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. 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 (Baldi 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)
$$\bf{y} = \bf{Xb} + \bf{Za} + \bf{Wm} + \bf{e}$$ \hspace{1cm} (4) \\
$$\bf{y} = \bf{Xb} + \bf{Za} + \bf{Wm} + \bf{Spe} + \bf{e}, \text{ with } \sigma(\bf{a, m}) = 0$$ \hspace{1cm} (5) \\
$$\bf{y} = \bf{Xb} + \bf{Za} + \bf{Wm} + \bf{Spe} + \bf{e}$$ \hspace{1cm} (6)

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

The (co)variance structure of the analysis is

$$\text{Var}(\bf{a}) = \bf{A}\sigma_a$$
$$\text{Var}(\bf{m}) = \bf{A}\sigma_m$$
$$\text{Var}(\bf{pe}) = \bf{I}\sigma_{pe}$$
$$\text{Var}(\bf{e}) = \bf{I}\sigma_e$$
$$\text{Cov}(\bf{a, m}) = \bf{A}\sigma_{AM}$$

Where $\bf{A}$ is the numerator relationship matrix and $\bf{I}$ 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 first model (Model 1) was a simple animal model with direct genetic effect as the only random effect. Model 2 included a permanent maternal environment as an additional random effect. Model 3 on the one hand had both the animal effect and the maternal effect as random effects, with their covariance being zero. Model 4 on the other hand was similar to Model 3 but the covariance between direct and maternal effect is assumed to be non-zero. Model 5 and 6 were similar to each other i.e. both of them have animal, maternal and permanent environmental effects as random. However, while Model 5 assumed that animal and maternal effects were not correlated, Model 6 assumed that they were correlated.

The Restricted Maximum Likelihood method of the Wombat software (Meyer, 2007) was used to estimate the various (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

$$h^2_r = (\sigma_a^2 + 0.5*\sigma_m^2 + 1.5*\sigma_{am})/\sigma_p^2.$$ 

where the phenotypic variance ($\sigma_p^2$) was:

$$\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_e^2$$
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).

\[
\begin{align*}
\text{Table 1. Estimate of variance component and genetic parameters for weaning weight} \\
\hline
\text{Weaning weight} & \text{Model 1} & \text{Model 2} & \text{Model 3} & \text{Model 4} & \text{Model 5} & \text{Model 6} \\
\text{Direct genetic variance} (\sigma^2_d) & 545.3 & 517.1 & 477.2 & 999.4 & 477.2 & 1002.6 \\
\text{Maternal genetic variance} (\sigma^2_m) & 71.7 & 280.8 & 71.7 & 262.5 \\
\text{Maternal permanent environmental variance} (\sigma^2_{pe}) & 37.4 & 0.001 & 19.1 \\
\text{Residual variance} (\sigma^2_e) & 1142.7 & 1129.2 & 1134.9 & 880.7 & 1134.9 & 872.9 \\
\text{Direct maternal covariance} (\sigma_{AM}) & -415.80 & -414.11 \\
\text{Phenotypic variance} (\sigma^2_y) & 1688.0 & 1683.8 & 1683.7 & 1745.0 & 1683.7 & 1742.9 \\
\text{Direct heritability} (h^2_d) & 0.32 & 0.30 & 0.28 & 0.57 & 0.28 & 0.58 \\
\text{Maternal heritability} (h^2_m) & 0.04 & 0.16 & 0.04 & 0.15 \\
\text{Covariance of maternal and genetic correlation} (r_{AM}) & 0.31 & 0.02 & 0.40 & 0.31 & 0.000000593 & 0.01 \\
\text{Total heritability} (h^2_t) & 0.32 & 0.31 & 0.30 & 0.29 & 0.31 & 0.29 \\
\text{Log Likelihood} & -185213.0 & -184154.2 & -184048.1 & -183868.2 & -184048.1 & -183866.1 \\
\hline
\end{align*}
\]

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, \( \hat{\sigma}_{AM}^2 = \sigma^2_A - \sigma_{AM}^2/\sigma^2_M \), as well as the conditional direct heritability, \( h^2_{AM} = \sigma^2_{AM}/\sigma^2_y \) 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.

\[
\begin{align*}
\text{Table 2. Additive genetic variance given maternal effect} (\sigma^2_{AM}); \sigma^2_A - \sigma^2_{AM}/\sigma^2_M \text{ estimates along with its resulting heritability} (h^2_{AM}), \\
\text{corresponding unconditional values are given for comparison} \\
\hline
\text{Weaning weight} & \text{Genetic Parameters} & \text{Genetic parameters*} \\
& \text{Model 3} & \text{Model 4} & \text{Model 5} & \text{Model 6} & \text{Model 4} & \text{Model 6} \\
\sigma^2 & 477.2 & 383.69 & 477.2 & 349.3 & 999.4 & 1002.6 \\
h^2 & 0.28 & 0.23 & 0.28 & 0.20 & 0.57 & 0.58 \\
\hline
\end{align*}
\]

*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 covariance 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 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 negative 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 sire 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.

**REFERENCES**


