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ORIGINAL ARTICLE

Impact of genomic preselection on subsequent ssGBLUP evaluation of preselected animals for scarcely recorded feed intake in pigs

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Abstract

We have previously shown that single-step genomic best linear unbiased prediction (ssGBLUP) estimates breeding values of genomically preselected animals without preselection bias for widely recorded traits, that is traits recorded for the majority of animals in the breeding population. This study investigated the impact of genomic preselection (GPS) on accuracy and bias in ssGBLUP evaluation of genomically preselected animals for a scarcely recorded trait, that is a trait recorded for only a small proportion of the animals, which generally has a lower prediction accuracy than widely recorded traits, mainly due to having a much smaller number of phenotypes available. We used data from a commercial pig breeding program, considering feed intake as a scarcely recorded target trait, being available for ~30% of the animals with phenotypes for any trait, and average daily gain, backfat thickness and loin depth as widely recorded predictor traits, being available for >95% of the animals with phenotypes for any trait. The data contained the routine GPS implemented by commercial animal breeding programs, and we retrospectively implemented two scenarios with additional layers of GPS by discarding pedigree, genotypes and phenotypes of animals without progeny. The ssGBLUP evaluation following GPS used records only from the target trait, only from the predictor traits, or both. Accuracy for feed intake did not differ statistically across GPS scenarios, although it tended to decrease with more intense GPS. The accuracy had average values of 0.37, 0.44, and 0.45 across all GPS scenarios when, respectively, records from only the target trait, only the predictor traits, or both were used in the ssGBLUP evaluation. Considerable deflation of the genomic breeding values for feed intake was observed in the most stringent GPS scenario, due to the variance components being underestimated as a result of the limited amount of strongly preselected data. As long as (co)variance components were unbiased, no or only marginal bias was observed. These results for accuracy and bias were observed whether records of the scarcely recorded

target trait, of the predictor traits, or both were used in the ssGBLUP evaluation. Our results show that for the scarcely recorded feed intake in pigs, ssGBLUP is able to estimate breeding values of preselected animals without preselection bias, similarly as previously observed for widely recorded traits.

KEYWORDS

bias, genomic preselection, scarcely recorded traits

1 | INTRODUCTION

The importance of recording phenotypes in animal breeding cannot be overemphasized. Some traits are measured routinely on the majority of animals in a breeding population. We refer to such traits as widely recorded traits. Other traits, however, are difficult or expensive to measure, and are therefore only measured on a small proportion of animals in each generation of a breeding population. We refer to such traits as scarcely recorded traits. Examples of scarcely recorded traits include individual feed intake in all livestock species, and carcass quality traits in meat animals. The small numbers of animals with records for scarcely recorded traits mean that reference populations for genomic evaluation of animals for such traits are small as well, and this may result in genomic estimated breeding values (GEBV) with low accuracies (e.g. Calus and Veerkamp, 2011; Pszczola et al., 2013). It has been shown that multi-trait evaluation of animals for scarcely recorded traits together with predictor traits, which usually are widely recorded traits that are moderately to highly genetically correlated with scarcely recorded traits, gives more accurate and less biased genetic evaluation for scarcely recorded traits compared to single-trait evaluation (Ducrocq, 1994; Philipsson et al., 1995; Calus and Veerkamp, 2011; Pszczola et al., 2013; Manzanilla-Pech et al., 2020). Phenotypes of animals for predictor traits mainly help in genetic evaluation of scarcely recorded traits by enabling more accurate estimation of Mendelian sampling (MS) terms of selection candidates, thereby increasing accuracy and reducing bias (Thompson and Meyer, 1986; Ducrocq, 1994; Philipsson et al., 1995; Calus and Veerkamp, 2011; Jia and Jannink, 2012; Pszczola et al., 2013; Manzanilla-Pech et al., 2020).

Selection of parents of the next generation usually involves multiple stages, such as a genomic preselection (GPS) of young selection candidates and a subsequent selection when the preselected candidates have records. Genetic evaluation models implicitly assume that the datasets analysed are unselected or are random subsets of the unselected datasets. In reality however, the datasets analysed at subsequent selection stages are neither unselected nor are they random samples of the unselected datasets, since preselection usually skews the distribution of the datasets (e.g. Henderson, 1975; Pollak et al., 1984; Patry and Ducrocq, 2011; Sullivan, 2019). In our previous study (Jibrila et al., 2022), we investigated the impact of GPS on accuracy and bias in subsequent single-step genomic best linear unbiased prediction (ssGBLUP) evaluation of preselected animals, using data from a commercial pig breeding program. We were able to show that ssGBLUP in subsequent evaluation estimates GEBV of genomically preselected animals without preselection-related bias and accuracy loss. In this previous study (Jibrila et al., 2022), we studied impact of GPS in subsequent evaluation of animals for widely recorded traits, that is traits that were measured for >95% of the animals that had phenotypes for any trait. The traits were average daily gain, backfat thickness and loin depth, which are some of the most important widely recorded production traits in a typical pig sire line (e.g. Dekkers et al., 2011).

Following the argument that ssGBLUP is able to estimate unbiased GEBV of preselected animals by making use of genotypes of the preselected animals and their parents to estimate the MS terms of preselected animals (Jibrila, 2022), it can be expected that the ability of ssGBLUP to prevent accuracy loss and bias due to preselection applies to both widely recorded and scarcely recorded traits. Nevertheless, with reduced recording, such as the case for scarcely recorded traits, GEBV may rely even more on information of close relatives, while this may not be available for all selection candidates in the presence of GPS (Patry and Ducrocq, 2011; Jibrila et al., 2020). From this perspective, an important question is whether ssGBLUP can still yield unbiased GEBV for scarcely recorded traits in the presence of GPS, if the amount of data available becomes very small. The aim of this study, therefore, was to investigate the impact of GPS on accuracy and bias in subsequent ssGBLUP evaluation of preselected animals for a scarcely recorded trait. To investigate the impact of the number of records used, and whether or not any bias could be alleviated by multitrait modelling, we either used phenotypes of: (1) only the scarcely recorded trait, (2) only predictor traits, or (3) both. Like in the work of Jibrila et al., 2022, we used a full dataset derived from a commercial pig breeding program as reference, and

retrospectively implemented additional layers of GPS. We used feed intake as scarcely recorded trait, which was measured for ~30% of the animals that had phenotypes for any trait. Since in every generation GEBV were used to select the parents of the next generation, we implemented our additional layers of GPS by discarding pedigree, genotypes and phenotypes of the animals that did not have progeny in the data. We compared accuracy and bias of subsequent ssGBLUP evaluation using the remaining data after these additional layers of GPS against those obtained for the full available data.

2 | MATERIALS AND METHODS

2.1 | Data

We obtained data for pig production traits of a sire line from Topigs Norsvin, collected between 1970 and 2020. The data included two scarcely recorded feed intake traits—feed intake from the start to the end of performance testing (FI_{SE}), and feed intake from the middle to the end of performance testing (FI_{ME}). Animals could only have records for one of the two feed intake traits, and the number of animals that had records was slightly higher for FI_{SE} than for FI_{ME}—there were about 12,000 and 10,500 animals with records for FI_{SE} and FI_{ME} in the complete dataset, respectively (Table 1). The data also included four widely recorded traits, including average daily gain during performance testing (ADG_T), average daily gain throughout the lifetime (ADG_L), backfat thickness, and loin depth, each with more than 70,000 animals with records in the complete dataset (Table 1). These production traits were part of the breeding goal of this line, and this was the basis for (pre)selection on these traits. Details on the amount of data used in this study are in Table 1. The data were recorded on animals that were routinely preselected by Topigs Norsvin. In the pedigree, animals with one or both parents missing were assigned to genetic groups (Westell et al., 1988), according to line and year of birth of each animal. We used the same data in our previous study (Jibrila et al., 2022), except that there (1) we did not use FI_{SE} and FI_{ME}, and (2) we additionally used a dataset from a dam line.

2.2 | Training and validation generations

Animals born before or on January 31, 2017 were used as training population. Animals born after January 31, 2017 that met the following requirements were selected as validation animals: (1) they had phenotyped progeny, and (2) their parents were born before or on January 31, 2017. The first requirement enabled comparing GEBV of the validation animals against their progeny yield deviation (PYD) (Mrode and Thompson, 2014), and the second

TABLE 1 Data used in subsequent ssGBLUP[a] evaluation following each preselection scenario

	Whether records of animals in the validation generation were included or excluded in the subsequent ssGBLUP evaluation					
	Included			Excluded		
Number of animals with	Reference[b]	VGP[c]	MGP[d]	Reference	VGP	MGP
Pedigree entry	81,875	60,950	12,777	81,875	60,950	12,777
FI_{SE}[e] records	12,136	8648	248	8610	8610	210
FI_{ME}[e] records	10,607	8389	240	8257	8257	108
ADG_T[f] records	71,859	51,811	5939	50,463	50,463	4591
ADG_L[f] records	74,893	54,053	6064	52,683	52,683	4694
Backfat thickness records	74,411	53,674	6058	52,304	52,304	4688
Loin depth records	73,544	52,803	5943	51,433	51,433	4573
Records for ≥1 trait	75,129	54,217	6065	52,846	52,846	4694
Genotypes	33,506	23,315	5131	33,506	23,315	5131
FI_{SE} records and genotypes	8393	5369	237	5331	5331	199

[a]Single-step genomic best linear unbiased prediction.
[b]The subsequent ssGBLUP evaluation used the entire available data until the validation generation.
[c]Validation generation preselection (VGP) scenario, in which all animals in the validation generation without progeny in the data were discarded.
[d]Multi-generation preselection (MGP) scenario, in which all animals in the validation and training generations without progeny in the data were discarded.
[e]Feed intake from the start (FI_{SE}) or the middle (FI_{ME}) to the end of performance testing.
[f]Average daily gain during performance testing (ADG_T) or throughout life (ADG_L).

requirement ensured that our validation animals were from only one generation. Since records on validation animals were included in some of our subsequent evaluation scenarios (as explained later), we chose to use PYD as our proxy for true breeding value (TBV) because PYD is estimated from phenotypes that were not included in the subsequent genetic evaluation. Using January 31, 2017 as the cut-off date to split the data into training and validation generations allowed us to have one generation of validation animals with phenotyped offspring.

2.3 | Genomic data and quality control

The genomic data included genotypes for about 21,000 segregating autosomal single nucleotide polymorphisms (SNP), genotyped using a custom SNP chip. Per GPS scenario (as described later), animals and SNP with call rates less than 90% were removed, as well as SNP that had a minor allele frequency below 0.005, or deviated from Hardy–Weinberg equilibrium (Hardy–Weinberg equilibrium exact test p value = 10^{-15}). The 0.005 cut-off for minor allele frequency in the MGP scenario, with the lowest number of genotyped animals retained (5131), corresponds with observing at least 51 times the minor allele. We expect that this number is sufficient to enable relatively accurate estimation of SNP effects, but also to avoid including SNPs that segregate in only one or a few families (Edriss et al., 2013), or that are actually not segregating at all, but only appear to be segregating as a result of genotyping errors. Across the GPS scenarios, the number of remaining SNP ranged from 20,550 to 20,963. All quality control steps were undertaken using Plink software (Purcell et al., 2007).

2.4 | Computation of precorrected phenotypes

We used precorrected phenotypes (y_c) as records in our genetic evaluations, to avoid that after implementing the GPS scenarios (as described in the next section), some classes of non-genetic effects in the model could be left with only one or a few animals (Jibrila et al., 2022). To compute y_c, we first ran a six-trait pedigree-based animal model. The model statement for every trait (j) is

$$\mathbf{y_j} = \mathbf{X_j b_j} + \mathbf{W_j p_j} + \mathbf{Z_j u_j} + \mathbf{e_j}, \quad (1)$$

where $\mathbf{y_j}$ was the vector of phenotypes; $\mathbf{b_j}$ was the vector of fixed effects (e.g. sex and batch), with incidence matrix $\mathbf{X_j}$; $\mathbf{p_j}$ was the vector of non-genetic random effects (including pen and common litter), with incidence matrix $\mathbf{W_j}$; $\mathbf{u_j}$ was the vector of breeding values, with incidence matrix $\mathbf{Z_j}$; and $\mathbf{e_j}$ was the vector of residuals. The model assumed $\mathbf{u_j}$ and $\mathbf{e_j}$ to be normally distributed and uncorrelated, each with mean of zero. For all traits and across all animals, $\mathbf{u}$ and $\mathbf{e}$ had variance–covariance matrices $\mathbf{A} \otimes \mathbf{G}$ and $\mathbf{I} \otimes \mathbf{R}$, respectively, where $\mathbf{A}$ was the pedigree relationship matrix among animals, $\mathbf{I}$ was an identity matrix with dimensions equal to the number of animals with records, and $\mathbf{G}$ and $\mathbf{R}$ were respectively the trait by trait additive genetic and residual variance–covariance matrices. Then, the vector of precorrected phenotypes for trait j ($\mathbf{y_{cj}}$) was computed as

$$\mathbf{y_{cj}} = \mathbf{y_j} - \mathbf{X_j}\hat{\mathbf{b}}_\mathbf{j} - \mathbf{W_j}\hat{\mathbf{p}}_\mathbf{j} = \mathbf{Z_j}\hat{\mathbf{u}}_\mathbf{j} + \hat{\mathbf{e}}_\mathbf{j}. \quad (2)$$

2.5 | Preselection

We implemented a reference scenario and two scenarios with additional layers of GPS, as described in Jibrila et al. (2022). Briefly, the reference scenario used all available data until the validation generation, and thus only included the routine GPS implemented by Topigs Norsvin. The other two scenarios implemented additional GPS in the validation generation (validation generation preselection; VGP), or in the validation and training generations (multi-generation preselection; MGP). This was achieved by discarding the pedigree, genotypes and phenotypes of all animals in the validation generation (VGP), or all animals in the validation generation and those in the training generations with no progeny in the data (MGP). Note that the last two scenarios do not occur in real breeding programs, but implementing these GPS scenarios enabled us to investigate the impact of GPS on subsequent genetic evaluations of preselected animals using real data, by including different amounts of pedigree, genomic and phenotypic information in the subsequent genetic evaluations. An overview of all finally remaining animals for each of the GPS scenarios is shown in fig. 1 in Jibrila et al. (2022).

2.6 | Subsequent ssGBLUP evaluation

For each GPS scenario, a subsequent ssGBLUP evaluation was performed with all animals that survived the GPS. Progeny of validation animals were not included in the subsequent ssGBLUP evaluation. The subsequent ssGBLUP evaluation was conducted with or without records on the animals in the validation generation (see Table 1). We assumed three situations in conducting the subsequent evaluation, where records were available for: (i) only the scarcely recorded target trait, (ii) only the predictor traits, and (iii) both the scarcely recorded target trait and the predictor traits. For the situation where the only records

available were of the scarcely recorded target trait, we still analysed FI_{SE} and FI_{ME} together, as this mimicked reality. We however decided to only report results of subsequent evaluation for FI_{SE}, as FI_{ME} had only 70 validation animals, while FI_{SE} had 944 validation animals.

The multi-trait model used for estimation of GEBV for every trait (j) was

$$\mathbf{y_j} = \mathbf{1_j}\mu_j + \mathbf{Z_j}\mathbf{u_j} + \mathbf{e_j}, \quad (3)$$

where for every trait (j), $\mathbf{y_j}$ was the vector of precorrected phenotypes; $\mathbf{1_j}$ was a vector of 1's, and $\mathbf{Z_j}$ was an incidence matrix, linking precorrected phenotypes to the overall mean μ_j and random animal effects, respectively; $\mathbf{u_j}$ and $\mathbf{e_j}$ and their assumptions are the same as for Equation (1). However, the matrix $\mathbf{A}$ in the variance–covariance matrix of $\mathbf{u}$ in Equation (1) was replaced in Equation (3) by the matrix $\mathbf{H}$, the combined genomic-pedigree relationship matrix among animals.

The inverse of $\mathbf{H}$ ($\mathbf{H^{-1}}$) was obtained as follows (Aguilar et al., 2010; Christensen and Lund, 2010):

$$\mathbf{H^{-1}} = \mathbf{A^{-1}} + \begin{bmatrix} 0 & 0 \\ 0 & \left(0.95\mathbf{G_t} + 0.05\mathbf{A_{22}}\right)^{-1} - \mathbf{A_{22}^{-1}} \end{bmatrix}, \quad (4)$$

where $\mathbf{A^{-1}}$ was the inverse of the pedigree relationship matrix, and $\mathbf{A_{22}}$ was part of the pedigree relationship matrix referring to genotyped animals. Inbreeding was considered in setting up both $\mathbf{A^{-1}}$ and $\mathbf{A_{22}}$, following the recommendation by (Tsuruta et al., 2019). The adjusted genomic relationship matrix $\mathbf{G_t}$ was computed as follows (Powell et al., 2010; Vitezica et al., 2011):

$$\mathbf{G_t} = \left(1 - \bar{f}_p\right)\mathbf{G_r} + 2\bar{f}_p\mathbf{11'}, \quad (5)$$

where $\bar{f}_p$ was the average pedigree inbreeding coefficient across genotyped animals being equal to 0.08 when including all 33,506 genotyped animals, $\mathbf{G_r}$ was the raw genomic relationship matrix computed following the first method of VanRaden (VanRaden, 2008), and $\mathbf{11'}$ was a matrix of 1's. As the animals with genotypes in this study were selectively genotyped, this transformation made sure that the impact of selective genotyping was taken care of and that $\mathbf{G}$ and $\mathbf{A_{22}}$ were on the same scale and therefore compatible (Vitezica et al., 2011; Hsu et al., 2017). To compute $\mathbf{G_r}$, we computed current allele frequencies using all available genomic data after quality control.

For every GPS scenario, the data used in the subsequent evaluation (as in Table 1) were used in a pedigree version of Equation (3) in ASReml (Gilmour et al., 2009) to estimate scenario-specific variance components. We used these scenario-specific variance components in the subsequent genetic evaluation, to ensure that the variance components used were appropriate for the precorrected phenotypes. All estimations of breeding values were done using MiXBLUP (ten Napel et al., 2020).

2.7 | Measures of accuracy and bias

We used progeny yield deviation (PYD) (Mrode and Thompson, 2014) to compute GEBV accuracy and bias. To compute PYD, we ran a multi-trait pedigree-based animal model in MiXBLUP, with precorrected phenotypes as records and an overall mean as the only fixed effect (Equation [3]). We computed approximate reliability of PYD for each validation animal for each trait, and used this approximate reliability as the weighting factor to compute accuracy and bias, to account for differences in number of progeny used to estimate PYD for different validation animals.

Validation accuracy was computed as weighted Pearson's correlation coefficient between PYD and GEBV of all validation animals, using the "cor.test" function of the "stats" package in R (R Foundation for Statistical Computing, 2020). We computed the standard errors (SE) of the estimates from the confidence intervals (CI) produced by the "cor.test" function. We computed two types of bias. Firstly, level bias was computed as the weighted mean difference between PYD and half of the GEBV across all validation animals, expressed in additive genetic standard deviation (SD) units of the trait. Secondly, dispersion bias was measured by the weighted regression coefficient of PYD on GEBV of all validation animals. We used the "lm" function of the "stats" package in R (R Foundation for Statistical Computing, 2020) to compute both the estimates and SE of the regression coefficients. We always used a one-tailed two-sample t-test at 5% significance level to determine whether two estimates (of accuracy, bias and heritability) were different. For a full description of all details of the calculations of the PYD and the associated approximate reliabilities, as well as the level and dispersion bias, see Jibrila et al. (2022).

3 | RESULTS

3.1 | Effectiveness of the additional GPS scenarios

Table 2 shows normalized means and SD of precorrected phenotypes of the traits analysed in this study, following the implemented GPS scenarios. The results show that our additionally implemented GPS was effective, as the line was (pre)selected for, among others, increased

TABLE 2 Normalized[a] means and standard deviations (in brackets) of precorrected phenotypes of the traits used in this study, following each genomic preselection scenario

	Mean and SD in validation generation		Mean and SD in the full data	
Trait/preselection scenario	**Reference[b]**	**VGP[c] & MGP[d]**	**VGP**	**MGP**
FI_{SE}[e] (g/day)	−0.08 (1)	0.14 (0.83)	−0.12 (1.00)	−0.01 (0.91)
FI_{ME}[e] (g/day)	−0.30 (1)	−0.11 (0.82)	−0.29 (1.00)	−0.10 (0.86)
ADG_T[f] (g/day)	0.12 (1)	0.51 (0.80)	−0.08 (1.00)	0.38 (0.84)
ADG_L[f] (g/day)	0.03 (1)	0.41 (0.85)	−0.11 (1.00)	0.31 (0.86)
Backfat thickness (mm)	−0.27 (1)	−0.29 (0.95)	−0.01 (1.00)	−0.10 (0.96)
Loin depth (mm)	0.26 (1)	0.26 (0.97)	0.17 (1.00)	0.20 (0.97)

[a]The values were normalized by dividing them by the standard deviations of their corresponding reference scenarios.

[b]The subsequent ssGBLUP evaluation used the entire available data until the validation generation.

[c]Validation generation preselection (VGP) scenario, in which all animals in the validation generation without progeny in the data were discarded.

[d]Multi-generation preselection (MGP) scenario, in which all animals in the validation and training generations without progeny in the data were discarded.

[e]Feed intake from the start (FI_{SE}) or the middle (FI_{ME}) to the end of performance testing.

[f]Average daily gain during performance testing (ADG_T) or throughout life (ADG_L).

TABLE 3 Estimated heritabilities (diagonal), genetic correlations (below diagonal) and phenotypic correlations (above diagonal) for the traits used in this study, using the full data

Traits	**FI_{SE}[a]**	**FI_{ME}[a]**	**ADG_T[b]**	**ADG_L[b]**	**Backfat**	**Loin depth**
FI_{SE}	**0.37 (0.02)**	0.85 (0.01)	0.70 (0.00)	0.72 (0.00)	0.43 (0.01)	−0.16 (0.01)
FI_{ME}	0.97 (0.02)	**0.35 (0.02)**	0.76 (0.00)	0.78 (0.00)	0.43 (0.01)	−0.19 (0.01)
ADG_T	0.79 (0.02)	0.78 (0.02)	**0.24 (0.01)**	0.91 (0.00)	0.20 (0.01)	−0.17 (0.01)
ADG_L	0.80 (0.02)	0.77 (0.02)	0.92 (0.00)	**0.26 (0.01)**	0.20 (0.01)	−0.17 (0.01)
Backfat	0.60 (0.02)	0.54 (0.03)	0.27 (0.02)	0.32 (0.02)	**0.58 (0.01)**	−0.04 (0.01)
Loin depth	−0.33 (0.03)	−0.35 (0.03)	−0.29 (0.02)	−0.30 (0.02)	−0.11 (0.02)	**0.55 (0.01)**

[a]Feed intake from the start (FI_{SE}) or the middle (FI_{ME}) to the end of performance testing.

[b]Average daily gain during performance testing (ADG_T) or throughout life (ADG_L).

The values in bold are heritabilities.

feed efficiency (i.e. slightly higher feed intake, and much higher average daily gain), slightly decreased backfat, and slightly increased loin depth. As the validation generation for both VGP and MGP scenarios only contained the preselected animals, means and SD of the precorrected phenotypes of the traits are the same for these two preselection scenarios when only considering the animals in the validation generation. When only the validation generation was considered (i.e. the middle part of Table 2), the average precorrected phenotypes of FI_{SE}, FI_{ME}, ADG_T and ADG_L increased going from the reference scenario to the VGP/MGP scenario. At the same time, SD of the precorrected phenotypes of these traits decreased from reference to VGP/MGP scenarios. For backfat thickness, both the mean and the SD only slightly decreased from reference to VGP and MGP scenarios. The change was also only slight for loin depth, with the mean remaining the same at least up to two decimal places, and the SD slightly decreasing, from reference to VGP and MGP scenarios. Higher effectiveness of MGP over VGP can be seen from the means and SD computed across the entire data (i.e. the right part of Table 2). For the positively (pre)selected traits (i.e FI_{SE}, FI_{ME}, ADG_T, ADG_L and loin depth) means were higher for MGP than for VGP. And for backfact thickness, which was negatively (pre)selected, the mean was lower for MGP than for VGP.

3.2 | Heritabilities and correlations among the traits

Table 3 shows estimated heritabilities (in bold, on the diagonal), genetic correlations (below diagonal) and phenotic correlations (above diagonal) for the traits analysed in this study, using the full data. All the traits have moderate to high heritabilities, ranging from 0.24 for ADG_T to 0.58 for backfat thickness. The two feed intake traits have close-to-unity genetic and phenotypic correlations with each other (0.97 and 0.85, respectively). They also have moderate to high genetic correlations and low to moderate phenotypic correlations with the other traits (absolute values of genetic correlations ranged from 0.33 to 0.80,

and absolute values of phenotypic correlations ranged from 0.16 to 0.78).

3.3 | Accuracy and bias

Accuracy and bias of subsequent ssGBLUP evaluation of FI_{SE} are presented in Table 4. We included estimated heritabilities in Table 4 because they help in explaining the results of accuracy and bias. The estimated heritability had a tendency (i.e. an inclination that may not be statistically significant) to decrease with more preselection, whether records on animals in the validation generation were included or excluded in estimating the heritabilities.

3.3.1 | Subsequent ssGBLUP evaluation only using records of the target trait

Validation accuracy did not differ across reference and VGP scenarios, but decreased in the MGP scenario (Table 4), due to the steep reduction of the number of phenotypes included in the analyses. We observed this whether records on animals in the validation generation were included or excluded in the subsequent evaluation. Level bias was present, and increased with more preselection when records on animals in the validation were included in the subsequent evaluation. However, when records on animals in the validation generation were excluded from the subsequent evaluation, level bias did not differ across GPS scenarios. Nevertheless, level bias was in all cases only marginal, as its estimate deviating the most from 0 across all GPS scenarios was only −0.17 additive genetic SD units. Dispersion bias (inflation in this case) was present in reference and VGP scenarios, and did not differ between the two scenarios, whether records on animals in the validation generation were included or excluded in the subsequent evaluation. Deflation was observed (i.e. the regression coefficient was bigger than the expected value of 0.5) with MGP when records on animals in the validation generation were included in the subsequent evaluation. When we repeated the subsequent evaluation for this MGP scenario using the (co)variance components estimated under the reference scenario (Table 5), the deflation disappeared. For the MGP scenario when records on animals in the validation generation were excluded from the subsequent evaluation, there was no significant dispersion bias, although a tendency towards deflation was observed (Table 4).

3.3.2 | Subsequent ssGBLUP evaluation only using records of the predictor traits

Validation accuracy did not differ across GPS scenarios (Table 4). Level bias was always present, but did not differ across GPS scenarios. Similar to the subsequent ssGBLUP

TABLE 4 Accuracy and bias in subsequent ssGBLUP evaluation of FI_{SE}[a] (SE in brackets)

		Whether records of animals in the validation generation were included or excluded in the subsequent ssGBLUP evaluation					
		Included			Excluded		
Measure	Traits used	Reference[b]	VGP[c]	MGP[d]	Reference	VGP	MGP
Heritability	All	0.37 (0.02)	0.35 (0.02)	0.24 (0.09)	0.36 (0.02)	0.36 (0.02)	0.32 (0.10)
Accuracy	$FI_{SE} + FI_{ME}$[a]	0.45 (0.03)	0.40 (0.03)	0.32 (0.03)	0.39 (0.03)	0.39 (0.03)	0.24 (0.03)
	Predictors[e]	0.46 (0.03)	0.45 (0.03)	0.45 (0.03)	0.42 (0.03)	0.43 (0.03)	0.40 (0.03)
	All	0.49 (0.02)	0.47 (0.03)	0.45 (0.03)	0.44 (0.03)	0.44 (0.03)	0.40 (0.03)
Level bias	$FI_{SE} + FI_{ME}$	−0.07 (0.02)	−0.12 (0.02)	−0.17 (0.03)	−0.11 (0.02)	−0.11 (0.02)	−0.14 (0.03)
	Predictors	−0.18 (0.02)	−0.21 (0.02)	−0.16 (0.03)	−0.19 (0.02)	−0.19 (0.02)	−0.14 (0.03)
	All	−0.06 (0.02)	−0.11 (0.02)	−0.17 (0.03)	−0.09 (0.02)	−0.09 (0.02)	−0.15 (0.03)
Dispersion bias	$FI_{SE} + FI_{ME}$	0.42 (0.03)	0.42 (0.03)	0.82 (0.08)	0.39 (0.03)	0.40 (0.03)	0.56 (0.07)
	Predictors	0.48 (0.03)	0.51 (0.03)	0.71 (0.05)	0.47 (0.03)	0.47 (0.03)	0.57 (0.04)
	All	0.45 (0.03)	0.47 (0.03)	0.69 (0.04)	0.44 (0.03)	0.44 (0.03)	0.55 (0.04)

[a]Feed intake from the start (FI_{SE}) or the middle (FI_{ME}) to the end of performance testing.

[b]The subsequent ssGBLUP evaluation used the entire available data until the validation generation.

[c]Validation generation preselection (VGP) scenario, in which we discarded all animals in the validation generation with no progeny in the data.

[d]Multi-generation preselection (MGP) scenario, in which we discarded all animals in the validation or training generations with no progeny in the data.

[e]The predictor traits are average daily gain during performance testing or throughout life, back fat thickness, and loin depth.

TABLE 5 Dispersion bias in subsequent ssGBLUP evaluation of FI_{SE}[a], under MGP[b] scenario with records on animals in the validation generation included (SE in brackets), using variance components estimated from the full data

Traits used	Dispersion bias	Level bias	Accuracy
$FI_{SE}+FI_{ME}$[a]	0.54 (0.05)	−0.13 (0.02)	0.46 (0.04)
Predictors[c]	0.53 (0.03)	−0.13 (0.02)	0.65 (0.04)
All	0.50 (0.03)	−0.13 (0.02)	0.66 (0.04)

[a]Feed intake from the start (FI_{SE}) or the middle (FI_{ME}) to the end of performance testing.

[b]Multi-generation preselection (MGP) scenario, in which we discarded all animals in the validation or training generations with no progeny in the data.

[c]The predictor traits are average daily gain during performance testing or throughout life, back fat thickness, and loin depth.

evaluation based on records from the target trait, level bias was always only marginal, with the highest estimate being −0.21 additive genetic SD units. There was generally no dispersion bias, whether records of the animals in the validation generation were included or excluded in the subsequent evaluation. The only exception is the MGP scenario with records on animals in the validation generation included in the subsequent evaluation, where there was deflation. Similar to the subsequent ssGBLUP evaluation based on records from the target trait, the deflation disappeared when we repeated the subsequent ssGBLUP evaluation for this MGP scenario using the (co)variance components estimated under the reference scenario (Table 5).

3.3.3 | Subsequent ssGBLUP evaluation using records of all traits

Results from the subsequent ssGBLUP evaluation based on all traits were very similar to those based on records from the predictor traits only. Validation accuracy did not differ across GPS scenarios (Table 4). Marginal level bias was present, with the highest estimate being −0.17 additive genetic SD units, and increased with more GPS. Dispersion bias was absent in most scenarios, except for the observed deflation for the MGP scenario with records on animals in the validation generation included in the subsequent evaluation. Just like in the previous subsections, the deflation disappeared when we repeated the subsequent ssGBLUP evaluation for this MGP scenario using the (co)variance components estimated under the reference scenario (Table 5).

4 | DISCUSSION

We studied the impact of GPS on accuracy and bias in subsequent ssGBLUP evaluation of preselected animals, for a scarcely recorded trait. We used data from a commercial pig breeding program in which routine preselection was already implemented, and retrospectively implemented additional layers of GPS by excluding animals with no progeny in the complete dataset from the subsequent evaluation. The data was on production traits in a sire line, with feed intake as scarcely recorded target trait, and average daily gain, backfat thickness and loin depth as widely recorded predictor traits. In the subsequent evaluation, we assumed that records were available for only the scarcely recorded target trait, only the predictor traits, or both. We performed the subsequent ssGBLUP evaluation either including or excluding records on animals in the validation generation, and in all cases without progeny of validation animals. We observed that validation accuracy generally only tended to decrease with more GPS. We also observed that although level and dispersion biases were sometimes present, the former was generally only marginal, and the latter did not differ across GPS scenarios.

Our reference GPS scenario already contains the routine preselection implemented in commercial animal breeding programs (Jibrila et al., 2022). The VGP and MGP scenarios implemented in our study do not happen in reality, but represent hypothetical scenarios where the breeding program was able to avoid phenotyping animals that later on were not selected to produce offspring, either only in the validation (VGP) or all generations (MGP). In this paper and in Jibrila et al. (2022), the three preselection scenarios implemented (i.e. reference, VGP and MGP scenarios) can be considered to represent different preselection intensities, although the increase in preselection intensity from VGP to MGP is across generations and not within one generation. Previously, using simulations we showed that following increasing preselection selection intensities of up to 5% in males and 12.5% in females, subsequent ssGBLUP still yielded unbiased GEBV (Jibrila et al., 2020). Especially the MGP scenario is much more extreme than what is possible in practice, as it retrospectively removes more accurately animals that will end up not being used for breeding purposes. As such, these scenarios are used here to investigate the ability of ssGBLUP to estimate GEBV of preselected animals without preselection bias in subsequent evaluation in real breeding programs, with more stringent preselection than will be encountered in practice. The idea is that if ssGBLUP in subsequent evaluation of the scenarios with additional GPS is able to estimate GEBV of preselected animals as unbiased as in the subsequent evaluation of our reference scenario, then it is also able to estimate GEBV of preselected animals without preselection bias in subsequent evaluation in real breeding programs. Our results have shown that just like for widely recorded traits (Jibrila et al., 2022), ssGBLUP in subsequent evaluation for scarcely recorded feed intake in pigs is able to estimate GEBV of preselected animals without preselection bias. Nevertheless, bias was observed in

some cases. The observed increase in dispersion bias moving from reference and VGP scenarios to MGP scenario was due to biased (co)variance components, most likely resulting from the small amount of data which came from heavily preselected animals in our MGP scenario. Note that in the MGP scenario there were only about 250 animals with records of the scarcely recorded target trait that were almost all genotyped (Table 1). However, when we repeated the subsequent ssGBLUP evaluation using the (co)variance components of the reference scenario, the dispersion bias in the MGP scenario disappeared, regardless of whether only the scarcely recorded target trait, only the predictor traits, or both were used in the analysis (Table 5). It is also interesting that the deflation observed in the MGP scenario was significant when records of the animals in the validation generation were included in the subsequent evaluation, but not significant when records of the animals in the validation generation were excluded from the subsequent evaluation. Underestimation of heritability in the MGP scenario was much bigger (i.e. the heritability was lower) when records of the animals in the validation generation were included than when they were excluded from the subsequent evaluation (Table 4). This lower heritability has resulted in less variable GEBV for the validation animals in the MGP scenario when records of validation animals were included rather than excluded from the subsequent evaluation. This explains the larger regression coefficient (i.e. bigger deflation) observed in the MGP scenario when records of the animals in the validation generation were included compared to when they excluded from the subsequent evaluation. This also explains why repeating the subsequent evaluation of the MGP scenario using the (co)variance components of the reference scenario eliminated the dispersion bias initially observed in the MGP scenario (Table 5). In summary, our results suggest that ssGBLUP in subsequent evaluation of animals for scarcely recorded traits is able to estimate GEBV of preselected animals without preselection bias, provided that the (co)variance components used are unbiased.

For level bias, the consistently small negative level bias observed throughout Table 4 can most likely be attributed to biased PYD. In this study, we computed PYD using a PBLUP model. The animals that were recorded on feed intake were intensely preselected based on an index mainly including traits genetically correlated to feed intake. As a result, the EBV of the preselected animals for feed intake are expected to be underestimated even in multi-trait PBLUP evaluation like the one we performed to estimate PYD. Because level bias was computed as the weighted mean difference between PYD and half of the GEBV across all validation animals, a consistent underestimation of the PYD would explain the consistent small negative level bias. Finally, the accuracy loss we observed in this study with more preselection, is as expected, as with more preselection there are less relatives with records (Patry and Ducrocq, 2011; Jibrila et al., 2020), and with more preselection the achieved heritability decreased. It is common knowledge that accuracy changes with heritability. Interestingly, when we repeated the subsequent ssGBLUP evaluation using the (co)variance components of the reference scenario (Table 5), the accuracy achieved from the MGP scenario increased to a level higher than the corresponding accuracy of the reference scenario (Table 4). This increase in accuracy can be explained by the higher heritability and presence of records only on animals with progenies (i.e. only the validation animals and their ancestors have records).

4.1 | Impact of preselection tended to be larger when using records of the target trait

Although results were in all cases not statistically different between corresponding reference and VGP scenarios, tendencies of accuracy to decrease and of dispersion bias to increase from reference to VGP to MGP scenarios were bigger when using records of feed intake compared to when using only records of the predictor traits. Since records of the target trait (feed intake in this case) are by default scarce, any further reduction in the amount of these records is likely to cause a bigger impact than a corresponding reduction in records of predictor traits. With fewer records that are also more intensely preselected, validation accuracy reduces, and there is more shrinkage to the mean, making the GEBV less variable, thereby leading to larger dispersion bias. This underlines the importance of obtaining enough records for scarcely recorded traits.

4.2 | Impact of predictor traits

Accuracy of predicting FI_{SE} tended to be higher when only records on predictor traits were used than when only records on feed intake itself were used. This shows that most of the information provided by the relatively few records of FI_{SE} and FI_{ME} had already been provided by the relatively more abundant records of the predictor traits. Indeed, the predictor traits had 3 to 15 times more records than the two feed intake traits combined, depending on the preselection scenario (Table 1). In previous studies, higher prediction accuracies have been reported for scarcely recorded traits when only records of predictor traits were used compared to when only records of the scarcely recorded traits themselves were used (Philipsson et al., 1995; Pszczola et al., 2013; Manzanilla-Pech et al., 2020). It has been shown that for a predictor trait to increase prediction accuracy of a scarcely recorded

trait, the two traits have to be moderately to highly genetically correlated (i.e. ≥0.3, e.g. Ducrocq, 1994; Calus and Veerkamp, 2011; Pszczola et al., 2013), and the two traits have to be more genetically than phenotypically correlated (e.g. Schaeffer, 1984; Thompson and Meyer, 1986). All our predictor traits had reasonably high correlations with FI_{SE}, and the genetic correlations are higher than their corresponding phenotypic correlations (Table 3). It has also been shown that the contribution of a predictor trait to the prediction accuracy of a scarcely recorded trait increases with an increasing difference in heritabilities of the two traits, if the predictor trait has the higher heritability (Thompson and Meyer, 1986; Ducrocq, 1994; Jia and Jannink, 2012; Manzanilla-Pech et al., 2020). All our predictor traits had moderate to high heritabilities, and backfat thickness and loin depth had higher heritabilities than FI_{SE} (Table 3). As long as genetic and phenotypic correlations among traits are reliably estimated (Mrode and Thompson, 2014), accuracy of prediction of a scarcely recorded trait increases with more predictor traits included in a multi-trait evaluation (e.g. Pszczola et al., 2013; Manzanilla-Pech et al., 2020). All the factors discussed in this paragraph likely contributed to some extent to the increase in accuracy of predicting FI_{SE} moving from only using records of the scarcely recorded FI_{SE} and FI_{ME} to only using records of the predictor traits.

In this study, we had predictor traits that all had moderate to high heritabilities and moderate to high genetic correlations with the target trait. In situations where heritabilities of the predictor traits and genetic correlations between predictor and target traits are smaller, we expect smaller prediction accuracies. However, even in such situations, we expect ssGBLUP in subsequent evaluation of animals for the scarcely recorded target traits to be able to estimate GEBV of preselected animals without preselection bias. This is because, as discussed in Jibrila (2022), ssGBLUP estimates unbiased GEBV of preselected animals mainly because it is able to obtain unbiased estimates of the Mendelian sampling terms of preselected animals from genotypes of the preselected animals and their parents, which are not affected by heritability and genetic correlations among traits. Indeed, in our study most of the validation animals (>80%) had both their parents genotyped.

5 | CONCLUSIONS

Our results show that as long as the (co)variance components used are unbiased, ssGBLUP in subsequent evaluation of pigs for scarcely recorded feed intake is able to estimate GEBV of preselected animals without preselection bias. We observed this whether records on animals in the validation generation were included or excluded in the subsequent evaluation, and whether the subsequent evaluations were done using records only from the scarcely recorded target trait, only from the predictor traits, or from both the target and the predictor traits. The presented approach with additional preselection implemented allows to evaluate the impact of preselection using real data from an ongoing breeding program. Existing preselection in the data may affect derived proxies for true breeding value, but this can be detected based on analysis of the full data. Results from this study confirm that multi-trait evaluation of animals for scarcely recorded traits together with predictor traits gives more accurate and less biased (G)EBV of animals for scarcely recorded traits compared to single-trait evaluation.

AUTHOR CONTRIBUTIONS

All authors participated in the conception and the design of the study and of the analysis of the dataset. RB provided the dataset, IJ analysed the dataset and wrote the first draft of the manuscript, and all authors participated in revising the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

ETHICS APPROVAL

The data used for this study were collected as part of routine data recording in a commercial breeding program. Samples collected for DNA extraction were used for routine diagnostic purposes of the breeding program. Data recording and sample collection were conducted in line with local laws on protection of animals.

DATA AVAILABILITY STATEMENT

The data used in the present study were provided by Topigs Norsvin and are not publicly accessible.

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REFERENCES

Aguilar, I., Misztal, I., Johnson, D. L., Legarra, A., Tsuruta, S., & Lawlor, T. J. (2010). Hot topic: A unified approach to utilize phenotypic, full pedigree, and genomic information for genetic evaluation of Holstein final score. *Journal of Dairy Science*, *93*(2), 743–752. https://doi.org/10.3168/jds.2009-2730

Calus, M. P. L., & Veerkamp, R. F. (2011). Accuracy of multi-trait genomic selection using different methods. *Genetics Selection Evolution*, *43*, 26. https://doi.org/10.1186/1297-9686-43-26

Christensen, O. F., & Lund, M. S. (2010). Genomic prediction when some animals are not genotyped. *Genetics Selection Evolution*, *42*, 2. https://doi.org/10.1186/1297-9686-42-2

Dekkers, J. C., Mathur, P. K., & Knol, E. F. (2011). Genetic improvement of the pig. In M. F. Rothschild & A. Ruvinksky (Eds.), *The genetics of the pig* (pp. 390–425). CABI.

Ducrocq, V. (1994). Multiple trait prediction: Principles and problems. In *Proceedings of the World Congress on Genetics Applied to Livestock Production* (pp. 455–462). University of Guelph.

Edriss, V., Guldbrandtsen, B., Lund, M. S., & Su, G. (2013). Effect of marker-data editing on the accuracy of genomic prediction. *Journal of Animal Breeding and Genetics*, *130*(2), 128–135. https://doi.org/10.1111/j.1439-0388.2012.01015.x

Gilmour, A. R., Gogel, B. J., Cullis, B. R., & Thompson, R. (2009). *ASReml user guide release 3.0*. VSN International Ltd.

Henderson, C. R. (1975). Best linear unbiased estimation and prediction under a selection model. *Biometrics*, *31*(2), 423–447. https://doi.org/10.2307/2529430

Hsu, W.-L., Garrick, D. J., & Fernando, R. L. (2017). The accuracy and bias of single-step genomic prediction for populations under selection. *G3: Genes|Genomes|Genetics*, *7*(8), 2685–2694. https://doi.org/10.1534/g3.117.043596

Jia, Y., & Jannink, J.-L. (2012). Multiple-trait genomic selection methods increase genetic value prediction accuracy. *Genetics*, *192*(4), 1513–1522. https://doi.org/10.1534/genetics.112.144246

Jibrila, I. (2022). *Impact of preselection in genomic evaluations*. PhD thesis. Wageningen University.

Jibrila, I., ten Napel, J., Vandenplas, J., Veerkamp, R. F., & Calus, M. P. L. (2020). Investigating the impact of preselection on subsequent single-step genomic BLUP evaluation of preselected animals. *Genetics Selection Evolution*, *52*(1), 42. https://doi.org/10.1186/s12711-020-00562-6

Jibrila, I., Vandenplas, J., ten Napel, J., Bergsma, R., Veerkamp, R. F., & Calus, M. P. L. (2022). Impact of genomic preselection on subsequent genetic evaluations with ssGBLUP using real data from pigs. *Genetics Selection Evolution*, *54*(1), 48. https://doi.org/10.1186/s12711-022-00727-5

Manzanilla-Pech, C. I. V., Gordo, D., Difford, G. F., Løvendahl, P., & Lassen, J. (2020). Multitrait genomic prediction of methane emissions in Danish Holstein cattle. *Journal of Dairy Science*, *103*(10), 9195–9206. https://doi.org/10.3168/jds.2019-17857

Mrode, R. A., & Thompson, R. (2014). *Linear models for the prediction of animal breeding values*. CABI.

Patry, C., & Ducrocq, V. (2011). Evidence of biases in genetic evaluations due to genomic preselection in dairy cattle. *Journal of Dairy Science*, *94*(2), 1011–1020. https://doi.org/10.3168/jds.2010-3804

Philipsson, J., Ral, G., & Berglund, B. (1995). Somatic cell count as a selection criterion for mastitis resistance in dairy cattle. *Livestock Production Science*, *41*(3), 195–200. https://doi.org/10.1016/0301-6226(94)00067-H

Pollak, E. J., Vanderwerf, J., & Quaas, R. L. (1984). Selection bias and multiple trait evaluation. *Journal of Dairy Science*, *67*(7), 1590–1595. https://doi.org/10.3168/jds.S0022-0302(84)81481-2

Powell, J. E., Visscher, P. M., & Goddard, M. E. (2010). Reconciling the analysis of IBD and IBS in complex trait studies. *Nature Reviews Genetics*, *11*(11), 800–805. https://doi.org/10.1038/nrg2865

Pszczola, M., Veerkamp, R. F., de Haas, Y., Wall, E., Strabel, T., & Calus, M. P. L. (2013). Effect of predictor traits on accuracy of genomic breeding values for feed intake based on a limited cow reference population. *Animal*, *7*(11), 1759–1768. https://doi.org/10.1017/S175173111300150X

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M. A. R., Bender, D., Maller, J., Sklar, P., de Bakker, P. I. W., Daly, M. J., & Sham, P. C. (2007). PLINK: A tool set for whole-genome association and population-based linkage analyses. *The American Journal of Human Genetics*, *81*(3), 559–575. https://doi.org/10.1086/519795

R Foundation for Statistical Computing. (2020). R: A language and environment for statistical computing. Vienna, Austria.

Schaeffer, L. R. (1984). Sire and cow evaluation under multiple trait models. *Journal of Dairy Science*, *67*(7), 1567–1580. https://doi.org/10.3168/jds.S0022-0302(84)81479-4

Sullivan, P. G. (2019). Mendelian sampling variance tests with genomic preselection. *Interbull Bulletin*, *54*, 1–4.

ten Napel, J., Calus, M. P. L., Lidauer, M., Stranden, I., Mäntysaari, E., Mulder, H. A., & Veerkamp, R. F. (2020). MiXBLUP, user-friendly software for large genetic evaluation systems. Wageningen, the Netherlands.

Thompson, R., & Meyer, K. (1986). A review of theoretical aspects in the estimation of breeding values for multi-trait selection. *Livestock Production Science*, *15*(4), 299–313. https://doi.org/10.1016/0301-6226(86)90071-0

Tsuruta, S., Lourenco, D. A. L., Masuda, Y., Misztal, I., & Lawlor, T. J. (2019). Controlling bias in genomic breeding values for young genotyped bulls. *Journal of Dairy Science*, *102*(11), 9956–9970. https://doi.org/10.3168/jds.2019-16789

VanRaden, P. M. (2008). Efficient methods to compute genomic predictions. *Journal of Dairy Science*, *91*(11), 4414–4423. https://doi.org/10.3168/jds.2007-0980

Vitezica, Z. G., Aguilar, I., Misztal, I., & Legarra, A. (2011). Bias in genomic predictions for populations under selection. *Genetics Research*, *93*(5), 357–366. https://doi.org/10.1017/S001667231100022X

Westell, R. A., Quaas, R. L., & Vanvleck, L. D. (1988). Genetic groups in an animal model. *Journal of Dairy Science*, *71*(5), 1310–1318. https://doi.org/10.3168/jds.S0022-0302(88)79688-5

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