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# CHALLENGES IN BLUP-BASED GENETIC EVALUATION OF PIGS WITH HIGH LEVELS OF IMPORTED GERMPLASM

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**Abstract:** Accurate estimation of breeding values is essential for effective selection in pig breeding programs. The Best Linear Unbiased Prediction (BLUP) method integrates pedigree, phenotypic, and, when available, genomic information to estimate breeding value. However, in pig populations with a high proportion of imported germplasm, progeny of imported sires often receives underestimated breeding value in the early stages of evaluation. This bias primarily arises from the lack of local performance data and genetic connectedness between imported parents and the domestic reference population. Without domestic phenotypic records, BLUP tends to regress breeding value of such animals toward the population mean, leading to lower selection indices despite potentially high genetic merit. Several approaches can mitigate this underestimation. The use of genetic groups or phantom parent groups can account for differences in genetic level between imported and domestic animals. Genomic evaluations (GBLUP) provide an additional solution by capturing relationships through DNA marker information, increasing connectedness even in the absence of phenotypic records. Rapid accumulation of domestic performance data from progeny also reduces bias over time. International genetic evaluations allow the incorporation of foreign breeding value into national evaluations, aligning genetic bases between countries. Addressing this issue is particularly important in small or developing breeding programs where imported germplasm represents a significant proportion of genetic improvement. Properly accounting for imported genetic material ensures fair evaluation of all candidates, optimizes selection decisions, and accelerates genetic progress.

**Key words:** pigs, breeding values, accuracy, import

# Introduction

Intensive pig breeding is oriented to achieving high performing animals' through strong genetic selection and high input systems. For that reason, breeding programmes in pig production are oriented to intensive genetic progress, often based on import of germplasm from foreign breeding programmes. Genetic improvement in economically important traits, such as growth, fertility or meat quality traits, is the basis for economic success of pig production. For that purpose, import of animals that are considered to be genetically superior has an important role in achieving economic success of production. This can be confirmed by partitioning genetic trends for traits in selection (Škorput et al., 2015), where genetic progress for economically important traits in small populations under selection can significantly be affected by imported germplasm and result in significant genetic improvement.

Moreover, the goal of importing foreign germplasm is to increase genetic variance of domestic population. While genomic selection is increasingly becoming the dominant approach in modern breeding programs, BLUP (*Best Linear Unbiased Prediction*) procedure based on mixed model methodology (*MMM*) continues to play a crucial role in smaller national breeding schemes where resources and reference populations may be more limited. BLUP has numerous advantages over earlier methods: it uses a combination of own results of the individual; data on relatives of the evaluated individuals; and data on environmental factors (Henderson, 1973) and remains a powerful tool in estimation of breeding values in livestock.

However, if included in BLUP genetic evaluation, imported animals and their progeny sometimes surprise with a bad proof (Peškovičová et al., 2004). Such a situation can cause a biased evaluation of selection candidates, and economic loss for breeders who invested into foreign seamen or boars. Moreover, discouraging breeders and associations from occasional import of genetic material might result with impaired genetic diversity in the population and slowed genetic improvement that arises from imported germplasm. This can be especially important for small breeds and populations and breeding programmes without the possibility of genotyping animals and applying genomic selection. Thus, solutions to override biased evaluations via BLUP and ranking evaluated animals is required to ensure genetic progress and genetic variability of the population.

The aim of the paper is to analyse reasons for underestimation of selection candidates and their progeny when BLUP is used as a method of choice for genetic evaluation in pigs. Moreover, the goal is to define relevant approach for solving this problem to avoid underestimation of animals and the economic losses that might occur because of biased evaluation.

## 2. Systematic Underestimation of Genetic Merit in BLUP Models

Proposed by Henderson (1973), BLUP has been one of the most influential tools in animal breeding. Its widespread adoption stems from its ability to separate genetic effects from environmental influences and to provide unbiased estimates of breeding values under the assumption of complete and well-connected data (Henderson, 1984). However, despite its strengths, a recurring challenge in the application of BLUP is the systematic underestimation of genetic merit, particularly in cases where imported sires or animals with incomplete pedigrees are involved. Imported animals are a base animals with no breeding values till enough progeny has been born and performance tests have been conducted to produce a new breeding value that is significant in the imported country (Van Vleck, 1990). Thus, the analysis of the value of domestic and imported germplasm is not trivial, because foreign data is often not available in sufficient amounts or easy to integrate into domestic evaluations, although methodology for such integrations exists (e.g., Vandenplas and Gengler, 2012).

This problem has been noticed early and discussed by Webb (1976), Hofer et al. (1992) and Peškovičová et al. (2004). According to Misztal et al. (2013), ignoring missing pedigrees, unknown selection processes, or inclusion of several populations can result with biased genetic predictions even when genomic information is included in evaluations. One of the primary causes of underestimation of breeding values lies in the structure of pedigree information. When pedigrees are incomplete or when imported animals lack genetic connectedness to the domestic population, BLUP tends to shrink estimated breeding values towards the population mean (Hofer et al., 1992; Misztal et al., 2013). This shrinkage is mathematically desirable to reduce variance and avoid overestimation, but it simultaneously penalizes animals that are truly superior yet lack adequate progeny or connectedness. As a result, the offspring of imported boars, for instance, may receive lower estimated breeding values than their true genetic potential would justify (Peškovičová et al., 2004; Krüger, 2015).

Another important factor contributing to bias of the estimations is the presence of preferential treatment and environmental differences. Imported sires may be used in herds with management practices that differ from the national average. If such environmental effects are not properly accounted for in the model, BLUP may incorrectly attribute part of the environmental advantage or disadvantage to the genetic component, further distorting accuracy (Arnason, 1999). This problem is particularly relevant in smaller breeding populations, where management heterogeneity tends to be greater and genetic ties across herds are weaker.

# 3. Tools for Reducing the Underestimation of Imported Animals in BLUP

Several methodological approaches are available for overriding problem of biased estimation of breeding values for animals from different groups using BLUP (Table 1).

**Table 1.** Tools and methods to reduce BLUP underestimation

| Tool/Method | Principle | Advantage | References |
|---|---|---|---|
| Unknown Parent Groups (UPG) | Group animals with missing pedigrees into genetic groups | Reduces bias for imported sires with incomplete pedigree | Quaas, 1988; Misztal et al., 2013 |
| Metafounders | Generalization of UPG, estimating relatedness of base populations | Accounts for base population differences; reduces bias | Legarra et al., 2015; Legarra et al., 2024 |
| Single-Step Genomic BLUP (ssGBLUP) | Combine genomic, pedigree, and phenotypic data in one step | Improves accuracy and fairness, reduces underestimation | Christensen et al., 2012 |
| Genomic Relationship Matrices (G-matrix) | Use SNP-based relationship matrices instead of pedigree | Captures realized relatedness; works without full pedigree | VanRaden, 2008 |
| Preferential Treatment Adjustments | Model herd × year × season or management group effects | Separates genetic from management/environmental effects | Arnason, 1999 |
| International Genetic Evaluations | Use international evaluation systems to improve connectedness | Enhances genetic connectedness across populations | Schaeffer, 1994 |
| Bayesian Genomic Methods (BayesA, BayesB, BayesCπ) | Bayesian methods model marker effects with different prior assumptions | Flexibility, better handling of unequal information | Meuwissen et al., 2001 |

## 3.1. Unknown parent groups

Quaas (1988) proposed a solution to handle differences in genetic values of base animals through genetic groups or unknown parent groups (UPG). The method involves assigning animals with unknown or poorly connected parents—such as imported sires—to specific “genetic groups” that account for systematic differences between base populations. For example, imported sires can be placed into separate groups reflecting their country or breeding line of origin. By doing so, the use of genetic groups prevents the underestimation of progeny of imported animals since their genetic merit is not forced towards population mean of domestic herd. Peškovičová et al. (2004) analysed the effect of genetic groups on the efficiency of selection on several traits, such as backfat thickness and average daily gain. Using model with genetic groups showed significant increase of selection efficiency, while using the model without genetic groups significantly reduced selection response. Škorput et al. (2013) used the model with genetic groups to estimate genetic trends on backfat thickness for Landrace and Large White pig and showed that the use of genetic groups is justified when there is a high proportion of imported animals in the breeding programme. Genetic trends for backfat thickness and time on test were partitioned by Škorput et al (2015) using method by Garcia-Cortes et al. (2008) with emphasis on the difference between domestic and imported genetics. Correlations between estimated breeding values from models with or without genetic groups indicated changes in estimated breeding values when genetic groups were included in the model.

Misztal et al. (2013) analysed the use of UPG in single-step genomic BLUP (ssGBLUP). For ssGBLUP, UPG equations also involve contributions from genomic relationships. When those contributions are ignored, UPG solutions and genetic predictions can be biased. The bias can be removed by making appropriate contributions to mixed model equations, by treating UPGs explicitly in the model, by refinements to definitions of UPGs or by adding an additional animal effect to the model. Phocas and Laloe (2004) considered the fitting of genetic groups in BLUP evaluation and concluded that the inclusion of genetic groups should be considered only with many animals per group.

Legarra et al. (2015) proposed the use of metafounders that represent the extension of the UPG concept. Unlike classical UPG, which treat base population groups as unrelated, metafounders explicitly model the genetic relationships among these base groups. This allows evaluations to capture both differences between populations and the degree of connectedness among them. The use of metafounders showed increased the accuracy of evaluation in both pedigree-based and ssGBLUP scenarios. The method was extended by Legarra et al. (2024), new definitions of the concept of meta-founders in terms of cross-product of allele frequencies of populations with new definitions that can be related to existing concepts of genetic distances, heterozygosity or inbreeding, and can be integrated easily into genomic and pedigree-based predictions.

## 3.2. Bayesian methods

Bayesian genomic methods such as BayesA, BayesB, and BayesCπ have become important alternatives to classical BLUP and genomic BLUP (GBLUP) in animal breeding, particularly when populations are small or include imported animals with limited pedigree connectedness. Traditional BLUP and GBLUP assume that all loci contribute to genetic variance in a similar way and therefore apply uniform shrinkage of estimated marker effects toward the mean (VanRaden, 2008). While this approach is computationally efficient and effective in large, well-connected populations, it can result in systematic underestimation of the genetic merit of imported sires and their progeny. This bias arises because rare alleles, often introduced through importation, are either poorly represented or absent in the domestic reference population, leading to insufficient recognition of their true contribution to performance traits. The relevance of these methods for imported animals lies in their ability to reduce the shrinkage of rare but important alleles. When imported sires introduce novel haplotypes, BLUP tends to undervalue their progeny because the estimation process regresses unknown animals toward the mean of the domestic population (Hofer et al. 1992; Peškovičová et al. 2004). In contrast, Bayesian methods give disproportionate weight to SNPs with larger observed effects, thereby capturing the genetic value of alleles unique to imported lines. This is particularly beneficial in pig breeding, where international exchange of boar semen is common and where imported lines are often carriers of superior growth or carcass traits not well represented in local germplasm (Kruger, 2015).

A relevant methodological development in this context is the work of Garrick and Fernando (2022), who proposed an approach to obtain exact single-step GBLUP results for non-genotyped descendants even when the genomic relationship matrix of ancestors is not available. Their method showed that it is not always necessary to have complete pedigree or genomic information for all ancestors; instead, posterior breeding values and covariance estimates from external evaluations can be incorporated into the local analysis to achieve identical results to a full single-step evaluation. This is particularly relevant for imported animals, where pedigree and genomic data are often incomplete or withheld for proprietary reasons. In such cases, the lack of connectedness leads to systematic underestimation of progeny breeding values under classical BLUP.

## 3.3. Genomic selection

The integration of genomic selection into animal breeding programs has transformed the way genetic merit is estimated, particularly in cases where pedigree information is incomplete or international genetic exchange plays a central role (Meuwissen et al., 2001). Imported animals, such as boars in pig breeding programs, present a unique challenge in classical BLUP systems, where their breeding values are often systematically underestimated due to weak or missing pedigree connections with the domestic population. Genomic selection provides an effective framework to overcome these limitations and to more accurately evaluate the contribution of imported genetics. Imported animals, which frequently lack full pedigree records in the importing country, are particularly vulnerable to this effect. By contrast, genomic selection employs marker-based relationship matrices that capture realized genetic relatedness among individuals. This enables more accurate estimation of breeding values for imported animals, even in the absence of complete pedigree data (Christensen et al., 2012). Genomic selection plays an important role in maintaining genetic diversity. Imported lines often introduce novel alleles that are underrepresented or absent in the domestic population. Classical pedigree-based BLUP, with its shrinkage effect, may undervalue these lines and discourage their use. Genomic selection, however, ensures that their genetic contributions are recognized and appropriately weighted, thereby promoting genetic diversity and long-term sustainability of breeding programs (Lourenco et al., 2014; Maiorano et al., 2019). Another important advantage of genomic selection is the ability to provide early and accurate evaluations. Imported animals often lack sufficient local phenotypic data, and their progeny may only just be entering performance testing, which significantly reduces the accuracy of BLUP estimates. With genomic information, breeding values can be estimated immediately after genotyping, without waiting for large progeny test records (Mei et al., 2022). This reduces generation interval and prevents valuable genetic lines from being discarded due to initially underestimated evaluations. In addition to accuracy, genomic selection also contributes to reducing environmental bias. Imported sires often originate from production systems with different management practices. If these environmental effects are not accounted for, BLUP may mistakenly attribute part of the variation to genetics. By integrating genomic information, evaluations can more effectively separate true genetic potential from environmental influences (Misztal et al., 2013).

## 3.4. International genetic evaluation

Unlike in cattle, where breeding values can be compared across herds and countries, international genetic evaluation of pigs is more complex and harder to realise. Although artificial insemination is also widely used, boars tend to be replaced more frequently, and herds are often smaller and more fragmented, resulting in weaker genetic connectedness. Also, there is no international body that unifies data across countries. Instead, evaluations are conducted within proprietary breeding programs managed by large international companies. Each company operates a closed nucleus scheme, and breeding values are calculated independently, making breeding values not directly comparable across herds, companies, or countries. However, the problem becomes more expressed in breeding programmes of small populations without sufficient resources such as in large international companies (Škorput et al., 2017). This lack of standardization in such populations has significant implications for imported animals. When boars are introduced into a new population, their progenies are often systematically underestimated in BLUP evaluations due to incomplete pedigrees and weak genetic connectedness with the local herd base unlike cattle, where international evaluations can adjust for base population differences, pigs lack a harmonized framework to correct for such biases.

## 4. Conclusion

Reliable genetic evaluation is essential for achieving sustainable genetic progress in pig production. While BLUP has served as the base of modern evaluation methods, its reliance on complete pedigree and strong connectedness makes it vulnerable to bias, particularly in the case of imported germplasm and progeny. Systematic underestimation of genetic merit not only undermines the efficiency of selection but also discourages the use of valuable foreign germplasm, thereby limiting both genetic gain and diversity.

A range of methodological improvements has been developed to address this challenge. Tools such as UPG and metafounders offer corrections for incomplete pedigrees. More importantly, the development of genomic selection and approaches like single-step genomic BLUP (ssGBLUP) have provided robust solutions by incorporating genomic relationships that capture hidden genetic connectedness between populations. These approaches not only improve the accuracy of evaluations for imported sires but also preserve genetic diversity by ensuring that novel alleles introduced from abroad are fairly represented.

In a globalized breeding industry, where international exchange of genetic material is indispensable, overcoming underestimation bias is critical. The integration of genomic information, combined with appropriate statistical and management tools, represents the most effective path forward. However, BLUP still remains a valuable tool, especially in smaller national programs, but its limitations must be recognized and mitigated. By embracing genomic selection and complementary methodologies, breeding programs can ensure more accurate and globally competitive genetic evaluations—ultimately driving faster and more sustainable genetic improvement.

**Conflict of interest**

The authors declare that they have no conflict of interest.

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