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MATERNAL GENETIC ADDITIVE VARIABILITY OF CONFORMATION TRAITS IN HALF-BRED HORSES

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ABSTRACT

Direct and maternal additive genetic variances as well as covariances between these effects were estimated via derivative-free restricted maximum likelihood algorithm under an animal model. 2750 half-bred mares from four Studes were recorded. The following three traits were analysed: height of wither, circumference of chest, circumference of canon. The breed group, year of birth and place of birth were included as fixed effects. The computations were performed using two genetic models (with and without maternal effects). Direct additive heritability estimates were 0.539 for height of wither, 0.345 (and 0.442 from maternal model) for circumference of chest and 0.233 for circumference of cannon. Using the likelihood ratio test it was concluded that the maternal effects were significant for the analysed traits. Generally, negative correlation estimates between direct and

maternal genetic effects were found for single traits. The performed studies indicate the advisability of inclusion of maternal effects into the genetic evaluation of horses.

Key words:

INTRODUCTION

One of the first experiments (described in literature) concerning the maternal effects was performed by Walton and Hammond in 1938 (Walton and Hammond, 1938). They presented the effects of a diallel cross of two horse breeds (Shire and Shetland). However, the maternal influence on some horse traits has not still been clearly established. It should be noted that the phenotypic value of offspring comprises a direct genetic effect and a maternal effect. The maternal effect is environmentally relative to the progeny, but differences among dams for the maternal effect may be expressed in the phenotypic value of offspring. Hence, these effects are divided in genetic and environmental. Some authors (Robinson, 1996) reported an antagonistic relationship between maternal and direct genetic effects. A negative correlation between these effects can conflict with the improvement of a trait.

The objective of this study was to estimate the variance due to direct and maternal additive effects as well as covariances between these effects for conformation traits in horses.

MATERIALS AND METHODS

2750 mares from four Masurian Studs (Rzeczna, Kadyny, Liski, Nowa Wioska) were studied. These individuals were born between 1932-1994. The following traits were included:

- height of wither
- circumference of chest
- circumference of canon

Since the studied population is genetically heterogeneous, the collected material was divided into six breed groups:

- Pure Trakhen and East-Prussian breeds (2093 individuals)
- Hanoverian breed (118 individuals)
- crossbreeds of Trakehnen or East-Prussian and Hanoverian (128 individuals)
- English thoroughbred (94 individuals)
- Anglo-Arab (4 individuals)
- other mares included into one common group (313 individuals)

A short statistical characteristics of the dataset is given in [Table 1](#).

Table 1. Description of the data-sets.

Trait	Number of individuals	Average	Standard deviation
Height of withers	2484	163.224	4.70103
Circumference of chest	2475	194.541	8.80886
Circumference of cannon	2483	20.664	1.18856

The following single trait mixed model were used:

$$\mathbf{y} = \mathbf{X}_1\boldsymbol{\beta}_1 + \mathbf{X}_2\boldsymbol{\beta}_2 + \mathbf{X}_3\boldsymbol{\beta}_3 + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e},$$

where:

\mathbf{y} is the $n \times 1$ vector of observations,

$\boldsymbol{\beta}_1$ is a $p_1 \times 1$ vector of fixed effects of place of birth,

$\boldsymbol{\beta}_2$ is a $p_2 \times 1$ vector of fixed effects of breed,

$\boldsymbol{\beta}_3$ is a $p_3 \times 1$ vector of fixed effects year of birth,

\mathbf{a} is a $qx1$ a vector of random direct additive genetic effects,

\mathbf{m} is a $q \times 1$ a vector of random maternal additive genetic effects,

\mathbf{e} is a $n \times 1$ a vector of random errors

n, p_1, p_2, p_3, q are the number of observations (recorded individuals), places of birth, breeds, years of birth and number of evaluated individuals, respectively.

$\mathbf{X}_1, \mathbf{X}_2, \mathbf{X}_3, \mathbf{Z}_1, \mathbf{Z}_2$ are the known incidence matrices associated with respective effects.

The assumptions of the model:

$$E \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \text{ and } D \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{A}\sigma_{am} & \mathbf{0} \\ \mathbf{A}\sigma_{am} & \mathbf{A}\sigma_m^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

Thus:

$$E(\mathbf{y}) = \mathbf{X}_1\boldsymbol{\beta}_1 + \mathbf{X}_2\boldsymbol{\beta}_2 + \mathbf{X}_3\boldsymbol{\beta}_3$$

$$D(\mathbf{y}) = \mathbf{Z}_1\mathbf{A}\mathbf{Z}_1'\sigma_a^2 + \mathbf{Z}_2\mathbf{A}\mathbf{Z}_2'\sigma_m^2 + \mathbf{Z}_1\mathbf{A}\mathbf{Z}_2'\sigma_{am} + \mathbf{Z}_2\mathbf{A}\mathbf{Z}_1'\sigma_{am} + \mathbf{I}\sigma_e^2$$

where: σ_a^2, σ_m^2 and σ_e^2 are the direct and maternal genetic variance as well as residual variance, respectively; σ_{am} is the covariance between direct and maternal effects; \mathbf{A} is the numerator relationship matrix.

The following genetic parameters were estimated:

- direct heritability (h_a^2) expressed as $h_a^2 = \sigma_a^2 / \sigma_p^2$

- maternal additive heritability h_m^2 as $h_m^2 = \sigma_m^2 / \sigma_p^2$

- correlation between direct and maternal effects ($r_{am} = \sigma_{am} / \sigma_a \sigma_m$)

These estimates were obtained by use of derivative-free restricted maximum likelihood (DFREML) (Graser et al., 1987).

To evaluate the significance of the maternal genetic effects, a simpler genetic model (after excluding the maternal effects) was also considered. An inference about the significance of the maternal effects is based on the following statistics (Dobson, 1990):

$$\chi^2 = -2(L_a - L_m) \sim \chi_{\alpha,1}^2$$

where: L_m is the logarithm likelihood for the model including maternal effects, L_a is the logarithm likelihood for the model without maternal effects.

The computations were performed by use of the DFREML package programmes (Meyer 1993).

RESULTS AND DISCUSSION

The obtained results are listed in [Tables 2-4](#). As already mentioned, two models were employed to estimate the genetic parameters. Generally, the so-called direct heritability estimates were similar for both models within each trait. The estimates are highest for the height of withers (0.539 for the genetic direct model and 0.515 for the second model), whereas relative small levels of heritability were found for the circumference of cannon (0.232 for both models). However, differences in these estimates were observed for the circumference of chest. The heritability estimates for these traits have already been reported by several authors (Koenen et al., 1995; Samore et al., 1997)). In general, their results were compatible with our studies. On the other hand, a majority of them were obtained from a simpler genetic model, namely sire model (see e.g. Kapron et al., 1993). Dong et al. (1988) concluded that the omission of some genetic relationships between individuals leads to biased estimates of heritability. It should be stressed that relationships of sires were here assumed as null. Hence, for instance inbreeding effects cannot be included in the employed models. It seems that relatively large genetic variability of these traits, in our study, resulted from the heterogeneity of the population analysed. As opposed to other horse breeds, the Wielkopolska breed was official registered in 1962 as many crossbreed lines.

Table 2. Direct and maternal additive genetic variance estimates as well as estimates of covariances between direct and maternal effects.

Trait	σ_a^2 (I)	σ_a^2 (II)	σ_m^2	σ_{am}
Height of withers	7.0971	6.7983	0.5700**	-0.1065
Circumference of chest	21.5123	27.8629	16.1932**	-11.3988
Circumference of cannon	0.2817	0.0004**	0.2806	-0.0103

Note on symbols:

σ_a^2 (I) - estimate of direct additive genetic variance obtained from model I;

σ_a^2 (II) - estimate of direct additive genetic variance obtained from model II;

σ_m^2 - estimate of maternal additive genetic variance;

σ_{am} - estimate of covariance between direct and maternal effects

**) - significance of maternal additive genetic effects at $P < 0.01$

Table 3. Direct and maternal heritability estimates and correlation estimates between direct and maternal additive genetic effects.

Trait	h_a^2 (I)	h_a^2 (II)	h_m^2	r_{am}
Height of withers	0.5395 ±0.0417	0.0434 ±0.0407	0.5151 ±0.0118	-0.0541
Circumference of chest	0.3453 ±0.0334	0.4425 ±0.0378	0.2572 ±0.0288	-0.5366
Circumference of cannon	0.2332 ±0.0274	0.2332 ±0.0274	0.0003 ±0.0001	-1.0000

Note on symbols:

h_a^2 (I) – estimate of direct additive heritability obtained from model I;
 h_a^2 (II)- estimate of direct additive heritability obtained from model II;
 h_m^2 - estimate of maternal additive heritability;
 r_{am} - correlation between direct and maternal effects

Table 4. Residual variance estimates for two genetic models.

Trait	Residual variance estimate – model I	Residual variance estimate – model II
Height of withers	6.058	5.859
Circumference of chest	40.796	30.308
Circumference of cannon	0.926	0.932

For two traits (height of wither and circumference of cannon), the maternal heritability estimates were moderately low (Table 3), whereas the heritability obtained from maternal additive variance of circumference of chest were above 0.2. Unfortunately, no comparable literature estimates were found for [X].

Negative correlation estimates between direct and maternal genetic effects (for all traits) were found in this study, as had been expected. To our knowledge, no animal model REML estimates of the direct maternal covariance of conformation horse traits are known, so most reports (concerning mainly beef cattle) in the literature are negative (see e.g. Shi, 1993). Robinson (1996) concluded that negative correlations resulted not only from genetic antagonism, but sometimes also because of additional sire or sire x year variation or negative dam offspring covariances. It must be noted that a highly negative correlation (-1) for the circumference of cannon is associated with small maternal variance and a small negative covariance between the genetic effects (see Table 3).

Should maternal effects be included in the model of a genetic evaluation in horses? In this study, two criteria of model adequacy were applied. It was concluded that the maternal effects were significant for all the analysed traits (even for circumference of cannon when maternal additive genetic variability constituted only a minor proportion of the total

phenotypic variance). Similar situations, when inclusion of small genetic effect in a model resulted in an improved log likelihood, were reported by other authors (Cloete et al., 1998, Dobek et al. 1999). On the other hand, currently the likelihood ratio test is recommended as the best approach of detection to fit the alternative models and assess respective genetic effects (Robinson, 1996).

Another criterion of model adequacy used here was a residual variance estimate. The model fitting direct and maternal additive effects was regarded as the most suitable one, first of all, for the circumference of chest.

The conformation traits of horses are one of several factors determining their racing and sport performances (Pietrzak, 1988; Kedzierski, 1988). Hence from a practical point of view, the improvement of horse exterior is of considerable importance. Over the last decades, the mixed model methodology is widely implemented in livestock breeding strategy, especially for dairy and beef cattle. However, the Polish breeding programmes for horses are still based on NON-BLUP methods (Swidzinska; 1988). Horse breeders have long believed in special attributes of certain mare lineages and the obtained results indicate that inclusion of maternal effects into genetic evaluation would lead to an increase of the selection efficiency associated with breeder's intuition.

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