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The role of maternal lineages in horse breeding: Effects on conformation and performance traits

N. Krattenmacher[1], J. Tetens[1], S. Hedt[1], E. Stamer[2] and G. Thaller[1]
[1] CAU, Institute of Animal Breeding and Husbandry, Hermann-Rodewald-Straße 6, 24098 Kiel, Germany, [2] TiDa GmbH, Bosseer Straße 4c, 24259 Westensee/Brux, Germany

ABSTRACT: Maternal lineage effects, probably indicative of mitochondrial DNA differences, are considered important in horse breeding. 8,098 Holstein warmblood horses representing 493 maternal lineages were studied to assess lineage effects on conformation and performance traits recorded at studbook inspections. Furthermore, field performance traits were analyzed using data from 2,329 mares representing 381 maternal lineages. Variance components were estimated using animal models considering the fixed effects age and year-season of assessment (for studbook inspection traits), and test year and location (for traits measured at mare performance tests), respectively. Additive genetic and lineage effects were modelled as random. Heritability estimates ranged from 0.10 (0.02) to 0.39 (0.06). Maternal lineage accounted for up to 2.1% of the phenotypic variation in the traits. Future research should examine the degree of molecular variation among mitochondrial genomes of different maternal lineages and its relationship to phenotypic differences.
Keywords: Holstein horse breed; maternal lineage; mitochondrial DNA

Introduction

A majority of horse breeders believe in special attributes of certain maternal lineages. However, the question whether the importance of female lineages is a myth or real has not yet been satisfactorily answered. Indeed, as in other mammals, equine mitochondrial DNA (mtDNA) is inherited exclusively from the dam without paternal contribution (Hutchison et al. (1974)) and mitochondrial genetic variation might contribute to lineage specific differences in performance traits.

Although the mitochondrial genome harbors only 13 protein coding genes, it plays a striking part in energy metabolism as all of these genes contribute to the respiratory chain. This suggests a role in important performance traits as already raised more than 40 years ago (Wagner (1972)). However, the knowledge gathered in livestock is still limited, while extensive research has been conducted in the context of human mitochondrial disorders and bioenergetics. Mitochondrial diseases are heterogeneous and primarily affect tissues with a high energy demand. Consequently, they have been implicated in blindness, dementias, cardiomyopathies and other severe syndromes (Wallace (2010)). However, with respect to performance traits in the horse, the role of mitochondrial variation in human athletic performance is of much more interest. Certain mitochondrial haplogroups have been shown to be directly associated with elite endurance status and response to endurance training (Castro et al., (2007); Dionne et al. (1991); Scott et al. (2009)). Encouraged by these results, we investigated the relative importance of maternal lines for conformation and performance traits in Holstein warmblood horses. Two data sets containing information of all active Holstein broodmares were used for variance component estimation. The proportion of phenotypic variance due to additive genetic variance was compared with the contribution of lineage variance to total phenotypic variance.

Materials and Methods

In Holstein horses, extensive pedigree records are available. Female lineages can be traced back to the early 19th century. Based on those records, 8,098 broodmares presented at studbook inspections of the breeding association "Holsteiner Verband" between 1990 and 2012 were assigned to a total of 493 maternal lineages. During studbook inspections, mares were evaluated on type, conformation and movement, and marked for each trait on a 1-point scale of 0 (not shown) to 10 (excellent). In addition, field test performance data recorded between 1993 and 2012 were available for 2,329 broodmares representing 381 maternal lineages. If a mare completed more than one performance test, only the last test result was considered for the analyses. Scores on a 0.5-point scale from 0 (not shown) to 10 (excellent) were given for movement under rider (walk, trot, canter), rideability (evaluated by judging commission and test rider) and free-jumping. Table 1 provides an overview of the descriptive statistics for both data sets.

Table 1. Descriptive statistics of the conformation and performance traits recorded at studbook inspections (N=8,098 mares) and mare field performance tests (N=2,329 mares)

Trait	Mean (SD)	Range
Studbook inspection		
Type	7.04 (0.61)	5-9
Topline conformation	6.61 (0.64)	4-9
Front limb conformation	6.69 (0.55)	4-8
Hind limb conformation	6.20 (0.58)	3-8
Walk (loose)	6.74 (0.75)	4-9
Trot (loose)	7.03 (0.73)	4-9
Canter (loose)	7.04 (0.73)	4-10
Field performance test		
Walk (with rider)	7.11 (0.92)	3-10
Trot (with rider)	7.01 (0.77)	4-10
Canter (with rider)	7.30 (0.77)	5-10
Free jumping	8.02 (1.09)	5-10

Rideability	7.37 (0.80)	4-10
Test rider assessment	7.57 (0.95)	4-10

Variance components were estimated using animal models considering the fixed effects age (5 classes: <1,075 days; 1,075-1,135 days; 1,136-1,405 days; 1,406-2,598 days; >2,601 days) and year-season of assessment (91 classes) for the studbook inspection traits, and test year (N=20) and location (N=8) for traits recorded at the mare performance tests, respectively. Additive genetic and lineage effects were treated as random effects. The pedigree file consisted of 141,071 animals. Lineage size ranged from 1 to 359 (16 female members with records, on average; studbook inspection data set), and from 1 to 112 (6 female members with records, on average; mare field performance test data set), respectively. Heritability and proportion of phenotypic variance due to lineage variance were estimated univariately via REML, using the software package VCE-6 (Kovač and Groeneveld (2007)).

Results and Discussion

The results suggest that effects of mitochondrial genome variation may exist for several conformation and performance traits in the Holstein horse breed. Estimates for additive genetic variances, lineage variances and residual variances for all analyzed traits are given in Table 2.

Table 2. Additive genetic variance (σ_a^2), lineage variance (σ_l^2), and residual variance (σ_e^2) for conformation and performance traits

Trait	σ_a^2	σ_l^2	σ_e^2
Studbook inspection			
Type	0.12262	0.00191	0.23789
Topline conformation	0.08703	0.00145	0.29074
Front limb conformation	0.02825	0.00197	0.24669
Hind limb conformation	0.03352	0.00275	0.28049
Walk (loose)	0.08105	0.00205	0.34108
Trot (loose)	0.11419	0.00000	0.30652
Canter (loose)	0.11825	0.00199	0.35847
Field performance test			
Walk (with rider)	0.09687	0.00452	0.64424
Trot (with rider)	0.19160	0.00782	0.37257
Canter (with rider)	0.13568	0.01172	0.40186
Free jumping	0.44293	0.00000	0.69902
Rideability	0.07889	0.00797	0.51317
Test rider assessment	0.14391	0.01691	0.70396

Heritability estimates ranged from 0.10 (0.02) to 0.39 (0.06) with the lowest values found for conformation traits and the highest values found for type, gaits and free jumping (see Table 3).

Table 3. Heritability (h^2) with standard error (SE) in parentheses, and proportion of the phenotypic variance that is due to lineage variance (h_l^2) for conformation and performance traits

Trait	h^2 (SE)	h_l^2 (SE)
Studbook inspection		
Type	0.34 (0.03)	0.005 (0.004)
Topline conformation	0.23 (0.03)	0.004 (0.003)
Front limb conformation	0.10 (0.02)	0.007 (0.005)
Hind limb conformation	0.11 (0.02)	0.009 (0.004)
Walk (loose)	0.34 (0.03)	0.005 (0.004)
Trot (loose)	0.31 (0.03)	0.000 (0.000)
Canter (loose)	0.36 (0.03)	0.004 (0.004)
Field performance test		
Walk (with rider)	0.13 (0.04)	0.006 (0.010)
Trot (with rider)	0.33 (0.06)	0.014 (0.010)
Canter (with rider)	0.25 (0.05)	0.021 (0.013)
Free jumping	0.39 (0.06)	0.000 (0.000)
Rideability	0.13 (0.04)	0.013 (0.011)
Test rider assessment	0.17 (0.05)	0.020 (0.013)

The mitochondrial genome is much smaller (about 17,000 base pairs; George and Ryder (1986)) than the nuclear genome (2,7 billion base pairs; Wade et al. (2009)). It is therefore not surprising that additive genetic effects contributed more to phenotypic variation than lineage effects, especially for studbook inspection traits. For these traits, maternal lineage accounted for maximal 0.9% of the phenotypic variation, whereas a higher amount of phenotypic variation was due to lineage effects in traits recorded at mare performance tests in field (range: 0 to 2.1%). It should be noted that the relative importance of lineage effects was highest in lowly heritable traits (e.g. hind limb conformation and rideability).

Mitochondrial DNA plays a decisive role in energy production. Therefore, we assumed that maternal lineage effects would especially have an influence on traits reflecting the energy output of a horse. There was, however, no clear evidence for this. Maternal lineage appears to have an influence on canter under the rider, for example, but not on free jumping which can be considered as a trait needing much energy supply. The latter result is in contrast to the findings of König et al. (2010) who reported relatively large lineage effects for own performance of Hanoverian stallions in show jumping. On the other hand, the present results indicate that 0.9% of the phenotypic differences in hind limb conformation are due to lineage effects. The evaluation of conformation includes the assessment of the horse's bones, muscles and associated soft tissues. The hind limbs should be fairly well muscled as they are the driving force for any forward and upward movement (speed, propulsion and jumping ability). Thus, a mediating effect may exist: mtDNA genes possibly affect jumping ability through their effect on the conformation or power of the hind limbs.

When interpreting the results, it should be noted that regions of mtDNA mutate at a much higher rate than nuclear DNA (Nachman et al. (1996); Schriner et al. (2000)). Therefore, heterogeneity on mtDNA level might exist even between horses belonging to the same female lineage, but this possibility was not considered in the present study. In addition, homogeneity of mtDNA between different female lines could have led to an underestimation of lineage effects (Huizinga et al. (1986)). Achilli et al. (2012) analyzed 83 mitochondrial genomes from a wide

range of horse breeds and found 18 major haplogroups. Kavar et al. (2002) found 37 different haplotypes in 56 maternal lineages represented by 212 Lipizzans. A smaller number of haplotypes was found in other breeds (e.g. Arabian horses; Bowling et al. (2000)). Up to date, no such studies have been performed for the Holstein horse breed, but it is most likely that some mare families share the same haplotype.

Because of its relatively small size, it is unlikely that the mitochondrial genome contains causal genes for a large number of traits. However, supposing that phenotypic variance caused by lineage is not due to preferential treatment of elite lineages, it is of special interest to gain a better insight into the impact of cytoplasmatic inheritance on conformation and performance traits, especially with regard to future breeding value estimation. If mtDNA genes have a significant influence on the performance of stallions, the breeding value of stallions would have to be corrected for this effect, because stallions do not pass the mtDNA to their progeny and the breeding value would be biased upward by favourable cytoplasmic contributions (Schachtner et al. (1992)). Mitochondrial DNA genetic diversity and its effect on all relevant traits should be determined. Knowledge of the spectrum of haplogroups in the Holstein horse breed is necessary to secure that all valuable lines (haplogroups) are maintained. In the analyzed data, size of maternal lines ranged from 1 to 357 active broodmares. The number of maternal lineages with only one female member used for breeding was quite high (N=64; studbook inspection data set) which highlights the importance of further studies on mtDNA diversity in the near future.

Conclusion

Maternal lineage accounted for up to 2.1% of the phenotypic variation in the analyzed traits (e.g. canter under the rider). Additional molecular genetic analyses are needed to determine whether and to what extent differences in conformation and performance traits between maternal lineages are due to genetic diversity on mtDNA level.

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