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Genomic Selection for Poultry Breeding and its Potential Applications in Developing Countries (Review)

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Abstract

This review article provides a general overview of advanced molecular techniques and their implementation in the genetic improvement of poultry and presents the potential application of these techniques in developing countries. Advances in molecular genetics have contributed to a significant rate of genetic progress in domestic fowl, especially for traits that are difficult to improve through conventional breeding methods. Compared to developed nations, however, the application of molecular techniques for the genetic improvement of poultry is limited in most developing countries due to a lack of infrastructure, capital, and human resources. This does not mean that it is an impossible task. To implement molecular techniques in developing countries, the potential merit of using these tools for the genetic improvement of poultry should be evaluated in terms of economic costs and benefits of the technology compared with conventional breeding. The existence of conventional genetic evaluation and selection programs is also a prerequisite, along with well-established research institutions and well-trained human resources. More important are the cooperation and partnership with academic and research institutions in developed countries to address challenges in applying molecular tools and associated infrastructures to implement genomic selection in developing countries.

Introduction

Demand for animal products has rapidly been increasing in many regions of the globe due to the growing population, rising incomes, and urbanization (FAO, 2018). As the world's population grows by 80 million people per annum (Preisinger, 2012), and is forecasted to hit 8.6 billion by 2030 (FAO, 2018), meeting the growing demand for animal products is one of the most significant challenges with current farm animal production (Eggen, 2012). Income growth and urbanization also result in shifting consumption patterns towards animal products and value-added foods (Hoffmann, 2005; FAO, 2011). Demand is significant in the poorest countries of the developing world (Rothschild and Plastow, 2014), where the livestock sector cannot provide quality and sufficient animal products for consumers because of its limited production efficiency. Poultry is one of the livestock subsectors in meeting these demands, as it offers affordable and high-quality proteins.

To date, genetic improvement of economically important traits in domestic animals has conventionally been based on phenotypic information (Boichard *et al*., 2016). The selection index and best linear unbiased prediction (BLUP) mixed linear methodologies are employed to accurately estimate the breeding values (BVs) of selection candidates based on phenotypic information of individuals and their relatives (Meuwissen *et al*., 2016). This method has contributed to a significant genetic progress in domestic fowl and livestock species, especially in easily recorded traits with moderate or high heritability. However, problems occur for hard to measure, low heritable, and measured later in life traits because the process of obtaining phenotypic information for those traits is less precise, costly, and

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time-consuming (Muir, 2003; Goddard and Hayes, 2007). Advances in molecular genetics, thereby the possible benefits of using markers linked to genes of interest (i.e., information at the DNA level), would create more genetic progress than genetic changes based on phenotypic information alone (Ruane and Sonnino, 2007; Dekkers, 2012; Meuwissen *et al*., 2016).

Advances in molecular genetics allow the use of genetic markers to identify genes or genomic regions that control traits of interest, that is, so-called quantitative trait loci (QTL). Consequently, the detected QTL could be utilized in marker-assisted selection (MAS) to enhance genetic progress (Dekkers, 2012; Heidaritabar *et al*., 2014; Heidaritabar, 2016). Despite the successful implementation of MAS for traits with a simple genetic determinism, its application has been practically limited in many more complex situations (Boichard *et al*., 2016). The emphasis has shifted to a variant of MAS, genomic selection, an alternative approach proposed by Meuwissen *et al*. (2001). Unlike MAS, which uses only a few detected QTLs, genomic selection (GS) uses a very huge number of genome-wide markers that potentially explain all the genetic variance (Goddard and Hayes, 2007; Toro, 2011). However, genomic technologies have not yet been applied to improve poultry (Psifidi *et al*., 2016) and other livestock species (Rothschild and Plastow, 2014; Mrode *et al*., 2018) in developing countries. This review provides a general overview of genomic selection and its implementation in the genetic improvement of poultry and presents its potential application in developing countries.

Advances in molecular genetics: From conventional selection to GS

Genetic improvement through conventional methods, which applies BLUP and uses information on phenotypes and pedigrees to predict BVs, has been very successful for traits with moderate or high heritability that can be measured in all selection candidates (Goddard and Hayes, 2007; Wolc, 2014). For instance, a substantial amount of genetic improvement has been obtained in body weight gain in the broilers, which can be measured on all selected candidates and has a moderate heritability (Bijma and Bovenhuis, 2009). However, costly phenotyping investments are required for traits measured in both sexes, hard-to-measure or low-heritable traits (Boichard *et al*., 2016) as well as for routinely recording phenotypes (Dekkers, 2012). Resistance to ascites is one of the traits mentioned as that is difficult to improve using conventional selection due to complicated and expensive phenotyping (Bijma and Bovenhuis, 2009).

Since most of the traits of interest, such as egg production and quality, are measurable only in mature females (sex-limited traits), the egg layer industry is particularly challenged (Fulton, 2008). Although both male and female birds contribute gene variants for these traits, a direct measurement can only be done in female birds (Fulton, 2008). For traits only recorded on females, birds are either required to be sacrificed (e.g., carcass quality traits) or accessible only under production conditions (e.g., disease resistance). For such traits, birds are indirectly selected on the genetic merit of their sisters and daughters (Muir, 2003; Fulton, 2008). This process can be more inaccurate, costly, and time-consuming than directly selecting birds based on their performance. Likewise, traits of economic importance in poultry, such as egg number, body weight, and feed efficiency are controlled by the combined effects of multiple genes and environmental factors (Muir, 2003). Environmental factors can affect genetic progress since genetically superior birds under poor environmental conditions would be culled, but birds would be retained for breeding if the reverse is the case (Muir, 2003). In other words, under poor environmental conditions, environmental variation due to inaccurate trait information can be far larger than the genetic variation that is being measured (Fulton, 2008).

Molecular genetics not only accelerates genetic gains in livestock but also helps address these challenges (Hayes *et al*., 2013). With sex-limited traits, for instance, molecular genetics allows direct selection on male birds (Fulton, 2008). Advances in molecular genetics also offer an opportunity to measure traits of selection candidates early in life (Dekkers, 2012). As DNA directs the trait expression in the birds early in life (i.e., at hatch), it is possible to measure genetic variation at day old than at later age (Fulton, 2008). Furthermore, problems caused by environment effects can be avoided as advances in molecular techniques allow selection to be applied directly to the genes themselves (Fulton, 2008). Thus, it will be necessary to address the potential challenges associated with conventional selection methods by fully exploiting molecular genetic techniques that allow an accurate estimate of the BVs of selection candidates.

Genetic markers and QTL detection

Moving from selection based on phenotypic information towards genetic selection based on genotype has been evident for several decades due to the potential benefits of using markers linked to genes of interest in breeding programs (Ruane and Sonnino, 2007). In the 1950s and the 1960s, studies conducted to detect QTL in livestock have used blood group polymorphisms, proteins, or enzymes as genetic markers (Weller, 2016). However, these studies failed to succeed due to the limited number of available genetic markers (Ruane and Sonnino, 2007). The breakthrough occurred with the advent of molecular

genetics, which enables the detection of DNA-level genetic markers in animal species (Flint and Woolliams, 2008; Weller, 2016). Different types of genetic markers, such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNA (RAPDs) markers, amplified fragment length polymorphisms (AFLPs), microsatellites, minisatellites, DNA sequence, single strand conformation polymorphism (SSCPs), and single nucleotide polymorphisms (SNPs) have become available to study the genetic architecture of traits and enabled the building of genetic maps for most important livestock species by locating genomic regions associated with quantitative traits (van Arendonk and Bovenhuis, 2003; Toro, 2011; Blasco and Toro, 2014; Wolc *et al*., 2014).

In order to use genetic markers to detect genes or QTLs, the relative positions of the genetic markers on the entire genome need to be known. Determining the relative position of markers is called "mapping" or "map development". Two types of maps are distinguished: linkage map, which shows the relative positions of loci on a chromosome (distance between markers) based on recombination events between the markers, and a physical map, which reflects the distance between loci in terms of base pairs. Morgan or centiMorgan (cM), after the American geneticist Thomas Hunt Morgan, is used as the basic unit for map distance (*d*). Using genomic markers, several QTLs have been mapped to better understand the passing on of chromosomal segments from parents to offspring and to trace if individuals that inherited alternative chromosomal segments differ for the quantitative trait. Two basic experimental designs are used to detect QTL (Toro, 2011; Blasco and Toro, 2014). In the first experimental design, linkage disequilibrium (LD) between markers and QTL generated by crossing two inbred lines or breeds is used. The crossbred animals (F1) are then either backcrossed to one of the parents or intercrossed to produce F2 crosses. The within-family LD, a design that is especially suitable for commercial populations which comprise large half-sib families (e.g., dairy cattle), is mainly used in the second design (Toro, 2011; Blasco and Toro, 2014).

Marker-assisted selection

Identifying genetic markers that are physically located alongside or even within genes of interest motivated MAS research in domestic animals (Ruane and Sonnino, 2007; Toro, 2011; Blasco and Toro, 2014; Boichard *et al*., 2016). MAS is a method of directly selecting regions of the genome influencing traits of economic importance (Fulton, 2012). In other words, animals can be selected for the phenotype of interest using markers that have a statistical association with a phenotypic trait. As noted by Toro (2011) and Blasco and Toro (2014), MAS is a three-step process. The first phase detects one or more marker associated with QTLs (i.e., indirect or non-functional genetic markers). The second stage determines the underlying gene (direct marker or causal mutation, i.e., genetic loci that have a known function ascribed to them). The third phase increases the frequency of the favorable allele, either using selection or introgression methods. In other words, if the regions were once identified, genetic markers could be used to differentiate those individuals with higher performance, and selection could be practiced at an early age (Fulton, 2012).

It is hard to find and prove direct markers for quantitative traits (van Arendonk and Bovenhuis, 2003), but they give direct information about genotype for the QTL (Dekkers and Hospital, 2002). Nevertheless, the linkage between indirect markers, which are abundant across the genome, and QTL can be shown by empirical associations of marker genotypes with trait phenotype. Therefore, the linkage between the marker and the QTL is essential to use indirect markers for QTL mapping and selection. According to Dekkers and Hospital (2002) and van Arendonk and Bovenhuis (2003), directed searches using candidate-gene approaches in unstructured populations and searches across the whole genome (genome scans) in specialized populations, such as F2 crosses are the two methods used to search indirect markers. Both candidate gene and QTL mapping approaches have been extensively utilized in domestic animals to discover genetic markers suitable for MAS, though their limitations are becoming apparent (Fan *et al*., 2010). Candidate-gene markers are often tightly linked to the QTL because they focus on polymorphisms in genes that are assumed to affect the trait (Dekkers and Hospital, 2002). Fan *et al*. (2010) noted that the regions with identified QTL are generally large, and further fine mapping is necessary. Also, the consistency of results from QTL mapping is often limited. Genome-wide association study (GWAS) is one of the most promising approaches to overcome these limitations (Fan *et al*., 2010). With genome scans thus, the entire DNA of an animal is searched systematically to identify only regions of the chromosomes that affect the trait (van Arendonk and Bovenhuis, 2003).

The success of molecular genetics for genetic improvement (MAS) is influenced by the linkage between the markers and genes of interest (Ruane and Sonnino, 2007). Pieces of literature distinguished three kinds of relationships: the marker is located within the gene of interest, the marker is in linkage disequilibrium (LD) with genes of interest across the population, and the marker is not in LD (i.e., it is in linkage equilibrium [LE]) with genes of interest throughout the whole population. In the former situation, one can refer to gene-assisted selection (GAS; Ruane and Sonnino, 2007). Population-wide

LD (i.e., the tendency of certain combinations of alleles to be inherited together) can be found when markers and QTL are very close to each other and/or when crosses between lines/breeds have been produced in recent generations. Selection using LD and LE can be referred to as LD-MAS and LE-MAS, respectively (Ruane and Sonnino, 2007). Selection using LE markers is the most difficult situation for applying MAS (Ruane and Sonnino, 2007). Compared to conventional selection methods, MAS has been successfully implemented to improve traits with a simple genetic determinism (Boichard *et al*., 2016). However, most of the selected traits are determined by a large number of genes, each with minor effects on phenotype (Meuwissen *et al*., 2016). MAS can be applied to support existing conventional breeding programs (Ruane and Sonnino, 2007).

Bijma and Bovenhuis (2009) argue that very few (if any) applications of MAS in commercial poultry breeding exist. The application of MAS was practically limited in commercial poultry breeding because most QTL mapping experiments are not very large and could only detect genes of large effect; for most QTL, the evidence cannot be fully informative and conclusive (Bijma and Bovenhuis, 2009; Fulton, 2012). The limited utilization of the MAS strategy is also attributed to the lack of genetic markers linking to QTL with significant effects and the expense of genotyping (Fan *et al*., 2010). Consequently, Meuwissen *et al*. (2001) introduced a novel approach of GS by which the BV (genomic estimated breeding value, GEBV) could be estimated from genetic markers covering the whole genome without having a precise knowledge of where specific genes are located on the genome. GS methodology, along with the identification of many thousands of SNPs (a point mutation of a single nucleotide), and SNP-chip genotyping technologies that reduce the genotyping costs of all these SNPs have resulted in the current widespread use of DNA information (Meuwissen *et al*., 2016). GS might become the most fundamental change to breeding and genetics in agricultural science due to the application of SNP arrays (Fan *et al*., 2010).

Genomic selection

Starting in the 21st century, rapid advances in molecular genetics, along with statistical and computational methods, have enabled the establishment of GS as a new tool to obtain a substantial amount of genetic gain in animal breeding (Stock and Reents, 2013; Heidaritabar, 2016). Genomic selection, also termed genomic evaluation/prediction or whole-genome selection, is a form of MAS, where thousands of SNPs covering the whole genome (instead of localizing QTL regions) are used to predict GEBV of animals, assuming that abundant SNPs scattered throughout the genome and LD relationships between SNPs and QTL is available (Goddard and Hayes, 2007; Bijma and Bovenhuis, 2009; Fan *et al*., 2010; Tixier-Boichard *et al*., 2012). Coupled with the advances in molecular genetics, conducive environment for whole-genome sequencing of several domestic species, collection of SNP libraries, and the development of informative and affordable SNP panels for multiple animal species have been created by the foundation of international consortia (Stock and Reents, 2013).

Several authors (Goddard and Hayes, 2007; Toro, 2011; Wolc *et al*., 2015; Boichard *et al*., 2016, Meuwissen *et al*., 2016) indicated that GS is a two-step process. In the first step, the reference or training population (i.e., a large number of animals with both phenotypes and marker genotypes) is used to estimate marker or SNP effects. Here, individual animals are genotyped with many markers (typically more than 10,000 SNPs) that are located across the whole genome. In the second step, these SNP effects are applied to selection candidates (also called the population) with marker genotype information but without known phenotypes. Then, the genomic EBV (GEBV) of selection candidates is estimated by combing their genotypes with the estimated marker effects. GS does not seek to identify genes or QTL regions, but simply estimates associations between chromosomal regions of interest in the reference population and uses these associations to predict the BVs of individuals for selection (Bijma and Bovenhuis, 2009). The practical application of this approach is very demanding in terms of both the number of genotyped individuals, and the number of markers in the genome (Boichard *et al*., 2016).

In contrast to BLUP-based conventional selection, the primary benefit of GS is to enhance genetic progress through a more precise prediction of GEBV compared with the accuracy of EBV (Wolc, 2014; Heidaritabar, 2016). It is also noted that GS does not require information from the pedigree population, which by contrast is essential for conventional EBV, and that the selection candidates are not necessarily trait recorded (Meuwissen *et al*., 2016). This approach identifies desirable DNA fragments by using commercial (non-pedigree) populations that may be selected for, within a nucleus (Flint and Woolliams, 2008). As the elite breeding population (i.e., selection candidates) is not necessarily trait recorded, GS can decrease the number of progenies to be phenotyped (Fulton, 2012). Potential benefits of GS also include identifying the relationship between parents and offspring, minimizing the number of individuals selected for breeding, decreasing the generation interval, overcoming age and sex limitations for traits, and a direct link between the genetic evaluation and the genome (Flint and Woolliams, 2008; Fulton, 2012).

Genomic selection in poultry breeding

High-throughput genotyping techniques make the use of high-density SNP possible in domestic fowl and other domestic species (Weller, 2016). Compared to dairy cattle breeding, where GS using high-density SNP panels was first implemented (Wolc *et al*., 2016), rapid genetic progress can be achieved in poultry breeding because of the short generation interval and a relatively large flock size (Wolc, 2014). GS is only possible with the development of high-density SNP chips, which enable rapid, massive, and relatively inexpensive genotyping (Wolc *et al*., 2016). The chicken genome sequencing projects (International Chicken Genome Sequencing Consortium, 2004) have enabled the availability of many high-density SNPs, which cover all major chromosomes, for GS to be used in chicken breeding programs. According to Wolc *et al*. (2016), the first chicken SNP chip had only 3,000 (3K) SNPs, which was insufficient. Due to a successive development in designing high-density chips, the density of SNP panels has increased from 6K to 12K, 42K, 60K and ultimately to 600K SNPs, which is anticipated to have a profound effect on the accuracy of GEBV prediction (Wolc *et al*., 2014; 2016). As a consequence, many poultry breeding companies have included this marker information for genetic improvement within their breeding programs of both layers and broilers (Fulton, 2012). Yet, not all of the results have been made available to the public, and this is an indication of commercialization impact on chicken breeding (Fulton, 2012; Stock and Reents, 2013).

Besides, the genotyping costs were reduced from $1 during the 1990s to below $0.01 per genotype by 2008. These costs were reduced further to approximately $0.002 per genotype within less than 10 years (Weller, 2016). Wolc *et al*. (2014) added that the cost required to determine a genotype at a single locus dropped from approximately $1.50 in 2010 for a microsatellite marker to less than $0.0005 per SNP on a high-density SNP chip. Such a decrease in genotyping costs indicates that high-density chips, and in the end, the whole genome would likely increase in availability. Likewise, the number of available genotypes for chicken genome sequencing has increased from 200 individuals per line during the early stages, in 2012, to more than 50,000 birds accumulated since 2012 (Wolc *et al*., 2014). The implementation of a cost-effective strategy for GS also provided a solution for the costs of large-scale genotyping, where training individuals are genotyped with a high-density panel and selection candidates with an evenly spaced, low-density panel (Wang *et al*., 2013). These have also motivated poultry breeding companies to incorporate marker information into their breeding plans. However, GS-based breeding programs need to be re-assessed and optimized regularly because genotyping technologies and costs are rapidly changing (Wolc *et al*., 2015).

As breeding objectives in commercial poultry breeding programs often include sex-limited traits, such as egg production or eggshell quality, and many other traits (e.g. disease resistance, feed efficiency, longevity, late production, and production persistency) hard to measure and improve using conventional breeding methods, breeding strategies should be benefited substantially from GS through more accurate selection at an earlier age and within families (Stock and Reents, 2013). Genomic selection is more efficient than conventional method to improve low heritability (e.g. hatchability and viability), sex-influenced (e.g. bodyweight) and post-slaughtering (e.g. carcass quality) traits in poultry industry. For these traits, GS provides an opportunity to do direct selection on both sexes, early in life and even prior to hatch (Fulton, 2008; 2012).

In their study aimed to quantify genetic gains from GS, Wolc *et al*. (2014) evaluated both layer and broiler breeder populations. They subdivided a brown egg layer population into two sublines. One of the sublines is used for GS and the other subgroup is used as control (i.e., a subline selected based on pedigree). They compared the two sublines for 16 economically important traits reflecting egg production and quality attributes. The GS subline outperformed the subgroup selected based on pedigree in 12 out of 16 traits, and GEBVs were more accurate and persistent than estimates based on phenotypic information (pedigree-based estimates). The generation interval in the birds selected based on genomic information was halved compared to the conventionally selected group. In fact, the GS group had six generations of selection by the time the conventionally selected group had only three generations of selection. The authors also demonstrated that the prediction accuracy of GS is advantageous than conventional selection based on pedigree, measured as the correlation between phenotype adjusted for fixed effects and pedigree/genomic EBV at the point of selection. Their comparison included estimates based on pedigree from multivariate BLUP and univariate GEBVs. In this study, authors found the relative improvement from the implementation of GS in terms of selection accuracy ranged between 20 and 70 percent when animals had no phenotypic information. This suggests that GS can be successfully used in poultry breeding to maximize genetic progress.

Efficiency of genomic selection

The main goal of animal breeding is to maximize responses to selection for all traits of economic importance in the long- and short-terms (Muir, 2003; Eisen, 2007). Usually, response to selection (or the rate of genetic progress/gain) measures the effectiveness of selection (Bourdon, 2014). For any

domestic species undergoing selection, factors summarized in what is often called the key (breeders) equation for genetic change affect the response to selection (Stock and Reents, 2013; Boichard *et al*., 2016). The equation states that the rate of genetic change is directly proportional to the accuracy of selection, selection intensity, and genetic variation and is inversely proportional to the generation interval (Bourdon, 2014). This suggests that genetic gain for a given trait can be maximized by an increase in selection intensity, a more accurate prediction of the genetic merit of breeding animals, and a reduction in the generation interval (Stock and Reents, 2013). Except for genetic variation, the other three determinants of selection efficiency can be modified by GS (Boichard *et al*., 2016). The benefit of GS over conventional selection in modifying generation interval and prediction accuracy has widely been reported for dairy cattle, though the breeding structures and the biological conditions in poultry breeding programs differ in several features from those in dairy cattle breeding programs (Sitzenstock *et al*., 2013). Therefore, this subsection briefly presents how GS can modify each of the parameters that influence prediction accuracy and enhance the response to selection in poultry breeding.

Genomic-based selection can be applied at an early age because animals under selection can be evaluated and selected without information on their own phenotype or their progeny (Boichard *et al*., 2016). Therefore, GS has the potential to shorten the generation intervals and increase the accuracy of the estimation of BV compared to conventional selection, changes which can be achieved due to the potential identification of the selection candidates at an early age (Preisinger, 2012; Blasco and Toro, 2014) and reliable methods of BV prediction (GEBVs; Heidaritabar *et al*., 2014). Several studies (Wolc *et al*., 2011; Sitzenstock *et al*., 2013; Calus *et al*., 2014; Wolc *et al*., 2014; 2015; Liu *et al*., 2017) indicated that GS can substantially increase selection efficiency in poultry breeding programs. Most of the accuracy in marker-based selection increase due to improved estimation of Mendelian sampling terms (Wolc *et al*., 2011). Accuracy at selection increased when genomic data was used in addition to the phenotypic information available in the conventional selection (Sitzenstock *et al*., 2013). In the same study, a substantial reduction in generation interval was observed in the selection based on a combination of pedigree and genomic information. In their simulation study, Wolc *et al*. (2015) found that the generation interval for GS was reduced by 50 percent compared to that of the conventional selection, which indicates that GS has the potential to reduce generation interval. Since the generation interval is already short in poultry, the increased accuracy of GEBV is more significant than the reduced generation interval (Heidaritabar, 2016). Therefore, the major benefit of GS over conventional selection is based on increases in the accuracy of estimated BVs at puberty and for sex-limited traits (Wolc *et al*., 2016).

As Calus (2010) and Fan *et al*. (2010) explained, factors including the LD extent between SNPs and the QTL, the size of the reference population, the heritability of the analyzed trait, the distribution of QTL effects, and the relationship between animals in the reference population and the evaluated animals influence the accuracy of GS. For a given trait, the accuracy of GS primarily depends on the size of the reference population (i.e., used to estimate SNP effects), which in turn are used to compute the GEBV of selection candidates (Boichard *et al*., 2016). The reference population may comprise genotyped males and females and their daughters, or a combination of the two (Moniruzzaman *et al*., 2014). In GS, accuracy is also a function of the LD between SNP and causal variants, which depends on the genetic architecture of the trait and the structure of the genome (Boichard *et al*., 2016).

In conventional selection programs, due to the limitation of costs, only a modest number of animals can be tested for some traits, such as egg production in the dam line of broilers (Muir, 2003). Selecting a small number of animals is the main factor responsible for the loss of genetic diversity, which leads to substantial decreases in selection intensity (Stock and Reents, 2013). With low genotyping costs, however, large number of candidates can be selected, and as a result, higher selection intensity will be achieved. Selecting a large number of candidates also allows better use of available animal genetic resources (Boichard *et al*., 2016). When it is difficult to record the trait on the candidate itself, the evaluation can be carried out for any trait recorded in the reference population (Boichard *et al*., 2016). This would lead to the conclusion that selection intensity can be substantially increased by increasing the size of the reference population.

Methods of genomic selection

With the new SNP arrays, more SNP effects need to be predicted than using phenotyped animals (Fan *et al*., 2010). GS involves estimation of the effect of each SNP on the high-density panel using models that fit all SNP simultaneously (Dekkers, 2012). As a result, different approaches have been developed to perform genomic evaluation (Boichard *et al*., 2016). Bayesian analysis methods were initially tested to predict GEBV using dense SNPs (Fan *et al*., 2010). In these methods, the effect of each SNP was assumed to be independent and random, and the variance of SNP effects was either assumed to be constant or locus-specific; then, SNP effects were estimated by a Bayesian procedure with a prior distribution for this

variance (Fan *et al*., 2010). The same authors explained that different statistical methods for GS, such as genomic BLUP (GBLUP) and mixed regression models, have been developed, derived from either non-parametric Bayesian models or parametric methods. In genomic evaluation, these statistical tools are used to combine phenotypes with high-density marker data to predict the genetic merit of individuals with complex traits (Vitezica *et al*., 2011).

In conventional BLUP selection, BV is estimated using the phenotypes of individuals and phenotypes of their relatives. Since GBLUP is an extension of the polygenic BLUP, it is closely related to the conventional BLUP method, except those genomic relationships replace pedigree relationships (Boichard *et al*., 2016; Meuwissen *et al*., 2016). Thus, GBV is estimated using phenotypes and genomic relationships based on dense marker data covering the whole genome (Meuwissen *et al*., 2016). With GBLUP, all markers have the same weight where the model neglects the true genetic determinism of the trait, and the covariance between the GBVs of two animals is proportional to the ratio of the genome they share (Boichard *et al*., 2016). Therefore, the genomic relationship between two individuals can be calculated as the correlation between their SNP genotypes across all the markers. GBLUP is especially efficient for very polygenic traits (Boichard *et al*., 2016), and its practical advantage is that all the conventional BLUP methods and software can still be applied by replacing pedigree with genomic relationships (Meuwissen *et al*., 2016).

Several Bayesian methods (such as Bayes-A, -B, -C, -R) have been proposed, which give larger weights to SNP potentially close to causal variants or assume that only a small proportion of the variants have a non-zero effect (Boichard *et al*., 2016). These methods are also called nonlinear methods because they use prior information in BLUP of SNP effects (SNP-BLUP and implicitly GBLUP), which assumes that SNP effects are normally distributed with the same variance for every SNP (Meuwissen *et al*., 2016). The same sources pointed out that Bayesian variable selection methods outperform GBLUP in simulation studies, but the methods are somewhat superior for some traits but not totally in real data. This is confirmed by the results of Wolc *et al*. (2014), who reported that Bayesian models outperformed GBLUP for egg weight traits, which were affected by a large QTL. In contrast, GBLUP had similar, or in some validation sets, higher accuracy for other traits. The models tested in this study (such as GBLUP, BayesB, BayesCPi, and their modifications) were not different in terms of their superiority over each other. On the contrary, Bayesian variable selection and GBLUP had similar accuracies (Calus *et al*., 2014). Using Bayesian variable selection methods, Wolc *et al*. (2011) found similar accuracies for methods that assume equal variance for all SNP, such as GBLUP and those that allow differential weighting and shrinkage of SNP effects.

Although GS models (such as Bayesian and GBLUP) have demonstrated advances in accuracy over pedigree-based conventional methods, they are inefficient in solving the problems related to low accuracy for a limited number of records and traits with low heritability (Wolc *et al*., 2014). As not all individuals with phenotypic information are genotyped (thereby, a smaller number of genotyped individuals) in GBLUP, the information from non-genotyped individuals can be summarized in pseudo-observations, a projection of the phenotypes of individuals close to the genotyped one, for genotyped animals (Vitezica *et al*., 2011; Wolc *et al*., 2011; Legarra *et al*., 2014; Misztal and Legarra, 2017). This multiple-step GBLUP is likely suboptimal for genomic prediction (Vitezica *et al*., 2011). Alternatively, single-step GBLUP (ssGBLUP), which uses a combined pedigree and genomic covariance matrix, where both genotyped and non-genotyped animals can be incorporated, was developed (Christensen and Lund, 2010). However, these methods are computationally demanding and require careful scaling of the genomic relationship matrix to be consistent with the pedigree-based relationship matrix (Wolc *et al*., 2011).

Chen *et al*. (2011) compared BLUP, ssGBLUP, and a multi-step procedure (Bayes A) in broiler chickens using all phenotypic data in the former two methods but only those of the genotyped individuals in the latter. For genotyped birds, Bayes A and ssGBLUP gave similar accuracies. The accuracy of Bayes A and ssGBLUP was similar for traits of high heritability and up to 50 percent better than BLUP. However, they found that ssGBLUP gave 4 to 6 times more accuracy than Bayes A and 50 percent better than BLUP for low heritable traits. In their review, Wolc *et al*. (2016) discussed several studies that evaluated the accuracies of GEBVs in layers and broilers for traits of economic importance using different methods (such as single-step methods, Bayesian methods, Bayesian LASSO, non-parametric methods, methods that dissect genetic variance into that from coding and non-coding regions, and approaches that capitalize on and include annotation information). They suggested that GEBVs were more accurate than pedigree-based EBVs in all the studies they have reviewed, but there was no clear superiority among the different genomic-based methods across traits and populations. However, the use of genomic-based methods was particularly promising for the traits difficult and expensive to measure, measured late in life, or sex-limited traits (Wolc *et al.*, 2016).

Implementation of GS in developing countries

Several molecular technologies (such as microsatellite markers, SNPs, SNP chips, genome-wide association studies or GWAS, sequencing, and other related technologies) have been practiced in developed countries (FAO, 2011; Rothschild and Plastow, 2014). Since their economies have grown quickly over the past decades, countries like Brazil and China have adopted many of these technologies. For example, in Brazil, poultry genomics research started in 1999, with the aim of mapping QTL for traits of economic importance in the poultry industry (Ledur *et al*., 2012). As a result, animal breeding companies, producers, and consumers in these countries have largely benefited from the implementation of these technologies and subsequent improvements in livestock production and animal health. Therefore, they are excluded as developing countries in this review. Nevertheless, the question that animal breeders and development practitioners rise is how applicable and beneficial are GS to the rest of the world, particularly in developing countries (Mrode *et al*., 2018).

The potential benefit of genome-based selection needs to be compared to those expected to achieve through conventional breeding methods (Moniruzzaman *et al*., 2014) based on the traits to be improved and the economic benefits of the methods. If the traits are not difficult to measure, are measured in both sexes, and can be measured at any age, the conventional selection will offer advantages (for example, in terms of cost) over GS. For example, conventional selection would be successful in broilers because most traits can be recorded in both sexes at an early age (Meuwissen *et al*., 2016). Thus, the implementation of GS should be financially beneficial to the breeding organizations in developing countries and to produce poultry breeds that can fulfill the growing demand for animal proteins in these countries.

Elsewhere in developing countries, poultry are kept under a wide range of agro-ecologies and diverse production systems, with production targets both subsistence and commercial farming (Hoffmann, 2005). According to the same author, the poultry sector in these countries is generally categorized into the commercial and small-scale subsector, where the former is dominated by developed-country-based and vertically integrated companies, while the latter is based on indigenous chickens, which can survive under harsh management and environmental conditions. As the small-scale subsectors differ in their degree of genetic improvement, investment in infrastructure, and challenges to and opportunities for, the application of GS will not follow the "one size fits all" approach (Mrode *et al*., 2018). This section, therefore, presents opportunities to use genomics and challenges limiting the implementation of GS for poultry improvement in developing countries.

Potential application of GS

Different molecular approaches (such as microsatellite and SNP markers) have been applied to identify genes or genomic regions linked with disease resistance and increased production (Psifidi *et al*., 2014; 2016), tolerance to environmental stresses (Fleming *et al*., 2016; 2017; Park *et al*., 2018), and to investigate genetic diversity (Lyimo *et al*., 2014; Ngeno *et al*., 2015; Okumu *et al*., 2017; Habimana *et al*., 2020) of indigenous chickens of developing countries in Africa. Much of such studies have been carried out through international collaboration, for example, with different institutes of the Consultative Group on International Agricultural Research (CGIAR; FAO, 2011). Broadly speaking, these findings provide a better understanding of the genetic diversity, structure, and adaptation of indigenous chickens. It is feasible to incorporate this information in designing conservation strategies and breeding programs to enhance productivity, immune response, thermal tolerance, and adaptation to disease and environmental stresses within and across indigenous chicken ecotypes. In the long term, incorporating these into breeding programs for increased productivity could be realized by utilizing gene or haplotype editing and other emerging breeding strategies (Mrode *et al*., 2018). This was shown in the initial poultry genomics research in Brazil, where the EMBRAPA F2 chicken resource population was used to identify genes and genomic regions associated with productive traits under the climatic conditions and production practices of the country (Ledur *et al*., 2012).

In their study, which examined the genetic make-up of different indigenous chicken ecotypes in Kenya, Ngeno *et al*. (2015) found a highly diverse major histocompatibility complex (MHC) -linked alleles. This suggests that an enormous amount of genetic variation exists in the MHC region of indigenous chickens and supports their reputation of being tolerant of harsh scavenging conditions and disease challenges (Ngeno *et al*., 2015). Genotyping microsatellite markers used in this study (or MHC-linked microsatellite markers) and others (e.g., Habimana *et al*., 2020) represent a relatively easy and inexpensive method to genotype and measure genetic diversity between populations, which might be affordable for developing countries (Rothschild and Plastow, 2014). Based on their results, Psifidi *et al*. (2016) noted that simultaneously selecting birds for enhanced productivity, immune response, and health would likely improve indigenous chickens in Ethiopia and other developing nations, thereby increasing the profitability of the poultry subsector and animal welfare in regions where veterinary service is not

available. This may be achieved by increasing the frequencies of target alleles and haplotypes within specific MAS or by improving the trait of interest through GS (Psifidi *et al*., 2016). As already suggested, however, the costs of genotyping individual birds with high-density SNP would be a determining factor for implementation in developing nations. Alternatively, several authors (Sitzenstock *et al*., 2013; Wang *et al*., 2013; Wolc *et al*., 2015; Psifidi *et al*., 2016) suggested the development of low-density SNP chips, which could provide relatively cost-effective strategies. Compared to SNP-based approaches (i.e., more accurately measures the whole genome-wide diversity among different populations), most polymorphic microsatellite markers, however, may lead to biased estimates, which may not accurately predict the overall genomic-wide diversity (Rothschild and Plastow, 2014).

In poultry, heat stress reduces production and reproductive efficiency, decreases product output and quality and feed intake, increases mortality, and causes various metabolic and physiological changes (Park *et al*., 2018). Research that investigated the transcriptome response of high-altitude and low-altitude chickens in Ethiopia to heat stress conditions (Park *et al*., 2018) has shown that heat stress affects high-altitude chickens. The long-term genetic solution requires, using genomics approaches, a fuller understanding of selection signatures related to heat stress, and individual genes associated with mechanisms to combat climate issues (Rothschild and Plastow, 2014). For instance, the genomic experiment aimed to examine indigenous chickens of Africa and Northern Europe for selection signatures that have allowed them to adapt to their local environments (Fleming *et al*., 2017) has revealed unique variations in the genomic regions under selection pressure from the environment for each group.

In small-scale systems, infectious diseases are a major cause of birds' mortality and reduced productivity due to extremely limited vaccination and little or no biosecurity measures (Psifidi *et al*., 2014; 2016). Selective breeding based on genomic technologies may offer a long-term solution (Rothschild and Plastow, 2014). Psifidi *et al*. (2016) studied the underlying genetic basis of antibody responses to major infectious diseases (including infectious bursal disease, Marek's disease, fowl typhoid, and fowl cholera) and resistance to Eimeria and cestode parasitism as well as body weight and body condition score in two Ethiopian indigenous chicken ecotypes. In this work, the authors identified SNPs significantly associated with immunity, disease, and production traits. They also found no significant genetic correlations between these traits, indicating that selection for altered antibody response and/or disease resistance does not affect production. The identification of markers associated with resistance to a particular disease will enable more focused selection, which does not involve the evaluation of breeding stock through welfare-unfriendly challenge experiments (Besbes *et al*., 2007). Introgression of the desirable allele at a target gene from a donor to a recipient breed can also be applied by multiple backcrosses to the recipient, followed by one or more generations of intercrossing (Dekkers and van der Werf, 2007). With the advent of GS, specific disease resistance alleles could be introduced into exotic breeds with improved production characteristics using an introgression strategy (i.e., marker assisted introgression; MAI) to make exotic birds more tolerant to the harsh environmental conditions in developing countries (Dekkers and van der Werf, 2007; Muchadeyi and Dzomba, 2017).

Challenges in implementing GS

Scholars (Fulton, 2012; Wolc *et al*., 2014) discussed some major challenges to implementing GS in poultry breeding programs elsewhere. These include the costs of large-scale genotyping of markers, a large number of selection candidates, and the limited value of individual candidates compared to the cost of genotyping, and integrating genomic information into existing breeding programs. To carry out GS, breeders will need to obtain DNA from individuals, and then a large number of SNPs (tens of thousands) would be typed in each sample (Flint and Woolliams, 2008). Substantial costs for the implementation of GS include the costs of DNA collection, genotyping, and analysis. According to Ruane and Sonnino (2007) and Moniruzzaman *et al*. (2014), these costs can be differentiated between development and running costs. Development costs, for instance, costs used for identifying markers on the whole genome and detecting their associations with the traits of interest, can be high. Thus, developing countries need to consider whether to develop their own technology or to import the technology (Ruane and Sonnino, 2007; Moniruzzaman *et al*., 2014). This suggests that capital is one of the major determining factors for the application of genomics to the improvement of agriculturally important species in developing countries (Ruane and Sonnino, 2007; Rothschild and Plastow, 2014). Therefore, the economic costs and benefits of GS and its potential benefits compared with conventional breeding should be weighed when assessing the possible virtues of applying molecular tools for the genetic improvement of poultry in developing nations. Evaluating the economic benefits of advanced molecular technologies to farmers also needs to be considered for a publicly funded breeding program (Ruane and Sonnino, 2007).

Genomic information has not yet been widely integrated into breeding programs in developing countries (FAO, 2011). GS provides precise tools that

can increase the rate of genetic gain and accuracy of selection decisions without performance testing. However, upstream performance testing for all traits of economic importance is a crucial requirement for the implementation of GS (Preisinger, 2012). This requires the existence of conventional genetic evaluation and selection programs, with capabilities and well-established infrastructure for phenotypic performance recording systems (Ruane and Sonnino, 2007; FAO, 2011; Mrode *et al*., 2018). Selection programs based on molecular markers have no relevance if efficient recording systems for traits of interest are not in place (FAO, 2011). Yet, only a few poultry breeding programs are mentioned to exist in developing countries because they are not able to compete with breeding companies in developed countries that have access to technology advantages and economies of scale, and the lack of indigenous breeds suitable for commercial production (Hoffmann, 2005). Eggen (2012) noted that GS builds on existing breeding programs in which the collection of pedigree information along with phenotypic data is already routine; it provides a new level of information that can be incorporated into the decision-making process to identify and select the most promising animals. On the contrary, Dekkers and Hospital (2002) argued that the effective implementation of molecular technologies might require a complete redesign of breeding programs and a capable breeding organization that can optimally combine genomic information to maximize the accuracy of BV's prediction. Nevertheless, a complete redesign is practically limited and still relatively expensive to be implemented in developing nations and even in developed nations. Therefore, decision-makers in developing countries need to consider whether it is cost-effective to develop new technologies or improving the existing conventional breeding program is more efficient instead of spending money and resources on developing and applying new technologies (Ruane and Sonnino, 2007).

In most developing nations, where the existing infrastructure and capacity are insufficient to run a sustainable conventional breeding program, advanced molecular technologies will not offer a shortcut to genetic improvement (Ruane and Sonnino, 2007). This means that molecular approaches are not alternatives to conventional ones but are complementary (FAO, 2011). Although the National Agricultural Research System (NARS) is in charge of executing agricultural research in many developing countries, they often have a limited capacity to develop the infrastructure required for genomic technologies. Besides the infrastructure, these countries have been constrained by the human resources necessary to undertake research in genomics (Sonnino *et al*., 2007; FAO, 2011). Consequently, the use of molecular markers seems less developed and limited or absent in most developing countries (Sonnino *et al*., 2007; FAO, 2011). The advancement and adoption of genomic technologies will require research institutions with their facilities and an increasing number of well-trained professionals with advanced degrees (Rothschild and Plastow, 2014). As suggested by Tixier-Boichard *et al*. (2012), communication and cooperation between academic institutions and the industry remain essential to address challenges relating to applying molecular tools and associated infrastructures to implement GS. Partnerships between developed and developing countries may also be a means to better realize the potential application of molecular techniques for improving livestock and poultry production (Sonnino *et al*., 2007). With such partnerships within or across regions, molecular marker techniques may potentially be used in genetic diversity studies to improve decision-making on the development of breeds and the identification of breeds to be conserved.

Concluding remarks

Either in developed or developing countries, the main goal of animal breeding is to genetically improve poultry and livestock populations. A substantial amount of genetic improvement has been obtained in important livestock species through conventional methods. The advent of molecular genetics provides a new opportunity for more successful genetic improvements by allowing the use of information at the DNA level. In developed countries, this information is incorporated into breeding programs; thus, GS is becoming a new paradigm for poultry breeding companies to genetically improve both broilers and layers. This review article demonstrates the successful implementation of GS by poultry breeding companies and its potential benefits over the conventional selection approach in improving the accuracy of GEBV. Although there is a long history of research into genomic technologies in developed countries, it has not yet been implemented in developing countries. The limitations with these countries are the absence of selection programs that record phenotypic information on pedigreed animals, the lack of infrastructure for data recording and analysis, and the lack of financial and human resources. Despite persistent challenges in developing countries, ample opportunities exist, which may allow the successful development of breeding programs incorporating marker information. Developing countries require support and cooperation with breeding and research institutions in the developed world to incorporate genomic technologies into their conventional poultry breeding programs. Thus, international organizations and donor agencies, particularly those focused on agricultural research

and development, need to support these countries through capacity building and infrastructure development to implement GS for poultry breeding.

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