Improving accuracy of direct and maternal genetic effects in genomic evaluations using pooled boar semen: a simulation study¹

Amanda M. Maiorano,^{†,‡,2} Alula Assen,^{‡,||,2} Piter Bijma,^{||} Ching-Yi Chen,[§]
Josineudson Augusto II Vasconcelos Silva,[†] William O. Herring,[§] Shogo Tsuruta,[‡] Ignacy Misztal,[‡] and
Daniela A. L. Lourenco^{‡,3}

[†]Department of Animal Science, Sao Paulo State University, Jaboticabal, SP 14884-900, Brazil; [‡]Department of Animal and Dairy Science, University of Georgia, Athens, GA 30602; ^{||}Animal Breeding and Genetics Centre, Wageningen University and Research, 6700 AH Wageningen, the Netherlands; and [§]Genus PIC, Hendersonville, TN 37075

ABSTRACT: Pooling semen of multiple boars is commonly used in swine production systems. Compared with single boar systems, this technique changes family structure creating maternal half-sib families. The aim of this simulation study was to investigate how pooling semen affects the accuracy of estimating direct and maternal effects for individual piglet birth weight, in purebred pigs. Different scenarios of pooling semen were simulated by allowing the same female to mate from 1 to 6 boars, per insemination, whereas litter size was kept constant ($N = 12$). In each pooled boar scenario, genomic information was used to construct either the genomic relationship matrix (**G**) or to reconstruct pedigree in addition to **G**. Genotypes were generated for 60,000 SNPs evenly distributed across 18 autosomes. From the 5 simulated generations, only animals from generations 3 to 5 were genotyped ($N = 36,000$). Direct and maternal true breeding values (**TBV**) were computed as the sum of the effects of the 1,080 QTLs. Phenotypes were constructed as the sum of direct TBV, maternal TBV, an overall mean of 1.25 kg, and a residual effect. The simulated heritabilities for direct and maternal effects were 0.056 and 0.19, respectively, and the genetic correlation between

both effects was -0.25 . All simulations were replicated 5 times. Variance components and direct and maternal heritability were estimated using average information REML. Predictions were computed via pedigree-based BLUP and single-step genomic BLUP (ssGBLUP). Genotyped littermates in the last generation were used for validation. Prediction accuracies were calculated as correlations between EBV and TBV for direct ($\text{acc}_{\text{direct}}$) and maternal (acc_{mat}) effects. When boars were known, $\text{acc}_{\text{direct}}$ were 0.21 (1 boar) and 0.26 (6 boars) for BLUP, whereas for ssGBLUP, they were 0.38 (1 boar) and 0.43 (6 boars). When boars were unknown, $\text{acc}_{\text{direct}}$ was lower in BLUP but similar in ssGBLUP. For the scenario with known boars, acc_{mat} was 0.58 and 0.63 for 1 and 6 boars, respectively, under ssGBLUP. For unknown boars, acc_{mat} was 0.63 for 2 boars and 0.62 for 6 boars in ssGBLUP. In general, $\text{acc}_{\text{direct}}$ and acc_{mat} were lower in the single-boar scenario compared with pooled semen scenarios, indicating that a half-sib structure is more adequate to estimate direct and maternal effects. Using pooled semen from multiple boars can help us to improve accuracy of predicting maternal and direct effects when maternal half-sib families are larger than 2.

Key words: genomic prediction, maternal ability, multiple sire, prediction accuracy

¹This study was partly supported by Genus PIC (Hendersonville, TN) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001 (scholarship number 88881.131671/2016-01). Comments by B. Fragomeni, Y. Masuda, and B. Valente are gratefully acknowledged.

²These authors contributed equally to this work.

³Corresponding author: danielino@uga.edu

Received May 8, 2019.

Accepted June 21, 2019.

© The Author(s) 2019. Published by Oxford University Press on behalf of the American Society of Animal Science. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com.

J. Anim. Sci. 2019.97:3237–3245

doi: 10.1093/jas/skz207

INTRODUCTION

Pooling semen is a common technique in swine production systems because it enhances the fertility success ratio of inseminations. This technique increased fertility in Duroc by 0.3 piglets relative to using single-boar semen (Pedersen, 2013). The same increase was observed in Landrace x Large White crossbred boars (Ferreira et al., 2015), where the average litter size was 12.4 for single-boar semen and 12.7 for pooled semen. For a combined group of Landrace, Yorkshire, and Duroc boars, the average increase in litter size by pooling semen was 0.6 piglets (Kuo et al., 2000). On the other hand, pooling semen affects the genetic resemblance levels within litters. This may be relevant for genetic evaluations, especially because the ability of inferring some random effects is sensitive to family structure. Maternal effects are likely examples of such effects.

Both parents directly influence their offspring phenotype by transmitting alleles, but sows also influence the offspring through the maternal environment provided. Multiple studies reported the importance of the inclusion of maternal effects in genetic models to improve the accuracy of evaluation for economically important traits (Roehe and Kennedy, 1993; Jasouri et al., 2017). However, obtaining accurate estimates of maternal effects in pigs is not straightforward, as the full-sib structure confounds maternal effects with additive direct and nonadditive effects. On the other hand, multiple paternity within a litter might provide better identifiability of maternal effects due to the presence of maternal half-sibs in the offspring. Maternal half-sibs are more favorable for the statistical separation of direct and maternal effects relative to full-sib families (Noble et al., 2014).

Genomic selection also has the potential to increase genetic gain for maternal-related traits such as litter weight and size (Lillehammer et al., 2011). The main overall benefit of adding genomic information to pedigree and phenotypic information is in the increase of prediction accuracy (Hayes et al., 2009). Genomics provide a more refined way to describe the genetic distances among maternal half-sibs and full-sibs, which combined with pooled semen may result in very favorable conditions to identify maternal effects. The objective of this study

was to investigate, through simulations, whether estimates of direct and maternal genetic effects for litter-related traits can be improved, under a genomic model, when pooled semen is used.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not needed because data were simulated.

Data Simulation

Phenotypes and genotypes for a purebred pig line were simulated using QMSim (Sargolzaei and Schenkel, 2009). A historical population starting with 100 founders and steadily increasing to 3,000 individuals after 100 generations was generated, allowing for the development of patterns of linkage disequilibrium, mutation, and drift. The number of males in the last historical generation was 100. The recent population was founded by 50 males and 1,000 females randomly chosen from the historical population. Subsequently, there were 4 generations of random selection with a replacement rate of 0.6 for boars and 0.45 for sows. After that process, 50 randomly chosen males were mated with 1,000 females selected based on phenotypic values. The mating structure mimicked either single-boar or multiple-boar inseminations (Figure 1). For the single-boar scheme, each sow was mated to a unique boar producing a litter of 12 full-sibs. For the remaining mating schemes, the population effect of pooling semen from different boars was emulated by allowing a multimating structure, given that QMSim (Sargolzaei and Schenkel, 2009) cannot explicitly simulate the pooled semen structure. Keeping litter size fixed at 12, the following 4 mating schemes for different number of pooled boars were adopted:

- 1) Each selected sow was mated to 2 boars producing 6 full sibs from each boar.
- 2) Each selected sow was mated to 3 boars producing 4 full sibs from each boar.
- 3) Each selected sow was mated to 4 boars producing 3 full sibs from each boar.
- 4) Each selected sow was mated to 6 boars producing 2 full sibs from each boar.

Although the simulation software considered that each mating in the pooled semen scheme was

Figure 1. Representation of the simulated population with pooled semen structure. Sub-generations G 5.1 to G 5.6 represent multiple matings mimicking pooled semen schemes to create generation 5.

in a different generation (e.g., 2 generations when sows were mated to 2 boars), mating females were not replaced and mating boars were replaced by boars from generation 4; therefore, the progeny from the pooled semen scheme can be considered the fifth generation of the recent population.

The total number of animals was 61,050 in all scenarios. All animals from generations 3 and 4, together with all 12,000 piglets in generation 5 were genotyped; therefore, 36,000 animals were genotyped in total. The Illumina PorcineSNP60k chip (Ramos et al., 2009) was used as a reference for simulating the genotypes. According to Groenen et al. (2012), the *Sus scrofa domestica* genome size is approximately 2,596 cM with 18 autosomes of different lengths. We defined chromosome 1 as the largest among the autosomes with a length of 298 cM and 7,600 evenly distributed SNP (Groenen et al., 2012). Conversely, chromosome 18 was defined as the smallest one with a length of 61 cM and 1,790 SNP. Overall, the total number of evenly distributed, biallelic SNP was 60,000 SNPs. The number of biallelic QTL simulated was 1080, and they explained 100% of all the genetic effects. The QTL effects were drawn from a Gamma distribution with shape parameter equal to 0.40, which resulted in several QTLs with small effects and few QTLs with large effects. All SNPs and QTL had initial allele frequency of 0.5 in the first historical generation, which changed afterwards by drift and mutations (2.5×10^{-5} mutations per meiosis per locus). Direct and maternal additive genetic variances were 0.005 and 0.017, respectively. These values were chosen to mimic

typical individual piglet birth weight heritabilities (Su et al., 2008).

The main objective of this study requires simulating both direct and maternal effects, but QMSim (Sargolzaei and Schenkel, 2009) can only generate one additive genetic effect. To tackle this restriction, the software was run twice using the same seed file and parameters, but different phenotypic variances as described in Lourenco et al. (2013). In a nutshell, the first run generated the direct additive genetic effects and the second generated the maternal additive genetic effects. The same seed was used to generate identical population structure in the two runs of QMSim; however, phenotypic variances changed to generate differences between direct and maternal effects. Phenotypic variances were 0.005 and 0.017 for the first and second run, respectively. As heritabilities for direct and maternal effects were assumed to be 0.99 in both runs, mostly all the phenotypic variances generated were actually genetic. This means that QMSim was used to simulate purely additive direct and maternal effects for the entire population based on QTL, whereas the other simulated effects were not taken into account in the composition of phenotypes. To mimic typical heritabilities for birth weight in pigs (i.e., 0.056 for direct and 0.19 for maternal), a residual effect [$e \sim N(0, \sigma_e^2 = 0.07)$] was simulated using a standalone software. Using a method described in VanVleck (1994), the genetic correlation between direct and maternal effects was set to -0.25 , which generated a covariance between direct and maternal effects of -0.0023 . True breeding values (TBV) for direct and maternal effects were computed as the sum of QTL

effects. Each individual phenotype was generated as the sum of its direct TBV, the maternal TBV from its dam, the residual effect, and a mean of 1.25 kg. For simplicity, maternal environmental effects and nonadditive effects were not simulated.

Before the wide availability of genomic information, using pooled semen would increase the missingness of pedigree because the sire of each piglet could not be identified. Regarding this issue, we investigated 2 scenarios. In the first one, sire information was missing in the pedigree but we relied on the genomic relationship matrix to recover information or pairwise genetic distances. In the second scenario, we assumed that genomic information was used not only to construct the genomic relationship matrix but also to identify individual sires. Therefore, pedigrees were considered complete for both ssGBLUP and BLUP in this scenario. All simulation scenarios were replicated 5 times.

Model and analysis. To check whether the simulated data structure allows the identifiability of parameter values, variance components were estimated based on pedigree and phenotypes using the AIREMLF90 software (Misztal et al., 2014) with the following model:

$$y = \mu + Za + Wm + e,$$

where y is the vector of birth weight, μ is the vector of mean birth weight, a is the vector of direct additive genetic effects, m is the vector of maternal additive genetic effects, e is the vector of random residual effects, and Z and W are incidence matrices for a and m , respectively. Direct and maternal heritabilities were calculated as

$$h_a^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{am} + \sigma_m^2 + \sigma_e^2},$$

$$h_m^2 = \frac{\sigma_m^2}{\sigma_a^2 + \sigma_{am} + \sigma_m^2 + \sigma_e^2},$$

where h_a^2 and h_m^2 are the heritabilities for direct and maternal genetic effects, σ_a^2 and σ_m^2 are additive direct and maternal variances, σ_{am} is the genetic covariance between direct and maternal effects, and σ_e^2 is the residual variance.

The same base model was used to compute traditional BLUP and single-step genomic BLUP (ssGBLUP) predictions using BLUP90IOD2 software (Misztal et al., 2014). When the single-boar semen scheme was used, pedigree information was complete for both BLUP and ssGBLUP. Under the pooled semen scheme, traditional BLUP considered missing boar information in the pedigree,

whereas ssGBLUP considered either unknown sire or sire assignment using genomic information.

It was assumed that direct and maternal effects were normally distributed with mean equal to 0 and (co)variance structure given by $\Sigma \otimes T$, where $\Sigma = \begin{bmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{bmatrix}$, T is A in the pedigree-based BLUP and H in ssGBLUP; H is the realized relationship matrix combining pedigree and genomic information. The inverse of H used in the mixed model equations had the following form (Aguilar et al., 2010):

$$H^{-1} = A^{-1} + \begin{pmatrix} 0 & 0 \\ 0 & G^{-1} - A_{22}^{-1} \end{pmatrix},$$

where A_{22}^{-1} is the inverse of the pedigree relationship matrix among genotyped animals and G^{-1} is the inverse of the genomic relationship matrix. The G matrix was created as in VanRaden (2008):

$$G = 0.95G^* + 0.05A_{22},$$

with

$$G^* = KK', \text{ and } K = \frac{(M - P)}{\sqrt{2 \sum_{j=1}^m p_j(1 - p_j)}},$$

where M is a matrix of m SNP genotypes for all genotyped animals and P is a matrix of 2 times the allele frequency of the second allele at locus j (i.e., $2p_j$ for every entry of the j th column of P).

Accuracies of EBV and genomic EBV (GEBV) for the direct effect were calculated as their correlations with TBV for genotyped animals in generation 5. Their phenotypes were not used to fit the model, instead, only phenotypes for animals from generations 1 to 4 were used. For the maternal effect, the correlation between maternal TBV of genotyped dams of animals in generation 5 and their (G)EBV for the maternal effect was calculated. Accuracies were compared for all the boar pooling schemes.

RESULTS AND DISCUSSION

The average (SE) estimates of direct and maternal heritability were 0.06 (0.004) and 0.21 (0.014), respectively, over all the boar pooling schemes (Table 1). These results agree with the parametric values used in the simulation, showing that the data structure generated is suitable for this study. To accurately estimate the maternal effect, dams should have a considerable progeny number. In the simulated data sets, a total of 3,350 dams had an average of 18 piglets during their productive life. Those dams were progeny of 1,291 dams that had

an average of 22 piglets. Tracing the dam side of the pedigree 5 generations back, it was observed all the dams in the pedigree were progeny of 31 different dams that produced an average of 17 piglets.

As a common practice, variance components obtained based only on phenotypes and pedigree were used to compute both BLUP and ssGBLUP (Fragomeni et al., 2016; Oliveira et al., 2019). Accuracies of breeding values for traditional and genomic evaluations for single-boar semen and pooled semen considering unknown and known boar information are in Tables 2 and 3, respectively. For the traditional BLUP method, accuracies of direct effects were greater when boars were known relative to the unknown boar scenario. This is expected as unknown parents can negatively affect predictions increasing bias and decreasing accuracy (Quaas, 1988; VanRaden, 1992). For

ssGBLUP, the inclusion of sires in the pedigree records of validation piglets did not change the accuracies for direct and maternal effects. The main reason is that the $\mathbf{G}$ matrix provides accurate genetic distance values for these piglets. The computation of these distances do not depend on pedigree information. Even though the missing parents affect $\mathbf{A}$, $\mathbf{G}$ has nonzero coefficients that reflect the proportion of alleles shared between them. Genomic EBV of validation animals is composed of parent average (PA) and direct genomic values (DGV). When boars are unknown, PA is based only on sows, which have usually less accurate EBV than boars. However, when validation animals have genotyped parents, the information in $\mathbf{A}^{-1}$ most likely is cancelled out by $\mathbf{A}_{22}^{-1}$ so that only the information in $\mathbf{G}^{-1}$ remains. Therefore, ssGBLUP can assess the realized relationship between a boar

Table 1. Simulated and estimated variance components for all scenarios

Variance components ¹	Simulated values	Number of boars				
		1	2	3	4	6
σ_a^2	0.005	0.005 ± 0.0004	0.005 ± 0.0003	0.005 ± 0.0003	0.005 ± 0.0002	0.004 ± 0.0002
σ_m^2	0.017	0.017 ± 0.0005	0.016 ± 0.0005	0.017 ± 0.0004	0.017 ± 0.0006	0.017 ± 0.0005
σ_{am}	-0.0023	-0.0023 ± 0.0005	-0.0021 ± 0.0005	-0.0023 ± 0.0004	-0.0023 ± 0.0004	-0.0025 ± 0.0003
σ_e^2	0.070	0.070 ± 0.0003	0.070 ± 0.0002	0.070 ± 0.0002	0.070 ± 0.0001	0.070 ± 0.0001
h_a^2	0.056	0.054 ± 0.0043	0.056 ± 0.0037	0.055 ± 0.0039	0.052 ± 0.0022	0.050 ± 0.0018
h_m^2	0.19	0.19 ± 0.0051	0.18 ± 0.0057	0.19 ± 0.0030	0.19 ± 0.0057	0.19 ± 0.0055
r_{am}	-0.25	-0.25 ± 0.0425	-0.23 ± 0.0469	-0.25 ± 0.0384	-0.27 ± 0.0371	-0.28 ± 0.0371

¹ σ_a^2 = additive genetic direct variance; σ_m^2 = maternal additive genetic variance; σ_{am} = genetic covariance between direct and maternal; σ_e^2 = residual variance; h_a^2 = heritability for direct effect; h_m^2 = heritability for maternal effect; r_{am} = genetic correlation between direct and maternal.

Table 2. Average accuracy of prediction, over 5 replicates, for direct and maternal effects for BLUP and ssGBLUP considering unknown boars in the pedigree, under the pooled semen scheme

Number of boars	BLUP		ssGBLUP	
	Direct	Maternal	Direct	Maternal
1 ¹	0.21 ± 0.02	0.52 ± 0.02	0.38 ± 0.02	0.58 ± 0.01
2	0.07 ± 0.01	0.55 ± 0.02	0.42 ± 0.02	0.63 ± 0.01
3	0.08 ± 0.02	0.6 ± 0.02	0.43 ± 0.01	0.65 ± 0.01
4	0.06 ± 0.01	0.59 ± 0.03	0.41 ± 0.01	0.66 ± 0.03
6	0.06 ± 0.01	0.53 ± 0.02	0.43 ± 0.01	0.62 ± 0.02

¹When only 1 boar was used, pedigree information was considered known.

Table 3. Average accuracy of prediction, over 5 replicates, for direct and maternal effects for BLUP and ssGBLUP considering known boars in the pedigree, under the pooled semen scheme

Number of boars	BLUP		ssGBLUP	
	Direct	Maternal	Direct	Maternal
1	0.21 ± 0.02	0.52 ± 0.02	0.38 ± 0.02	0.58 ± 0.01
2	0.24 ± 0.01	0.55 ± 0.02	0.42 ± 0.02	0.63 ± 0.01
3	0.27 ± 0.02	0.60 ± 0.02	0.43 ± 0.01	0.65 ± 0.01
4	0.22 ± 0.01	0.57 ± 0.04	0.41 ± 0.01	0.66 ± 0.03
6	0.26 ± 0.02	0.53 ± 0.02	0.43 ± 0.01	0.63 ± 0.02

and its offspring even in the absence of recorded pedigree.

Greater accuracies for direct effects were provided by ssGBLUP relative to BLUP independently of the boar pooling scheme, showing that accounting for genomic information improves predictions. The accuracy boost from the ssGBLUP models for direct effect was greater for the unknown boar scenario. When ssGBLUP was used instead of pedigree BLUP under 4 and 6 unknown pooled boars, predictive correlations improved from 0.06 to 0.41 and from 0.06 to 0.43, respectively. Therefore, correlations were approximately 7 times higher with ssGBLUP. Part of this dramatic improvement is due to the inclusion of animal's own genotype in the evaluations, which has a greater impact on the accuracy of its own GEBV. Similar results were found by [Tonussi et al. \(2017\)](#) studying scenarios with multiple sires and different levels of missing pedigree records in a simulated beef cattle population. They reported prediction accuracies for direct effects that are 5 to 6 times greater from ssGBLUP compared with traditional BLUP when sires are unknown.

The highest accuracies for maternal genetic effects were obtained when 3 to 4 boars were pooled. This pattern applied similarly to both known and unknown boar scenarios, either considering genomic information or not. When only 2 boars are pooled, the number of half-sib families may not yet be ideal to accurately separate direct and maternal variances. Conversely, when 6 boars were used, the full-sib families might have been smaller than the ideal for decomposing phenotypic variance within and among full-sib families. Under traditional BLUP and using only 1 boar, accuracy was 8 correlation points less than when using 3 boars, and 1 point less relative to using 6 boars. When using genomic information, the greatest improvement over traditional BLUP was observed in the 6 boars scheme (10 points). For ssGBLUP, the greatest increase in accuracy compared with using a single boar was 8 points in the 4 boars pooling scheme.

Results showed that including genomic information improves predictions for both direct and maternal genetic effects. This is important for maternally influenced traits such as litter birth weight in pigs, as improving inferences of both effects has a positive influence on the response to selection ([Willham, 1980](#); [Roehe and Kennedy, 1993](#)). Additionally, [Lourenco et al. \(2013\)](#) recommended the inclusion of maternal effects in the model to reduce bias in genomic predictions of maternally affected traits. Finally, [Lillehammer et al. \(2011\)](#) observed that genotyping dams in addition to the

male selection candidates should increase accuracy of the genomic breeding values, enhancing genetic gains, and decreasing rates of inbreeding in pigs.

Inaccurate predictions of maternal genetic effects reduce the genetic progress of litter traits. This effect is prone to weak identifiability from data as it is partly confounded with the contribution of the dam's direct effect, the maternal environmental effect, and the single sire genetic effect ([Willham, 1980](#)). According to [Willham \(1963\)](#) and [Willham \(1972\)](#), the maternal effect is better estimated when sows have multiple progeny in a half-sib structure. Mating females with different males helps identify maternal effects on the environment of the progeny. According to [Lynch and Walsh \(1998\)](#), in a paternal half-sib design where each mating generates several offspring (i.e., nested full-sib, half-sib mating design), the dam variance can be computed as the difference between full-sib and half-sib covariances. When a maternal half-sib design is used, the variance among dams should be proportional to the covariance of individuals with the same dams but different sires. In a full-sib design, the covariance of full sibs is the sum of sire and dam variances. [Willham \(1972\)](#) showed that the covariance between maternal half sibs, when direct and maternal effects are considered and there is no dominance effect, corresponds to the sum of $\frac{1}{4} \sigma_a^2$, σ_{am} , σ_m^2 , and maternal environmental variance.

Before the restricted maximum likelihood (REML; [Patterson and Thompson, 1971](#)) method was proposed, the estimation of maternal effects was conducted by comparing correlations between maternal and paternal half-sibs or between dam- and sire-offspring. The pooled semen scheme allows the generation of a maternal half-sib structure, or more precisely, a nested full-sib, half-sib design where dams have several half-sib families with replicates within families ([Lynch and Walsh, 1998](#)). As mentioned by [Noble et al. \(2014\)](#), families of maternal half-sibs allow for better statistical separation of additive from maternal genetic effects in comparison with full-sib families. In general, accuracies of both direct and maternal effects were lower in the single-boar scenario compared with pooling semen, indicating disadvantages of litters composed of a single large fullsib family. However, getting too close to litters consisting of half-sibs alone is not beneficial for maternal effect predictions, as indicated by a decrease in accuracy when using 6 boars per sow.

Reliable estimates of maternal effects for birth weight require suitable data and pedigree structure to correctly learn the target causal effects from the

observed phenotypic values (Meyer, 1992). The individual phenotype is composed by its own additive genetic effect and components from related animals and environment (Willham, 1963). Thus, the covariance among related animals in the data should be considered to separate possible components of a phenotypic value. Eisen (1967) and Cheng et al. (2009) reported that phenotypes from full sibs were not ideal to render direct, maternal, and environmental components identifiable, as they would have similar covariance structures. Full sibs of a litter resemble one another because of shared direct additive, dominance, maternal additive, and maternal common environmental effects (Meyer, 2008). Nongenetic covariances between full-sib litters arise because of the environmental component of the maternal effect and other environmental effects common to full sibs in a litter. However, Eisen (1967) suggested that half-sib family design is optimal for estimation of direct and maternal effects as well as the covariance of direct and maternal effects. Half-sib data can reduce environmental half-sib covariances, which is likely to improve the precision of the often highly confounded components to be estimated. If sows are inseminated with pooled semen, the piglets in a litter can possibly be from different sires (half sibs). In our study, we confirmed that using maternal half-sib litters from pooled semen from up to 4 boars can improve prediction of maternal effects compared with using full-sib litters from single-boar semen. The issue of genetically linking individual piglets in the litter to their respective sires when pooling semen can be elucidated by genotyping AI boars and piglets altogether.

Although a design with maternal half-sib families with replications within families helps disentangle maternal and nonmaternal effects, the separation between genetic and environmental maternal effects would still be challenging. In our study, the objective was to investigate only the former type of identifiability, and therefore, maternal environmental effects were not simulated. Willham (1980) pointed to several problems in estimating maternal effects, and the biggest one was the confounding between the contribution of the dam to the direct effect and the maternal effect itself, which is environmental for the progeny and expressed in the progeny's phenotype.

Our study attempted to mimic a purebred pig line where pooled semen is used. Extrapolations to different breeding systems, like crossbreeding, should be avoided because of the strength of nonadditive effects in such cases, likewise to

different traits with varying heritability and impact of maternal effects. In a purebred pig line, Vitezica et al. (2018) showed that although dominance and epistasis variances were considerable compared with additive, accuracy of predicting future performance was not improved by the inclusion of nonadditive effects into the model.

In real applications, pooling semen from a number of boars can cause a fertility dilution effect where some boars may produce fewer offspring than others (Roca et al., 2015). However, the simulation strategy used in this study to mimic pooled semen was rather simplistic and did not assume varying levels of fertility for different boars. Boar dominance effect could possibly lead to loss of accuracy as the size of some maternal full-sib families would be reduced. Additionally, even if there were no true fertility differences among boars, the number of piglets per boar would be expected to vary randomly due to sampling effects. Therefore, variation will always be observed independently of the assumption of boar dominance.

According to Sonderman and Luebbe (2008), the highest semen quality is observed in crossbred boars, proceeded from purebred terminal lines and purebred maternal lines. Usually, the pooled semen technique is heavily applied in commercial farms (Knox et al., 2008), with very limited application to multiplier farms and no application to genetic nucleus farms. This is because nucleus farms rely on pedigree information to keep the breeding programs running. However, if genotyping parents and all selection candidates is a reality, the pooled semen technique could be also applied to nucleus farms because the sire side of the pedigree can be determined based on genomic information. If genotyping and genomic evaluation methods are not adopted by the time the selection decisions are made, pooled semen should not be used at the top of the pyramid because of low accuracy of pedigree BLUP in such a case.

CONCLUSIONS

Using pooled semen from few boars can help us to improve accuracy of predicting maternal and direct effects, especially when the size of the maternal full-sib family is larger than 2. Even when paternity tests are not carried out and boar information is missing in the pedigree, using genomic information in a single-step genomic BLUP helps us to keep considerable levels of prediction accuracy for both direct and maternal effects.

LITERATURE CITED

- Aguilar, I., I. Misztal, D. L. Johnson, A. Legarra, S. Tsuruta, and T. J. Lawlor. 2010. Hot topic: a unified approach to utilize phenotypic, full pedigree, and genomic information for genetic evaluation of Holstein final score. *J. Dairy Sci.* 93:743–752. doi:10.3168/jds.2009–2730.
- Cheng, J., S. Janssens, and N. Buys. 2009. Full sib pens of pigs are not suitable to identify variance component of associative effect: a simulation study using gibbs sampling. *BMC Genet.* 10:9. doi:10.1186/1471-2156-10-9.
- Eisen, E. J. 1967. Mating designs for estimating direct and maternal genetic variances and direct-maternal genetic covariances. *Can. J. Genet. Cytol.* 9:13–22. doi:10.1139/g67-002.
- Ferreira, C. E., D. B. Sávio, A. C. Guarise, M. J. Flach, G. D. Gastal, A. O. Gonçalves, O. A. Dellagostin, R. V. Alonso, I. Bianchi, C. D. Corcini, et al. 2015. Contribution of boars to reproductive performance and paternity after homospermic and heterospermic artificial insemination. *Reprod. Fertil. Dev.* 27:1012–1019. doi:10.1071/RD13418.
- Fragomeni, B. O., D. A. Lourenco, S. Tsuruta, H. L. Bradford, K. A. Gray, Y. Huang, and I. Misztal. 2016. Using single-step genomic best linear unbiased predictor to enhance the mitigation of seasonal losses due to heat stress in pigs. *J. Anim. Sci.* 94:5004–5013. doi:10.2527/jas.2016-0820.
- Groenen, M. A., A. L. Archibald, H. Uenishi, C. K. Tuggle, Y. Takeuchi, M. F. Rothschild, C. Rogel-Gaillard, C. Park, D. Milan, H. J. Megens, et al. 2012. Analyses of pig genomes provide insight into porcine demography and evolution. *Nature* 491:393–398. doi:10.1038/nature11622.
- Hayes, B. J., P. J. Bowman, A. J. Chamberlain, and M. E. Goddard. 2009. Invited review: genomic selection in dairy cattle: progress and challenges. *J. Dairy Sci.* 92:433–443. doi:10.3168/jds.2008-1646.
- Jasouri, M., P. Zamani, and S. Alijani. 2017. Dominance genetic and maternal effects for genetic evaluation of egg production traits in dual-purpose chickens. *Br. Poult. Sci.* 58:498–505. doi:10.1080/00071668.2017.1336748.
- Knox, R., D. Levis, T. Safranski, and W. Singleton. 2008. An update on north american boar stud practices. *Theriogenology* 70:1202–1208. doi:10.1016/j.theriogenology.2008.06.036.
- Kuo, Y. H., S. Y. Huang, and K. H. Lee. 2000. Effects of sperm number and semen type on sow reproductive performance in subtropical area. *Asian Australas. J. Anim. Sci.* 13:6–9. doi:10.5713/ajas.2000.6.
- Lillehammer, M., T. H. Meuwissen, and A. K. Sonesson. 2011. Genomic selection for maternal traits in pigs. *J. Anim. Sci.* 89:3908–3916. doi:10.2527/jas.2011-4044.
- Lourenco, D. A. L., I. Misztal, H. Wang, I. Aguilar, S. Tsuruta, and J. K. Bertrand. 2013. Prediction accuracy for a simulated maternally affected trait of beef cattle using different genomic evaluation models. *J. Anim. Sci.* 91:4090–4098. doi:10.2527/jas.2012-5826.
- Lynch, M., and J. B. Walsh. 1998. *Genetics and analysis of quantitative*. Sinauer Associates, Sunderland, MA. p. 980.
- Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31:179–204. doi: 10.1016/0301-6226(92)90017-X
- Meyer, K. 2008. Likelihood calculations to evaluate experimental designs to estimate genetic variances. *Heredity (Edinb)*. 101:212–221. doi:10.1038/hdy.2008.46.
- Misztal, I., S. Tsuruta, D. A. L. Lourenco, I. Aguilar, A. Legarra, and Z. Vitezica. 2014. Manual for BLUPF90 family of programs. http://nce.ads.uga.edu/wiki/lib/exe/fetch.php?media=blupf90_all7.pdf (Accessed 21 January 2019.)
- Noble, D. W. A., S. E. McFarlane, J. S. Keogh, and M. J. Whiting. 2014. Maternal and additive genetic effects contribute to variation in offspring traits in a lizard. *Behav. Ecol.* 25:633–640. doi:10.1093/beheco/aru032.
- Oliveira, H. R., D. A. L. Lourenco, Y. Masuda, I. Misztal, S. Tsuruta, J. Jamrozik, L. F. Brito, F. F. Silva, and F. S. Schenkel. 2019. Application of single-step genomic evaluation using multiple-trait random regression test-day models in dairy cattle. *J. Dairy Sci.* 102:2365–2377. doi:10.3168/jds.2018-15466.
- Patterson, H. D., and R. Thompson. 1971. Recovery of interblock information when block sizes are unequal. *Biomet.* 58(3):545. doi:10.1093/biomet/58.3.545
- Pedersen, M. L. 2013. Fertility higher with pooled Duroc semen than with semen from one boar. *Pig Research Centre, Denmark*. p. 7. (Trial Report, 969). https://pdfs.semanticscholar.org/20db/5111f25aacc0c966c8b9f9667bbcc7725179.pdf?_ga=2.82947861.2003103432.1548764279-1563262216.1548764279 (Accessed 21 January 2019.)
- Quaas, R. L. 1988. Additive genetic model with groups and relationships. *J. Dairy Sci.*, 71:1338–1345. doi:10.1016/S0022-0302(88)79986-5.
- Ramos, A. M., R. P. Crooijmans, N. A. Affara, A. J. Amaral, A. L. Archibald, J. E. Beever, C. Bendixen, C. Churcher, R. Clark, P. Dehais, et al. 2009. Design of a high density SNP genotyping assay in the pig using snps identified and characterized by next generation sequencing technology. *PLoS ONE* 4:e6524. doi:10.1371/journal.pone.0006524.
- Roca, J., M. L. Broekhuijsse, I. Parrilla, H. Rodriguez-Martinez, E. A. Martinez, and A. Bolarin. 2015. Boar differences in artificial insemination outcomes: can they be minimized? *Reprod. Domest. Anim.* 50(Suppl 2):48–55. doi:10.1111/rda.12530.
- Roehe, R., and B. W. Kennedy. 1993. The influence of maternal effects on accuracy of evaluation of litter size in swine. *J. Anim. Sci.* 71:2353–2364. doi:10.2527/1993.719.2353x.
- Sargolzaei, M., and F. S. Schenkel. 2009. QMSIM: a large-scale genome simulator for livestock. *Bioinformatics* 25:680–681. doi:10.1093/bioinformatics/btp045.
- Sonderman, J. P., and J. J. Luebke. 2008. Semen production and fertility issues related to differences in genetic lines of boars. *Theriogenology* 70:1380–1383. doi:10.1016/j.theriogenology.2008.08.009.
- Su, G., D. Sorensen, and M. S. Lund. 2008. Variance and covariance components for liability of piglet survival during different periods. *Animal* 2:184–189. doi:10.1017/S1751731107001115.
- Tonussi, R. L., R. M. O. Silva, A. F. B. Magalhães, R. Espigolan, E. Peripolli, B. F. Olivieri, F. L. B. Feitosa, M. V. A. Lemos, M. P. Berton, H. L. J. Chiaia, A. S. C. Pereira, R. B. Lobo, L. A. F. Bezerra, C. U. Magnabosco, D. A. L. Lourenco, I. Aguilar, F. Baldi. 2017. Application of single step genomic BLUP under different uncertain paternity scenarios using simulated data. *PLoS ONE*. 12(9): e0181752. doi: 10.1371/journal.pone.0181752.

- VanRaden, P. M. 1992. Accounting for inbreeding and crossbreeding in genetic evaluation of large populations. *J. Dairy Sci.*, 75:3136–3144. doi: 10.3168/jds.S0022-0302(92)78077-1.
- VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. *J. Dairy Sci.* 91:4414–4423. doi:10.3168/jds.2007-0980.
- VanVleck, L. D. 1994. Algorithms for simulation of animal models with multiple traits and with maternal and non-additive genetic effects. *Rev. Bras. Genet.* 17:53–57.
- Vitezica, Z. G., A. Reverter, W. Herring, and A. Legarra. 2018. Dominance and epistatic genetic variances for litter size in pigs using genomic models. *Genet. Sel. Evol.* 50:71. doi:10.1186/s12711-018-0437-3.
- Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19:18. doi:10.2307/2527570.
- Willham, R. L. 1972. The role of maternal effects in animal breeding. 3. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35:1288–1293. doi:10.2527/jas1972.3561288x.
- Willham, R. L. 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* 7:405–418. doi: 10.1016/0301-6226(80)90080-9.