Review Paper:

Genomic Selection: Prospects and Challenges in Animal Breeding

Amedu Godwin, Joseph Michael Adinoyi*, Yisah Jato Lasisi, Abisoye Oluwaseyi Faith and Eboh Sule
Department of Animal Health and Production Technology, School of Agricultural Technology, Kogi State Polytechnic, Lokoja, Kogi State, NIGERIA
*michaeladinoyi2@gmail.com

Abstract

Taking careful look at animal breeding in general, appreciable gap is existing between animal breeding/ production and the demand of the world population. The effect of the conventional breeding methods for selection of animal populations on numerous traits of economic importance is however questionable in regards to the accuracy in breeding value. It has been discovered via simulation and experimental results that breeding values can be predicted with high accuracy via genomic selection for young animals without own performance.

Genomic selection is seen as a form of marker-assisted selection in which genetic markers covering the whole genome are used in a way that all quantitative trait loci (QTL) are in linkage disequilibrium with at least one marker. Genomic selection improves genetic gain by decreasing genetic interval and improving reliability. By this we can say it is the future of livestock breeding companies. This review paper is however centered on the prospects and challenges of genomic selection in the breeding of animals.

Keywords: Genomic Breeding, Genomic Estimated Breeding Value, Genomic Selection.

Introduction

According to Food and Agriculture Organization of the United Nations (FAO) to meet the consumption requirement of world population, food production should be doubled in the next coming years[28]. The expected productivity gap could be filled by improving genetic, health and perfection of animal husbandry. According to Ventura et al[91], animal breeding is related to intended human selection based on animal performance record and mostly selection is done based on more than one trait. Garner[31] reported that in the absence of molecular knowledge, breeders have effectively used traditional animal breeding methods (TAB) for production of superior animals.

In the TAB method, estimated breeding value (EBV) is based on animal own and family realistic physical character or phenotype, but with these methods animal's production remains questionable due to low reliability. During the past years, animal breeding based on quantitative genetics has remarkably increased animal production. However, the implementation of genetic markers into breeding programmes has been rather limited for technological reasons[24]. Presently, the availability of dense panels of single nucleotide polymorphism (SNP) markers has offered new opportunities to select the best fit animals for breeding purpose, commonly referred to as genomic selection. The basic concept of such methodology is to use the quantitative trait locus (QTL) linked with a particular phenotypic trait and exploit them for selection purpose.

The broad information of dense genetic markers has allowed the estimation of breeding values for young candidates with higher accuracy than before. According to de Koning[17], the principle of genomic selection is to take advantage of both genotypic and phenotypic data available in reference population to shape prediction equations of the genetic merit of individuals. The reliability of genomic selection is expected with larger reference male or female populations[3].

On the other hand, because of the reliable phenotypic information resulting from a large group of daughters, progeny-tested bulls often construct the training set of genomic selection. Zhou[98] reported that using a joint reference population by collecting different data from different populations has been expressed as an efficient method of improving the accuracy of genomic selection.

According to König et al[49] genomic selection has significantly increased the technical and economic efficiency of animal breeding program and its benefit was first reported for dairy cattle. These expected advantages are generally due to a reduction in the generation interval, increase in the accuracy of EBV and a reduction in costs for progeny testing[81]. Nevertheless, there are some challenges that are being faced in genomic selection even though the successes recorded so far cannot be overlooked when it comes to animal breeding in general and that is what this review is centered on.

Traditional breeding methods: Animal breeding involves the selection of domestic animals with the goal to improve quantitative or qualitative traits in the next generation.

According to Plieschke[70], a number of breeding methods have been used to improve animals, but the main aim has always been to improve the production of superior animals of desired traits. Traditionally, animals were selected for breeding purpose based on phenotypic recordings. Thus, traits difficult to be measured such as those later expressed, limited to sex or of low heritability are more difficult to be improved[11].

According to Henderson[37], best linear unbiased predictions (BLUP) combined individual records and those of relatives into EBV to improve the predictions of performance. Dekkers[23] reported that the BLUP method increases genetic response to selection by improving the reliability of EBV. This is so because the method can account for all systematic effects (e.g. batch, sex, production environment, age variation) that are often associated with traits of economic importance in farm animals. In addition, the BLUP method improves the reliability of EBV because in BLUP analysis, all pedigree information is exploited through a numerator relationship matrix to account for changes in additive genetic variance due to inbreeding or assortative mating[14].

Although animal selection based on EBV estimated from phenotype has been very successful, there are still a number of limitations. These mainly relate to the capability to regularly record phenotypic data of selected candidates and/or their close relatives in a timely manner which help to accelerate selection decisions at an early age to reduce generation intervals. Costly phenotype recording for traits difficult to be measured or with low heritability also plays an important role here.

Another limitation of TAB is the trait of interest which is only recorded late in life and only on one sex which requires animals to be sacrificed (meat quality) or exposed to conditions that would hamper the ability to market or export their germplasm (e.g. disease resistance). In addition, these breeding processes remain comparatively slow because of the considerable time required to collect adequate daughter phenotypes to calculate genetic evaluations with high precision.

Marker-assisted selection: The use of genomic information in addition to phenotypic information to increase reliability is known as Marker-Assisted Selection (MAS). According to Sax[77], the concept of MAS for selection of superior animals was first introduced as early as in 1900. Genes controlling specific traits are scattered all over the genome but pretty few in numbers have large effects with many more genes having gradually smaller effects[93] and in MAS, marker genes are used to indicate the presence of desirable genes[73].

According to Meuwissen et al[61], MAS depends on identifying association between genetic marker and linked Quantitative traits loci (QTL) and the association between marker, while that association depends on distance between marker and target traits[75].

The combination of traditional breeding method with molecular genetic methods is beneficial to the selection response. With the help of MAS, it becomes possible to recognize the trait of interest which will pass on to the next generation, regardless of environmental condition. This method also helps in identification of the trait with low phenotypic expression like disease resistance. Selection is

possible for recessive genes and mutants, in addition to MAS selection; process is faster because an individual's phenotype can be predicted at a very early stage[39]

According to Rothschild et al[76], MAS is profitable compared to TAB for sex-limited traits or traits with poor predictor of breeding value and traits that are expressed late in life. MAS could be particularly useful in cross-breeding programmes in which desirable genotypes are introgressed into productive local breeds with overall better breeding values. Although the MAS technique increases animal production by increasing reliability, it is not timely in animal breeding programs because most traits of interest are governed by a large number of loci.

VanRaden[90] opined that MAS could result in small genetic gain because the use of a limited number of loci can capture only part of the proportion of genetic variance. According to Baruch et al[6], complexity of the calculations involves the estimation of breeding values with incorporation of information molecular markers hampering the use of MAS.

Development of genomic selection: The MAS method is fruitful for traits with a simple genetic determinism, but delivers unsatisfactory outcomes in many more complex conditions.

According to Boichard[8], the two key causes for this low productivity were the limited part of the genetic variance and also the low association between markers and QTL at population level. Another limitation of MAS is the expensive cast of genotyping of selection candidates, due to the benefits of MAS in commercial breeding programs being clearly less than expected[21].

According to deKoning[17], the success of genomics in animal breeding set in with a new novel approach where the breeding value could be estimated from markers spanning the entire genome. Now parental relationships are no longer vital to make clear similar performances in animals because with the accessibility of low-cost whole-genome SNP panels, analogous performances can now be justified by the reality that animals share the same chromosome fragments[44].

According to Rabier[72], genomic selection is a type of MAS in which breeding value of animals can be accurately estimated with the help of dense maker map of chromosomes without information about their phenotype or that of close relatives.

Konig et al[49] also stated that genomic selection has improved animal production by reducing the generation interval and cost of proving bulls. The genomic selection is based on the analysis of 10.000 up to 800.000 SNP's[85]. According to Fan[27], whole genomes of many animals have been sequenced including chicken, horse, sheep, cattle, dog, cat and rabbit and it is shown clearly in the table 1.

Table 1
Summary of whole-genome sequence information of important animal species with year of completion1

Species	Genome Size (Gb)	Year
Cattle (*Bos taurus*)	2.67	2009
Sheep (*Ovis aries*)	2.61	2008
Goat (*Capra hircus*)	2.63	2012
Pig (*Sus scrofa*)	2.8	2009
Chicken (*Gallus gallus*)	1.04	2004
Rabbit (*Oryctolagus cuniculus*)	2.73	2009
Dog (*Caris familiaris*)	2.41	2003
Horse (*Equus caballus*)	2.47	2009
Cat (*Felis catus*)	1.64	2006
Turkey (*Meleagris gallopavo*)	1.06	2009
Spotted gar (*Lepisosteus oculatus*)	0.94	2011
Atlantic salmon (*Salmo solar*)	2.43	2011
Atlantic cod (*Gadnus morhua*)	0.82	2010

[1]Modified from Stock *et al*., (2013)

Table 2
Impact of genomic selection on genetic gain

Animals	Added Genetic Gain
Pig[35]	23-91%
Dairy sheep[80]	51.7%
Dairy goat[80]	26.2%
Dairy cattle[71]	60 -120%
Layers[82]	60%
Broilers[20]	20%
Meat sheep[80]	17.9%
Beef cattle[69]	15-44%

Principle of genomic selection: Considering the principles of genomic selection, the basic is the use of marker information for estimation of breeding value without having the information of gene location. In order to get this done, the first step is the collation of phenotypic and genotypic information of reference population. According to Boichard[8], for genotypic information, all animals in reference population are genotyped for SNPs of entire genome. Although genotyping of large population is expensive, increasing the numbers of animal in reference population will make results more precise[54].

According to Fernandes Junior[29], collected phenotypic and genotypic data are used to obtain predictive equation to calculate GEBV. These effects are then applied to candidates for selection with marker genotype information, but without known phenotypes. Neves[65] reported that the precision of GEBV depends on 3 factors: trait heritability ($h2$), animal number (N) in the reference population and q parameter.

Advantages of genomic selection: Genomic selection increases productivity by increasing the rate of genetic gain compared to traditional breeding methods and this is shown clearly in the table 2 with accurate references.

According to Ibañez-Escriche et al[41], genetic gain (ΔG) in animal breeding programs depends upon the intensity of selection (i), accuracy of predictions (r), genetic variance ($\sigma2g$) and generation interval (IG): $\Delta G = i * r * \sigma2g / IG$. Genomic selection increases the rate of genetic gain by decreasing generation interval[59] and increasing accuracy of prediction[36]. The key benefit of genomic selection is that candidates can be assessed without progeny and phenotypic information. Consequently, selection of animals can be done at very early age; it can be applied on embryos, thus, genomic selection could increase productivity by reducing generation interval. Moreover, by increasing the size of reference population, selection intensity could increase.

According to Hiendleder et al[39], the efficiency of genomic selection for sex-limited (milk yield), low heritable, or poor predictor breeding value traits (fertility) is high compared to traditional selections. Before the genomic era, genetic improvement depended on huge phenotypic record and thousands of bulls which were progeny tested and used for artificial insemination. However, Henryon et al[38] reported that with the development of genomic selection, progeny testing is no longer necessary, simplifying the selection process and decreasing its cost. Due to a strong reduction in generation interval, the yearly genetic trend could be doubled; due to their lower production cost, a much larger number of bulls could be selected and marketed leading to a better management of genetic resources, limiting inbreeding trends. Therefore, whole genomic selection is the effective

modern breeding method for production and selection of superior animals.

Implementation of genomic selection in livestock: Animal breeding has had a great influence on the improvement in livestock production. Genetic improvement has played an important role in improving the desired traits' efficiency in livestock including cattle, sheep, pigs and poultry. The advancement of gene technology allows livestock breeders and commercial livestock product producers to make breeding decisions based on gene marker technology.

Genomic selection in ruminants

Genomic selection in dairy cattle: In dairy cattle, it has been used to discover markers that will improve the reliability of traits associated with milk production, cow health and cow conformation. According to Bolormaa[9], Australia is the leading country in identifying genomic regions associated with milk production and several studies have also been completed in the United States, Canada[94], China[42] and some other countries. According to Lund[58] and Wiggans et al[95], the application of genomic estimation has caused significant changes in dairy cattle breeding; the reliability of genomic prediction in dairy cattle exceeds 0.8 for production traits and 0.7 for fertility and other traits.

Selection is mostly done on the sire side as bulls' semen is distributed via AI for breeding purpose and with the help of genomic selection, elite bulls can be selected at early age. The reliability of predicted GEBV in dairy cattle has already been evaluated in some countries like the United States, New Zealand, Australia and the Netherlands.

When the accuracy of GEBV for a bull calf at birth is equal to that of conventional breeding values after progeny test, cost reductions in the order of 90% appeared realizable. These experiments used reference populations between 650 and 4,500 progeny-tested Holstein-Friesian bulls which were genotyped for approximately 50,000 genome-wide markers.

According to Hayes[36], reliabilities of GEBV for young bulls without progeny test resulting in the reference population were between 20 and 67%. Gray et al[32] reported the possibility of implementing genomic selection by determining the effectiveness of genomic prediction of milk flow traits in Italian Brown Swiss population at the North Carolina State University (USA). The genetic worth for milk flow traits estimated from genomic markers indicated an increase in reliability in most cases compared to traditional pedigree-based evaluations. Across country evaluation of female fertility parameters has been done in Holstein Friesian (HF) cows distributed over Ireland, UK, Netherlands and Sweden.

Bayesian stochastic search variable selection using Gibbs sampling was done for bivariate genome-wide associations of traditional fertility parameters (viz. days to first service,

days to first heat, pregnancy rate to first service, number of services and calving interval) and fertility phenotype derived from milk progesterone profiles. According to Berry et al[7], it was concluded that sharing of data vis-à-vis utilizing the physiological measures of trait under investigation may increase the power of the GWAS.

Finlay et al[30] reported that the composite phenotype of genetic merit for tuberculosis susceptibility among the daughters of HF elite sires was studied at Trinity College Dublin, Ireland. They compared around 44K SNPs in 307 animals which revealed that 3 SNPs spanned over 65 kb region of chromosome 22 were associated with tuberculosis susceptibility. This genomic region harbours a transporter gene, SLC6A6, or TauT which is known to function in the immune system.

Genomic selection in beef cattle: According to Montaldo[63] in beef cattle breeding, selection of indices is often based on a specified market, but adoption is slower primarily due to trait of interest like growth rate, carcass, reproduction and health that contribute to profitability. Reliabilities of genomic prediction in beef cattle have been lower than in dairy cattle[88]. The lower reliability is due to lower quality and quantity of beef cattle population than dairy. According to Kuehn et al[50], the traits of interest in beef cattle are docility, growth, marbling pattern of beef, body composition traits (like sub-cutaneous fat thickness, 12th-13th rib by area, subcutaneous fat over the rump of the animal and intramuscular fat or marbling fat) as well as reproduction and health traits. Markers flagging the genomic regions associated with growth and feed efficiency have already been studied and identified in beef cattle[83,84].

Pimentel et al[69] reported that genomic selection of beef cattle has been done for three traits weight at 200 and 400 days as well as marbling score and muscling score using selection index theory. According to Elzo et al[26], illumina 3K-chip has been used for evaluating three different models namely genomic-polygenic, genomic and polygenic models for feed efficiency and postweaning growth in Angus-Brahman multibreed cattle. The study revealed that "Genomic-polygenic, genomic and polygenic predictions for all traits tended to decrease as Brahman fraction increased, indicating that calves with greater Brahman fraction were more efficient but grew more slowly than calves with greater Angus fraction".

Genomic Selection in Small Ruminants: According to Daetwyler et al[15,16], the feasibility of genomic selection in small ruminants has been evaluated recently in meat sheep in Australia and New Zealand[2], in dairy sheep in France and in dairy goats in France[12,13] and in the UK[64]. One of the key underpinning features of genomic selection is that a reference population should be created, whereby dense phenotyping occurs for animals that are genetically related to the wider population to link the genotypic information with the phenotype.

Legarra et al[53] reported that for New Zealand, which has 13,420 pure (mostly Romney) and crossbred sheep, the reference population sizes are still rather limited when compared with cattle, with around 1,900 Western Pyrenees dairy sheep breeds; around 2,400 and 2,700 UK and French goat populations respectively; 4,800 Lacaune dairy sheep[51] and up to 8,000 mutli-breed Australian meat sheep[15,16]. Within country, reference populations are generally composed of various breeds and crossbreeds. Purebred populations reached at maximum about 5,300 for New Zealand Romney, 4,000 for Australian Merino and 4,800 for French Lacaune, with all other populations being in the range of a few hundred to 2,000. Despite small reference populations, genomic best linear unbiased prediction (GBLUP) resulted in greater accuracies of EBV than pedigree-based BLUP although for some traits and population, the increase in accuracy was small.

According to Daetwyler et al[15,16], gains in GEBV accuracies were estimated to be on average between 0.05 and 0.10 for carcass traits and meat quality traits in Australian sheep and between 0.05 and 0.27 (mean = 0.13) per breed for meat, fleece and litter size traits in New Zealand as reported by Auvray et al[2]. Baloche et al[5] in their study assessed a similar gain in accuracy between 0.10 and 0.20 across milk production traits in Lacaune dairy sheep. The gain in GEBV accuracy in the French and UK dairy goat populations amounted to 0.06 for milk yield and 0.14 for fat and protein content[12].

Daetwyler et al[16] equally showed how the gain in accuracy was well correlated with the reference population size and the genomic heritability of the trait, thus suggesting that accuracy and expected genetic gain can increase in the future if reference populations increase in size. The gains of reliability provided by molecular information were lower than for cattle with respect to reference population size which is probably due to lower linkage disequilibrium (LD) due to higher effective population size and inclusion of crossbreds in sheep and goats.

According to Carillier et al[13], Brito et al[10] and Mucha et al[13], the extent of LD estimated by average $r2$ values between adjacent markers (50kb) ranged from 0.10 to 0.18 for Saanen and Alpine goat populations and was mostly between 0.08 and 0.12 in sheep[5,45]. Soay sheep[45] and boar goat[10] were exception with higher LD ($0.28 < r2 < 0.30$), which is probably due to low primary effective population size. The extent of LD was therefore lower than comparable estimates in Holstein dairy cattle ranging from 0.18 to 0.3[19,35] and in Landrace, Duroc, Hampshire and Yorkshire pigs (from 0.46 to 0.36)[4]. The LD results indicate that for some breeds, the addition of new genotypes is mandatory and that a denser SNP panel than the current 50K Beadchip could be beneficial.

Also, genomic evaluation methods can substantially improve the accuracies of GEBV estimation when applied to small ruminants and therefore accelerate response to selection. Indeed, the accuracy of methods that use only phenotypes of the genotyped animals and ignore records of the nongenotyped part of the population (e.g. GBLUP and BLUP-SNP) is limited when the reference population is small. Therefore, a single-step approach is the recommended method for such small reference populations. According to (Legarra et al[52] and Misztal et al[62], it integrates all of the available phenotypic, pedigree and genomic information in a single-step procedure to calculate genomic breeding values. It also avoids bias in the estimation of GEBV due to the preselection of candidates.

The method is easy to implement as it can use raw phenotypic records without the need to calculate deregressed proofs whereby records are adjusted to reflect the fact that there are different amounts of information between animals, coming from relatives. It also allows all animals to be evaluated (with and without genotypes) simultaneously.

According to Carillier et al[12], the single-step approach improved prediction accuracy of candidates from 22 to 37% for both Alpine and Saanen goat breeds compared with the two-step method. The gain in accuracy when comparing traditional pedigree-based genetic evaluations and single-step genomic evaluations for milk production traits was also significant i.e. from 5% up to 30%, in Western Pyrenees dairy sheep breeds despite very low reference population sizes[53]. Given the diversity of meat and dairy sheep and goat breeds and small population size for most of those breeds, multi-breed genomic evaluations have been preferred. The benefits from blending different breeds with similar breeding objectives and recorded traits were highly variable but generally limited.

Auvray et al[2] concluded that training datasets with Romney, Coopworth and Perendale animals all together usually predicted better than using just a pure breed training dataset for all traits except for a few traits in Perendales. In goats, Carillier et al[12] compared several models: a multi-breed model blending the two breeds together, a per-breed model and a multi-trait model considering each trait in a breed correlated to a similar one in the other breed. They found the best regression coefficients were obtained with the per-breed model.

Daetwyler et al[15] further discovered that accounting for the structure of their large multi-breed and crossbreed sheep population generally decreased the accuracy of across-breed genomic predictions. Accordingly and because of limited persistence of LD phases between breeds[5,12], a denser SNP panel than the current 50K Beadchip, or imputation from sequence data in key ancestors, might be beneficial if one expects substantial gain in accuracy for multi-breed genomic evaluations.

For some breeds that are bred in several countries with similar breeding objectives, blending populations on an

international basis could be highly profitable, but this depends on the level of genetic connection by commercial exchanges between populations. According to Legarra et al,[53] this might be the case for Texel meat sheep (Ireland, UK, France and New Zealand), Saanen goats and crossbreds (France, UK, Italy and Canada) and Boer goats (Canada, Australia and France) and has already been positively evaluated for some of a set of Western Pyrenees dairy sheep breeds in Spain and France.

Genomic selection in swine: According to Meuwissen et al,[60] the key step in pig breeding is the selection of elite boar in nucleus farm before which boar test recordings generally take place, consequently reduction in generation interval for genetic gain is limited, but genomic selection could still possibly reduce generation interval up to 25% compared to traditional methods. Hence, in pig breeding, genetic gain could be increased by improving the accuracy of EBV, particularly for traits which are difficult to improve in traditional methods; single-sex, late-in-life, low heritability and to measure. Genomic selection improves litter size in pig[87] but increases pre-weaning mortality in piglet because more number of live piglets than sows are capable of nursing.[1]

According to Rohrer et al,[74] wide genomic selection made it possible to make selection with high accuracy to increase the number of teats to ensure that sows can nurture all of their piglets. It is interesting that the use of genomic information could possibly increase the reliability of this trait up to 50%.[57] According to Knap,[46] post-weaning mortality is another example of a hard to measure trait, with low incidence and heritability, strong environmental influences, but very high economic value. With conventional methods, the accuracy of this trait could be increased, but only possible with high mortality incidence. Knol et al[47] reported that genomic selection also successfully increased the genetic gain of this trait in pig by increasing the accuracy of EBV up to 50%. In pigs, cross-breeding is widely used; hence, more effectual selection could be done by using cross-bred pigs as a reference population.

Lillehammer et al[55] reported on how they studied and compared the alternative designs for implementation of genomic selection to improve maternal traits in pigs. Genomic selection increased genetic gain and reduced the rate of inbreeding as compared to conventional selection without progeny testing. Incorporation of GS increased the genetic gain to 23-91% in contrast to 7% genetic gain obtained through progeny testing. They concluded that genomic selection can increase genetic gain for traits that are measured on females which included several traits with economic importance in maternal pig breeds. A study on genome wide assisted selection of swine farrowing traits by Schneider et al[78,79] aimed at determining the genetic parameters (using MTDFREML) and genomic parameters among swine farrowing traits like total number of piglets born, born alive, dead, still born etc.

The proportion of phenotypic variance explained by genomic markers generated by GenSel was ranging between 0 (number of piglets born dead) to 0.31 (average piglet birth weight). The results indicated that "genomic selection implemented at an early age would have similar annual progress as traditional selection and could be incorporated along with traditional selection procedures to improve genetic progress of litter traits".

Genomic selection in poultry: According to Knol et al,[47] poultry was first sequenced in 2004 and then in 2006 the second new build of chicken genome was released, which corrected some of the deficiencies found with the first version. According to Dekkers,[22] chicken breeding programs are in a pyramid form and the larger number of offspring in chicken allows more than double genetic improvement compared to cattle or pigs when using traditional breeding methods. Some studies showed the possibility to reduce generation interval in layer breeding programs by implementing genomic selection.[97] Breeding of layers for commercial egg production is an international business and is dominated by a few companies.

Wolc[96] reported that in 2013, Hy-Line Int. performed genomic selection in commercial layers, preceded by 3 years of genomic selection in an experimental line. At the end of experiment, birds that were selected based on genomic prediction outperformed those that were submitted to conventional selection for most of the 16 traits that were included in the index used for selection. According to Sitzenstock et al,[82] other companies also reported genomic selection as a promising alternative to conventional breeding for genetic improvement in layer chickens. Research on the application of genomic selection in broiler breeding was started shortly after the report of chicken genome sequence.

However, in broiler, the case for genomic selection is not as obvious as in layers because most traits can be recorded on both sexes at an early age. According to Wang,[92] in broiler chicken, the improvement in reliability of moderate heritable traits like fertility and egg production can range from 20-45%, while for highly heritable traits it can be greater than 50%.[96]

Genomic Selection in Horses: According to Koenen et al,[48] routine genetic evaluations have been established for riding horses in several riding horse populations with a focus on performance whereas further important breeding goal traits are not yet considered sufficient because of testing difficulties. The long generation interval in the equine implies large potential of GS to enhance the genetic gain and at the same time optimize the spectrum of selection traits. The available SNP chip has already been used for research,[68,79] and routine use of whole-genome data for breeding purposes may be expected in the near future.

According to Van Grevenhof et al,[89] collection of enough high-quality phenotype data is likely to be the major limiting

factor, but possible solutions have already been presented. However, collaborations between breeding organizations will be essential for assembly of the reference population and the networks in the equine industry may not yet be as close as in dairy cattle in the pre-genomics era where international information exchange via Interbull was already established.

Genomic Selection for Rabbits: According to Gyovai et al,[34] breeding programmes are usually based on mass selection for production traits like litter size, growth rate and meat characteristics, implying similar options for enhancing the genetic gain by genomic selection (GS) through earlier and particularly more accurate selection as, for example in pigs or chicken. However, the organization structure and overall weak financial power of commercial rabbit breeding make developments towards routine use of genomics unlikely in the near future.

Considering the important role of rabbits as experimental animals, science-driven advances can be expected, so single nucleotide polymorphism (SNP) chips may become available which could allow genomic selection (GS) at least in some larger and market oriented populations. Given the low value of individual breeding animals, affordable tools for whole-genome screening would facilitate stronger focus on the important low-heritability traits like disease and parasite resistance.[18]

Genomic Selection for Dogs: Dogs are used by humans for a broad variety of tasks including traditional and new fields of work (e.g. herding, therapy) and represent an important model species for research. According to Parker et al,[67] Ke et al[43] and Oliete,[66] the canine genome was fully sequenced already in 2003 followed by the development of single nucleotide polymorphism (SNP) arrays that have been used in different context for research.

Guo et al[33] reported that in 2011, the opportunities to efficiently select against disease conditions using GEBV were illustrated, implying possible move of dog breeding from science to routine use of whole-genome data. Dog breeding programmes usually consider several moderately to highly heritable conformation traits, but frequently also include strategies to reduce disease prevalences and to improve traits impacting the intended use of the dogs (e.g. behaviour, specific working abilities). For this category of traits, which have relatively low heritabilities and require considerable efforts for phenotype recording, genomic selection (GS) promises considerable enhancement of the genetic gain through more accurate selection at young age.

When compared to the livestock species, the cost factor for routine implementation of genomics may be less problematic, because many dog breeders already spend large amounts of money for increasing numbers of single-gene test, which may become dispensable with whole-genome screening.

Conclusion

No doubt genomic selection (GS) has been widely successful; nevertheless many remaining issues are still being identified and addressed. Genomic selection approach is still in its inception. It has equally been observed from the information gathered that genomic selection is more applicable in large animals than in the small ones due to the difference in the generation interval that directly affects the economic feasibility of the project and it is seen as a major challenge.

More theoretical studies following analyses of large field datasets are needed to fully understand the effects of long-term GS. It has been noted that fluctuations of genomic predictions reflect limited prediction accuracies and can be managed to reduce risk and achieve high genetic gains.

References

1. Andersen I.L., Naevdal E. and Boe K.E., Maternal investment, sibling competition and offspring survival with increasing litter size and parity in pigs (Sus scrofa), *Behavioral Ecology and Sociobiology*, **65(6)**, 1159-1167 **(2011)**

2. Auvray B., McEwan J.C., Newman S.A.N., Lee M. and Dodds K.G., Genomic prediction of breeding values in the New Zealand sheep industry using a 50K SNP chip, *J. Anim. Sci.*, **92(10)**, 4375–4389 **(2014)**

3. Azizian S., Effect of increasing accuracy of genomic evaluations on economic efficiency of dairy cattle breeding programmes, *Italian Journal of Animal Science*, **15(3)**, 379-385 **(2016)**

4. Badke Y.M., Bates R.O., Ernst C.W., Schwab C. and Steibel J.P., Estimation of linkage disequilibrium in four US pig breeds, *BMC Genomics*, **13**, 24 **(2012)**

5. Baloche G., Legarra A., Sallé G., Larroque H., Astruc J.M., Robert-Granié C. and Barillet F., Assessment of accuracy of genomic prediction for French Lacaune dairy sheep, *J. Dairy Sci.*, **97(2)**, 1107–1116 **(2014)**

6. Baruch E. and Weller J.I., Incorporation of genotype effects into animal model evaluations when only a small fraction of the population has been genotyped, *Animal: an International Journal of Animal Bioscience*, **3(1)**, 16-23 **(2009)**

7. Berry D.P., Bastiaansen J.W.M., Veerkamp R.F., Wijga S., Wall E., Berglund B. and Calus M.P.L., Genome-wide associations for fertility traits in Holstein–Friesian dairy cows using data from experimental research herds in four European countries, *Animal*, **6(8)**, 1206-1215 **(2012)**

8. Boichard D., Genomic selection in domestic animals: Principles, applications and perspectives, *Comptes Rendus Biologies*, **339(7-8)**, 274-277 **(2016)**

9. Bolormaa S., Multivariate analysis of a genome-wide association study in dairy cattle, *Journal of Dairy Science*, **93(8)**, 3818-3833 **(2010)**

10. Brito L.F., Jafarikia M.D., Grossi A., Kijas J.W., Porto-Neto L.R., Ventura R.V., Salgorzaei M. and Schenkel F.S.,

Characterization of linkage disequilibrium, consistency of gametic phase and admixture in Australian and Canadian goats, *BMC Genet.*, **16**, 67 **(2015)**

11. Calus M.P.L., Predicted accuracy of and response to genomic selection for new traits in dairy cattle, *Animal: An International Journal of Animal Bioscience*, **7(2)**, 183-191 **(2013)**

12. Carillier C., Larroque H. and Robert-Granié C., Comparison of joint versus purebred genomic evaluation in the French multi-breed dairy goat population, *Genet. Sel. Evol.*, **46**, 67 **(2014)**

13. Carillier C., Larroque H., Palhière I., Clément V., Rupp R. and Robert-Granié C., A first step toward genomic selection in the multi-breed French dairy goat population, *J. Dairy Sci.*, **96(11)**, 7294–7305 **(2013)**

14. Cowling W.A., Using the Animal Model to Accelerate Response to Selection in a Self-Pollinating Crop, *G3 (Bethesda, Md.)*, **5(7)**, 1419-1428 **(2015)**

15. Daetwyler H.D., Kemper K.E., van der Werf J.H.J. and Hayes B.J., Components of the accuracy of genomic prediction in a multi-breed sheep population, *J. Anim. Sci.*, **90(10)**, 3375–3384 **(2012a)**

16. Daetwyler H.D., Swan A.A., Van Der Werf J.H. and Hayes B.J., Accuracy of pedigree and genomic predictions of carcass and novel meat quality traits in multi-breed sheep data assessed by cross-validation, *Genet. Sel. Evol.*, **44**, 33 **(2012b)**

17. De Koning D.J., Meuwissen on genomic selection, *Genetics*, **203(1)**, 5–7 **(2016)**

18. De Rochambeau H., Licois D., Gidenne T., Verdelhan S., Coudert P. and Elsen J.M., Genetic variability of the resistance for three types of enteropathy in the growing rabbit, *Livest Sci*, **101**, 110–115 **(2006)**

19.de Roos A.P., Hayes B.J., Spelman R.J. and Goddard M.E., Linkage disequilibrium and persistence of phase in Holstein-Friesian, Jersey and Angus cattle, *Genetics*, **179(3)**, 1503–1512 **(2008)**

20. Dekkers J., Opportunities for genomic selection with redesign of breeding programs, *J Anim Sci*, **87(Suppl E)**, 275 **(2009)**

21. Dekkers J.C.M., Commercial application of marker- and gene-assisted selection in livestock: strategies and lessons, *Journal of Animal Science*, **82(E-Suppl)**, E313-328 **(2004)**

22. Dekkers J.C.M., Marker-assisted selection for commercial crossbred performance, *Journal of Animal Science*, **85(9)**, 2104-2114 **(2007)**

23. Dekkers J.C.M., Application of Genomics Tools to Animal Breeding, *Current Genomics*, **13(3)**, 207-212 **(2012)**

24. Deng T., Four novel polymorphisms of buffalo INSIG2 gene are associated with milk production traits in Chinese buffaloes, *Molecular and Cellular Probes*, **30**, 294-299 **(2016)**

25. der Werf J.H.J. and Hayes B.J., Accuracy of estimated genomic breeding values for wool and meat traits in a multi-breed sheep population, *Anim. Prod. Sci.*, **50(12)**, 1004–1010 **(2010)**

26. Elzo M.A., Lamb G.C., Johnson D.D., Thomas M.G., Misztal I., Rae D.O., Martinez C.A., Wasdin J.G. and Driver J.D., Study on Genomic-polygenic evaluation of Angus-Brahman multibreed cattle for feed efficiency and post weaning growth, *J. Anim. Sci.*, **90**, 2488-2497 **(2012)**

27. Fan B., Development and Application of High-density SNP Arrays in Genomic Studies of Domestic Animals, *Asian Australas. J. Anim. Sci*, **23(7)**, 833-847 **(2010)**

28. FAO (Food and Agriculture Organization of the United Nations), No World Agriculture: Towards 2030/2050—Interim Report, Food and Agriculture Organization of the United Nations, Rome, Italy **(2006)**

29. Fernandes Junior G.A., Genomic prediction of breeding values for carcass traits in Nellore cattle, *Genetics, Selection, Evolution: GSE*, **48**, 7 **(2016)**

30. Finlay E.K., Berry D.P., Wickham B., Gormley E.P. and Bradley D.G., A genome wide association scan of bovine tuberculosis susceptibility in Holstein-Friesian dairy cattle, *PLoS One*, **7(2)**, e30545 **(2012)**

31. Garner J.B., Genomic Selection Improves Heat Tolerance in Dairy Cattle, *Scientific Reports*, **6**, 34114 **(2016)**

32. Gray K.A., Vacirca F., Bagnato A., Samoré A.B., Rossoni A. and Maltecca C., Genetic evaluations for measures of the milk-flow curve in the Italian Brown Swiss population, *J. Dairy Sci.*, **94(2)**, 960-70 **(2011)**

33. Guo G., Zhou Z., Wang Y., Zhao K., Zhu L., Lust G., Hunter L., Friedenberg S., Li J., Zhang Y., Harris S., Jones P., Sandler J., Krotscheck U., Todhunter R. and Zhang Z., Canine hip dysplasia is predictable by genotyping, *Osteoarthr Cartil*, **19**, 420–429 **(2011)**

34. Gyovai P., Nagy I., Gerencser Z., Matics Z., Radnai I., Donko T., Bokor A., Farkas J. and Szendro Z., Genetic parameters for litter weight, average daily gain and thigh muscle volume measured by in vivo Computer Tomography technique in Pannon White rabbits, *Livest Sci.,* **144**, 119–123 **(2012)**

35. Habier D., Tetens J., Seefried F.R., Lichtner P. and Thaller G., The impact of genetic relationship information on genomic breeding values in German Holstein cattle, *Genet. Sel. Evol.*, **42**, 5 **(2010)**

36. Hayes B.J., Invited review: Genomic selection in dairy cattle: progress and challenges, *Journal of Dairy Science*, **92(2)**, 433-443 **(2009)**

37. Henderson C.R., Sire evaluation and genetic trends, *Journal of Animal Science*, **1973**, 10-41 **(1973)**

38. Henryon M., Berg P. and Sørensen A.C., Animal-breeding schemes using genomic information need breeding plans designed to maximise long-term genetic gains, *Livestock Science*, **166**, 38-47 **(2014)**

39. Hiendleder S., Bauersachs S., Boulesteix A., Blum H., Arnold G.J. and Fröhlich T., Functional genomics: tools for improving farm animal health and welfare, *Revue Scientifique et Technique (International Office of Epizootics)*, **24(1)**, 355-77 **(2005)**

40. Hong Thien Van, Thanh Truc Do, Thao Nguyen Luu, Van Son Le and Van Dat Doan, Chemical constituents and antibacterial activities of essential oils from aerial parts of three Limnophila species (Scrophulariaceae) in Southern Vietnam, *Res. J. Chem. Environ.*, **25(4)**, 12-19 **(2021)**

41. Ibañez-Escriche N. and Gonzalez-Recio O., Review: Promises, pitfalls and challenges of genomic selection in breeding programs, *Spanish Journal of Agricultural Research*, **9(2)**, 404-413 **(2011)**

42. Jiang L., Genome wide association studies for milk production traits in Chinese Holstein population, *PloS One*, **5(10)**, e13661 **(2010)**

43. Ke X., Kennedy L.J., Short A.D., Seppälä E.H., Barnes A., Clements D.N., Wood S.H., Carter S.D., Happ G.M., Lohi H. and Ollier W.E.R., Assessment of the functionality of genome-wide canine SNP arrays and implications for canine disease association studies, *Anim Genet*, **42**, 181–190 **(2011)**

44. Kemper K.E. and Goddard M.E., Understanding and predicting complex traits: knowledge from cattle, *Human Molecular Genetics*, **21(R1)**, R45-51 **(2012)**

45. Kijas J.W., Porto-Neto L., Dominik S., Reverter A., Bunch R., McCulloch R. and Hayes B.J., Linkage disequilibrium over short physical distances measured in sheep using a high-density SNP chip, *Anim. Genet.*, **45(5)**, 754–757 **(2014)**

46. Knap P., Pig breeding goals in competitive market, Proceedings, 10th World Congress of Genetics Applied to Livestock Production **(2014)**

47. Knol E.F., Nielsen B. and Knap P.W., Genomic selection in commercial pig breeding, *Animal Frontiers*, **6(1)**, 15 **(2016)**

48. Koenen E.P.C. and Aldridge L.I., Testing and genetic evaluation of sport horses in an international perspective, 7th WCGALP, 19-23 August 2002, Montpellier, France **(2002)**

49. Konig S., Simianer H. and Willam A., Economic evaluation of genomic breeding programs, *Journal of Dairy Science*, **92(1)**, 382-391 **(2009)**

50. Kuehn L.A., Keele J.W., Bennett G.L., McDaneld T.G., Smith T.P.L., Snelling W.M., Sonstegard T.S. and Thallman R.M., Predicting breed composition using breed frequencies of 50,000 markers from the US Meat Animal Research Center 2,000 Bull Project, *J. Anim. Sci.*, **89**, 1742–1750 **(2011)**

51. Larroque H., Barillet F., Baloche G., Astruc J.M., Buisson D., Shumbusho F. and Clément V., Toward genomic breeding programs in French dairy sheep and goats, In Proc. 10th World Congress on Genetics Applied to Livestock Production **(2014)**

52. Legarra A., Aguilar I. and Misztal I., A relationship matrix including full pedigree and genomic information, *J. Dairy Sci.*, **92(9)**, 4656–4663 **(2009)**

53. Legarra A., Baloche G.F., Barillet J.M., Astruc C., Soulas X., Aguerre F., Arrese L., Mintegi M., Lasarte F., Maeztu I., Beltrán de Heredia and Garte E., Within-and across-breed genomic predictions and genomic relationships for Western Pyrenees dairy sheep breeds Latxa, Manech and Basco-Bearnaise, *J. Dairy Sci.*, **97(5)**, 3200–3212 **(2014)**

54. Li H.D., Bao Z.M. and Sun X.W., Genomic selection and its application, *Yi chuan = Hereditas / Zhongguo yi chuan xue hui bian ji*, **33(12)**, 1308-1316 **(2011)**

55. Legarra A., Duchemin S.I., Colombani C., Baloche G., Larroque H., Astruc J.M., Barillet F., Robert-Granié C. and Manfredi E., Genomic selection in the French Lacaune dairy sheep breed, *J. Dairy Sci.*, **95(5)**, 2723-33 **(2011)**

56. Lillehammer M., Meuwissen T.H.E. and Sonesson A.K., Genomic selection for maternal traits in pigs, *Journal of Animal Science*, **89(12)**, 3908-3916 **(2011)**

57. Lopes M.S., Using markers with large effect in genetic and genomic predictions, *Journal of Animal Science*, **95(1)**, 59-71 **(2017)**

58. Lund M.S., A common reference population from four European Holstein populations increases reliability of genomic predictions, *Genetics Selection Evolution: GSE*, **43**, 43 **(2011)**

59. Meuwissen T. and Goddard M., Accurate prediction of genetic values for complex traits by whole-genome resequencing, *Genetics*, **185(2)**, 623-631 **(2010)**

60. Meuwissen T., Hayes B. and Goddard M., Genomic selection: A paradigm shift in animal breeding, *Animal Frontiers*, **6(1)**, 6 **(2016)**

61. Meuwissen T.H.E. and Goddard M.E., The use of marker haplotypes in animal breeding schemes, *Genetics, Selection, Evolution: GSE*, **28(2)**, 161-176 **(1996)**

62. Misztal I., Legarra A. and Aguilar I., Computing procedures for genetic evaluation including phenotypic, full pedigree and genomic information, *J. Dairy Sci.*, **92(9)**, 4648–4655 **(2009)**

63. Montaldo H.H., Opportunities and challenges from the use of genomic selection for beef cattle breeding in Latin America, *Animal Frontiers*, **2(1)**, 23-29 **(2012)**

64. Mucha S. et al, Estimation of genomic breeding values for milk yield in UK dairy goats, *J. Dairy Sci.*, **98(11)**, 8201–8208 **(2015)**

65. Neves H.H.R., Accuracy of genomic predictions in Bos indicus (Nellore) cattle, *Genetics, Selection, Evolution: GSE*, **46**, 17 **(2014)**

66. Oliete J.Q., Application of Genome- Wide Single Nucleotide Polymorphism Arrays to Understanding Dog Disease and Evolution, Ph.D. thesis, University of Barcelona, Barcelona **(2012)**

67. Parker H.G. and Ostrander E.A., Canine genomics and genetics: running with the pack, *PLoS Genet*, **1**, e58 **(2005)**

68. Petersen J.L., Mickelson J.R., Rendahl A.K., Valberg S.J. andersson L.S., Axelsson J., Bailey E., Bannasch D., Binns M.M., Borges A.S., Brama P., da C^amara Machado A., Capomaccio S., Cappelli K., Cothran E.G., Distl O., Fox-Clipsham L., Graves K.T., Gu_erin G., Haase B., Hasegawa T., Hemmann K., Hill E.W., Leeb T., Lindgren G., Lohi H., Lopes M.S., McGivney B.A., Mikko S., Orr N., Penedo M.C.T., Piercy R.J., Raekallio M., Rieder S., Røed K.H., Swinburne J., Tozaki T., Vaudin M., Wade C.M. and McCue M.E., Genome-wide analysis reveals selection for important traits in domestic horse breeds, *PLoS Genet*, **9**, e1003211, doi:10.1371/journal. pgen.1003211 **(2013)**

69. Pimentel E.C.G. and Konig S., Genomic selection for the improvement of meat quality in beef, *Journal of Animal Science*, **90(10)**, 3418-3426 **(2012)**

70. Plieschke L., Systematic genotyping of groups of cows to improve genomic estimated breeding values of selection candidates, *Genetics, Selection, Evolution: GSE*, **48(1)**, 73 **(2016)**

71. Pryce J.E. and Daetwyler H.D., Designing dairy cattle breeding schemes under genomic selection: A review of international research, *Animal Production Science*, **52(2-3)**, 107-114 **(2012)**

72. Rabier C.E., On the Accuracy of Genomic Selection, *PloS One*, **11(6)**, e0156086 **(2016)**

73. Ribaut J.M. and Ragot M., Marker-assisted selection to improve drought adaptation in maize: the backcross approach, perspectives, limitations and alternatives, *Journal of Experimental Botany*, **58(2)**, 351-360 **(2007)**

74. Rohrer G.A. and Nonneman D.J., Genetic analysis of teat number in pigs reveals some developmental pathways independent of vertebra number and several loci which only affect a specific side, *Genetics, Selection, Evolution: GSE*, **49**, 4 **(2017)**

75. Ron M. and Weller J.I., From QTL to QTN identification in livestock--winning by points rather than knock-out: a review, *Animal Genetics*, **38(5)**, 429-439 **(2007)**

76. Rothschild M.F. and Ruvinsky A., Marker-Assisted Selection for Aquaculture Species, In Aquaculture Genome Technologies, Blackwell Publishing Ltd., 199-214 **(2007)**

77. Sax K., The Association of Size Differences with Seed-Coat Pattern and Pigmentation in PHASEOLUS VULGARIS, *Genetics*, **8(6)**, 552-560 **(1923)**

78. Schneider J.F., Rempel L.A. and Rohrer G.A., GWAS of swine farrowing traits: Genetic and genomic parameter estimates, *J. Anim. Sci.*, (In Press) **(2012)**

79. Schröder W. et al, A genome-wide association study for quantitative trait loci of show-jumping in Hanoverian warmblood horses, *Anim Genet*, **43**, 392–400 **(2012)**

80. Shumbusho F., Potential benefits of genomic selection on genetic gain of small ruminant breeding programs, *Journal of Animal Science*, **91(8)**, 3644-3657 **(2013)**

81. Shumbusho F., Economic evaluation of genomic selection in small ruminants: a sheep meat breeding program, *Animal*, **10(6)**, 1033-1041 **(2015)**

82. Sitzenstock F., Efficiency of genomic selection in an established commercial layer breeding program, *Genetics Selection Evolution*, **45(1)**, 29 **(2013)**

83. Snelling W.M. et al, Genomewide association study of growth in crossbred beef cattle, *J. Anim. Sci.*, **88**, 837–848 **(2010)**

84. Snelling W.M. et al, Partial genome evaluation of post weaning feed intake and efficiency of crossbred beef cattle, *J. Anim. Sci.*, **89**, 1731–1741 **(2011)**

85. Sonesson A.K., Meuwissen T.H.E. and Goddard M.E., The use of communal rearing of families and DNA pooling in aquaculture genomic selection schemes, *Genetics, Selection, Evolution: GSE*, **42**, 41 **(2010)**

86. Stock K. and Reents R., Genomic selection: Status in different species and challenges for breeding, *Reproduction in Domestic Animals*, **48(Suppl. 1)**, 2-10 **(2013)**

87. Tusell L., Genome-enabled methods for predicting litter size in pigs: a comparison, *Animal: An International Journal of Animal Bioscience*, **7(11)**, 1739-1749 **(2013)**

88. Van Eenennaam A.L., Applied animal genomics: results from the field, *Annual Review of Animal Biosciences*, **2**, 105-139 **(2014)**

89. Van Grevenhof E.M., Van Arendonk J.A.M. and Bijma P., Response to genomic selection: The Bulmer effect and the potential of genomic selection when the number of phenotypic records is limiting, *Genet Sel Evol*, **44**, 26 **(2012)**

90. Van Raden P.M., Invited review: reliability of genomic predictions for North American Holstein bulls, *Journal of Dairy Science*, **92(1)**, 16-24 **(2009)**

91. Ventura R.V., Assessing accuracy of imputation using different SNP panel densities in a multi-breed sheep population, *Genetics, Selection, Evolution: GSE*, **48(1)**, 71 **(2016)**

92. Wang C., Accuracy of genomic prediction using an evenly spaced, low-density single nucleotide polymorphism panel in broiler chickens, *Poultry Science*, **92(7)**, 1712-23 **(2013)**

93. Wells D., Misica P. and Tervit H., Future opportunities in livestock production and biomedicine from advances in animal cloning, Proceedings of the New Zealand Society of Animal Production, **58**, 32-35 **(1998)**

94. Wiggans G.R., Selection of single-nucleotide polymorphisms and quality of genotypes used in genomic evaluation of dairy cattle in the United States and Canada, *Journal of Dairy Science*, **92(7)**, 3431-3436 **(2009)**

95. Wiggans G.R., Van Raden P.M. and Cooper T.A., The genomic evaluation system in the United States: Past, present, future, *Journal of Dairy Science*, **94(6)**, 3202-3211 **(2011)**

96. Wolc A., Response and inbreeding from a genomic selection experiment in layer chickens, *Genetics, Selection, Evolution: GSE*, **47**, 59 **(2015)**

97. Wolc A., Implementation of genomic selection in the poultry industry, *Animal Frontiers*, **6**, 23-31 **(2016)**

98. Zhou L., Consistency of linkage disequilibrium between Chinese and Nordic Holsteins and genomic prediction for Chinese Holsteins using a joint reference population, *Genetics, Selection, Evolution: GSE*, **45**, 7 **(2013)**.

*****