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# Maternal effects on the conformation traits in half-bred horses

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## ABSTRACT

Data on 4477 mares born between 1932 and 1995 from six studs were recorded. Three exterior traits were included: height at wither, chest girth, circumference of cannon. (Co)variance components were estimated by the DFREML procedure on the basis of four linear models. Model I included the fixed effects: period of birth, place of birth, breed effect (as covariable) and random effects: direct additive genetic and residuals. Model II was expanded by taking into account the maternal additive genetic effect. Third model included cytoplasmic effect as fixed (model IIIa) and random (model IIIb). Direct heritability estimates varied from 0.4 to 0.6 whereas maternal heritability estimates ranged between 0.01 and 0.25, cytoplasmic heritabilities were close to zero. Negative correlations between direct and maternal effects were estimated for all traits under study. Akaike Information Criterion suggested the highest adequacy of model I. However, other criteria (likelihood ratio test and error variance estimate) and negative covariance between direct and maternal genetic effects indicate that maternal effects should be included in the genetic evaluation of horses. In general, genetic trends were positive for the traits studied.

KEY WORDS: half-bred horses, maternal effects, heritability, conformation traits

## INTRODUCTION

Although maternal effects, which result from pre and postnatal influences of dam on progeny, were first described in horses (Walton and Hammond, 1938) the proportion of maternal variance in phenotypic variance has not been extensively

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studied in this species. A long generation interval, late maturing, only one progeny per year, and a lack of full-sib groups made the estimation of variance components difficult. However, the development of estimation methods, from crossing experiments (Robison, 1972), by sire and dam models (Tempelman and Burnside, 1990) to animal models enabled the estimation maternal and cytoplasmic variances (Southwood, 1989; Tess and Mac Neil, 1994). Currently, maternal effects are defined as any influence from a dam on its progeny, excluding the effects of directly transmitted genes. It should be noted that dependences between direct and maternal (indirect) effects exist. One of the maternally specific sources of genetic variation are genes located in mitochondrial DNA. Since an ovum contains about 100000 copies of mtDNA, whereas a spermatozoa only about 75 copies, both male and female progeny inherit mitochondrial DNA from mother. The influence of mitochondrial genes on some traits in livestock has been studied by many authors (Bell et al., 1985; Mannen et al., 1998).

The modern half-bred horse, as described by the American Trakehner Association, is expected to be a noble, harmonious riding horse with great lines, distinguished by its expression, nobility and striking features, rideable and talented for many uses. Therefore, the external features: appearance, type and conformation play an important role in the selection of horses. The basic elements of exterior evaluation are biometrical measurements: height at wither, chest girth, circumference of cannon. They enable an objective description of the development and type of animal. Moreover, several authors suggest that there is a correlation between the measurements and performance test results (see e.g., Koenen et al., 1995).

One of the most popular horse breeds in Poland is the Wielkopolski horse. The objective of the horse breeding has changed over time from working animals, through a multipurpose horse with emphasis on driving traits, to a modern riding horse. Recently, the Wielkopolski horse is expected to be gentle, multipurpose and suitable for riding sports - jumping, dressage, eventing and driving as well as for recreational riding (Chrzanowski and Łojek, 1998).

The objectives of this study were to estimate the direct and maternal additive genetic as well as cytoplasmic variances of exterior traits, to propose an adequate model for genetic evaluation of horses and to estimate genetic trends in the population of Wielkopolski horse.

## MATERIAL

A population of 5096 half-bred horses (including 4477 recorded mares) born between 1932-1995 was analysed. The breeding mares were kept at six studs (SK

Kadyny - 580, SK Liski - 1237, SK Nowa Wioska 318, SK Rzeczna - 614, SK Pępowo - 615, SK Posadowo - 1114).

It must be noted that until the end of the 1950s two types of these horses were bred depending on the region. The Masurian type based on East Prussian horses, and the Wielkopolski type based on local mares mated to Trakehner, East Prussian, Thoroughbred, Arabian, Hanoverian and other western breeds stallions. The exchange of breeding material unified the population, which since 1962 has formed the Wielkopolska breed. To account for differences in breed origin the proportion of breed components was determined (Table 1). The average inbreeding coefficient equaled 0.00048 and 1.9%, for all and 593 inbred individuals, respectively. Hence, inbreeding effect was omitted in the further analysis. To estimate cytoplasmic variance, 555 maternal lineages were distinguished. As only individuals with known dam can be included in the models with maternal effects, the data were analysed in two subsets DATA1 (all individuals, model I) and DATA2 (individuals with full pedigree information, models II, IIIa, IIIb). The description of the data is included in Table 2. The data was classified according to the following criteria: place of birth (six levels), period of birth (5 year periods with 14 levels), breed (7 levels).

TABLE 1

Proportion of breed components in the studied population

| Breed | Proportion of breed components, % | Regression coefficients | | |
|---|---|---|---|---|
| | | on height at wither | on chest girth | on circumference of cannon |
| Trakehner and East Prussian | 55.46 | 0.0887 | 0.8675 | 0.0257 |
| Hanoverian | 6.22 | 0.0959 | 0.8537 | 0.0297 |
| Thoroughbred | 22.82 | 0.0910 | 0.7813 | 0.0169 |
| Arabian | 0.92 | 0.0583 | 0.7346 | 0.0092 |
| Anglo-Arabian half-bred | 3.39 | 0.0526 | 0.8261 | 0.0167 |
| Other western breeds | 10.52 | 0.0792 | 0.3660 | 0.0223 |
| Unknown origin | 0.67 | 0.1018 | 0.8583 | 0.0283 |

TABLE 2

Phenotypic description of the studied Wielkopolski horse population

| Trait | DATA 1 | | DATA 2 | |
|---|---|---|---|---|
| | number of mares | mean ± SD | number of mares | mean ± SD |
| Height at wither | 4201 | 162.30 ± 4.84 | 3710 | 162.70 ± 4.68 |
| Chest girth | 4187 | 194.33 ± 7.52 | 3697 | 194.97 ± 7.31 |
| Circumference of cannon | 4194 | 20.62 ± 0.91 | 3704 | 20.69 ± 0.89 |

## METHODS

To improve the normality of the distribution, logarithmic transformation was applied. (Co)variance components were estimated by the derivative-free restricted maximum likelihood algorithm (Graser et al., 1987) based on the four linear models: Model I:

$$y_{ijk}=r_i + s_j + b_1x_{(1)ijk} + b_2x_{(2)ijk} + b_3x_{(3)ijk} + b_4x_{(4)ijk} + b_5x_{(5)ijk} + b_6x_{(6)ijk} + a_{ijk} + e_{ijk},$$

where: $y_{ijk}$ - observation of the *ijk*-th individual, $r_i$ - fixed effect of the *i*-th period of birth, $s_j$ - fixed effect of the *j*-th place of birth, $b_1, b_2, b_3, b_4, b_5, b_6$ - partial regression coefficients for respective covariables, $x_{(1)ijk}$ - proportion of Thoroughbred genes in the *ijk*-th individual, $x_{(2)ijk}$ - proportion of Arabian breed genes in the *ijk*-th individual, $x_{(3)ijk}$ - proportion of Trakener and East Prussian genes in the *ijk*-th individual, $x_{(4)ijk}$ - proportion of Hanoverian genes in the *ijk*-th individual, $x_{(5)ijk}$ - proportion of other western breed genes in the *ijk*-th individual, $x_{(6)ijk}$ - proportion of unidentified breed genes in the *ijk*-th individual, $a_{ijk}$ - random direct additive genetic effect of *ijk*-th individual, $e_{ijk}$ - random error related to *ijk*-th observation.

In the second model (Model II), random additive genetic maternal effect was included. The next two models are an alternative approach to cytoplasmic effects estimation: Model IIIa includes the additional maternal lineages effect (as fixed effect), whereas Model IIIb takes into account the random cytoplasmic effect.

The following parameters were estimated:

- direct heritability ($h_a^2$) defined as: $h_a^2=\hat{\sigma}_a^2/\hat{\sigma}_p^2$, where: $\hat{\sigma}_a^2$ - direct additive genetic variance, $\sigma_p^2$ - phenotypic variance estimate
- maternal heritability ($h_m^2$) defined as: $h_m^2 = \hat{\sigma}_m^2/\hat{\sigma}_p^2$, where: $\hat{\sigma}_m^2$ - maternal additive genetic variance
- ratio of covariance between direct and maternal genetic effects to phenotypic variance ($\hat{d}_{am}$) defined as: ($\hat{d}_{am}$) $=\hat{\sigma}_{am}/\hat{\sigma}_p^2$, where: $\hat{\sigma}_{am}$ - covariance between direct and maternal genetic effects
- total heritability ($h_T^2$) defined as (Willham, 1972): $h_T^2 = (\hat{\sigma}_a^2 + 0.5\hat{\sigma}_m^2+1.5\hat{\sigma}_{am})/\hat{\sigma}_p^2$
- cytoplasmic heritability ($h_c^2$) defined as: $h_c^2 = \hat{\sigma}_c^2/\hat{\sigma}_p^2$, where: $\hat{\sigma}_c^2$ - genetic cytoplasmic variance.

Phenotypic and genetic trends were defined as five year period phenotypic and genetic averages, respectively. The trends were estimated *via* model I.

The adequacy of the models was compared based on error variance estimates and Akaike Information Criteria - AIC (Akaike, 1977). Moreover, the significance of maternal effects was checked by the likelihood ratio test (Dobson, 1990). The computations were performed using the DFREML package programs (Meyer, 2000).

## RESULTS AND DISCUSSION

The logarithmic transformation applied in this study improved the normality of the distribution of all the analysed traits (Table 3). The genetic parameter estimates are listed in Table 4. Direct heritability of height at withers was equal to 0.57 according to model I, which corresponds to the results of Miserani et al. (2002), but is higher than the results of Starun and Socha (2002) for the Małopolski horse $h_a^2$ =0.305. One of the highest heritability estimates for this trait was obtained by Saastamoinen et al. (2002) for Finnish horses $h_a^2$=0.78. Similar pattern was found for the other two traits. For chest girth and circumference of cannon the direct heritability was equal to 0.44 and 0.55, respectively. These results correspond to the estimates of Miserani et al. (2002) 0.51 and 0.53. Lower estimates were reported by Starun and Socha (2002) $h_a^2$ =0.27, whereas in Finnish horses (Saastamoinen et al., 2002) higher estimates were found. The differences in parameter estimates between populations may result from differences in population size, methods and models, and different genetic backgrounds of the populations. Although genetic parameters are population specific they could be informative for populations with similar origin.

TABLE 3

Distribution parameters for the traits studied before and after logarithmic transformation

| Trait | Skewness | | Kurtosis | |
|---|---|---|---|---|
| | before transformation | after transformation | before transformation | after transformation |
| Height at wither | -0.276 | -0.185 | -0.222 | -0.201 |
| Chest girth | -0.382 | -0.295 | 0.451 | 0.110 |
| Circumference of cannon | -0.293 | -0.152 | 0.070 | 0.053 |

Low maternal heritability coefficients were estimated (Table 4). Of all the biometrical measurements, only for chest girth this parameter exceeded 0.2 according to models II and IIIa. Despite the fact that horses were the first species in which maternal effects were described (Walton and Hammond, 1938) and later many times confirmed (Pool-Anderson et al., 1994) there are only a few publications on the estimation of maternal effects based on multigenerational populations.

Although the estimates of maternal heritability were low, these effects could bias genetic evaluation because of a negative relationship between direct and maternal genetic effects. Except for the circumference of cannon in model IIIa, negative covariance between the effects was found. A negative relationship between direct and maternal effects was confirmed in the research on cattle (Lee et al., 1997). In

TABLE 4

Genetic parameters of conformation traits in horses

| Model | High at wither | | | | | Chest girth | | | | | Circumference of cannon | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $h_a^2$ | $h_m^2$ | $\hat{d}_{am}$ | $h_T^2$ | $h_c^2$ | $h_a^2$ | $h_m^2$ | $\hat{d}_{am}$ | $h_T^2$ | $h_c^2$ | $h_a^2$ | $h_m^2$ | $\hat{d}_{am}$ | $h_T^2$ | $h_c^2$ |
| I | 0.57 ± 0.066 | – | – | – | – | 0.44 ± 0.058 | – | – | – | – | 0.52 ± 0.063 | – | – | – | – |
| II | 0.58 ± 0.066 | 0.07 ± 0.023 | -0.04 | 0.55 ± 0.065 | – | 0.59 ± 0.067 | 0.22 ± 0.041 | -0.20 | 0.4 ± 0.055 | – | 0.69 ± 0.073 | 0.1 ± 0.028 | -0.14 | 0.57 ± 0.064 | – |
| IIIa | 0.59 ± 0.071 | 0.07 ± 0.025 | -0.07 | 0.51 ± 0.066 | – | 0.46 ± 0.063 | 0.25 ± 0.047 | -0.14 | 0.38 ± 0.057 | – | 0.44 ± 0.062 | 0.01 ± 0.009 | 0.01 | 0.46 ± 0.063 | – |
| IIIb | 0.10 ± 0.029 | 0.01 ± 0.009 | 0.01 | 0.09 ± 0.028 | b | 0.1 ± 0.029 | 0.01 ± 0.009 | -0.01 | 0.09 ± 0.028 | | 0.63 ± 0.074 | 0.09 ± 0.028 | -0.11 | 0.6 ± 0.072 | b |

note on symbols: $h_a^2$ - direct heritability, $h_m^2$- maternal heritability, $\hat{d}_{am}$- ratio of covariance between direct and maternal genetic effects to phenotypic variance, $h_T^2$ - total heritability, $h_c^2$ - cytoplasmic heritability, b - for $h_c^2 < 0.0001$

livestock the inclusion of maternal effects in selection programs to avoid the reduction in genetic gain was suggested by many authors (Gama et al., 1991; Van Vleck et al., 1996). Based on the results from the studied population, a similar conclusion can be drawn with respect to horse breeding. The exclusion of negative covariance between direct and maternal effects may lead to underestimation of the direct heritability.

Besides indirect maternal genetic effects, cytoplasmic effects were estimated as well, following two approaches (model IIIa as fixed effect of maternal lineage, and IIIb as random effect). Although Akaike's criterion favours model IIIb, according to other criteria this result is questionable. It corresponds with results obtained by Tess and MacNeil (1994). In the studied population cytoplasmic heritability estimates were close to zero ($h_c^2$<0.0001). Very low $h_c^2$ estimates were also found in sheep by Maniatis and Pollott (2002). Higher proportion of cytoplasmic variance was reported for some traits in dairy cattle by Schnitzenlehner and Essl (1999). Moreover, inclusion of the random cytoplasmic effect led to underestimation of other variance components. For height at wither, the direct heritability estimated in the first two models was higher than 0.5, whereas in model IIIb it was equal to 0.1. The results were similar for chest girth, but opposite for circumference of cannon. Contrary results suggest caution in drawing conclusions on cytoplasmic effects. It is possible that small population size and some mathematical approximations may bias the results. It must be noted that recent knowledge does not allow to ignore cytoplasmic effects, but analysis of mitochondrial DNA polymorphism may improve the accuracy of estimation (Bowling et al., 2000).

In order to verify the significance of maternal effects, the likelihood ratio test was applied (Dobson, 1990). Although this method has limited sensitivity (Southwood et al., 1989) it is widely used in analysis of model adequacy, including models with maternal effects in livestock (Robert-Granie et al., 1997; Maniatis and Pollott, 2002). The likelihood ratio test revealed significant maternal effects for all the traits studied. A second tool used to classify models according to their adequacy was Akaike Information Criterion (Lancelot et al., 2002). Another criterion suggested for population studies (Ptak and Żarnecki, 2000) was error variance estimate. Models were ranked on the basis of these criteria. The simplest model (I) appeared to be the most adequate. Almost as adequate was model II including maternal genetic effects. Both models with cytoplasmic effects performed worse which suggests the omission of this effect in genetic evaluation of horses. However, comparing random and fixed cytoplasmic effects, the random effects model was superior. The population size (2845-4201 individuals) may appear relatively small, however the estimates based on smaller populations are also found in literature (Wewala et al., 1988).

In general, the type traits described are characterized by high heritability coefficients. Such a result arises from a high genetic variability and low unification of the Wielkopolska breed. This relatively new breed was created on the basis of Trakehner and East Prussian genotypes (55.46%) with a high proportion of Thoroughbred (22.82%), Hanoverian and other Western breeds genes (16.74%). The proportions of other genotypes were marginal. The influence of breed components on the studied traits were balanced, which is expressed in even values of partial regression coefficients (Table 1). Height at wither was most strongly influenced by horses of unknown origin, whereas for chest girth and circumference of cannon the most significant components were Trakehner, East Prussian and Hanoverian breeds, respectively.

An analysis of genetic trends shows a gradual increase in the exterior traits of horses (Figure 2). Genetic trends are generally in agreement with breeding goals in the analysed period although these traits have never been directly selected for the preferences of the type of performance horses have varied in time. An initial (until late 1950s) lack of improvement in height at wither is related to continued production of the working horse for the field. Its increase in the 1960s resulted from the mechanization of agriculture, and therefore also from the changing role of horses. An increase in average genetic value for this trait was also caused by the introduction of imported stallions of the Hanoverian breed in the 1970s. The influence of those stallions was also reflected in the chest and cannon circumference. For these two traits maximal average breeding values were reached in the 1980s, since then the riding horse for sport and recreation was preferred. In turn, in the 1990s, Thoroughbred stallions were used to improve constitution and riding performance, which led to reduction of cannon and chest circumference. To sum up, it can be said that progress in agriculture has transformed the Polish half-breed horse from a traditional working animal into a modern riding horse (Figure 1).

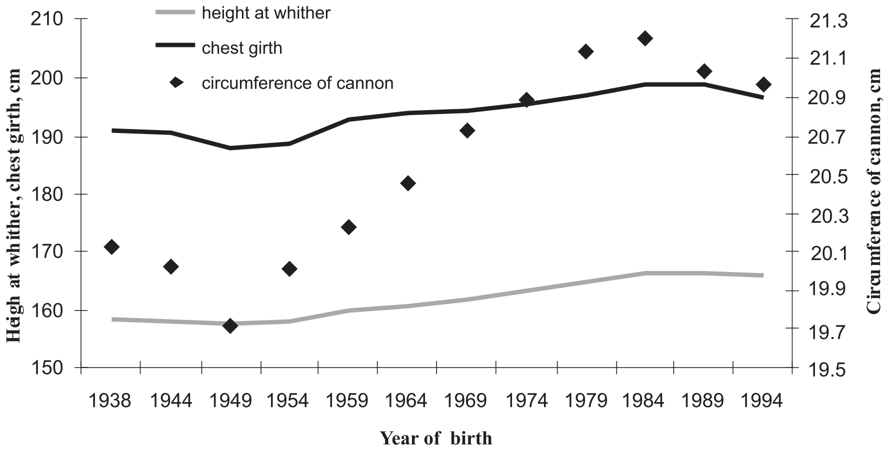

Figure 1. Phenotypic trends of conformation traits in Wielkopolski horses

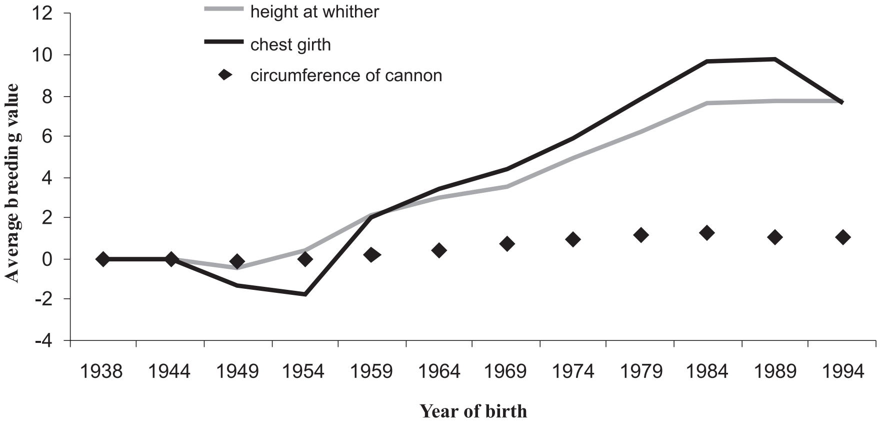

Figure 2. Genetic trends of conformation traits in Wielkopolski horses

## CONCLUSIONS

Moderate direct heritability was estimated for exterior traits in the studied population of Wielkopolski horses. The estimates of maternal heritability on low to moderate level, showing a negative covariance with the direct additive genetic effects, suggest the need of including this effect in the genetic evaluation of horses, whereas the cytoplasmic effects seem less relevant. Genetic and phenotypic trends confirm the effectiveness of the current selection system and the reasonable response to selection. Balanced influence of breed components on all traits was found.

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## STRESZCZENIE

### Ocena wpływów matczynych na cechy pokrojowe koni półkrwi

Analizą objęto dane o 4477 klaczach urodzonych w latach 1932-1995 w sześciu stadninach. Uwzględniono trzy cechy pokrojowe: wysokość w kłębie, obwód klatki piersiowej i obwód nadpęcia. Komponenty (ko)wariancji oszacowano przy pomocy algorytmu DFREML na podstawie czterech modeli liniowych. Model I uwzględniał efekty stałe: okres urodzenia, miejsce urodzenia, udział komponentów rasowych w genotypie klaczy (jako zmienne towarzyszące) oraz efekty losowe: genetyczny addytywny bezpośredni oraz błąd losowy. Model II został rozszerzony przez uwzględnienie efektu genetycznego addytywnego matczynego. W modelu trzecim uwzględniono efekt cytoplazmatyczny jako stały (model IIIa) lub losowy (model IIIb). Estymatory odziedziczalności bezpośredniej zawierały się w przedziale od 0,4 do 0,6, podczas gdy odziedziczalności matczyne przyjmowały wartości między 0,01 a 0,25, odziedziczalność cytoplazmatyczna była natomiast bliska zeru. Dla wszystkich badanych cech oszacowano negatywne korelacje między efektem genetycznym bezpośrednim a matczynym. Kryterium Akaike wskazuje na najwyższą adekwatność modelu I. Jednakże, inne kryteria (test logarytmu wiarogodności oraz estymator wariancji błędu) oraz negatywna kowariancja między efektami genetycznymi bezpośrednimi a matczynymi sugerują uwzględnianie efektów matczynych w ocenie wartości hodowlanej koni. Trendy genetyczne były dodatnie dla wszystkich badanych cech.