Towards Genomic Selection in Danish Warmblood Horses: Expected Impacts and Selective Genotyping Strategy

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ABSTRACT: The aim was to investigate the sensitivity of different selective genotyping strategies, and to approximate the impact of different genomic selection strategies on genetic gain in Danish Warmblood horses using selection index theory. An index for selective genotyping was presented based on reliabilities for multiple traits and average unrelatedness. This index was robust to varying weights on information sources considered. Compared to selective genotyping based on dressage alone, the index had negligible impact on prospects of genomic selection for dressage, while benefiting prospects for jumping. Compared with current practice (no genotypes; stepwise selection), the expected genetic gain in dressage from stallion selection was 4.3 times higher with a reference population of 5000 genotyped stallions and selection at 1 years of age. Benefits were smaller (1.6 times higher gain) with 500 stallions genotyped, partly because 3-year olds were selected to restrict inbreeding.
Keywords: Genomic selection, Sport horses, Selective genotyping

Introduction

Breeding of sport horses is characterized by long generation intervals (~10yr) because horses are quite old before they can obtain reliable breeding values for the main breeding goal traits. Genomic selection has revolutionized breeding opportunities for other domestic animals either by reducing generation intervals (e.g. dairy cattle) or improving accuracy of selection at an unchanged age of selection (e.g. pigs and poultry). Particularly in dairy cattle, genomic selection is having a major impact by enabling accurate young bull selection. A similar large impact of genomic selection may be expected for sport horse breeding. Here the generation interval is even longer than it was in dairy cattle before genomic selection and the reliabilities of estimated breeding values (EBV) for the main breeding goal traits in horses (i.e. dressage and jumping in competitions) is lower than for dairy cattle. Thus there is potentially more to be gained from genomic information in horses. On the other hand, the horse sector in Denmark and elsewhere is not prepared to allocate as many resources to maintain and develop genetic evaluation systems as is the case for cattle. With limited resources available it is interesting to investigate relative simple genomic selection strategies that rely on a limited number of genotyped horses as a starting point.

The primary breeding goal of Danish Warmblood (DWB) horses is to improve their ability to compete in either dressage or jumping competitions. Dressage is the main trait though and the DWB breeding association is determined to further strengthening its international position in especially dressage competitions. They see genomic selection as a useful tool to improve its breeding program. Therefore resources for genotyping (70K SNP chip) at least 500 of the most informative DW horses have been allocated to develop and investigate the feasibility of genomic selection in DWB horses. It is important to identify and genotype those horses that will contribute most to the reliability of genomic EBVs for a young horse chosen at random from the DWB population. The available genotypes should be used to predict EBVs for all traits currently evaluated for DWB horses using multiple-trait single-step genomic selection models. However, with a relatively limited number of genotypes available it was unclear whether to focus all resources on improving dressage evaluations or whether some focus should also be directed towards jumping as well.

The aim of this study was to investigate the sensitivity of different selective genotyping strategies and to assess the potential impact of different genomic selection strategies in DWB horses on genetic gain.

Materials and Methods

Selective genotyping index. The following information sources were considered for each horse to decide whether the horse should be genotyped or not: 1) The reliability of EBVs (r^2_{IA}) for dressage competition results, 2) r^2_{IA} for jumping competition results, 3) r^2_{IA} for young horse gaits (indicator of future dressage ability), 4) r^2_{IA} for young horse jumping test, and 5) r^2_{IA} for conformation traits (also recorded at young age), and 6) average unrelatedness which was defined as 1-a, where a is the average genetic relationship between a horse and all other horses that could potentially be selected for genotyping. These horses were already a pre-selected group as only horses which already had an available blood or hair sample were considered. Blood or hair samples have been routinely collected by the DWB association since 1990 on all horses entering conformation and young horse tests (~ 30 of the best young stallions and ~200 mares annually).

The initial relative weights for these variables are given in Table 1 (reference) and were chosen somewhat arbitrarily. Double weight was given to dressage compared to jumping because dressage is the main discipline for DWB horses. Young horse traits were considered, despite the performance in actual competition results being the target trait, for three reasons: 1) the impact of genomic selection should be maximized when the first genomic EBVs are expected to be made official which is expected to last at least a couple of years. At that time horses with own/progeny information for young horse traits are also expected to have own/progeny information for competition traits, 2) young horse traits are planned to be included in the evaluation of competition traits via a multiple-trait single-

step genomic model and the genotypes can help to connect this information with EBV for future competition ability, and 3) it is desirable to have genotypes on young horses which are more likely selection candidates than older horses. Unrelatedness was considered to get a more balanced distribution of alleles in the reference population.

Expected reliability (approximation). The information source reliability method (Harris and Johnson (1998)) was used to combine the following information sources which were assumed independent: 1) parent average (contribution of 0.2 to the reliability was assumed), 2) own competition records (rounded average of no. records at different ages for 3 actual DWB elite stallions were used), 3) progeny information (also based on actual statistics for the 3 elite stallions), 4) genomic information. Basic selection index equations were used to derive the reliability due to own and progeny results (e.g. disregarding effect of inaccurate estimation of environmental effects). The contribution to the reliability from genomic information was approximated using the formula given by Goddard (2008), assuming an infinitesimal model, as well as population specific parameters for the DWB population, i.e. an effective population size of 263 (Jensen (2008)) and heritabilities of 0.21 (dressage) and 0.11 (jumping).

Results and Discussion

Sensitivity of selective genotyping index. Table 1 shows the weights chosen for different information sources in the reference index, whereas Table 2 shows the impact of varying these index weights. There was little difference in the selected horses regardless of whether dressage or jumping reliabilities were prioritized. This was because most of the older stallions had progeny information for both dressage and jumping. The impact of varying the weight on average unrelatedness was higher than varying weights between reliabilities of different traits. The impact appeared higher when quantified in terms of percent common horses than in terms of average reliabilities and unrelatedness. This implies that while somewhat different sets of horses were selected, it is not expected to have a major impact on the usefulness of the genomic predictions. Using an index of information sources rather than one source alone means that small sacrifices for a given trait can be offset by larger benefits from other traits. Generally the index was quite robust to changes in the weights applied. Based on these results, it was decided to use the reference index for actual selection of DWB horses for genotyping.

Expected reliability and impact of different genomic selection scenarios on genetic gain for dressage. Regardless of whether a small (500 genotypes) or larger (5000 genotypes) reference population was available there was substantially more to be gained from directing selection pressure towards young horses (Table 3). With a reference size of 500 genotyped horses, the expected genetic gain achieved by selecting stallions at 3 years of age was about 1.5 and 2.5 times higher than when stallions were selected at 6 and 11 years of age, respectively. The advantage of early selection became even greater with a larger number of genotyped horses. The expected genetic gains were higher

from selecting horses at 1 rather than 3 years of age (or older). However, here the parent average explains most of the EBV and substantial inbreeding could be the result of such early selection unless the number of genotyped animals are large (e.g. 5000) so that mendelian sampling terms are fairly accurately predicted from genotype information (see Fig. 1). Therefore strong selection of 1-year old horses is probably not advisable when only 500 genotyped horses are available and definitely not when no genotypes are available. The impact of genomic selection on inbreeding is difficult to foresee. While it is beneficial with more information about mendelian sampling terms it also becomes tempting to use younger stallions with high genetic merit intensively. Implementation of genomic selection should be accompanied with restrictions on how much each young stallion can be used. Similar gains in reliability as for stallions are also expected for mares, at least at relative young ages.

Ricard et al. (2013) found a reliability for genomic jumping EBVs of 0.4 based on 800 French horses. This figure was for genomic information alone and corresponds exactly to Fig. 1. They did, however, not blend the genomic EBVs with other information sources. Hence a practical validation of Fig. 2 remains to be seen.

The results presented here are based on single-trait genomic evaluations. Even higher accuracies can be achieved by multiple-trait genomic analyses and especially for 3-4 year old horses with own young horse trait records (Jönsson et al. (2014)). Also, the impact on actual genetic gains may be even larger than the figures presented here, because genomic selection facilitates an objective genetic comparison of domestic and foreign horses which – although it is completely lacking today – is very important for horses. Genomic selection may offer new possibilities for international collaboration. Countries can benefit from genotype exchanges and especially joint genomic evaluations. This can happen despite larger link-providing populations being reluctant to collaborate because the genotypes will provide direct genetic links.

Continued research. The feasibility of implementing a multiple-trait single-step genomic selection evaluation (Misztal et al. (2009); Christensen and Lund (2010)) for dressage and jumping traits, respectively, will be investigated after genotyping results are ready in the near future. Advantages of this method are that: 1) it can easily be integrated with current practice, 2) non-genotyped horses are included, which is vital because there are many more of those than genotyped horses, 3) advantages of the current evaluation system remains, and the system is easily extended, e.g. to multiple-traits and heterogeneous variance. Furthermore, simulations of genomic breeding schemes will be conducted to investigate the impact on genetic gain and especially inbreeding more precisely than in this study.

Conclusion

Genomic selection can substantially increase genetic gains in sport horse breeding through reduced generation intervals. Challenges include 1) establishing sufficiently large reference populations, which may be achieved through international collaboration, and 2)

convincing breeders to have a systematic approach to breeding which also considers restrictions to control inbreeding. An index for selective genotyping was presented based on reliabilities for multiple traits and average unrelatedness. This index was robust to varying weights on the information sources considered.

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Table 1. Information sources considered in reference index for selecting horses for genotyping, its mean and standard deviation, and associated final index weight[¤].

Info	mean	s.d.	weight
Reliability for dressage	0.78	0.22	**28**
Reliability for jumping	0.57	0.36	**14**
Reliability for YH gaits[&]	0.68	0.33	**12**
Reliability for YH jumping[&]	0.26	0.27	**6**
Conformation	0.68	0.25	**5**
Average relationship	0.006	0.004	**35**

[&]YH = Young horse trait; [¤]Statistics computed on selected top 500 horses

Table 2. Sensitivity[&] (relative to reference index in Table 1) to specific changes in weights of selective genotyping index. The sensitivity with respect to the difference in average reliability of dressage competition breeding values (Δr^2_{IA}), difference in average relationship with rest of population (Δa), and percent selected stallions in common with reference index is given.

Change[¤]	Δr^2_{IA}	Δa	%common
2× weight_dressage	0.011	0.000	96
0% weight_jumping	0.008	0.000	96
100% weight_dressage	0.012	0.000	96
100% weight_jumping	-0.105	0.000	83
100% weight_unrelated	-0.119	-0.002	79

[&] $\Delta r^2_{IA} = r^2_{IA(changed\ index)} - r^2_{IA(reference\ index)}$.

Δa = mean(mean relationship)$_{changed\ index}$ - mean(mean relationship)$_{ref.\ index}$.

[¤] The changes that were tested, in order as they appear in the table, were:
- Weight on reliabilities of EBV for dressage competition results were doubled compared to reference index while all other weights were unchanged
- The weights on jumping traits (both competition and young horse) were set to zero while the other weights were unchanged
- The weights on unrelatedness, conformation and the 2 jumping traits were set to zero while weights on the 2 dressage traits were unchanged
- Weights on unrelatedness, conformation and the 2 dressage traits were set to zero while weights on the 2 jumping traits were unchanged
- 100 % weight on unrelatedness (i.e. low average relationship)

Table 3. Impact on genetic gain (accuracy / generation interval)[&] for three genetic evaluation scenarios and different ages of selection

Age of stallion (years)	Genetic evaluation scenario (# genotypes)		
	none	500	5000
1	0.22	0.30	0.39
3	0.11	0.15	0.20
6	0.08	0.10	0.12
7	0.08	0.09	0.10
11	0.06	0.06	0.07
12	0.07	0.07	0.07

[&]The accuracies (r_{IA}) were as in Fig. 2 for the 3 scenarios. The generation interval (L) was the age of the stallion in the 1st column plus 1 year (gestation length + semen collection and use). The impact was r_{IA}/L which is proportional to the genetic gain.
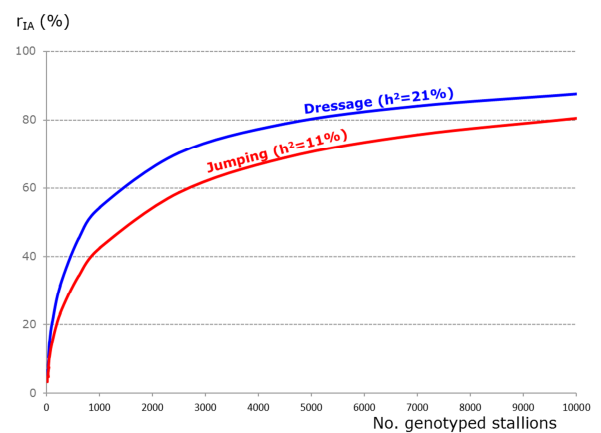

Figure 1. The expected accuracy of breeding values for dressage and jumping, respectively, due to genomic information alone as a function of the number of genotyped stallions.
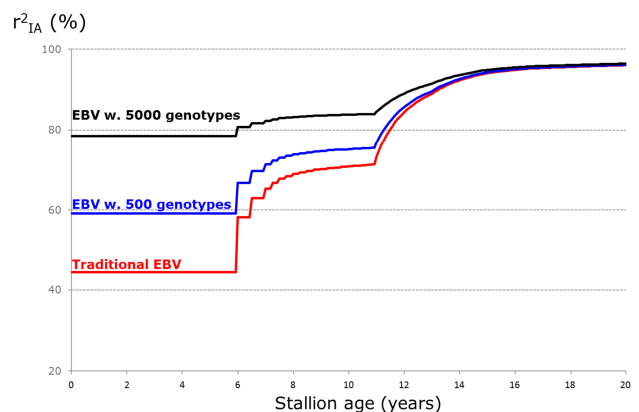

Figure 2. The expected reliability of breeding values for dressage competition results (r^2_{IA}) over the life time of an elite stallion for different sizes of reference populations (i.e. 0, 500 and 5000 horses). The increase in r^2_{IA} from 6 years of age is due to repeated own records and the increase from 11 years of age is due to progeny records.