Single-Step Genomic Evaluation With a Metafounder for Feed Conversion Ratio and Average Daily Gain in Danish Landrace and Yorkshire Pigs

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Single-step genomic evaluation with a metafounder for feed conversion ratio and average daily gain in Danish Landrace and Yorkshire pigs

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Abstract

Background

Single-step genomic best linear unbiased prediction (SSGBLUP) method is an effective approach for genetic evaluation. To overcome the issue that pedigree and genomic relationship matrices refer to different base populations, a single-step genomic method with a metafounder (MF-SSGBLUP) was put forward. The aim of this study was to compare the predictive abilities and bias of genomic evaluation based on MF-SSGBLUP compared with standard SSGBLUP. We did this for feed conversion ratio (FCR) and average daily gain (ADG) in DanBred Landrace (LL) and DanBred Yorkshire (YY) pigs using both univariate and bivariate models. Additionally, optimal weighting factors (ω) on pedigree-based relationship matrices for ADG and FCR in both SSGBLUP and MF-SSGBLUP were also investigated.

Results

In general, SSGBLUP and MF-SSGBLUP methods showed similar predictive abilities and biasedness of GEBVs. In LL, for ADG, the predictive ability for SSGBLUP was up to 0.355, while MF-SSGBLUP reached a highest predictive ability of 0.356; for FCR, the predictive ability for MF-SSGBLUP together with a bivariate model was highest (0.196) among all the different scenarios. In YY, performances of genomic prediction for ADG were almost similar among different scenarios and predictive ability for ADG was up to 0.347; for FCR, the highest predictive ability (0.355) was obtained in MF-SSGBLUP. In biasedness, SSGBLUP and MF-SSGBLUP performed

nearly the same, and bivariate models generally had less biasedness than univariate models. Additionally, in terms of the optimal weighting factors (ω), in LL, regardless of a univariate or a bivariate model was used, the optimal ω for ADG were around 0.2 in both SSGBLUP and MF-SSGBLUP; for FCR, 0.70 and 0.55 were the optimal ω in SSGBLUP and MF-SSGBLUP method, respectively. In YY, the optimal ω ranged from 0.25 to 0.35 for ADG and from 0.10 to 0.30 for FCR in different scenarios.

Conclusions

This study indicated that MF-SSGBLUP method performed at least as good as SSGBLUP for genomic evaluation. The optimal weighting factors (ω) in SSGBLUP and MF-SSGBLUP are not dramatically different. Overall, MF-SSGBLUP in combination with a bivariate model was recommended for single-step genomic evaluation for ADG and FCR in DanBred Landrace and Yorkshire pigs.

Keywords: Single-step GBLUP, Metafounder, Weighting factor, Model, Pigs

Background

Single-step genomic best linear unbiased prediction (SSGBLUP) has been successfully used as a standard genomic evaluation method in the pig industry [1]. Through using SSGBLUP, genomic selection (GS) can be implemented even if some animals are not genotyped, as it has an ability to integrate information from

phenotypic records, pedigree and genomic information on all the relevant animals [2, 3]. However, in regular SSGBLUP, some issues need to be solved. First, allele frequencies that are used to construct the genomic relationship matrix theoretically should be obtained from the base population [4]. Nevertheless, the base allele frequencies are usually unknown, since the animals in the base population have usually been dead for many years, and therefore are not genotyped [5]; second, genomic relationship matrix and pedigree relationship matrix should refer to the same (base) population to make them compatible. However, the (base) population is usually unknown and the beginning of pedigree is often regarded as the base population, which is an arbitrary choice. Thus, pedigree-based and marker-based relationship matrices are not directly compatible [6]; third, the optimal weighting factors (ω) on pedigree-based relationship matrix in a single-step genomic evaluation method might be breed-specific and trait-specific, which need to be further investigated. Currently, there are a few imperfect solutions to the above-mentioned issues. For example, instead of using base allele frequencies, allele frequencies of the current population are used to construct the genomic relationship matrix. Some studies adjusted the marker-based relationship matrix to make it compatible with the pedigree-based relationship matrix [7-9]. Breeding companies usually use a same weighting factor (ω) for different traits, rather than using an optimal ω for each trait, leading to a decreased accuracies of estimated breeding values [10]. Although these solutions have been widely used in regular SSGBLUP and seemed to be effective in practice, the

85 above-mentioned issues in regular SSGBLUP were not totally solved and SSGBLUP
86 had to be further developed and improved.
87 To overcome these issues, based on Christensen [6], Legarra et al. [5] developed a
88 concept of metafounder. A metafounder is assumed to be a finite-sized pool of
89 gametes, and animals in the base population randomly extract alleles from this pool to
90 form diploids [5]. With the concept of metafounder, genomic relationships should be
91 constructed using allele frequencies of 0.5, and a pedigree-based relationship matrix
92 needs to refer to the base allele frequencies as well, which resulted in automatic
93 compatibility between pedigree-based and marker-based relationship matrices. In
94 other words, the issues of unknown allele frequencies in base populations and
95 compatibility between two relationship matrices in SSGBLUP were in principle
96 solved.
97 Since then, a few studies have focused on the applications of single-step genomic
98 evaluation with metafounders (MF-SSGBLUP). For instance, Garcia-Baccino et al.
99 [11] used simulated data to investigate the optimal ways of estimating the relatedness
100 of animals in the base population (γ); Xiang et al. [12] employed MF-SSGBLUP on
101 purebred pigs for their crossbred performances and Bradford et al. [13] compared the
102 performances of SSGBLUP with three unknown parent groups with MF-SSGBLUP in
103 dairy cattle and recommended the use of MF-SSGBLUP for genomic prediction；
104 Macedo et al. [14] concluded that MF-SSGBLUP yielded unbiased estimates when
105 pedigree information was not complete. Nevertheless, to our knowledge, there is lack

of studies on the comparison of how MF-SSGBLUP performs in genomic evaluation for productive traits (e.g.: feed convention ratio, FCR and average daily gain, ADG) in pigs with the standard SSGBLUP method, especially that such records are available at the time of selection, and also using a multi-trait model, which is comprehensively used in pig breeding program. Besides, there were no studies investigating the effect of different weighing factors on pedigree-based relationship matrix in MF-SSGBLUP method. Therefore, the aims of this study are: (1) to compare the predictive abilities of genomic evaluation in SSGBLUP and MF-SSGBLUP; (2) to investigate the accuracies and biasedness of GEBVs in univariate and bivariate animal models in both SSGBLUP and MF-SSGBLUP methods; (3) to find optimal weighting factors (ω) on pedigree-based relationship matrices for ADG and FCR, in both SSGBLUP and MF-SSGBLUP. Results from this study can be applied directly in pig breeding industry.

Materials and Methods

Phenotypic recordings

In this study, all the datasets were provided by SEGES Danish Pig Research Centre. The traits of ADG (ADG = weight gain/days) and FCR (FCR = feed intake/weight gain) in the interval 30 to 100 kg were measured in both DanBred Landrace (LL) and DanBred Yorkshire (YY) pigs. In LL, ADG were recorded on 686,420 pigs, among which 18,889 pigs also had FCR recordings. In YY, ADG and FCR were recorded on

570,493 pigs and 19,387 pigs, respectively. All the phenotypic recordings were measured between the year 2000 and 2017. Pedigrees of the two breeds were traced back to the date 1 January 1994, and thus, there are 700,960 LL pigs and 582,114 YY pigs in the two pedigrees.

Genotypes

A total of 37,699 LL pigs and 37,845 YY pigs were genotyped with either the Illumina PorcineSNP60 Genotyping BeadChip v1 or v2. i.e. about 50% animals with each version. The two different chip versions were taken into account when applying a quality filter on SNPs. SNPs were mapped to pig chromosomes using the pig genome build 10.2 [15]. Quality controls were applied in LL and YY separately as follows: animals with call-rate smaller than 90% were first removed; SNPs with call-rate smaller than 90% were removed as well; SNPs with minor allele frequency smaller than 0.05 were filtered out; SNPs that deviated strongly from Hardy Weinberg equilibrium within breed ($p < 10e\text{-}7$) were also excluded. Fimpute v2.2 [16] was used to impute the missing SNPs. After quality control, 37,621 SNPs on 37,699 LL and 36,687 SNPs on 37,845 YY were retained for further analysis.

Methods of constructing relationship matrix

In SSGBLUP, the inverse of combined marker-based and pedigree-based relationship matrix was constructed according to Christensen and Lund [3] and Christensen et al. [9], which was:

$$\boldsymbol{H}^{-1} = \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{G}_{\omega}^{-1} - \boldsymbol{A}_{22}^{-1} \end{bmatrix} + \boldsymbol{A}^{-1},$$

where $\boldsymbol{G}_{\omega} = (1-\omega)\boldsymbol{G} + \omega\boldsymbol{A}_{22}$ and $\boldsymbol{A}_{22}$ contained pedigree-based relationships among genotyped pigs; $\boldsymbol{G}$ matrix was constructed following Vanraden [4] method 1: $\boldsymbol{G} = \frac{(\boldsymbol{m}-2\boldsymbol{p}_i)(\boldsymbol{m}-2\boldsymbol{p}_i)^T}{\sum 2\boldsymbol{p}_i(1-\boldsymbol{p}_i)}$, where $\boldsymbol{m}$ is a matrix with entries m_{ij} = 0, 1, 2 for genotypes *AA*, *AB* and *BB*, respectively. In theory, $\boldsymbol{p}_i$ should be allele frequencies in the base population, but as we mentioned above, in practice, $\boldsymbol{p}_i$ were often computed from observed genotypes. To be compatible with the pedigree-based relationship matrix, $\boldsymbol{G}$ matrix was scaled to create a $\boldsymbol{G}_a$ matrix, following Christensen et al. [9]: $\boldsymbol{G}_a = \beta\boldsymbol{G} + \alpha$, where β and α were obtained by solving the following equations: $Avg\big(diag(\boldsymbol{G})\big)\beta + \alpha = Avg(diag(\boldsymbol{A}_{22}))$ and $Avg(\boldsymbol{G})\beta + \alpha = Avg(\boldsymbol{A}_{22})$. This $\boldsymbol{G}_a$ matrix was used instead of matrix $\boldsymbol{G}$ in the formula for combined marker-based and pedigree-based relationship matrix above. To test the effects of different weighting factors (ω) between the pedigree-based and marker-based relationship matrices on genomic predictions, ω values between 0.05 and 0.95 with a gap of 0.05 were investigated for the SSGBLUP method. Inverse pedigree-based relationship $\boldsymbol{A}$ matrix was constructed according to the Henderson rule [17].

In MF-SSGBLUP, to construct the inverse combined relationship matrix, the first step was to estimate a parameter γ in both LL and YY, respectively, which represents the relatedness for base animals. In this study, we followed Garcia-Baccino et al. [11] and Xiang et al. [12] using the method of generalized least squares (GLS) for estimating γ. Christensen [6] and Garcia-Baccino et al. [11] showed that $\gamma = 8\sigma_p^2$ and σ_p^2 is variance of true allele frequencies in the base population. In other words, to estimate

γ, the σ_p^2 needs to be estimated first, which was done by GLS method in this study. The detailed steps of obtaining σ_p^2 and γ can be found in our previous study [12]. After getting γ for both LL and YY, the inverse combined relationship matrix $\boldsymbol{H}(\gamma)^{-1}$ was constructed as follows:

$$\boldsymbol{H}(\gamma)^{-1} = \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{G}_{\omega}^{-1} - \boldsymbol{A}(\gamma)_{22}^{-1} \end{bmatrix} + \boldsymbol{A}(\gamma)^{-1},$$

where the marker-based relationship matrix $\boldsymbol{G} = \left(\boldsymbol{m} - \mathbf{1}\boldsymbol{1}'\right)\left(\boldsymbol{m} - \mathbf{1}\boldsymbol{1}'\right)' /s$ and $\mathbf{m}$ is the allele contents matrix with entries 0, 1, 2 for genotypes *AA*, *AB* and *BB*, respectively, and s is a scaling parameter, which is half of the number of used markers [18]. This method was the same as ssGBLUP_M in Garcia-Baccino et al. [11]. In this study, 37,621 SNPs and 36,687 SNPs were used for LL and YY, respectively and thus s was 18,810.5 and 18,343.5 for LL and YY, respectively. To capture the residual polygenetic effects, matrix $\boldsymbol{G}$ was replaced by $\boldsymbol{G}_{\omega} = (1 - \omega)\boldsymbol{G} + \omega\boldsymbol{A}(\gamma)_{22}$. Similar to SSGBLUP, values of ω between 0.05 and 0.95 with a gap of 0.05 were investigated. The inverse of pedigree-based relationship matrix $\boldsymbol{A}(\gamma)^{-1}$ was constructed according to the usual rule [5], and matrix $\boldsymbol{A}(\gamma)_{22}$ was constructed following Colleau [19]. Matrix $\boldsymbol{A}(\gamma)_{22}^{-1}$ is the inverse of matrix $\boldsymbol{A}(\gamma)_{22}$.

Statistical models

Both univariate and bivariate animal models were applied for ADG and FCR in LL and YY, respectively. The statistical models for ADG and FCR were as follows:

$$\boldsymbol{y}_{ADG} = \boldsymbol{X}_{ADG}\boldsymbol{\beta}_{ADG} + \boldsymbol{Z}_{ADG}\boldsymbol{a}_{ADG} + \boldsymbol{M}_{ADG}\boldsymbol{litter}_{ADG} + \boldsymbol{W}_{ADG}\boldsymbol{pen}_{ADG} + \boldsymbol{e}_{ADG},$$

$$\boldsymbol{y}_{FCR} = \boldsymbol{X}_{FCR}\boldsymbol{\beta}_{FCR} + \boldsymbol{Z}_{FCR}\boldsymbol{a}_{FCR} + \boldsymbol{e}_{FCR},$$

where $\boldsymbol{y}_{ADG}$ and $\boldsymbol{y}_{FCR}$ contain phenotypic recordings for ADG and FCR, respectively; $\boldsymbol{X}_{ADG}\boldsymbol{\beta}_{ADG}$ and $\boldsymbol{X}_{FCR}\boldsymbol{\beta}_{FCR}$ represent fixed effects, which include section (physical unit for animals present at the same point of time) effect, sex effect and covariates of the starting weights for ADG and FCR, respectively; $\boldsymbol{a}_{ADG}$ and $\boldsymbol{a}_{FCR}$ are additive effects for ADG and FCR, respectively; $\boldsymbol{litter}_{ADG}$ and $\boldsymbol{pen}_{ADG}$ are random birth litter effects and random pen effects for ADG; $\boldsymbol{Z}$, $\boldsymbol{M}$, $\boldsymbol{W}$ are the respective incidence matrices; $\boldsymbol{e}_{ADG}$ and $\boldsymbol{e}_{FCR}$ are the random residual effects. It was assumed that random litter effects and pen effects follow normal distributions, as: $\boldsymbol{litter}_{ADG} \sim N(\mathbf{0}, \boldsymbol{I}\sigma^2_{litter})$ and $\boldsymbol{pen}_{ADG} \sim N(\mathbf{0}, \boldsymbol{I}\sigma^2_{pen})$, where $\boldsymbol{I}$ is an identity matrix. In the univariate models, vectors $\boldsymbol{a}_{ADG}$ and $\boldsymbol{a}_{FCR}$ were assumed normally distributed with mean $\mathbf{0}$ and (co)variance structures equal to $var(\boldsymbol{a}_{ADG}) = \boldsymbol{H}\sigma^2_{a\_ADG}$ and $var(\boldsymbol{a}_{FCR}) = \boldsymbol{H}\sigma^2_{a\_FCR}$ in SSGBLUP, and $var(\boldsymbol{a}_{ADG}) = \boldsymbol{H}(\gamma)\sigma^2_{a\_ADG}$ and $var(\boldsymbol{a}_{FCR}) = \boldsymbol{H}(\gamma)\sigma^2_{a\_FCR}$ in MF-SSGBLUP. In the bivariate model, $\boldsymbol{a}_{ADG}$ and $\boldsymbol{a}_{FCR}$ were assumed to follow a multivariate normal distribution: $\begin{pmatrix}\boldsymbol{a}_{ADG}\\ \boldsymbol{a}_{FCR}\end{pmatrix} \sim N\left(\mathbf{0}, \begin{pmatrix}\sigma^2_{a\_ADG} & \sigma_{a\_ADG,a\_FCR}\\ \sigma_{a\_FCR,a\_ADG} & \sigma^2_{a\_FCR}\end{pmatrix} \otimes \boldsymbol{H}\right)$ in SSGBLUP and $\begin{pmatrix}\boldsymbol{a}_{ADG}\\ \boldsymbol{a}_{FCR}\end{pmatrix} \sim N\left(\mathbf{0}, \begin{pmatrix}\sigma^2_{a\_ADG} & \sigma_{a\_ADG,a\_FCR}\\ \sigma_{a\_FCR,a\_ADG} & \sigma^2_{a\_FCR}\end{pmatrix} \otimes \boldsymbol{H}(\gamma)\right)$ in MF-SSGBLUP, where $\sigma^2_{a\_ADG}$, $\sigma^2_{a\_FCR}$ and σ_{a_ADG,a_FCR} are additive genetic variances for ADG, additive genetic variances for FCR and additive genetic covariance between ADG and FCR, respectively. Note that in MF-SSGBLUP, (co)variance components cannot be directly compared with the normal scale that assumes animals in the base population are

unrelated. For this purpose, all the genetic (co)variance components in the MF-SSGBLUP were multiplied by $(1-\gamma/2)$, where γ is from the respective LL or YY population [5, 18].

Scenarios and genetic parameters

Estimates of (co)variance components and heritabilities (h^2) was investigated in four different scenarios for both ADG and FCR: (1) SSGBLUP method in a univariate model (*UNI_SSGBLUP*); (2) MF-SSGBLUP method in a univariate model (*UNI_MF-SSGBLUP*); (3) SSGBLUP method in a bivariate model (*BI_SSGBLUP*) and (4) MF-SSGBLUP method in a bivariate model (*BI_MF-SSGBLUP*). Estimates of genetic correlation between ADG and FCR (r_g) was only studied in the two bivariate scenarios: *BI_SSGBLUP* and *BI_MF-SSGBLUP.* All of the four scenarios were studied in both LL and YY populations. For heritabilities, with the SSGBLUP method, they were calculated as $h^2_{ADG} = \frac{\sigma^2_{a\_ADG}}{\sigma^2_{a\_ADG}+\sigma^2_{litter}+\sigma^2_{pen}+\sigma^2_{e\_ADG}}$ and $h^2_{FCR} = \frac{\sigma^2_{a\_FCR}}{\sigma^2_{a\_FCR}+\sigma^2_{e\_FCR}}$ for ADG and FCR, respectively. In scenarios *UNI_MF-SSGBLUP* and *BI_MF-SSGBLUP,* as mentioned above, all the variance components had to be scaled first. Thus, the heritabilities for ADG and FCR in scenarios *UNI_MF-SSGBLUP* and *BI_MF-SSGBLUP* were calculated as: $h^2_{ADG} = \frac{\sigma^2_{a\_ADG}*(1-\gamma/2)}{\sigma^2_{a\_ADG}*(1-\gamma/2)+\sigma^2_{litter}+\sigma^2_{pen}+\sigma^2_{e\_ADG}}$ and $h^2_{FCR} = \frac{\sigma^2_{a_{FCR}}*(1-\gamma/2)}{\sigma^2_{a\_FCR}*(1-\gamma/2)+\sigma^2_{e\_FCR}}$. In terms of genetic correlation between ADG and FCR (r_g), in both *BI_SSGBLUP* and *BI_MF-SSGBLUP,* r_g was calculated as: $r_g = \frac{\sigma_{a\_ADG,a\_FCR}}{\sqrt{\sigma^2_{a\_ADG}*\sigma^2_{a\_FCR}}}$. Software DMU was used to estimate the variance components [20].

Predictive abilities

To compare the performances of genomic evaluation between SSGBLUP and MF-SSGBLUP and investigate the effects of different weighting factors (ω) on genomic predictions, the predictive abilities were measured as correlation between corrected phenotypes ($\boldsymbol{Y}_c$) and genomic estimated breeding values ($\widehat{\boldsymbol{a}}$) in different scenarios ($cor(\boldsymbol{Y}_c, \widehat{\boldsymbol{a}})$), following Christensen et al. [9]. A Hotelling-Williams t-test at a 5% confidence level was applied to evaluate the statistical significance of the differences between predictive abilities in different scenarios. Phenotypes were corrected for all the fixed effects and random effects other than additive genetic effect ($\boldsymbol{Y}_c = \widehat{\boldsymbol{a}} + residuals$). To avoid the possible preference of a specific single-step method in the process of calculating $\boldsymbol{Y}_c$, traditional BLUP method in combination with a univariate model was used to obtain $\boldsymbol{Y}_c$.

Data recordings were split into training populations and validation populations by using a cut-off date of 1 May 2016. Validation populations consisted of young pigs born between 1 May 2016 and 1 February 2017. Thus, 654,908 LL and 541,301 YY were included in the training populations, respectively, and among them, 29,825 LL and 30,144 YY were genotyped, respectively. The validation populations contained 31,515 LL and 29,192 YY, respectively, while 7,700 LL and 7,645 YY were genotyped, respectively. Validation populations were divided into subgroups of genotyped and non-genotyped animals. For each of the YY and LL populations, predictive abilities were investigated in the two subgroups as well as in the whole validation population. Meanwhile, regression coefficients of $\boldsymbol{Y}_c$ on $\widehat{\boldsymbol{a}}$ in different

scenarios were calculated as an indicator of biasedness of the genomic predictions. Table 1 provides an overview of the numbers of animals in the different datasets.

Results

Estimation of γ in MF-SSGBLUP

In MF-SSGBLUP, before constructing the inverse combined relationship matrix, parameter γ should be estimated first. The estimates were $\hat{\gamma}_L = 0.605$ for LL and $\hat{\gamma}_Y = 0.553$ for YY.

Scenarios and genetic parameters

Table 2 shows estimated genetic parameters for ADG and FCR in all the scenarios, and genetic correlations (r_g) between ADG and FCR in bivariate scenarios (*BI_SSGBLUP, BI_MF-SSGBLUP*) in LL and YY populations.

In LL, additive genetic variances of ADG ($\sigma^2_{a\_ADG}$) and FCR ($\sigma^2_{c\_FCR}$) were similar among the four scenarios. Heritabilities for ADG ($h^2_{a\_ADG}$) and FCR ($h^2_{a\_FCR}$) were almost constant across different scenarios ($h^2_{a\_ADG}$ ranged from 0.23 to 0.24 and $h^2_{a\_FCR}$ ranged from 0.10 to 0.11). For genetic correlations between ADG and FCR, r_g in scenario *BI_MF-SSGBLUP* (-0.27) showed higher negative correlations than that in scenario *BI_ SSGBLUP* (-0.19).

In YY, as a whole, we obtained similar results as in LL. All the four scenarios generally showed similar estimated variance components, except for the estimates of additive genetic variances for ADG ($\sigma^2_{a\_ADG}$) and FCR ($\sigma^2_{a\_FCR}$). In the two

metafounder scenarios (*UNI_MF-SSGBLUP* and *BI_MF-SSGBLUP*), $\sigma^2_{a\_ADG}$ and $\sigma^2_{a\_FCR}$ were slightly higher than that in other two SSGBLUP scenarios. Heritabilities were stable across different scenarios, where $h^2_{a\_ADG}$ varied between 0.26 and 0.28 and $h^2_{a\_FCR}$ varied between 0.19 and 0.20. Genetic correlations between ADG and FCR were same (-0.46) in scenarios *BI_MF-SSGBLUP* and *BI_ SSGBLUP*.

Predictive abilities

The diagrams of correlation coefficients between corrected phenotypes ($\boldsymbol{Y}_c$) of ADG and FCR, and genomic estimated breeding values ($\widehat{\boldsymbol{a}}$) in different scenarios ($cor(\boldsymbol{Y}_c, \widehat{\boldsymbol{a}})$) with a dynamic ω are shown in Figure 1.

In LL, for ADG, four scenarios performed nearly the same (highest $cor(\boldsymbol{Y}_c, \widehat{\boldsymbol{a}}) = 0.355$), and the optimal weighting factors (ω) were 0.20, 0.15, 0.20 and 0.25 in scenarios *UNI_SSGBLUP*, *UNI_MF-SSGBLUP*, *BI_SSGBLUP* and *BI_MF-SSGBLUP,* respectively. For FCR, predictive abilities in bivariate scenarios (0.19) were a bit higher than those in the univariate scenarios (0.16). The optimal ω were 0.70 in both *UNI_SSGBLUP* and *BI_SSGBLUP*, and 0.55 in both *UNI_MF-SSGBLUP* and *BI_MF-SSGBLUP.*

In YY, for ADG, curves of predictive abilities in four scenarios were almost on top of each other. The highest predictive abilities (0.347) appeared when ω was set at around 0.30 in different scenarios. For FCR, univariate models performed slightly better than bivariate models when ω were lower than 0.85. In univariate models, highest predictive abilities of FCR were 0.355, where ω were set to 0.10 and 0.15 in

294 *UNI_SSGBLUP* and *UNI_MF-SSGBLUP,* respectively. In bivariate models, when ω
295 were set to 0.25 and 0.30 in *BI_SSGBLUP* and *BI_MF-SSGBLUP,* highest predictive
296 abilities of 0.344 turned up.
297 As a whole, with same ω, performances of genomic evaluation were not much
298 different among four scenarios. Meanwhile, we observed that scenario
299 *BI_MF-SSGBLUP* potentially had some superiority of predictive abilities compared to
300 other scenarios in genomic evaluation.
301 In addition, to compare the performances of genomic evaluation in genotyped and
302 non-genotyped animals, validation populations were first divided into genotyped
303 subgroups and non-genotyped subgroups in both LL and YY, and then predictive
304 abilities were calculated on both subgroups with the estimated optimal ω. Predictive
305 abilities of genomic prediction with an optimal ω in the validation populations for
306 ADG and FCR are displayed in Table 3. For same trait and same population, based on
307 the Figure 1, the optimal ω in SSGBLUP and MF-SSGBLUP were nearly the same.
308 Thus, we only investigated the performances of genomic evaluation on both
309 genotyped and non-genotyped animals with four optimal ω: 0.20, 0.70, 0.25 and 0.10
310 for ADG in LL, FCR in LL, ADG in YY and FCR in YY, respectively.
311 According to Table 3, no matter if a univariate model or a bivariate model was used,
312 SSGBLUP and MF-SSGBLUP showed similar predictive abilities for genotyped
313 subgroups and non-subgroups. Within each scenario, animals in genotyped subgroups
314 always presented higher predictive abilities than those in non-genotyped subgroups.

Biasedness of genomic predictions was investigated as regression coefficients of corrected phenotypes ($\boldsymbol{Y}_c$) on the genomic estimated breeding values ($\widehat{\boldsymbol{a}}$). The changes of biasedness for both ADG and FCR in different scenarios in both LL and YY with ω ranging from 0.05 to 0.95 with a gap of 0.05 are shown in Figure 2. In general, regression coefficients increased with the weighting factors (ω). In LL, among different ω, when ω was 0.95, the regression coefficients were closest to 1. More specifically, for ADG, the changes of regression coefficients were nearly the same in all the four scenarios; for FCR, regression coefficients in univariate models deviated more from 1 than those in bivariate models. In YY, for ADG, scenario *BI_MF-SSGBLUP* was best among the four different scenarios since the regression coefficients were closest to 1. For FCR, there were no dramatic differences among the four scenarios. When ω was 0.15, genomic predictions presented smallest biasedness in all the scenarios.

Similarly, the biasedness of genomic predictions was studied separately in both genotyped and non-genotyped subgroups of validation populations. The results of biasedness with an estimated optimal ω in the four scenarios are shown in Table 4. Overall, animals in the non-genotyped animals had less biasedness of genomic prediction than those in the genotyped subgroup.

Discussion

In this work, we compared the performances of genomic evaluation in both regular

SSGBLUP and MF-SSGBLUP for the important productive traits ADG and FCR in both DanBred Landrace and DanBred Yorkshire pigs. We first estimated γ for constructing $\boldsymbol{H}(\gamma)^{-1}$ matrix in MF-SSGBLUP, then compared genetic parameters and predictive abilities between SSGBLUP and MF-SSGBLUP, either in a univariate or a bivariate model. Through this study, we also detected the optimal weighting factors for ADG and FCR in both SSGBLUP and MF-SSGBLUP.

Estimation of γ in MF-SSGBLUP

In the current study, γ estimates were 0.605 and 0.553 in MF-SSGBLUP of LL and YY populations respectively, which were different from other estimates in these populations (0.756 of LL and 0.730 of YY) [12]. As mentioned in Legarra et al. [5], several factors influence the values of γ, such as effective population size, and the SNP panel used. The current study and previous studies originated from the same ancestors, and thus it is not the differences of effective population size that affect these estimates. However, the SNP used in this study are fewer than in the previous study, about 37,500 SNP in this study compared to the 41,000 SNP were used in the previous study. The cause of this difference is the difference in criteria on minor allele frequencies (MAF) used in the two studies: In the current study, the criteria of MAF was 0.05 in each of the two populations, whereas in Xiang et al. [12] the criteria was 0.01 across LL and YY populations. The additional low MAF SNPs used in Xiang et al. [12] have increased the estimates of the metafounder parameter γ since there are more homozygote genotypes for such low MAF markers. In practice, γ needs to be

357 estimated depending on the SNP used in the analysis.

358 **Genetic parameters**

359 Before being compared to genetic parameters in SSGBLUP, variance components in
360 MF-SSGBLUP were scaled to be comparable with the results from regular
361 population that assumed base individuals are unrelated [5, 18]. Overall, estimates in
362 MF-SSGBLUP were not far from those in regular SSGBLUP method. In YY, additive
363 genetic variances of ADG and FCR in two metafounder scenarios were slightly higher
364 than estimates in regular SSGBLUP scenarios. For environmental variances, estimates
365 were nearly the same in all the four scenarios. Thus, the heritabilities of ADG and
366 FCR in two metafounder scenarios were also a little higher than results in the regular
367 SSGBLUP scenarios.

368 For both MF-SSGBLUP and SSGBLUP, although univariate models and bivariate
369 models gave similar estimates of genetics variances, the slight decrease of standard
370 errors in bivariate models indicated that compared with univariate models, bivariate
371 models would further reduce the uncertainty of the estimated genetics parameters.
372 Genetic correlations between ADG and FCR (r_g) were estimated in bivariate models.
373 Although MF-SSGBLUP in LL showed more negative correlation (-0.27) than that in
374 SSGBLUP (-0.19), taking the standard error (0.10) into account, there were no
375 significant differences for the estimated r_g in MF-SSGBLUP and in SSGBLUP.

376 **Predictive abilities**

377 Predictive abilities changed slightly with different weighting factors (ω). We termed

the weighting factor ω that resulted in a highest predictive abilities as the optimal ω. For ADG, optimal ω were almost the same in LL and YY (around 0.2), but for FCR, optimal ω were dramatically different in LL (around 0.7) and YY (around 0.1). A possible reason could be that for different traits and populations, proportions of genetic variances that could be accounted by 50K SNP markers were quite different. For FCR, genes that largely affected FCR were not consistent in LL and YY [21] and thus, the linked SNP markers captured different proportion of total genetic variances. Martini et al. [22] reported that high ω would increase inflation by increasing the variance of EBVs. Thus, choosing an optimal ω to construct combined pedigree-based and genomic-based relationship matrix is crucial in genomic evaluation.

Magnitudes of predictive abilities in this study were higher than those in a previously published study [9]. The main reason for enhanced predictive ability was due to the increased population size. In addition, based on the published results from the same populations, accuracies for ADG and FCR in SSGBLUP in this study were higher than accuracies of total number of piglets born [23]. This could due to a fact that total number of piglets born had lower heritabilities than those in ADG and FCR. As shown in Table3, genotyped subgroups had higher predictive abilities than non-genotype subgroups in all scenarios for ADG and FCR in LL and YY populations. Similar results were reported in some previous studies [9, 12]. However, Guo et al. [24] reported that reliabilities of non-genotyped subgroups were higher than those of genotyped subgroups for total number of piglets born and litter size at Day 5 after

399 birth in LL population. They interpreted that phenomenon as decreased relationships
400 between phenotypes and genotypes due to pre-selection of genotyped animals. Forni
401 et al. [25] also reported that marker information only increased accuracies of
402 genotyped individuals in SSGBLUP method. In this study, although genotyped
403 animals were pre-selected, genomic information from large number of genotyped
404 animals still provided enough information to improve the performance of genomic
405 prediction. Nevertheless, one consequence of pre-selection was that genotyped
406 subgroups showed more biasedness in genomic prediction than non-genotyped
407 subgroups, whereas biasedness in non-genotyped subgroup was similar to that in the
408 whole population.
409 Compared with SSGBLUP, there was a trend that MF-SSGBLUP method performed
410 slightly better in genomic predictions for ADG and FCR, although the differences
411 were not always statistically significant. This finding was in agreement with the
412 theory that MF-SSGBLUP should perform at least as good as SSGBLUP method [5].
413 All in all, MF-SSGBLUP was recommended to be used for pig genomic evaluation.
414

415 Conclusion

416 MF-SSGBLUP method was successfully implemented in genomic prediction for ADG
417 and FCR in Danish Landrace and Yorkshire populations. The method of single-step
418 genomic evaluation with a metafounder performed at least as good as regular
419 single-step method in genomic evaluation for ADG and FCR in Danish Landrace and

Yorkshire populations. Bivariate models were recommended instead of univariate models for the metafounder approach for the correlated productive traits. The optimal weighting factors (ω) in SSGBLUP and MF-SSGBLUP methods were not completely identical.

Availability of data and materials

The datasets in the current study are not publicly available since they are owned by SEGES, but are available from the corresponding author on reasonable request and if agreed by SEGES.

Abbreviations

SSGBLUP: Single-step genomic best linear unbiased prediction

MF-SSGBLUP: a single-step genomic method with a metafounder

FCR: feed conversion ratio

ADG: average daily gain

LL: DanBred Landrace

YY: DanBred Yorkshire

GEBVs: genomic estimated breeding values

GS: genomic selection

GLS: generalized least squares

MAF: minor allele frequencies

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Contributions

CF and TX performed data analysis and wrote the manuscript. OFC, TX and TO conceived the study, made substantial contributions to the interpretation of results and revised the manuscript. TO provided with the data and improved the manuscript and added valuable comments during the study. All authors read and approved the final manuscript.

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Ethics declarations

Ethics approval and consent to participate

Data recording and sample collection were conducted following Danish laws of management and welfare procedures for pig production.

Competing interests

The authors declare that they have no competing interests.

Table and figure

Table1 numbers of animals with records of ADG and FCR in the training and in the validation dataset, respectively, as well as the numbers of genotyped animals in the two datasets

LL	Training	Validation
ADG	654,908	31,512
FCR	17,901	988
Genotyped	29,825	7,700
Genotyped and FCR	2,660	902

YY	Training	Validation
ADG	541,301	29,192
FCR	18,478	909
Genotyped	30,144	7,645
Genotyped and FCR	2,802	870

ADG = average daily gain; FCR = feed conversion ratio.

Note: all genotyped animals have ADG record, but only some have FCR record.

558 Table2. Variance components,[1] heritabilities,[2] and genetic correlations between ADG and FCR with SE in LL and YY populations, respectively

Model	scenario	Breed	$\sigma^2_{a\_ADG}$	σ_{a_ADG,a_FCR}	$\sigma^2_{a\_FCR}$	σ^2_{pen}	σ^2_{litter}	$\sigma^2_{e\_ADG}$	$\sigma^2_{e\_FCR}$	$h^2_{a\_ADG}$	$h^2_{a\_FCR}$	r_g
BLUP	all	LL	1916.33	-0.56 (0.44)	4.12*10-3	633.35	455.57	4544.12	2.82*10-2	0.25	0.13	-0.20
			(98.71)		(2.55*10-3)	(69.57)	(77.25)	(96.21)	(2.49*10-3)	(0.05)	(0.06)	(0.11)
		YY	2039.74	-1.19 (0.22)	3.60*10-3	577.24	445.98	5144.01	1.55*10-2	0.25	0.19	-0.44
			(117.88)		(6.4710-4)	(57.33)	(62.07)	(94.21)	(6.19*10-3)	(0.05)	(0.05)	(0.15)
	UNI_SSGBLUP	LL	1899.91	-	3.44*10-3	669.29	510.24	4787.67	2.87*10-2	0.24	0.11	-
			(99.30)		(2.61*10-3)	(64.02)	(81.99)	(95.34)	(2.53*10-3)	(0.04)	(0.06)	
		YY	2168.95	-	3.75*10-3	571.73	422.21	5092.61	1.54*10-2	0.26	0.19	--
			(116.30)		(5.95*10-4)	(56.91)	(61.32)	(93.86)	(5.69*10-3)	(0.04)	(0.04)	
SSGBLUP(w=0.25)	*BI_ SSGBLUP*	LL	1882.02	-0.48 (0.42)	3.35*10-3	691.50	527.58	4885.49	2.88*10-2	0.24	0.10	-0.19
			(96.75)		(2.42*10-3)	(50.15)	(63.81)	(90.25)	(2.47*10-3)	(0.04)	(0.06)	(0.09)
		YY	2174.28	-1.28 (0.31)	3.58*10-3	568.85	418.41	5080.37	1.56*10-2	0.26	0.19	-0.46

			(110.43)		(5.26*10-4)	(54.42)	(70.61)	(100.25)	(4.22*10-3)	(0.03)	(0.04)	(0.13)
	UNI_MF-SSGBLUP	LL	1885.58	-	3.46*10-3	721.22	529.21	4894.98	2.88*10-2	0.23	0.11	-
			(102.48)		(2.59*10-3)	(59.25)	(65.23)	(95.54)	(2.61*10-4)	(0.04)	(0.07)	
		YY	2305.03	-	3.79*10-3	570.11	415.72	5077.82	1.56*10-2	0.27	0.20	-
			(122.34)		(6.31*10-4)	(56.87)	(61.25)	(93.91)	(5.72*10-4)	(0.03)	(0.03)	
MF-SSGBLUP(w=0.25)	*BI_MF-SSGBLUP*	LL	1887.71	-0.68 (0.43)	3.48*10-3	727.64	532.84	4916.36	2.87*10-2	0.23	0.11	-0.27
			(97.14)		(2.41*10-3)	(53.62)	(63.94)	(91.40)	(2.50*10-3)	(0.05)	(0.05)	(0.10)
		YY	2311.95	-1.37 (0.22)	3.86*10-3	567.00	411.53	5065.37	1.55*10-2	0.28	0.20	-0.46
			(118.92)		(5.91*10-4)	(60.40)	(57.75)	(88.41)	(5.01*10-4)	(0.03)	(0.03)	(0.12)

[1]Variance components for genetic parameters correspond to the usual genetic variance, which is the variance among unrelated individuals in base population:

In SSGBLUP, $\sigma^2_{a\_ADG}$ is the additive genetic variance for ADG, and in MF-SSGBLUP $= \sigma^2_{a\_ADG} * (1 - \gamma_L/2)$ for LL and $\sigma^2_{a\_ADG} * (1 - \gamma_Y/2)$ for YY; in SSGBLUP, $\sigma^2_{a\_FCR}$ is the additive genetic variance for FCR, and in MF-SSGBLUP $= \sigma^2_{a\_FCR} * (1 - \gamma_L/2)$ for LL and

563 $\sigma^2_{a_{FCR}} * (1 - \gamma_Y/2)$ for YY; in SSGBLUP σ_{a_ADG,a_FCR} is genetic covariance between ADG and FCR, and in MF-SSGBLUP $= \sigma_{a\_ADG,a\_FCR} *$

564 $(1 - \gamma_L/2)$ for LL and $\sigma_{a\_ADG,a\_FCR} * (1 - \gamma_Y/2)$ for YY; σ^2_{pen} is the variance of pen effect for ADG; σ^2_{litter} is the variance of litter effect for

565 ADG; $\sigma^2_{e\_ADG}$ is the residual variance for ADG; $\sigma^2_{e\_FCR}$ is the residual variance for FCR. Numbers between brackets are the SE of the

566 corresponding parameters.

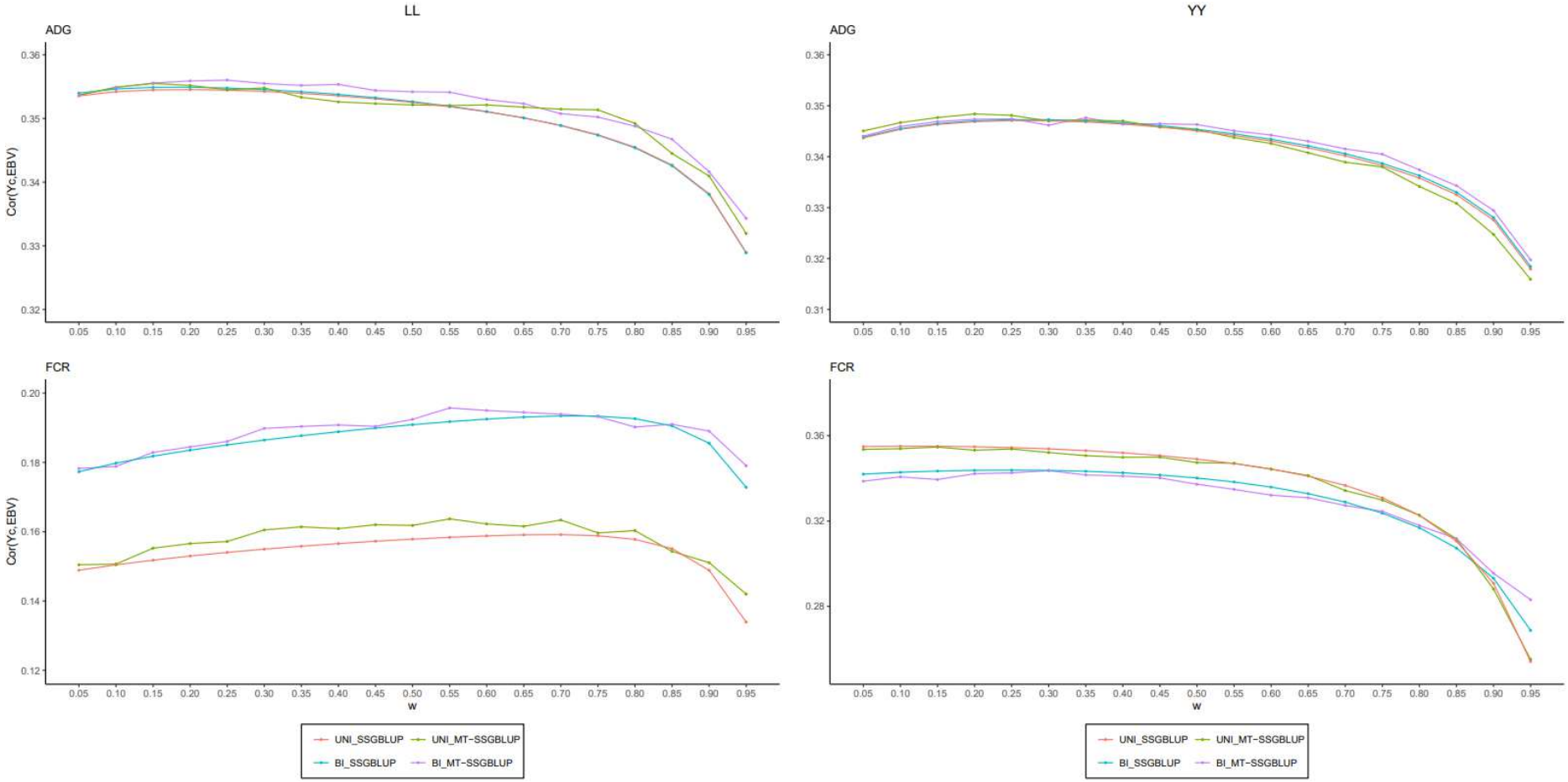
567 [2]Heritablity, in SSGBLUP, $h^2_{ADG} = \frac{\sigma^2_{a\_ADG}}{\sigma^2_{a\_ADG}+\sigma^2_{litter}+\sigma^2_{pen}+\sigma^2_{e\_ADG}}$ for ADG, and in MF-SSGBLUP, $= \frac{\sigma^2_{a\_ADG}*(1-\gamma_L/2)}{\sigma^2_{a\_ADG}*(1-\gamma_L/2)+\sigma^2_{litter}+\sigma^2_{pen}+\sigma^2_{e\_ADG}}$ for LL and

568 $\frac{\sigma^2_{a\_ADG}*(1-\gamma_Y/2)}{\sigma^2_{a\_ADG}*(1-\gamma_Y/2)+\sigma^2_{litter}+\sigma^2_{pen}+\sigma^2_{e\_ADG}}$ for YY; in SSGBLUP, $h^2_{FCR} = \frac{\sigma^2_{a\_FCR}}{\sigma^2_{a\_FCR}+\sigma^2_{e\_FCR}}$ for FCR, and in MF-SSGBLUP, $= \frac{\sigma^2_{a\_FCR}*(1-\gamma_L/2)}{\sigma^2_{a\_FCR}*(1-\gamma_L/2)+\sigma^2_{e\_FCR}}$ for LL

569 and $\frac{\sigma^2_{a\_FCR}*(1-\gamma_Y/2)}{\sigma^2_{a\_FCR}*(1-\gamma_Y/2)+\sigma^2_{e\_FCR}}$ for YY.

570 [3]Genetic correlation $r_g = \frac{\sigma_{a\_ADG,a\_FCR}}{\sqrt{\sigma^2_{a\_ADG}*\sigma^2_{a\_FCR}}}$

571 Figure 1



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573

574 Table3. Accuracies of the optimal weighting factors (ω) in four scenarios from different validation groups for ADG and FCR

Population	Trait	Validation group	*UNI_SSGBLUP*	*UNI_MF-SSGBLUP*	*BI_SSGBLUP*	*BI_MF-SSGBLUP*
LL	ADG (ω=0.20)	All	0.3545[a]	0.3555[a]	0.3549[a]	0.3560[a]
		Genotyped	0.4096[a]	0.4098[a]	0.4101[a]	0.4102[a]
		Non-genotyped	0.3269[a]	0.3268[a]	0.3264[a]	0.3269[a]
	FCR (ω=0.70)	All	0.1921[a]	0.1933[a]	0.1934[a]	0.1957[b]
		Genotyped	0.2001[a]	0.2060[b]	0.2013[a]	0.2064[b]
		Non-genotyped	0.1672[a]	0.1703[a]	0.1786[b]	0.1795[b]
YY	ADG (ω=0.25)	All	0.3471[a]	0.3472[a]	0.3473[a]	0.3474[a]
		Genotyped	0.3946[a]	0.3945[a]	0.3942[a]	0.3941[a]
		Non-genotyped	0.3086[a]	0.3088[a]	0.3092[a]	0.3081[a]
	FCR	All	0.3550[a]	0.3547[a]	0.3438[b]	0.3435[b]

	(ω=0.10)	Genotyped	0.3699[a]	0.3671[a]	0.3574[b]	0.3561[b]
		Non-genotyped	0.1179[a]	0.1214[a]	0.1167[a]	0.1139[a]

575 Four scenarios are *UNI_SSGBLUP*, *UNI_MF-SSGBLUP*, *BI_SSGBLUP* and *BI_MF-SSGBLUP.*

576 Validation groups include a validation population of all young pigs born between 1 May 2016 and 1 February 2017, and a genotyped and a

577 non-genotyped subgroup which were separated by the validation population.

578 Different superscripts of small letters among scenarios indicate significant differences ($p<0.05$) by Hotelling-Williams t-test

579 Figure 2

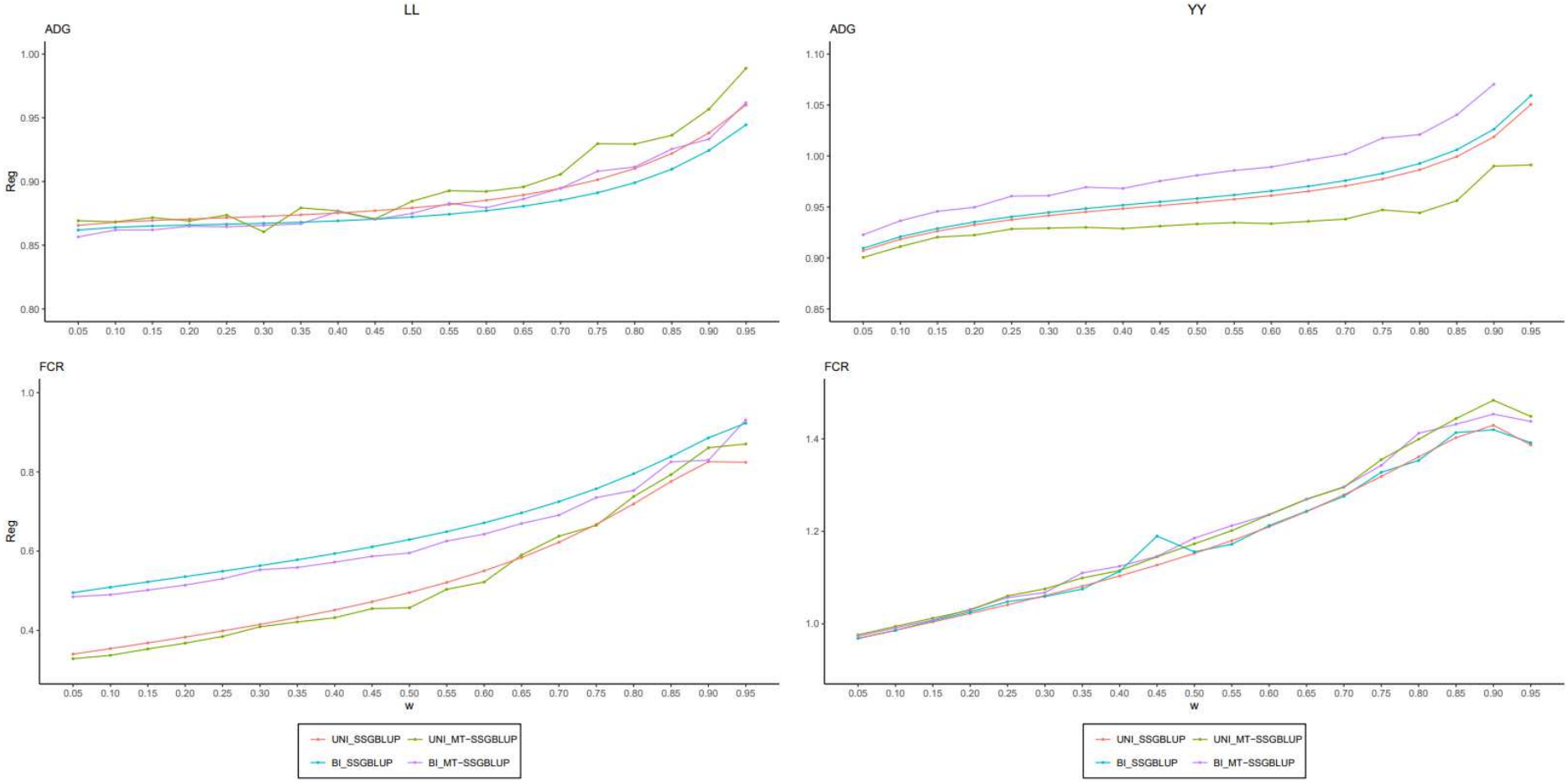

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Table4. Biases of the optimal weighting factors (ω) in four scenarios from different validation groups for ADG and FCR

Population	Trait	Validation group	*UNI_SSGBLUP*	*UNI_MF-SSGBLUP*	*BI_SSGBLUP*	*BI_MF-SSGBLUP*
LL	ADG (ω=0.20)	All	0.9600	0.9888	0.9445	0.9618
		Genotyped	0.7334	0.7386	0.7324	0.7375
		Non-genotyped	0.8379	0.8394	0.8289	0.8281
	FCR (ω=0.70)	All	0.8241	0.8705	0.9230	0.9310
		Genotyped	0.5419	0.4789	0.5650	0.5241
		Non-genotyped	1.0776	1.2833	0.7638	0.8809
YY	ADG (ω=0.25)	All	0.9994	0.9912	1.0060	1.0019
		Genotyped	0.7425	0.7418	0.7498	0.7595
		Non-genotyped	0.8668	0.8655	0.8704	0.8856

	FCR (ω=0.10)	All	1.0040	1.0122	1.0064	1.0080
		Genotyped	0.4721	0.4876	0.4832	0.5019
		Non-genotyped	1.0064	0.9962	1.0054	0.9991

Four scenarios are *UNI_SSGBLUP*, *UNI_MF-SSGBLUP*, *BI_SSGBLUP* and *BI_MF-SSGBLUP.*

Validation groups include a validation population of all young pigs born between 1 May 2016 and 1 February 2017, and a genotyped and a non-genotyped subgroup which were separated by the validation population.

Figures

Figure 1

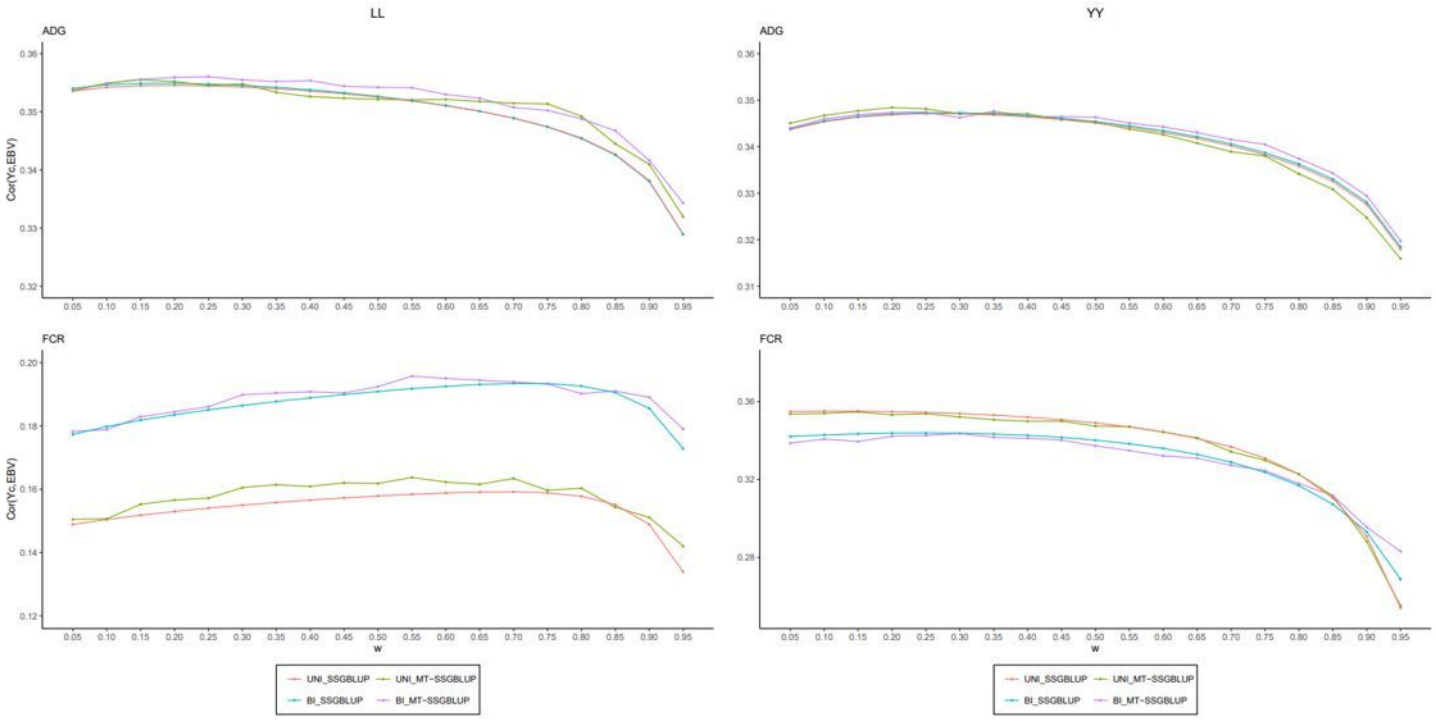

Figure 1

The diagrams of correlation coefficients between corrected phenotypes (Yc) of ADG and FCR, and genomic estimated breeding values (â) in different scenarios (cor(Yc,â)) with a dynamic ω are shown in Figure 1.

Figure 2

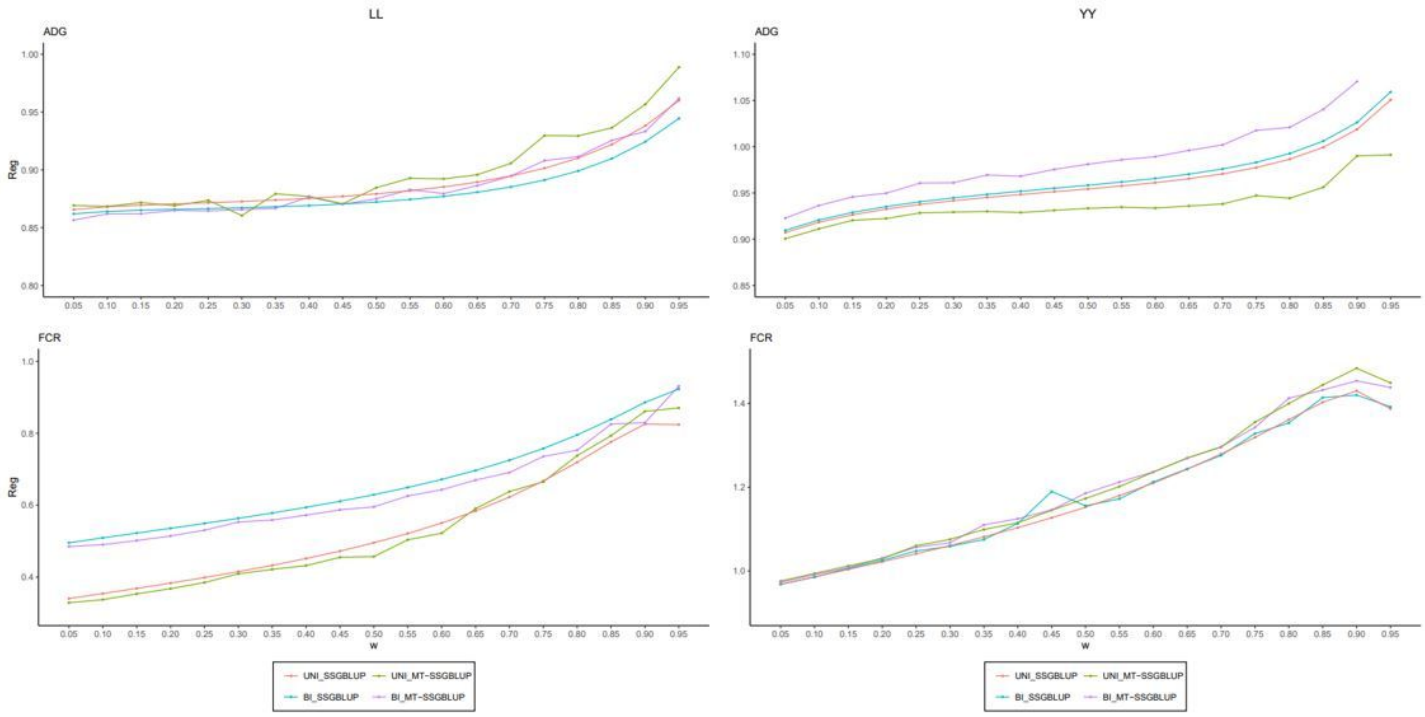

Figure 2

The changes of biasedness for both ADG and FCR in different scenarios in both LL and YY with ω ranging from 0.05 to 0.95 with a gap of 0.05 are shown in Figure 2.