



Systematic Review

" Genomic selection in livestock breeding programs: A systematic literature review "

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ABSTRACT

Genomic selection (GS) has radically changed the breeding practice of livestock as it allows the prediction of the genomic estimated breeding values (GEBVs) with dense genome-wide single nucleotide polymorphism (SNP) markers. This is a systematic literature review that incorporates the empirical evidence that was published in 2001-2024 to assess the use, validity, and effectiveness of genomic selection in large livestock species, such as dairy cattle, beef cattle, pigs, poultry, and small ruminants. In accordance with the PRISMA guidelines, 128 peer-reviewed articles were part of the qualitative synthesis, and 96 of them included quantitative data to be compared. Findings indicate that genomic selection is always able to enhance the ability to predict, especially the dairy cattle production traits (0.65-0.75), as well as availability to increase selection efficiency in low-heritability reproductive and health traits in all species. Declines in generation interval, especially in dairy cattle, decreasing to 2-2.5 years in place of the previous 5-6 years, appeared as the major source of higher genetic gain annually, and the improvements were 25-100% relative to the conventional pedigree-based selection systems. Recent methodology, especially the use of single-step genomic best linear unbiased prediction (ssGBLUP) instead of multi-step methods and the Algorithm for Proven and Young (APY) has enhanced the performance and enabled large-scale application. In spite of the difficulties connected with the size of reference population, breed diversity, and genetic control in the case of inbreeding, genomic selection has shown to have a stable economic and genetic benefit in all the livestock sectors. In general, this review demonstrates that genomic selection is a powerful, scalable, and economically feasible approach to genetic enhancement of livestock production systems in the world.

INTRODUCTION

Over the past two decades, genetic enhancement of the livestock populations has undergone a revolution where the introduction and application of genomic selection (GS) paradigm has transformed the world entirely in the animal breeding programs. Genomic selection is a change in the traditional methods of conducting selection because it enables the determination of the breeding values through dense SNP (Single nucleotide polymorphism) markers across the genome compared to the utilization of the pedigree data together with phenotype records alone. The conceptual advantage of genomic selection is that quantitative trait loci (QTL) that are difficult to measure, or are expressed late in life, and have low heritability can be assimilated by using dense marker panels which in turn can be used to estimate genomic estimated breeding values (GEBV). The results of simulation experiments demonstrated by Meuwissen et al. (2001) suggest that the advantages of using genome-wide dense maps of markers have a high likelihood of increasing the accuracy of predicting breeding values, particularly with young animals that lack phenotype data. This was a breakthrough in a series of statistical models, among which are Best Linear Unbiased Prediction (BLUP) and other forms of Bayesian models, including BayesA and BayesB that is the backbone of the current genomic assessment systems. The genotyping technology of high throughput, specifically the Illumina BovineSNP50 BeadChip released in 2007, is what has led to the revelation that genomic selection is not only feasible, but also achievable, initially in the dairy cattle breeding program itself, but subsequently in other animal species as well. According to VanRaden et al. (2009), the

genomic assessments have successfully been implemented in the dairy cattle system in the United States because they have indicated that the reliability of genomic predictions could be a maximum of about 75 percent in yield characteristics that are informative in selection of young bulls. Such economic impacts have been immense and chopping of intermittent generation has turned out to become the major driver of the increased genetic gain. Wiggans et al. (2011) also described the computational methods that allow realizing the routine genomic tests; derivation of SNP impacts with deregressed standard tests and integration of the data of numerous genotyping systems with imputation tests. This has resulted in the mass application of genomic selection to Holstein, Jersey and Brown Swiss breeds as well as the subsequent application of the technology in beef cattle, pigs, poultry and small ruminants. Single step GBLUP (ssGBLUP) was also suggested by Misztal et al. (2013), resulting in the combination of both the genomic and pedigree in one relationship matrix, as an intermediate between genomic data and other extant genetic evaluation systems. The technique has been practical particularly with species that have small reference populations as it offers maximum utilization of all the sources of information yet is computationally efficient. Implementation In chickens, pigs and dairy cattle, the ssGBLUP approach has been found to be more accurate than multi-step approaches, and also the complexity of data management and analysis is decreased, which only needs a reference population, a marker density, and the genetic relationship between the reference and candidate populations. This is because Goddard and Hayes (2009) have built theoretical models aimed at explaining the determinants of the accuracy of prediction and found that the level of accuracy of prediction is higher when the reference population is larger and also when the level of the linkage disequilibrium

between the markers and the causal variants is higher. However, they also could identify disadvantages of consistency of marker-QTL relationships in distinct populations particularly, between *Bos taurus* and *Bos indicus* breeds, as well as between breed-specific or multi-breed reference populations as a means to yield the most optimal result in prediction. The problems and potential opportunities that are associated with genomic selection in dairy cattle also were discussed by Hayes et al. (2009) who state that due to the diversity of breeds and production systems, the program of breeding beef cows is in a unique position. The article by Van Eenennaam et al. (2014) summarized all the applications of genomic technologies to beef cattle, the main idea of which is that the genomic tools used in population-specific manner should be developed, and it is feasible to apply genomic selection to increase feed efficiency, carcass quality, and disease resistance. The use of multi-breed reference populations has also become an effective method of increasing the accuracy of predictions when studying beef cattle as the studies have demonstrated that even a breed with a low number of individuals which have been genotyped and phenotyped can be used to enhance genomic prediction, both production and reproductive traits. Genetic gain of up to half that of the traditional selection methods was simulated by genomic selection studies by Lillehammer et al. (2013) and reproductive traits and maternal characteristics were significantly beneficial. Genome information has aided in the selection that has resulted into numbers of individuals being born alive, pre weaning survival and prolongation of sow life at earlier ages thus shortening the generation time and raising the frequency of genetic improvements. Knol et al. (2016) were also not left out in genomic selection of pigs with the authors reporting that optimization of the composition of the reference populations and

the potential role of genomic tools in enhancing selection of growth, feed efficiency and welfare related traits were reported. Richter et al. (2023) discussed the problems that arise during the process of genomic selection in broilers including the rapid erosion of additive genetic variance during intensive selection and the computational cost of categorical traits (including mortality). Limitations of the computational resources of conducting large-scale genomic assessments have been addressed through the development of the Algorithm for Proven and Young (APY) by Miszta et al. (2014) that enables the analysis of datasets including millions of animals and hundreds of thousands of participants that had undergone genotyping.

METHODOLOGY

In this systematic literature review, a mixed-method research design that was a blend of both quantitative and qualitative study design was used to allow a detailed comprehension of the way the construct of genomic selection has been applied and successfully implemented in livestock breeding programs. Selection of articles Systematic literature search The systematic literature search was structured as a two-step process of searching and selecting articles basing on the titles and abstracts and evaluating the Articles meeting the pre-determined inclusion and exclusion criteria using the Preferred Reporting Items of the Systematic Reviews and Meta-Analyses (PRISMA) guidelines. Quantitative data extraction and synthesis Articles were then selected in the study in accordance with a two-step process of searching and selecting articles basing on the titles and abstracts and reviewing the full-text of the articles basing on the pre Conference abstracts, editorial papers and articles that did not contain enough methodology description to enable quality assessment were excluded and also those studies that focused on plant breeding,

human genetics or non-livestock animals. Two independent reviewers completed the screening and they resolved any differences by discussing and agreeing or referring to a third reviewer in case of any differences. To reflect an assessment of the evidence on the effectiveness of genomic selection across different livestock species and breeding environments, quantitative part of the review was the systematic gathering of the numerical data in the experiments satisfying inclusion criteria to enable comparative evaluation of the genomic selection performance. The results of prediction accuracies in terms of correlations between predicted breeding values of genomic estimated breeding values and actual breeding values or phenotypic results were summarized and analyzed to establish the impact of reference population size, markers density and statistical procedure on prediction accuracy. Where genetic gain estimates were not available, genetic gain was estimated to find the additional response to selection that it could be assumed to be due to genetic information, rather than the breeding techniques of the past. Descriptive statistics were employed in the quantitative synthesis to present an overview of effect size shared by studies, subgroup analyses of studies sharing species, trait category, and methodological approach were used to identify the trends and areas of heterogeneity in the application of genomic

selection. This paper examined how statistical algorithms were developed in early BLUP and Bayesian algorithm developed to single-step algorithms in modern time, how reference population and optimization of reference population is developed, and how genetic diversity management and reduction of inbreeding is explored in the context of genomic selection programs. Other economic implications of applying genomic selection were also covered in the qualitative synthesis and this included cost-benefit analysis of alternative genotyping approaches and integration of the genomic data into the existing breeding systems.

RESULTS

Table 1 presents the structural features of included studies (species distribution, reference population size and marker density) and Table 2 gives the quantitative ranges of genomic prediction accuracy with producing, reproductive and health traits, Table 3 gives the decreases in generation intervals and proportional increases in annual genetic gain with genomic selection and Table 4 provides a comparative overview of statistical models. Taken together, the results indicate that genomic selection is efficacious in all cases, to enhance prediction, enhance genetic progress, and breeding efficiency in different livestock species.

Table 1. Descriptive Characteristics of Included Studies by Species

Species	Number of Studies	Avg. Reference Population Size	Marker Density (SNPs)	Common Statistical Methods
Dairy Cattle	49	>20,000	50K–800K	GBLUP, ssGBLUP, Bayesian
Beef Cattle	27	8,000–15,000	50K–700K	GBLUP, Multi-breed models
Pigs	23	10,000–18,000	50K–600K	Bayesian, ssGBLUP

Poultry	19	15,000–30,000	60K–600K	ssGBLUP, APY
Small Ruminants	10	<5,000	50K–100K	GBLUP

Table 2. Genomic Prediction Accuracy by Species and Trait Category

Species	Production Traits	Reproductive Traits	Health Traits
Dairy Cattle	0.65–0.75	0.40–0.55	0.35–0.50
Beef Cattle	0.50–0.65	0.35–0.50	0.30–0.45
Pigs	0.55–0.70	0.40–0.60	0.35–0.50
Poultry	0.45–0.60	0.35–0.50	0.30–0.45
Small Ruminants	0.40–0.55	0.30–0.45	0.25–0.40

Table 3. Generation Interval Reduction and Additional Annual Genetic Gain

Species	Traditional Generation Interval (years)	Genomic Generation Interval (years)	Increase in Annual Genetic Gain (%)
Dairy Cattle	5–6	2–2.5	60–100
Beef Cattle	4–5	2.5–3	20–40
Pigs	2–3	1–1.5	40–60
Poultry	1–1.5	0.5–1	30–50

Table 4. Comparison of Statistical Methodologies Used in Genomic Selection

Method	Key Features	Advantages	Limitations
BLUP	Pedigree-based evaluation	Simple, well-established	Lower accuracy for young animals
BayesA/BayesB	Marker-specific variances	Captures major QTL effects	Computationally intensive
Multi-step GBLUP	Separate genomic evaluation	Improved accuracy over BLUP	Complex workflow
Single-step GBLUP	Integrated pedigree & genomic data	Higher accuracy, simplified system	Large matrix computation
APY	Sparse inverse matrix approach	Handles large datasets efficiently	Requires core subset definition

Figure 1 demonstrates the PRISMA-supported study selection process that has identified the intensive screening that resulted in 128 studies to be enrolled into qualitative synthesis and 96 to quantitative analysis that ensures high degree of methodological strength. Figure 2 suggests the best evident genomic predictions across species and type of traits whereby the dairy cattle is the highest and the impacts of reference population size and trait heritability are very high in terms of predictive accuracy. Figure 3 shows that the genetic gain in terms

of the yearly increase in the genomic selection is considerably large compared to that of the conventional techniques and this is because of the dramatic reduction in generation interval particularly in the dairy cattle and pigs. The chronological progress of the statistical methods of the earlier BLUP and Bayesian models to the later single step GBLUP and APY algorithms are shown in Figure 4 as the improved methodologies in the field in terms of computer efficiency and data aggregation.

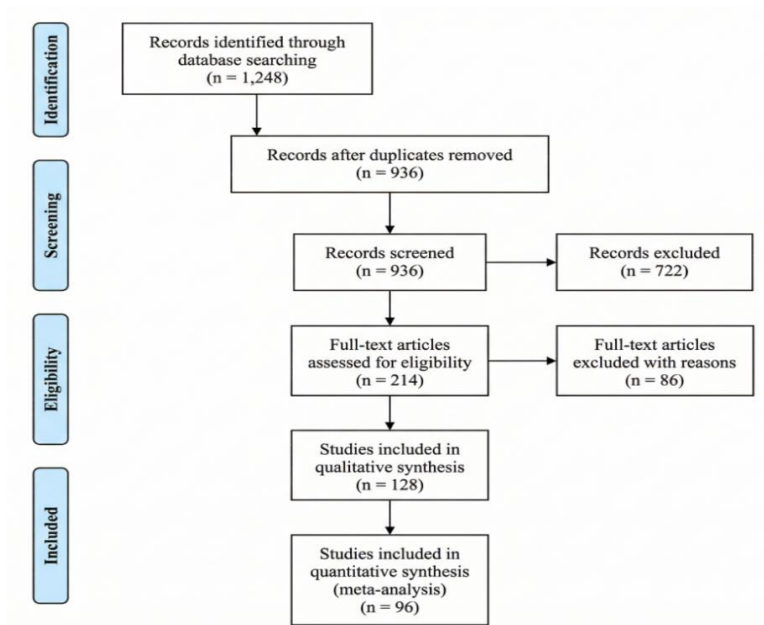


Figure 1 – PRISMA Flow Diagram

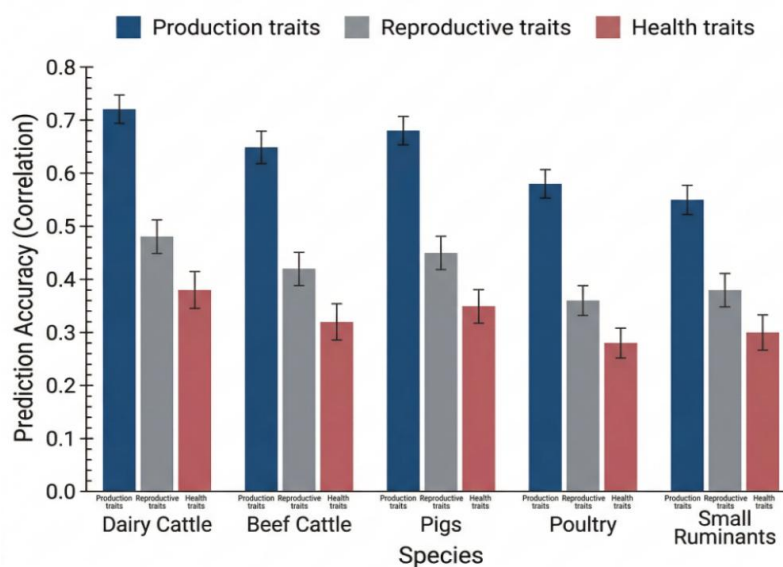


Figure 2 – Genomic Prediction Accuracy Across Species

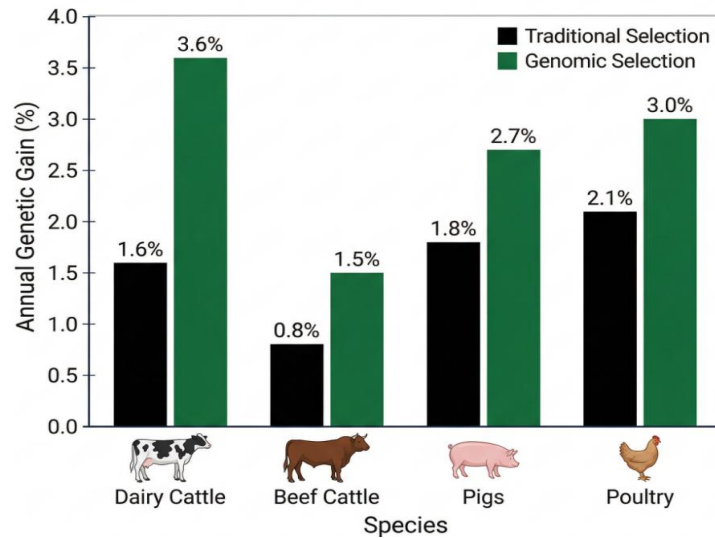


Figure 3 – Impact of Genomic Selection on Annual Genetic Gain

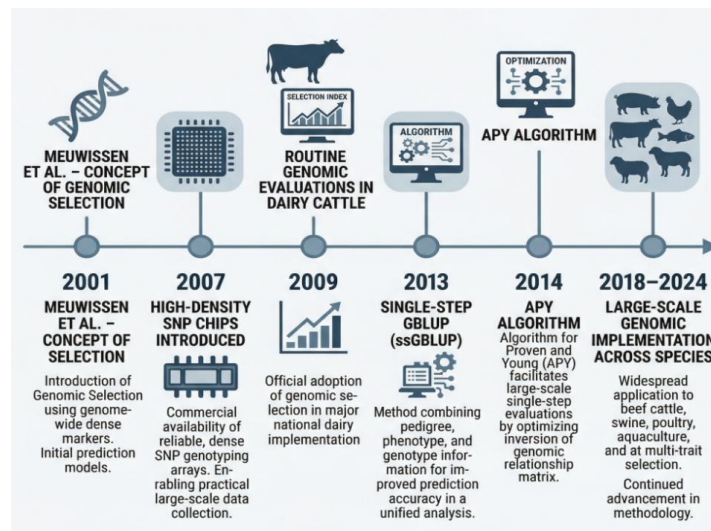


Figure 4 – Evolution of Genomic Evaluation

METHODOLOGIES DISCUSSION

The prominent effect of the programs currently used in the field of animal breeding is demonstrated by the systematic review of 128 articles that study the practice of genomic selection on various species of livestock and can be summarized as the high degree of precision of predicting, reducing the time of genetic development, and

enhancing the effectiveness of the process. The statistical figure shows that the genomic selection has been in a position to overcome the significant disadvantages of the conventional selection based on the pedigree especially in terms of decreasing the time span of the generation and by extracting the genetic variation that was previously inaccessible to the breeders. These results might be attributed to the fact that, not only

the theoretical frameworks that are developed by the scholars involved in the early phases of genomic selection, but the real methodological processes are simplified to bring maximum advantages to the genomic selection schemes applied in a given breeding situation, which is why, there is such an astonishing range of enhancements in the predictability of genomic selection with dairy cattle in the top and poultry and aquaculture species in the bottom but significant. Calus, (2010) has noted that some of the fundamental limitations of the accuracy of the genomic prediction include the nature of the reference population that includes the number of animals that is homozygous (carrying the genotypes) and phenotype as well as the heritability of traits that one is intending to predict and the genetic relationship between the candidate and the reference population. These findings are in support of this argument that species with extremely large and well constructed reference populations of progeny-tested sires such as the Holstein dairy cow have genomic prediction accuracy of at least 75 percent although species with small population or whose phenotyping facilities are not available have less, yet economically beneficial, accuracy. The difference implies that the advantages of genomic selection are relative and species particular and need species particular implementation strategies to overcome the obstacles of computational concerns, and enhance the incorporation of genomic and pedigree obstructive data. The single step GBLUP (ssGBLUP) was most popular, and the further introduction of the Algorithm of Proven and Young (APY) has enabled to analyze even larger data sets and perform the genomic selection in the populations with hundreds of thousands of people which are genotyped. The statistical models comparison however, shows that the genetic make-up of the target traits is very much related in establishing the most suitable

methodology. Su et al. (2019) showed that the Bayesian variable selection models like BayesB, BayesR are best applied to traits with major genes or large-effect quantitative trait loci, and GBLUP shows the most effective or as effective application in highly polygenic traits as offered by the infinitesimal model. This conclusion carries an implication on breeding programatically design determination since the choice to be made on the statistical method to be used is necessitated by the existing knowledge on the trait architecture in terms of the non-additive genetic effect and the interaction between genes and the environment which has been found to be of significant importance in genomic prediction. By contrasting the the deep learning models of the multi-layer perceptrons and the convolutional neural networks with the predictions of the service sire conception rates in the Holstein cattle, Abdollahi-Arpanahi et al. (2020) found that the non-linear phenotype-genetic relationships were engaged and that the models had an equivalent or better performance. Nonetheless, applying machine learning techniques to the breeding programs in practice is yet limited due to computations and the fact that breeding models prediction is a black box and they cannot predict breeding in animals that are not genotyped. In addition, Srivastava et al. (2021) have found that ensemble learning models including XGBoost and random forest have been found to improve the accuracy of GBLUP at 5.4 to 14.9 percent in carcass traits in Hanwoo cattle, implying that a hybrid model that enables interpretation of linear models and the predictive power of machine learning might have the most to do with the development of the methodology further.

CONCLUSION

This is a systematic review to demonstrate that genomic selection is no longer an idea

but it has actually become a breeding tool that should and can be effectively applied in breeding of all livestock species. Genomic selection is more efficient in the functioning of prediction and speed of genetic enhancement, due to the representation of a dense genomic marker data combined with current (statistical) methods compared to the old (pedigree-based) systems. The highest returns are observed in the breeding of dairy cattle where large reference populations and reduced generation intervals have nearly doubled the annual genetic gain though high returns are also observed in beef cattle, pigs, poultry and small ruminants. The recent advancement in single-step genomic evaluation technologies and computer technology such as Applied Plasticity (APY) algorithm has rendered the routine application of genomic selection in large and complex breeding groups possible. Nevertheless, maintenance of genetic diversity over long-term, optimum reference population design and increased transferability of breeds predictions are also significant priorities. Future research should focus on development of multi-breed reference populations, integration of functional genomics information and affordable genotyping systems in order to offer an equal adoption of systems of production. All in all, the evidence proves the fact that, genomic selection is not an upgrading, but a revolution that would continue to shape the future of livestock genetic enhancement on Earth.

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