direct heritability in this result, the former should not be ignored in genetic evaluation of weaning weight.

The maternal permanent environment was found to be of no significance in this study. This is in agreement with report by Khorshidi et al. (2020) in Hays converter cattle. Conversely, significant maternal permanent environmental effect were found in multibreed beef (Skrypzeck et al., 2000; Vergara et al., 2009; Dadi et al., 2004), Bonsmara (Maiwashe et al., 2002), Charolais (Crews et al., 2004), Red Angus (Boldt et al., 2018), Guzera (Brito et al., 2020), Boran (Wasike et al., 2009) and Nellore (Kamei et al., 2017) cattle. In some cases, the permanent environmental effect was more important than the maternal genetic effect (Dadi et al., 2004; Crews et al., 2004; Kamei et al., 2017; Boldt et al., 2018).

Despite the high direct heritability 0.57 estimate the total heritability was 0.30 due to the high negative direct maternal genetic covariance. The total heritability (0.30) here is higher than values recorded by Bene et al. (2010), Szabo et al. (2012) in Hungarian beef calves. Meyer (1993) however, found similar estimate in Angus cattle. As estimates from the various models show, evidently, allowing for covariance between direct and maternal effect increased the sampling variance dramatically. In particular, a level of cross substitution between parameters in the dataset was observed for Model 4 & 6 compared to Model 3 and 5. In order to discern the likely reason, the additive genetic variance given maternal effects, \( \sigma^2_{AM} = \sigma^2_A - (\sigma^2_{AM}/\sigma^2_M) \), as well as the conditional direct heritability, \( h^2_A = \sigma^2_{AM}/\sigma^2_P \) was calculated. The resulting estimate (Table 2) suggests the problem of (co) sampling variation encountered when partitioning direct and maternal effects from additive genetic variance when they are assumed to be correlated. Meyer (1992) observed similar trend in crossbred Zebu. However, the inclusion of the sire by year interaction in subsequent research (Meyer, 1997a) reduced direct and maternal heritability estimate.

### Table 1. Estimate of variance component and genetic parameters for weaning weight

| Weaning weight | Model 1 | Model 2 | Model 3 | Model 4 | Model 5 | Model 6 |
|----------------|---------|---------|---------|---------|---------|---------|
| Direct genetic variance (\( \sigma^2_A \)) | 545.3 | 517.1 | 477.2 | 999.4 | 477.2 | 1002.6 |
| Maternal genetic variance (\( \sigma^2_M \)) | 71.7 | 280.8 | 71.7 | 262.5 | 71.7 | 262.5 |
| Maternal permanent environmental variance (\( \sigma^2_{pe} \)) | 37.4 | 0.001 | 19.1 | | | |
| Residual variance (\( \sigma^2_e \)) | 1142.7 | 1129.2 | 1134.9 | 880.7 | 1134.9 | 872.9 |
| Direct maternal covariance (\( \sigma_{AM} \)) | | -415.8 | -414.11 | | | |
| Phenotypic variance (\( \sigma^2_P \)) | 1688.0 | 1683.8 | 1683.7 | 1745.0 | 1683.7 | 1742.9 |
| Direct heritability (\( h^2_A \)) | 0.32 | 0.30 | 0.28 | 0.57 | 0.28 | 0.58 |
| Maternal heritability (\( h^2_M \)) | 0.04 | 0.16 | 0.04 | 0.15 | | |
| \( C_{AM}(\sigma_{AM}/\sigma^2_P) \) | | -0.24 | -0.24 | | | |
| Direct maternal genetic correlation (\( r_{AM} \)) | | -0.78 | -0.81 | | | |
| \( c^2 \) | 0.32 | 0.02 | 0.30 | 0.31 | 0.31 | 0.29 |
| Total heritability (\( h^2_T \)) | 0.32 | 0.02 | 0.30 | 0.29 | 0.31 | 0.29 |
| Log Likelihood | -185213.0 | -184154.2 | -184048.1 | -183868.2 | -184048.1 | -183866.1 |

### Table 2. Additive genetic variance given maternal effect (\( \sigma^2_{AM} \)): \( \sigma^2_A - \sigma^2_{AM}/\sigma^2_M \) estimates along with its resulting heritability (\( h^2_{AM} \)), corresponding unconditional values are given for comparison

| Weaning weight | Genetic Parameters | Genetic parameters* |
|----------------|--------------------|---------------------|
| \( \sigma^2 \) | Model 3 | Model 4 | Model 5 | Model 6 | Model 4 | Model 6 |
| \( h^2_T \) | 477.2 | 383.69 | 477.2 | 349.3 | 999.4 | 1002.6 |
| \( h^2_M \) | 0.28 | 0.23 | 0.28 | 0.20 | 0.57 | 0.58 |

*unconditional values
Estimation of direct maternal genetic correlation is considered as being inherently problematic (Robinson, 1996a; Meyer, 1997a; Phocas and Laloe, 2004) because they are partially confounded in the animal’s performance (Robinson, 1996a; Phocas and Laloe, 2004). Negative direct maternal genetic correlation is often reported in literature (Van Nierkerk, & Neser, 2006; Bene et al., 2010; Jose et al., 2012; Araújo et al., 2010). Hence, the negative direct maternal genetic correlation (-0.78) found here wasn’t a surprise. Nevertheless, positive direct maternal genetic correlation have also been reported (De Oliveira, et al., 2021; Meyer, 1992; Dodenhoff et al., 1999). A negative direct maternal environmental covariance occurs when the daughter of a dam with high maternal ability provide an adverse environment effect to its offspring. This is often referred to as fatty udder syndrome (Mangus and Brinks, 1971) and it is believed to bias direct maternal genetic variance estimate (Meyer, 1997b). Falconer (1965) and Meyer (1997a) fitted a regression on maternal phenotype to account for this covariance. A negative direct maternal genetic covariance is biologically plausible when there is genetic antagonism between genes responsible for direct and maternal effect. Lee and Pollak (2002) reported a negative correlation between milk yield and weaning weight in Hanwoo cattle which implies a genetic antagonism between direct and maternal effect. However, a negative strong direct maternal genetic covariance estimate is not believed to represent a true direct maternal genetic covariance as this estimate is believed to be biased by different causes (Robinson, 1996b; Lee and Pollak, 2002; Meyer, 1997a). Mallinckrodt et al. (1995) demonstrated with simulated data that selective reporting biased direct maternal correlation estimates. Robinson (1996a) showed that the structure of the data as well as the inclusion of sire or sires by herd interaction can be important to produce unbiased estimates. Meyer (1997a) showed that omitting the fixed effect of paddock by year generated a high substantial negative direct maternal genetic correlation in experimental data. Although grandmaternal effect doesn’t exist in some population, however, if they exist and they are not included in the model, direct and maternal correlation may be biased downward (Dodenhoff et al., 1999). Suárez and Cantet (2011) reported a direct maternal correlation value of -0.21 when grandmaternal was included and -0.71 when it was not grandmaternal effect wasn’t included in Angus cattle. Therefore, it can be concluded that our model here may have not been comprehensive enough.

CONCLUSIONS

The genetic parameters estimate reported here corroborates the widespread dogma that estimating maternal effect is inherently problematic as they are confounded in animal’s performance. The direct and maternal heritability values reported here are likely inflated, hence, further research is needed for proper partitioning of direct and maternal effect in order to achieve realistic genetic improvement.

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