Genomic applications in horse breeding

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Abstract

Rapid technical advances in molecular genetics and bioinformatics have enabled the integration of genomic information in increasing numbers of routine applications in animal breeding in the last decade. This shift from conventional genetic evaluations to genomic evaluations has started a “new era of breeding” (Eggen, 2012). Especially in dairy cattle, the concept of genomic selection (GS) was rapidly adopted and has radically changed the breeding schemes and structures (Dürr and Philipsson, 2012). Today, GS is successfully used in all major dairy populations worldwide. Genomic selection has facilitated accurate early selection and has substantially reduced the generation interval in dairy cattle breeding. At the same time, it has also made it easier to control inbreeding, which is partly due to more information available about Mendelian sampling terms relative to parent averages and wider screening of potential young sires (Schefers and Weigel, 2012). Based on large-scale access to genotype data, new approaches for the detection and management of genetic defects and improved selection and mating strategies that account for genetic diversity and inbreeding were presented (e.g., Pryce et al., 2012), contributing to a new, powerful genomic toolbox for animal breeders.

In horses, much less genomic data is so far available and used than in dairy cattle although there is little doubt that GS has enormous potential for horses as well (Stock and Reents, 2013; Mark et al., 2014). The long generation interval and the trait spectrum in, for example, sport horse breeding imply substantial gain by earlier and more reliable support of selection decisions (Haberland et al., 2012). Relating to the diversity of uses of horses, the much lower proportion of professionals among breeders of horses than of other livestock species, and the often substantial monetary and affective value of individual horses, population management and design of breeding programs are sometimes challenging. At the same time, selection decisions are increasingly requested to be knowledge based, balanced, and sustainable, and genomics could provide valuable information that genomics can contribute, so faster genetic progress can be achieved (Van Grevenhof et al., 2012).

The aim of this paper is to review the framework of equine genomic research and innovation and the implementation status of genomic applications for different groups of traits and populations as well as their prospective development in horse breeding. Potential implications for future horse breeding schemes will be discussed, with a focus on sport horses.

Introduction

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Genome Sequence and Key Determinants of Genomic Applications in Horses

Knowledge of the genome sequence is advantageous and often a prerequisite for efficient working with molecular genetic information in research and routine (Nicholas and Hobbs, 2013). As the result of the collaborative
efforts of researchers from more than 20 countries, the genome sequence of the domestic horse was completed, and a first draft assembly was published in 2007 (EquCab1.0; HGP, 2007). With the second assembly (EquCab2.0), an improved reference sequence became available in 2009, indicating new and better opportunities for equine genomic research and development toward practical applications (Wade et al., 2009). Further improvements are expected from the third assembly that is supposed to be fully annotated and may become available soon (Kalbfleisch et al., 2014).

In this context, the generated dense map of single nucleotide polymorphisms (SNPs) and the installation of comprehensive marker libraries were particularly valuable: The abundance of SNPs, together with technical properties, allowed establishing the SNP array technology; this implies easy and affordable accessibility of genomic data suitable for a broad range of scientific and also commercial applications (Eggen, 2012). Genomic selection as we know it today relies on the high-throughput SNP genotyping, and genome-wide SNP chips are today offered for multiple species and in a demand-driven range of formats from low to high density (Stock and Reents, 2013). The rapid development of better and cheaper genotyping tools is expected to continue, and methodologies like genotyping by sequencing may increase in relevance for routine applications in animal breeding (Gorjanc et al., 2015).

For horses, EquCab2.0 allowed compilation of intermediate-density SNP chips, where the 50k array with about 54,000 SNPs was later replaced by the 70k array to further increase the number of informative genetic variants for different breeds and breed groups (McCue et al., 2012). Only recently, a high-density SNP chip (670k) became available for more refined genomic studies. Sequence data are also available on an increasing number of horses through research projects but are still too expensive to be used in large-scale applications. When assessing the cost–benefit ratio, it should also be noted that sequence information does not necessarily provide added value for all applications, e.g., standard genomic selection procedures based on genomically enhanced relationship matrices (Pérez-Enciso et al., 2015).

According to the studies of the structure of the equine genome, especially the patterns of linkage disequilibrium (LD) and haplotypes in ancient and modern breeds, a panel of approximately 100,000 SNPs was supposed to provide sufficient power for successful association mapping (Wade et al., 2009). Although considerable breed differences were seen, implying that trait-associated sequence variants are easier to identify in some long-LD breeds like the Thoroughbred than in other horse breeds or across-breed approaches (McCue et al., 2012), there are multiple examples of successful use of the intermediate-density marker panel in studies of a wide range of phenotypes and in various breeds (Petersen et al., 2013; Finno and Bannasch, 2014).

The increasingly better framework for genomic studies is reflected by the speed with which new mutations for Mendelian traits have been discovered. The annual numbers of publications on mutation discoveries have more than doubled in the last decade compared with the early 2000s when only linkage maps were available. Today, well-annotated genome assemblies and SNP chips are available as screening tools for genome-wide association studies (Nicholas and Hobbs, 2013). In the Online Mendelian Inheritance in Animals (OMIA) database, where update lists of scientifically described Mendelian traits in non-laboratory species can be found, the number of entries for horses is much lower than that for other species, particularly dogs. As shown in Table 1, the number of Mendelian traits that has been described in horses until August 2015 is about six times smaller than in dogs and five times smaller than in cattle. Furthermore, coat color genetics make up a relatively larger part in horses (24.4%) than in both dogs (5.7%) and cattle (5.8%). However, the equine and canine mutation discovery rates are very similar and around 70%, so clearly higher than in cattle (51.4%) and above the average across species (52.3%; OMIA, 2015). In such comparison, several aspects must be taken into account to avoid misinterpretation, including, for example: differences in the diversities of breeds and their drivers and developments with respective impact on the genome structures and phenotype distributions within and across populations; the intensities of genomic research, linked to the suitability as model species for humans; and the roles of monogenic traits with simple Mendelian inheritance versus polygenic and multifactorial (complex) traits.

### Table 1. Overview of traits with Mendelian inheritance, scientifically described in horses, dogs, and cattle, according to the Online Mendelian Inheritance in Animals (OMIA) database, accessed on 21 Aug. 2015.

| Trait Description                                      | Horse | Dog | Cattle |
|--------------------------------------------------------|-------|-----|--------|
| Total number of Mendelian traits                        | 45 (11) | 263 (15) | 208 (12) |
| Number of Mendelian traits with known mutation          | 32 (10) | 193 (12) | 107 (10) |
| Mutation discovery rate including coat color traits     | 71.1% | 73.4% | 51.4% |
| Mutation discovery rate excluding coat color traits     | 64.7% | 73.0% | 49.5% |

**Genome-Wide Association Studies and Their Importance for Horse Breeding**

Across species, the majority of breeding goal traits is determined by multiple genetic and non-genetic factors, and the success of animal breeding using additive models justifies the assumption that very often large numbers of genes and genetic modifiers with mostly small contributions to the overall trait variance are involved (Meuwissen et al., 2001). However, the importance of genomic regions for a particular polygenic trait may vary widely, and those with stronger effects on the trait expression can be identified in genome-wide association studies (GWAS).
Identification of such regions can be important for better understanding the biology of underlying complex traits, which may give useful hints for biomedical developments as well as improved genomic prediction models. Target traits for GWAS in horses accordingly range from traits with presumably, based on clearly recognizable inheritance patterns, mono- or oligogenic origin to multifactorial traits with complex genetic backgrounds. A driver for such research is that genome-wide associations provide statistical evidence for some link between phenotype and specific genomic regions, which may be later supported by identification of the causal variants in the genetic code, allowing the transition from marker-based to direct gene tests.

As long as there is no phenocopy of the trait of interest, i.e., it has a uniform genetic basis, such tests allow maximum efficiency of breeding measures by reliable identification of horses with the mutation.

Famous examples of traits with known mutations and commercially available gene tests are hyperkalemic periodic paralysis (HYPP; Rudolph et al., 1992), also referred to as periodic paralysis II, and overo lethal white foal syndrome (OLWFS; Santschi et al., 1998) where the mutations are linked to some breed-specific and desired phenotype and, as such, are difficult to eliminate from the populations (further examples can be found in Finno and Bannasch, 2014). Routine genetic testing allows responsible planning of matings such that no risk is taken to produce affected foals. When compared with rigorous elimination of all carriers of the mutated allele from breeding, population management can gain a lot from systematic use of these genomic tools, particularly if the effective population size is small and the frequency of the unfavorable allele is high.

An interesting example of how the detection of a mutation can increase our understanding of evolution, selection, and the genetic architecture of traits is polysaccharide storage myopathy type I (PSSM I). Exertional rhabdomyolysis and related phenotypes were originally considered as a complex trait with large environmental sensitivity. However, genomic studies revealed that a single mutation is responsible for a significant proportion of cases in several breeds (McCue et al., 2008), and that the Mendelian inheritance pattern was only blurred by the phenotypic similarity of equine disease conditions and involvement of secondary, modifying genes (McCue et al., 2009). While most disease-causing variants of the genetic code are mediated by reduced or complete loss of function of the protein produced, PSSM I was found to be caused by a gain-of-function missense mutation in the skeletal muscle glycogen synthase (GYS1) gene, the relevance of which had changed dramatically over time. When horses were used for regular and heavy work in either an agricultural (e.g., field work) or urban setting (transportation), the faster replenishment of muscular glycogen storages was an advantage, so human selection increased the frequency of the mutated allele. Signatures of selection were identified around the GYS1 gene on equine chromosome 10 (ECA10), supporting this hypothesis and explaining segregation in several breeds, whereas founder effects in the context of specific population dynamics may have played only a minor role (McCoy et al., 2014). With the remarkable changes of use and environment of horses, the better ability to cope with strenuous daily exercise at low input became detrimental. Occurrence of clinical cases of exertional rhabdomyolysis is strongly influenced by environmental factors, particularly feeding and exercise practices. Accordingly, genetic testing for PSSM I is not only important from the breeder’s perspective, but also allows horse owners to account for the higher demands in management of genetically predisposed horses and, by that, avoid bouts of myolysis, pain, and suffering. Although this second dimension of improved disease management by using genomic tools may be identified for a much smaller number of traits for which gene tests are offered, it can be of high practical relevance for particular breeds. Today,
the performance of riding horses. In the formation of several horse and as objective measures of performance, it is more difficult to characterize narrowing of the genetic basis with its detrimental long-term effects, and breeders should try to avoid further breeding may need to be seen in the light of the small genetic basis of that of reducing wastage of racehorses. Opportunities for more specialized training and career planning and thereby also contribute to the efforts of riding horses. In the formation of several horse and such opportunities exist especially for American Quarter Horses and related breeds (Finno and Bannasch, 2014).

Phenotypes relating to performance are in most breeds playing central roles in the breeding programs of horses, implying high motivation of science and practice to benefit from new genomic applications in this field. However, performance traits in horses are usually regarded as classical examples for complex traits where some multi-faceted interplay of factors influences how well the individual horse performs in riding or racing. Only recently it has been demonstrated that this does not preclude the existence of single mutations that capture a substantial amount of the genetic variation of certain performance traits. The focus of Thoroughbred breeding has always been on racing performance, suggesting particular selection pressure on cardio-respiratory and musculo-skeletal function. The important role of muscle metabolism was supported by GWAS results, in which the myostatin gene (MSTN) was found to allow discrimination between short- and long-distance gallopers (Binns et al., 2010; Hill et al., 2010a; Petersen et al., 2013). Improved choice of the best racing distance with the help of the now offered speed gene test may provide valuable support for efficient training and career planning and thereby also contribute to the efforts of reducing wastage of racehorses. Opportunities for more specialized breeding may need to be seen in the light of the small genetic basis of that breed, with recognizable impact on genome structure (high LD), genetic diversity, and inbreeding (Corbin et al., 2010; McCue et al., 2012). Within their closed studbook, Thoroughbred breeders should try to avoid further narrowing of the genetic basis with its detrimental long-term effects, and genomic tools can support that, too (Scheifers and Weigel, 2012).

When compared with racing where racing time and speed are available as objective measures of performance, it is more difficult to characterize the performance of riding horses. In the formation of several horse and pony breeds, the ability to perform alternate gaits in addition to walk, trot, and canter was and still is an important and rather specific criterion, for which strong and consistent selection pressure has been and still is exerted. The Icelandic horse is probably the most famous example of a breed with gaitedness as an important breeding goal. The so-called four-gaiters show the basic gaits and tölt, characterized as typical regular ambling gait, whereas five-gaiters show the basic gaits, tölt, and pace, characterized as synchronized lateral two-beat gait. Genome-wide association studies for these gaiting abilities in the Icelandic horse revealed a strong association on the equine chromosome 23 (Andersson et al., 2012) that initiated an impressive story of success of equine genomic research: A mutation in the DMRT3 gene was identified as the cause of the strong association signal. The importance of the gene and the polymorphism across species and the working mechanism were demonstrated in an experimental setting (mouse model) and later complemented with extensive studies of allele frequencies within and across horse breeds (Jäderkvist et al., 2014, 2015; Promerová et al., 2014; Kristjansson et al., 2014; Jäderkvist et al., 2015; Ricard, 2015). The allele frequency studies showed that the mutation had, through its role in the coordination of limb movement, an impact on the ability for a wider range of alternate gaits, gait quality, and also trotting race performance. This important role of a single gene, which is expressed in a distinct fraction of neurons in the spinal cord, for locomotion in quadrupeds allows using the offered SynchroGait gene test as a genomic tool for decision support in management and breeding.

Further examples of successful GWAS for performance-related phenotypes are found in Table 2. However, it is unrealistic to assume that the genetic variation of complex breeding goal traits for sport horses including performance can be adequately captured by a few single locus tests. The validity and success of linear additive genetic models in animal breeding were
in the last decade again proven and multiplied by the introduction of genomic selection—first in dairy cattle breeding and later for other livestock and plant species (e.g., De los Campos et al., 2013). Accordingly, GWAS can, by identification and subsequent functional characterization of specific sites in the genome, valuably contribute to our understanding and possibly add information for improved decision making for traits controlled by at least one large QTL (Meira et al., 2013). Even if association signals were not always consistent across study populations, they provided hints toward the roles of certain genes in determining performance and health (Schröder et al., 2011; Distl, 2013; Brard and Ricard, 2014). Nevertheless, the potential of genomic selection is substantially larger with regard to the range of traits, the explanatory value and reliability, and the long-term usability mediated through opportunities for updating and re-adjusting the prediction algorithms (Meuwissen et al., 2013). Genomic evaluations may therefore be seen as the major field of genomic applications in horse breeding, implying a continuous move toward the center of current and near-future research and development activities worldwide.

Genomic Selection in Horses

Because most breeding goal traits in horses have a multifactorial background and are controlled by several genes, limitations of single-locus approaches are obvious. Even if major genes exist and single gene tests are marketed worldwide, their results describe only a limited fraction of the total genetic variance. In contrast, GS is a holistic approach and is jointly considering multiple sites of the genome, implying clear superiority in a setting where few genes with large effects and many genes with small effects influence a particular trait—which is most frequently encountered in animal breeding (Goddard and Hayes, 2009). Furthermore, applying GS based on genome-wide data as obtained via the commercially available SNP panels gives access to information on possible effects on other traits, and awareness of unfavorable pleiotropic effects supports balanced and sustainable breeding decisions.

Through GS, breeding schemes for some livestock and plant species have been revolutionized by enabling accurate selection decisions at a young age. In dairy cattle, first to adopt the new technology, GS has been used to substantially reduce the generation interval. In other species such as pigs and poultry, it was mainly the increase of accuracy of selection on an unchanged time of selection (i.e., sexual maturity) that increased the genetic gain. In horses, the generation interval is even longer than it used to be in dairy cattle breeding before GS, and accuracies of breeding values are lower. Hence, GS can be argued to have even greater potential for sport horse breeding provided the necessary willingness to invest in an efficient implementation of the technology. Today, the stepwise selection of horses is limited in efficiency due to the fact that information on the main performance traits becomes available late, so horses are at least 9–10 yr old (i.e., when offspring start competing) before they may get accurate conventional estimated breeding values (EBV). For large parts of the equine breeding stock, EBV accuracies remain low or rise much slower. A main advantage of genomic information is that it is available before sexual maturity (i.e., newborn foals or even embryos) and for any horse regardless of gender and origin, implying considerably improved support of selection decisions.

Apart from the gain in time and accuracy in stallion selection, genomic breeding values for the first time allow equally accurate selection of mares, which may be particularly important when the best female genetics is supposed to be identified for reproduction programs. Embryo transfer is only slowly increasing in popularity in sport horses, and genomic breeding values can serve as a good and relatively inexpensive screening tool, helping to reduce the financial risk of the individual breeder. Because genomic information does not discriminate between the Mendelian and parent average part of the breeding value, GS may also with increased selection intensity result in less inbreeding than the traditional breeding systems.

Given the substantial exchange of genetic material across studbooks and countries, sport horse breeding can especially benefit from GS because it gives access to breeding values for foreign horses with otherwise no objective and comparable information in a given country. Close enough genetic connectedness is a precondition for reliable genomic predictions, and previous studies in European sport horse populations give reason to assume good prospects for collaboration with regard to GS (Thorén Hellsten et al., 2008; Ruhlmann et al., 2009). In a situation where the small size of many countries’ horse populations interferes with running efficient national breeding programs and exchange of genetic material across country borders create potential bias in EBVs, joint initiatives can be crucial and generate strength by allowing objective genetic comparisons (Viklund et al., 2015).
compared with pedigree-based relationship matrices, genomic data allow improved consideration of connectedness among populations. Accordingly, genomics may compensate sparsely recorded pedigree ties and effectively link populations (Ricard et al., 2013) with positive impact on the feasibility of joint international genetic and genomic evaluations.

A further benefit of genomics for the whole equine sector may arise from the new opportunities of optimized management and use of horses, going beyond the improved selection for breeding. For example, knowledge about the genetically predetermined responsiveness to intense training can substantially support targeted investments in the sports career of individual horses. Although the cost–benefit ratio is expected to be most favorable for breeders and raisers who can select among larger numbers of young horses, general advantages should arise from strengthening and objectifying the decision basis by using genomic tools.

Despite this enormous potential of genomic applications in horses, the scientific literature on GS in an equine setting is very sparse, and there are so far no GS routines and practical experiences with its implementation and use in populations of, for example, racing or riding horses. Major parts of the turnover in the equine sector are today still related to traditional strategies of marketing hope and trust, based on expert phenotypic classification and performance. Accordingly, broader accessibility of objective quality measures of horses might be least welcomed by some established and successful sellers whose opinion is actually listened to by many. After the recent financial crisis, it has become more important for the weakened horse sector, though, to minimize the economic risk around the breeding, keeping, and trading of horses. With appropriate and target group–specific communication strategies, the interested studbooks should accordingly have good prospects to succeed in increasing the openness toward the use of genomic applications among their breeders and customers.

Besides some reluctance of the equine industry to adopt new technologies, limited resources and funding options have likely contributed to the lacking indications of development toward GS and genomically enhanced horse breeding programs. Considerable efforts are needed to compile the genotypic and phenotypic data basis of appropriate size, structure, and quality, which allows reliable predictions for complex breeding goal traits like dressage and show jumping performance. According to simulation studies, thorough selection of the horses for genotyping can help to maximize the information value for the whole population and, by that, assist efficient GS development (Mark et al., 2014). Using real data, new approaches have been presented to meet phenotype-related challenges of GS implementation (Ricard et al., 2013). In this French study involving 908 stallions with 50k SNP genotypes, the superiority of genomic evaluation over the conventional system was only minor. However, methodological adjustments that allow integration of information on non-genotyped horses and optimal usage of genomic and phenotypic data could help to increase the reliabilities and overall performance of GS. In the two-step genomic evaluation, commonly used in dairy cattle, SNP effects are regularly estimated in a reference population with phenotype and genotype information, and the summary prediction formula is then applied to the whole population, such that genomic breeding values become available for all genotyped individuals regardless of whether or not phenotype data is available for them. Reliabilities can be improved by combining genomic and conventional polygenic breeding values (blending; Goddard and Hayes, 2007). Alternatively, all available phenotypic, genomic, and pedigree information can be simultaneously used for genomic predictions, i.e., all animals are considered jointly, and genomic breeding values are computed directly by combining pedigree and genomic information. Such a single-step procedure avoids bias due to selective and goal-trait related genotype availability and implies optimal usage of information (Aguilar et al., 2010), which is particularly relevant when only a small part of the population is genotyped—as it will likely be the case in horses in the foreseeable future. However, technical issues need to be addressed, and utilization of a properly scaled and augmented relationship matrix in one integrated step has been shown to be crucial for proper comparison of animals across generations and with different sources of information (Vitezica et al., 2011). Single-step procedures have been found to be less biased and more accurate also in presence of selection, so methods like H-BLUE are expected to gain in importance also among the routines for dairy cattle (Koivula et al., 2012). For sport horses, multiple-trait single-step procedures may be prioritized to cope with the specific data structures and implementation conditions of GS (Mark et al., 2014).

Development of Genomic Applications in Horse Breeding

Given the different purposes of use of horses and their relation to the origins and historical development of breeds, selective sweeps as found in comparative multi-breed analyses are likely to include regions of the equine genome that influence performance (Petersen et al., 2013). Over the years, our understanding of the genetic determination of some important traits in horse breeding has improved, and particularly the GWAS results for performance traits have attracted interest of the horse industry.

However, several positively selected loci with putative exercise-related genes were reported for the Thoroughbred, and significant marker associations with performance in flat races (Hill et al., 2010a) indicate the limitations of a single gene test (e.g., considering only MSTN) as offered today or possibly a set of single-locus tests. Cost–benefit ratio and long-term perspectives suggest that only genome-wide approaches may gain practical relevance in Thoroughbred breeding, provided that the widespread traditionalism will allow adoption of the new genomic tools for the racehorse industry.

For sport horses, the situation is similar with regard to the possible gene testing for gaiting abilities and gait quality (DMRT3), which may help to make breeders and owners familiar with genomics in another context than testing for genetic defects. Nevertheless, only GS promises significant benefits as required with regard to the spectrum of traits and long-term perspective in sport horse breeding. Recent intensification of research and development activities in the field of new traits like health (Hartig et al., 2013; Jönsson et al., 2014; Stock et al., 2014) has already been driven by the now better opportunities to consider them in the breeding programs through GS. The now increased engagement of studbooks for improved routine data recording results in more informative and objective phenotypes that become available for conformation and performance (Duensing et al., 2013); this may benefit the development of GS and allow refined genomic predictions. However, to overcome the shortcomings of initiatives of single studbooks or countries and achieve the power for successful implementation of GS in the sport horse, collaboration may be crucial as was the case in dairy breeding (Dürr and Philipsson, 2012). Sharing of costs and data among studbooks, efficient use of know-how and resources, and improved conditions for establishing best practices for routine GS are strong arguments for new alliances in the sport horse sector.
Anne Ricard has graduated at AgroParisTech and was recruited by French National Stud (IFCE) to work at the French Institute of agricultural research (INRA) under the supervision of B. Langlois in the 1980s. Since then, she is responsible for the horse breeding evaluation and is member of the international Interstallion working group where she was responsible for the second pilot project on genetic correlations in sport horses among European countries. Her principal fields of work are: analysis of sport performances, optimization of breeding plans, and now genomics. She published the first application of genomic evaluation in horses.

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Stock, K.F., and R. Reents. 2013. Genomic selection: Status in different species and challenges for breeding. Reprod. Domest. Anim. 48(Suppl. 1):2–10. doi:10.1111/rda.12201.

Vitezica, Z.G., I. Aguilar, I. Misztal, and A. Legarra. 2011. Bias in genomic predictions for populations under selection. Genet. Res. 93(5):357–366. doi:10.1017/S000166721100022X.

Wade, C.M., E. Giulotto, S. Sigurdsson, M. Zoli, S. Gnerre, F. Imsland, T.L. Lear et al. 2009. Genome sequence, comparative analysis and population genetics of the domestic horse (Equus caballus). Science 326:865–867. doi:10.1126/science.1178158.