

ANIMAL GENETICS AND GENOMICS

Optimal definition of contemporary groups for crossbred pigs in a joint purebred and crossbred genetic evaluation

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Abstract

In the pig industry, purebred animals are raised in nucleus herds and selected to produce crossbred progeny to perform in commercial environments. Crossbred and purebred performances are different, correlated traits. All purebreds in a pen have their performance assessed together at the end of a performance test. However, only selected crossbreds are removed (based on visual inspection) and measured at different times creating many small contemporary groups (CGs). This may reduce estimated breeding value (EBV) prediction accuracies. Considering this sequential recording of crossbreds, the objective was to investigate the impact of different CG definitions on genetic parameters and EBV prediction accuracy for crossbred traits. Growth rate (G_p) and ultrasound backfat (BF_p) records were available for purebreds. Lifetime growth (G_x) and backfat (BF_x) were recorded on crossbreds. Different CGs were tested: **CG_all** included farm, sex, birth year, and birth week; **CG_week** added slaughter week; and **CG_day** used slaughter day instead of week. Data of 124,709 crossbreds were used. The purebred phenotypes (62,274 animals) included three generations of purebred ancestors of these crossbreds and their CG mates. Variance components for four-trait models with different CG definitions were estimated with average information restricted maximum likelihood. Purebred traits' variance components remained stable across CG definitions and varied slightly for BF_x . Additive genetic variances (and heritabilities) for G_x fluctuated more: 812 ± 36 (0.28 ± 0.01), 257 ± 15 (0.17 ± 0.01), and 204 ± 13 (0.15 ± 0.01) for **CG_all**, **CG_week**, and **CG_day**, respectively. Age at slaughter (**AAS**) and hot carcass weight (**HCW**) adjusted for age were investigated as alternatives for G_x . Both have potential for selection but lower heritabilities compared with G_x : 0.21 ± 0.01 (0.18 ± 0.01), 0.16 ± 0.02 (0.16 ± 0.01), and 0.10 ± 0.01 (0.14 ± 0.01) for **AAS** (**HCW**) using **CG_all**, **CG_week**, and **CG_day**, respectively. The predictive ability, linear regression (**LR**) accuracy, bias, and dispersion of crossbred traits in crossbreds favored **CG_day**, but correlations with unadjusted phenotypes favored **CG_all**. In purebreds, **CG_all** showed the best LR accuracy, while showing small relative differences in bias and dispersion. Different CG scenarios showed no relevant impact on BF_x EBV. This study shows that different CG definitions may affect evaluation stability and animal ranking. Results suggest that ignoring slaughter dates in CG is more appropriate for estimating crossbred trait EBV for purebred animals.

Key words: commercial pigs, grading, model validation, predictive ability, sequential selection

Abbreviations

AAS	age at slaughter
BF _p	backfat in purebred animals
BF _x	backfat in crossbred animals
CG	contemporary group
CG _{all}	contemporary group based on farm, sex, birth year, and birth week
CG _{day}	contemporary group based on farm, sex, birth year, birth week, and slaughter day
CG _{week}	contemporary group based on farm, sex, birth year, birth week, and slaughter week
EBV	estimated breeding value
EW	weight at end of growth test period (measured in purebred animals)
G _p	growth in purebred animals
G _x	growth in crossbred animals
HCW	hot carcass weight (measured in crossbred animals)
IGE	indirect genetic effects
LR	linear regression, or Legarra-Reverter, method

Introduction

Crossbreeding is a common practice in the pig industry. Similar traits measured in crossbred and purebred animals may be considered as effectively different traits (Wei and van der Werf, 1994; Lutaaya et al., 2001; Christensen et al., 2014). This difference can largely be attributed to environmental factors. However, traits may also be measured or determined differently. For instance, growth in purebred animals is often calculated as live weight at the end of a growth test divided by age, whereas crossbred growth is calculated as hot carcass weight (HCW) divided by age. These differences in cross- and purebred performances are important since purebred animals are selected to produce crossbred animals expected to perform optimally in a commercial environment. As these traits are different and genetic merits for them are likely influenced by different genetic factors, the animals that produce the best purebred offspring may not produce the best crossbred offspring (Lutaaya et al., 2001).

Crossbred and purebred animals perform in considerably different environments. Housing conditions are better controlled for purebred animals, while conditions for crossbred animals may be harsher and more variable. The environmental effects accounted for in purebred animals may not be as relevant in crossbred animals and vice versa. Additionally, crossbred animals are kept in pens with large pen mate groups, which can affect growth adversely, especially for the smallest pigs. This is known as social interaction (or competition) effects, which is an indirect genetic effect (IGE) that individuals have on their peers (Bijma, 2014). Because of the resulting growth rate heterogeneity, crossbred pen mates reach the market size/weight (based on visual inspection) in different time periods and are removed from the pen sequentially (i.e., fast growers are removed first). This practice helps to create more space for the smallest pigs to grow and allows the pork industry to have more uniform carcasses. However, as a consequence, there is usually no single point at which all animals in the pen are measured together, and not all animals initially in the pen experience the same IGE until slaughter. Conversely, purebreds remain in the same group over the growth test period and are measured together at the conclusion of the test.

The fact that crossbred animals in the same pen are slaughtered, and, therefore, phenotyped at different times should, at best, be accounted for by the model to increase the accuracy of estimated breeding values (EBV) and avoid bias. Including selection day in the construction of contemporary groups (CGs) creates multiple small groups that compare only the best animals in the pen at that time. These superior animals could be unfairly penalized by never being compared with their more inferior contemporaries, while the inferior animals can benefit. Age adjustments are questionable since animals are removed from the pen based on size, regardless of age, producing growth curves that are not truly reflective of the physiological process. Additionally, it has been shown that earlier weights are poor predictors of later growth of pigs within the same pen. Shull (2013) found that only 57.8% of pigs were in the same live weight quartile at 10- and 22-wk postwean, and the rank correlation between birth weight and weaning weight was only 0.50. When CGs have more animals, the accuracy of evaluation may increase because of better estimation of CG effects. However, the ideal CGs should not only be larger but also appropriately defined. Bias can be introduced if animals in the group are not exposed to the same conditions (Carabaño et al., 2004; Vasconcelos et al., 2008; Crump et al., 2010).

The objective of this study was to find an optimal CG definition to evaluate crossbred traits for both purebred and crossbred animals when recording is incomplete, and animals are sequentially phenotyped based on prior visual inspection.

Materials and Methods

Animal Care and Use Committee approval was not needed because the information was obtained from preexisting databases.

Data

Data from three crossbred farms recorded from January 2016 to May 2020 were used for this study, totaling 124,709 animals. Crossbred animals had phenotypes for growth (G_x) and backfat (BF_x). The purebred population included three generations of ancestors of the crossbred individuals as well as their CG mates. Purebred ancestors of crossbred pigs totaled 12,533 individuals but only 1,793 of them had measurements for both growth (G_p) and ultrasound backfat (BF_p). The total number of purebred animals with measurements was 62,274. The pedigree included 203,374 animals, of which 1,430 were sires and 22,758 were dams. The instrumentations used to measure BF_x may differ between harvest sites. These instrumentation effects are accounted for through the inclusion of farm in the CG definition. To further reduce potential bias introduced by different instruments, purebred sires are represented across farms. The G_p was calculated as the live weight at the end of the growth test divided by age, whereas G_x was calculated as the carcass weight divided by age. Therefore, G_p and G_x make two major assumptions—growth has a linear behavior and birth weight is zero for all animals. The summary statistics for traits and age are presented in Table 1. Purebred animals were measured at a considerably younger age than crossbred animals, thus traits in each group may capture different phases of the growth curve. Additionally, purebred animals remained in the same pen for the duration of the weight test, whereas crossbred animals were removed for slaughter at different time points based on visual inspection. The remaining animals

Table 1. Summary statistics for traits and effects on purebred and crossbred animals

Trait	N	Min	Max	Mean	SD
HCW, kg	124,709	60	144.24	98.16	8.89
EW ¹ , kg	62,274	62.6	182.5	121.5	14.61
G _p , g/d	62,274	450.3	1,106.1	766.6	90.72
G _x , g/d	124,709	301	758	528.4	60.63
BF _p , mm	62,274	5	32.7	8.56	2.13
BF _x , mm	124,709	5	38.7	14.82	4.05
Age _{purebred} ¹ , d	62,274	127	200	158.6	7.02
Age _{crossbred} ¹ , d	124,709	143	250	186.2	13.20

¹EW, end weight of purebreds; Age_{purebred}, purebred age; Age_{crossbred}, crossbred age.

were not weighed at the time when selected pen mates were removed.

Pen information was not available to be included in CGs, but pen sizes were known to accommodate 30 to 60 pigs. CG for purebred animals was compiled of farm, line, sex, birth year, and birth week. Three different CG compositions for crossbred traits were tested, including 1) **CG_all**, which was compiled of birth farm, sex, birth year, and birth week; 2) **CG_week**, which was compiled of birth farm, sex, birth year, birth week, and slaughter week; and 3) **CG_day**, which was compiled of birth farm, sex, birth year, birth week, and slaughter day. In the CG_{day} scenario, there were 10,598 groups with size ranging from 1 to 231 animals, with an average of 11.8 animals. Within these groups, 1,928 (18.2%) had only one animal and 2,981 (28.1%) only included individuals sired by the same single boar. In the CG_{week} scenario, there were 5,850 groups with sizes ranging from 1 to 266 animals, with an average size of 21.3 animals. Within these groups, 532 (9.09%) had only one animal and 813 (13.9%) only included individuals sired by the same single boar. There were, on average, 1.5 slaughter dates within each group. CG_{all} had 970 groups ranging from 1 to 566 animals, with an average size of 128.6 animals. Only 2 (0.21%) groups had only one animal and 12 (1.24%) had all individuals sired by the same single boar. There was an average of 9 slaughter dates per group, with 359 groups (37.01%) having 10 or more slaughter dates, up to a maximum of 22. Only CGs with more than four animals were considered for variance component estimation. However, all animals were included for breeding value prediction. Primarily, a four-trait model for G_p, BF_p, G_x, and BF_x was used:

$$y = Xb + Wc + Zu + e$$

where y is the vector of phenotypes; b is a vector of solutions for fixed effects, while X is an incidence matrix relating phenotypes to these effects (all traits had CG as a fixed effect, but BF_p and BF_x also included weight as a covariate); c is a vector of random litter effects, while W is an incidence matrix relating phenotypes to these effects; u is a vector of direct additive genetic effects, while Z is an incidence matrix relating phenotypes to the additive effect; e is a vector of residuals. Vector c is distributed as multi-variate normal [MVN(0, I₀)] where:

$$L_0 = \begin{bmatrix} \sigma_{IGP}^2 & \sigma_{IGP,IBFP} & 0 & 0 \\ \sigma_{IBFP,IGP} & \sigma_{IBFP}^2 & 0 & 0 \\ 0 & 0 & \sigma_{IGX}^2 & \sigma_{IGX,IBFX} \\ 0 & 0 & \sigma_{IBFX,IGX} & \sigma_{IBFX}^2 \end{bmatrix};$$

vector a is distributed as MVN(0, A \otimes G₀) where:

$$G_0 = \begin{bmatrix} \sigma_{aGP}^2 & \sigma_{aGP,aBFP} & \sigma_{aGP,aGX} & \sigma_{aGP,aBFX} \\ \sigma_{aBFP,aGP} & \sigma_{aBFP}^2 & \sigma_{aBFP,aGX} & \sigma_{aBFP,aBFX} \\ \sigma_{aGX,aGP} & \sigma_{aGX,aBFP} & \sigma_{aGX}^2 & \sigma_{aGX,aBFX} \\ \sigma_{aBFX,aGP} & \sigma_{aBFX,aBFP} & \sigma_{aBFX,aGX} & \sigma_{aBFX}^2 \end{bmatrix};$$

vector e is distributed as MVN(0, I \otimes R₀) where:

$$R_0 = \begin{bmatrix} \sigma_{eGP}^2 & \sigma_{eGP,eBFP} & 0 & 0 \\ \sigma_{eBFP,eGP} & \sigma_{eBFP}^2 & 0 & 0 \\ 0 & 0 & \sigma_{eGX}^2 & \sigma_{eGX,eBFX} \\ 0 & 0 & \sigma_{eBFX,eGX} & \sigma_{eBFX}^2 \end{bmatrix},$$

where σ_a^2 is the additive variance, σ_l^2 is the litter variance, and σ_e^2 is the residual variance. Age at slaughter (AAS) and carcass weight (HCW) were also investigated as potential replacement traits for crossbred growth. Accordingly, models for these two traits included the relevant CG as fixed effect and litter and additive genetic effects as random effect. Furthermore, HCW included AAS as a covariate. This should be a reflection of G_x since G_x is measured as HCW divided by age, while this approach is HCW adjusted for age. However, regression coefficients are recalculated at every genetic evaluation and are, therefore, dependent on data changes. We used AIREMLF90 to estimate variance components and BLUP90IOD to compute EBV. Both programs belong to the BLUPF90 software family (Misztal et al., 2014). The variance of the solutions for CG was used to measure the amount of variance absorbed by the CG effect when different CG definitions are used for G_x and BF_x.

Cross-validation tests were used to compare models with different CG definitions. The accuracy of predicting future EBV and the ability to predict future performance were evaluated for purebreds and crossbreds. The crossbred validation data set consisted of 66,585 animals born in 2018 and 2019. The purebred validation set consisted of parents of the crossbred validation animals, totaling 7,454 animals, out of which 377 had both G_p and BF_p measurements. Predicted breeding values of validation animals were obtained with all data (\hat{u}_{whole}) and without phenotypes of crossbred validation animals ($\hat{u}_{partial}$). Different validation measures were used to evaluate the changes in accuracy, including the linear regression (LR) method (Legarra and Reverter, 2018), the predictive ability, and Pearson correlations between \hat{u}_{whole} and unadjusted phenotypes. Different measures to evaluate stability included the regression coefficient (dispersion), difference between \hat{u}_{whole} and $\hat{u}_{partial}$ (bias), and Pearson correlations between the \hat{u}_{whole} obtained using different CG definitions. The LR method (Legarra and Reverter, 2018) calculates validation accuracy as follows:

$$acc_{LR} = \sqrt{\frac{COV(\hat{u}_{whole}, \hat{u}_{partial})}{(1 - \bar{F})\sigma_a^2}},$$

where acc_{LR} stands for accuracy from the LR method, \bar{F} is the average inbreeding coefficient of the validation population, and σ_a^2 is the additive genetic variance. The dispersion was measured as the regression coefficient (b_1) of the regression of \hat{u}_{whole} on $\hat{u}_{partial}$:

$$b_1 = \frac{COV(\hat{u}_{whole}, \hat{u}_{partial})}{VAR(\hat{u}_{partial})},$$

and bias as $\widehat{\mathbf{u}}_{\text{partial}} - \widehat{\mathbf{u}}_{\text{whole}}$. The Pearson correlation between $\widehat{\mathbf{u}}_{\text{whole}}$ and $\widehat{\mathbf{u}}_{\text{partial}}$ was to measure the stability of model-based predictions when phenotypes are added to the data.

The ability to predict future performance (i.e., predictive ability) was calculated on the basis of $\text{cor}(\mathbf{y}_{\text{adj}}, \widehat{\mathbf{u}}_{\text{partial}})$. However, this correlation was transformed for each trait to the accuracy scale as:

$$\text{acc}_{\text{PRED}} = \text{cor}(\mathbf{y}_{\text{adj}}, \widehat{\mathbf{u}}_{\text{partial}}) / h,$$

where acc_{PRED} stands for accuracy transformed from predictive ability, \mathbf{y}_{adj} is the vector of phenotypes adjusted for all other effects in the model, and h is the square root of trait heritability (Legarra et al., 2008). Since only crossbred animals have phenotypes for G_x and BF_x , this could only be estimated for crossbred animals.

Because fixed effects for crossbred phenotypes changed across scenarios, the benchmark for each model was different. Therefore, we calculated Pearson correlations between unadjusted phenotypes for crossbred animals and $\widehat{\mathbf{u}}_{\text{partial}}$ or $\widehat{\mathbf{u}}_{\text{whole}}$. The $\widehat{\mathbf{u}}_{\text{whole}}$ estimated under different CG definitions were also compared with each other with Pearson correlations.

Results

Estimated values for variances of crossbred traits (Table 2) decreased in general as CG composition became more specific (from CG_all to CG_day). The additive genetic variance for G_x using CG_all was exceptionally large (812 vs. 257 for CG_week and 204 for CG_day). The variances of the solutions for CG effect on G_x (and BF_x) were 23,451 (25.68), 35,313 (34.60), and 67,842 (60.09) for CG_day, CG_week, and CG_all, respectively.

Variance estimates for purebred traits are not included in the table. Estimates for litter, additive, and residual variances remained stable for purebred traits, which is expected since no changes were made to CGs of purebred animals themselves. The estimated values for variance components for G_p and BF_p were 809 ± 25 and 0.20 ± 0.01 for litter effects, $1,404 \pm 77$ and 1.41 ± 0.05 for additive genetic effects, and $3,022 \pm 43$ and 1.84 ± 0.03 for residuals, respectively.

Heritability and genetic correlation estimates for G_p , BF_p , G_x , and BF_x are presented in Table 3. The heritability estimates remained stable for G_p , BF_p , and BF_x , whereas the heritability for G_x increased as the CG became more inclusive. Genetic correlations between BF_x and purebred traits remained relatively stable under all CG definitions. The correlations between G_x and BF_p were more sensitive to change and became stronger as the CG size increased. Correlations between G_x and G_p showed the greatest discrepancy. The standard errors of genetic parameters remained stable across different CG definitions.

Heritability and genetic correlation estimates with AAS replacing G_x in the four-trait model are presented in Table 4. Heritability estimates for AAS halved as CG size decreased from CG_all to CG_day and are lower than G_x heritability under the

analogous four-trait model. The correlation between G_p and AAS was also favorable (i.e., negative) but weaker relative to the G_p - G_x association (-0.46 ± 0.07 vs. 0.56 ± 0.06 , respectively).

Heritability and genetic correlation estimates when HCW replaces G_x in the four-trait model are presented in Table 5. The heritability estimates for HCW using CG_all were substantially lower than that of G_x in an analogous four-trait model (0.18 vs. 0.28) but similar for CG_week (0.16 vs. 0.17) and CG_day (0.14 vs. 0.15). Correlations of purebred traits with HCW were stronger than those with G_x using CG_week and CG_day, but weaker when using CG_all.

Model comparison results based on the LR method for purebred animals and crossbred animals are presented in Tables 6 and 7, respectively. The breeding values obtained using different variance components and CG did not lead to marked changes for BF_x . Accuracies, dispersion, bias, and correlations remain similar across scenarios for BF_x in purebred validation animals and barely changed for crossbred validation animals. Conversely, more performance variability was observed for G_x for both purebred and crossbred validation sets. The LR accuracy was highest for purebred animals for CG_all at 0.36 vs. 0.33 for CG_day and 0.31 for CG_week. Bias was least for CG_day (0.02) and most for CG_all (0.06). For G_x in crossbred animals, the predictive ability was highest for CG_day (0.30) and lowest for CG_all (0.27). LR accuracy was also highest for CG_day (0.28) but lowest for CG_week (0.26). Relatively greater performance discrepancies are observed for correlations (0.53, 0.49, and 0.43 for CG_day, CG_week, and CG_all), dispersion (1.00, 0.97, and 0.86 for CG_day, CG_week, and CG_all), and bias (0.03, 0.38, and 0.88 for CG_day, CG_week, and CG_all). The covariances between $\widehat{\mathbf{u}}_{\text{whole}}$ and $\widehat{\mathbf{u}}_{\text{partial}}$ for crossbred traits in purebred validation animals were generally higher than those for crossbred validation animals, which may explain the higher LR accuracies of crossbred traits in purebred animals compared with crossbred animals. As an illustration, the covariances for G_x in purebred (and crossbred) validation animals were 22.53 (16.82), 24.05 (17.93), and 105.42 (58.20) for CG_day, CG_week, and CG_all, respectively.

The Pearson correlation between $\widehat{\mathbf{u}}_{\text{partial}}$ of crossbred validation animals and their unadjusted phenotype for G_x was highest for CG_all (0.08), followed by 0.06 for both CG_week and CG_day. These differences are small enough to be negligible. Correlations with unadjusted BF_x barely varied between scenarios (0.26, 0.26, and 0.27 for CG_all, CG_week, and CG_day, respectively). Correlations between unadjusted phenotype and $\widehat{\mathbf{u}}_{\text{whole}}$ of crossbred validation animals for G_x (BF_x) were 0.70 (0.72), 0.47 (0.69), and 0.43 (0.67) using CG_all, CG_week, and CG_day, respectively. Correlations between $\widehat{\mathbf{u}}_{\text{whole}}$ of G_x (and BF_x) for crossbred validation animals were 0.95 (0.98) between CG_day and CG_week, 0.73 (0.95) between CG_day and CG_all, and 0.76 (0.97) between CG_all and CG_week, while correlations of G_x (and BF_x) for purebred validation animals were 0.94 (0.97) between CG_day and CG_week, 0.76 (0.94) between CG_day and CG_all, and 0.79 (0.97) between CG_week and CG_all.

Table 2. Variance components and standard errors estimated with AI-REML when using different CGs

	Additive variance		Litter variance		Residual variance	
	G_x	BF_x	G_x	BF_x	G_x	BF_x
CG_all	812 ± 36	4.28 ± 0.13	322 ± 11	0.50 ± 0.03	1,790 ± 20	5.69 ± 0.07
CG_week	257 ± 15	4.03 ± 0.12	116 ± 5	1.72 ± 0.03	1,130 ± 9	5.16 ± 0.07
CG_day	204 ± 13	4.00 ± 0.12	78 ± 4	0.36 ± 0.03	1,084 ± 8	5.04 ± 0.07

Table 3. Heritability estimates (diagonal) and genetic correlations (off-diagonal) for G_p , BF_p , G_x , and BF_x

	G_p	BF_p	G_x	BF_x
CG_all				
G_p	0.27 ± 0.01	0.45 ± 0.02	0.56 ± 0.06	0.23 ± 0.05
BF_p		0.41 ± 0.01	0.17 ± 0.06	0.78 ± 0.03
G_x			0.28 ± 0.01	0.27 ± 0.02
BF_x				0.41 ± 0.01
CG_week				
G_p	0.27 ± 0.01	0.46 ± 0.03	0.44 ± 0.07	0.21 ± 0.06
BF_p		0.41 ± 0.01	0.11 ± 0.06	0.78 ± 0.03
G_x			0.17 ± 0.01	0.24 ± 0.03
BF_x				0.42 ± 0.01
CG_day				
G_p	0.27 ± 0.01	0.46 ± 0.02	0.49 ± 0.07	0.22 ± 0.05
BF_p		0.41 ± 0.01	0.10 ± 0.06	0.78 ± 0.03
G_x			0.15 ± 0.01	0.19 ± 0.03
BF_x				0.42 ± 0.01

Table 4. Heritability estimates (diagonal) and genetic correlations (off-diagonal) for G_p , BF_p , AAS, and BF_x

	G_p	BF_p	AAS	BF_x
CG_all				
G_p	0.27 ± 0.01	0.46 ± 0.03	-0.46 ± 0.07	0.23 ± 0.05
BF_p		0.41 ± 0.01	-0.14 ± 0.06	0.78 ± 0.03
AAS			0.21 ± 0.01	-0.12 ± 0.03
BF_x				0.41 ± 0.01
CG_week				
G_p	0.27 ± 0.01	0.46 ± 0.02	0.20 ± 0.09	0.21 ± 0.06
BF_p		0.41 ± 0.01	0.11 ± 0.07	0.77 ± 0.03
AAS			0.16 ± 0.02	-0.06 ± 0.04
BF_x				0.42 ± 0.01
CG_day				
G_p	0.27 ± 0.01	0.46 ± 0.02	0.19 ± 0.10	0.22 ± 0.06
BF_p		0.41 ± 0.01	0.13 ± 0.08	0.77 ± 0.03
AAS			0.10 ± 0.01	-0.02 ± 0.05
BF_x				0.42 ± 0.01

Discussion

The genetic parameters obtained with CG_all are the most favorable, with the highest heritability estimate for G_x , similar heritability estimates for other traits, and stronger correlations with crossbred traits. Such values would indicate a possibility of a faster response to the selection provided that they best represent the “true” population parameters. Parameters estimated under CG_all were also most favorable when replacing G_x with AAS or HCW. The additive genetic variance estimated for G_x was more than three times higher for CG_all than for the other scenarios. Using simulated data, Gao et al. (2019) found decreased additive genetic variance estimates when ignoring dropout animals (reflecting our CG_day and CG_week scenarios). More specifically, the additive genetic variance was only 69% of estimates obtained when animals never dropped out. Their group size was 12 animals, and a total of 15% of the worst-performing animals were dropped over six different time periods. Weights for all animals were available for each time period and used in a regression model. The number of animals per pen in our study was large (30 to 60 animals), and the average

Table 5. Heritability estimates (diagonal) and genetic correlations (off-diagonal) for G_p , BF_p , HCW, and BF_x

	G_p	BF_p	HCW	BF_x
CG_all				
G_p	0.27 ± 0.01	0.46 ± 0.02	0.47 ± 0.07	0.24 ± 0.05
BF_p		0.41 ± 0.01	0.16 ± 0.06	0.78 ± 0.03
HCW			0.18 ± 0.01	0.32 ± 0.03
BF_x				0.41 ± 0.01
CG_week				
G_p	0.27 ± 0.01	0.46 ± 0.03	0.48 ± 0.07	0.21 ± 0.05
BF_p		0.41 ± 0.01	0.13 ± 0.06	0.78 ± 0.03
HCW			0.16 ± 0.01	0.23 ± 0.03
BF_x				0.42 ± 0.01
CG_day				
G_p	0.27 ± 0.01	0.46 ± 0.02	0.50 ± 0.07	0.21 ± 0.05
BF_p		0.41 ± 0.01	0.12 ± 0.06	0.78 ± 0.03
HCW			0.14 ± 0.01	0.19 ± 0.03
BF_x				0.42 ± 0.01

Table 6. Validation statistics for G_x and BF_x in purebred animals

Trait	Scenario	$cor(\hat{u}_{whole}, \hat{u}_{partial})^1$	b_1^2	Bias ³	acc_{LR}^4
G_x	CG_all	0.59	1.01	0.06	0.36
	CG_week	0.58	1.00	0.05	0.31
	CG_day	0.61	1.01	0.02	0.33
BF_x	CG_all	0.60	1.01	-0.01	0.41
	CG_week	0.60	1.03	-0.01	0.42
	CG_day	0.60	1.03	-0.02	0.41

¹Correlation between EBV with whole and partial data.

²Coefficient of the regression of EBV with partial data on EBV with whole data.

³Defined as the difference between average EBV with partial and whole data.

⁴Accuracy based on LR metrics.

CG size ranged from 11.77 for CG_day and 128.57 for CG_all. The variance captured by CG (as measured by the variance of the solutions for the CG effect) also increased as our CG definition became less specific.

Additive genetic variance for CG_all in our study could be overestimated, the degree of which will depend on the suitability of CG compilation and accounting for either the relative time spent in the pen or relative space allowance (Ask et al., 2020). Total genetic variance in pigs for traits measured in group housing conditions is composed of the direct genetic effect of the individual and the IGE of the group mates (Bijma et al., 2007). The IGE in a group also depends on a dilution parameter, since the effect of one animal on another in the group will be smaller when the group is large (Arango et al., 2005; Bijma, 2010; Heidaritabar et al., 2019). The reason for this expectation is that pairwise interactions are less frequent in large groups, leading to larger dilution parameter values (Canario and Bijma, 2010). In the current study, IGE is less of a concern since food was available ad libitum in large troughs, which decreases, although does not eliminate, the social effect on growth (Bergsma et al., 2008). Neither the IGE nor the dilution parameter could be inferred in our study due to the lack of pen information. Additionally, animals that were removed first were always sharing a pen with a large number of animals. Conversely, animals remaining until the latest dates (after other animals were removed several times before) were housed with fewer pen mates for part of

Table 7. Validation statistics for G_x and BF_x in crossbred animals

Trait	Scenario	$\text{cor}(\hat{u}_{\text{whole}}, \hat{u}_{\text{partial}})^1$	b_1^2	Bias ³	acc_{LR}^4	$\text{acc}_{\text{PRED}}^5$
G_x	CG_all	0.43	0.86	0.88	0.27	0.27
	CG_week	0.49	0.97	0.38	0.26	0.28
	CG_day	0.53	1.00	0.03	0.28	0.30
BF_x	CG_all	0.54	1.03	0.01	0.37	0.41
	CG_week	0.54	1.03	0.00	0.37	0.42
	CG_day	0.55	1.03	-0.02	0.38	0.43

¹Correlation between EBV with whole and partial data.

²Coefficient of the regression of EBV with partial data on EBV with whole data.

³Defined as the difference between average EBV with partial and whole data.

⁴Accuracy based on LR metrics.

⁵Accuracy based on predictive ability.

their growing period. This means that although some scenarios have small CGs, this should not be understood as if they would have more pairwise social interactions because CG sizes are not reflecting the number of pen mates. Pen information is often not recorded in pig breeding, but the inclusion thereof may be essential to avoid biased genetic parameters, even when the pen size is the same (Bergsma et al., 2008).

The definition of growth in this study considers that G_x and G_p are essentially indices of both weight and growth, instead of weight change over time. Also accommodating an initial weight, such as birth weight or weaning weight, would be useful to capture growth alone, but these weights may not be available, especially for crossbreds. The birth weight of piglets has an influence on future growth, with piglets that are heavier at birth growing faster (Shull, 2013). AAS is an attractive alternative trait, especially because it is easy to measure and less susceptible to human error, unlike carcass weight. This latter trait is particularly prone to be affected by various factors that day. The heritability of 0.21 for AAS with CG_all suggests that it would respond to selection, albeit less than G_x (0.28). The heritability estimates are even lower for CG_week and CG_day. Although AAS is not commonly researched as a trait, Torres Filho et al. (2004) found heritability estimates ranging from 0.13 to 0.20 for age at 100 kg body weight, which is similar to the range of heritability estimates in this study (0.10 to 0.21). Santos et al. (2015) used a few hundred genomic markers and found heritability estimates ranging from 0.02 to 0.23 for AAS depending on the model used and the number of markers selected. In Irish beef cattle, the heritability of deviation of AAS ranged from 0.23 to 0.26 (Berry et al., 2017).

The AAS also shows weaker correlations with other traits. The negative correlation between GP and AAS for CG_all suggests that the selection for faster growth in purebred animals may lead to earlier slaughter age for crossbred offspring, which is desirable. However, this correlation is not only weaker but also positive when using CG_week and CG_day. The genetic parameters in this study suggest that, although it is possible to use AAS as a replacement for G_x , genetic change is expected to be faster when using G_x . Furthermore, the inconsistency of the correlation between AAS and G_p when using different CGs makes G_x a safer choice. The results suggest that HCW could be a more appropriate alternative trait to use if CGs are based on week or day, but not when excluding slaughter information.

Although CG_all has the most favorable variance component estimates, CG_day delivered the highest predictive ability, highest validation accuracy, least dispersion, and least bias. Validation accuracy measured as predictive ability is a measure of how well the model is correcting for effects, but not

an indication whether the effects themselves are appropriate. Additionally, Legarra and Reverter (2018) showed that using adjusted phenotypes as a benchmark is questionable when variance components are wrong or when fixed effects have a large number of levels. In the latter, the error associated with the estimation of effects of all levels is high if the number of observations per level is small, causing an upward bias. The bias is then inversely proportional to the number of levels of a fixed effect. The higher predictive ability achieved with CG_day can be partially explained by the far greater number of CGs in the model (10,589 groups for CG_day, 5,850 for CG_week, and only 970 for CG_all). Correlations with adjusted phenotypes will also be influenced by the overall populations accuracy, heritability, and errors in estimating the fixed effects (Legarra and Reverter, 2018).

The accuracy measured by the LR method remained essentially unchanged for BF_x across CG scenarios, at around 0.41 for purebred animals and 0.37 for crossbred animals. The higher values for purebred validation animals were driven by the higher covariances between breeding values with all the data and breeding values computed without measurements of the crossbred validation animals. The LR accuracies for G_x in crossbred animals essentially remained unchanged (between 0.26 and 0.28), while differences in predictive ability are slightly bigger (0.27 to 0.30). These small differences make it difficult to draw a definitive conclusion regarding crossbred animals. However, the differences in accuracy for G_x in purebred animals varied more—0.36, 0.31, and 0.33 for CG_all, CG_week, and CG_day. In the pig industry, purebred animals are selected for crossbred performance, and, therefore, the breeding value accuracies for G_x and BF_x are crucial. CG_all gave the highest accuracy for G_x in purebred animals, but the second highest for crossbred animals. Based on these results, CG_all is the most appropriate for G_x selection in purebred animals, but CG_day may be the most appropriate in crossbred animals. Although the LR method for calculating accuracy is designed to overcome some flaws of predictive ability tests, it relies on the estimated additive variances. As discussed above, estimating the true additive variance with dropout animals is difficult.

The correlations between EBV obtained under different CG definitions indicate how these definitions affect the animals. Smaller CG comparing similar animals could be a disadvantage for the superior animals and an advantage for inferior animals. This would be reflected in a negative correlation. Results in this study show high correlations (>0.94) for BF_x for all comparisons and both purebred and crossbred animals, while correlations for G_x are lower, but still positive, for all comparisons. Comparisons

of G_x between CG_day and CG_week show strong correlations, suggesting little difference in ranking. Greater differences are observed when comparing results to CG_all, where correlations are between 0.71 and 0.76. This indicates significant changes in ranking, although the overall trend will be similar. Adjusting measurements for age is an attractive option but it may not be a suitable reflection of the true growth curve. Although animals are weighed at different ages, they are chosen for slaughter based on size and only weighed once in their lifetime. Thus, weights are more or less similar regardless of age. Multiple records over time would allow better adjustments for age. Additionally, age is used in the calculation of growth. Adjusting for a factor that is part of the trait may remove some of the genetic components of the trait.

A higher Pearson correlation between EBV and less bias is not necessarily indications of improvement since it shows the magnitude of changes from parent average to a breeding value based also on phenotypic records, not whether the change is moving toward the true breeding value (which is unknown). A model that gives a higher correlation will be more stable between evaluations, indicating less changes when phenotypes are recorded, but it might not be the most correct.

Correlations between EBV of crossbred validation animals and their unadjusted phenotypes favored CG_all, especially when phenotypes were included in the evaluation (\hat{u}_{whole}). This reflects the higher heritability estimate calculated using this CG definition. It may be that, under CG_all, less statistical signals are captured by CG and more remain for the breeding value. Caution should be used when interpreting correlations with unadjusted phenotype, but these higher values may suggest that the exclusion of slaughter date from CG was able to better capture the genetic merit of animals. However, some traits may be more sensitive to CG changes than others, as was the case of growth but not backfat in our study.

Conclusions

This study reflects the complexity of evaluating the appropriateness of CG compilation and the accuracy of breeding values. Accuracy measures assume that the model was able to adequately correct for all effects and that the estimated variance components are correct, which may not be true. Selecting purebred animals for crossbred growth is essential in the pig industry. Results suggest that, for the estimation of crossbred traits in purebred animals, it is best to include all crossbred animals finished together in a single CG, as opposed to multiple groups based on slaughter date. Routine pen information recording would allow finer tuning of CGs and the estimation of IGEs. AAS shows potential as an alternative growth trait for crossbreds. However, heritability estimates are lower and correlations with other traits are weaker.

Acknowledgments

We are grateful to Jorge Hidalgo for his useful input. This study was partially funded by Genus PIC.

Conflict of interest statement

The authors declare that there are no conflicts of interest.

Literature Cited

- Arango, J., I. Misztal, S. Tsuruta, M. Culbertson, and W. Herring. 2005. Estimation of variance components including competitive effects of Large White growing gilts. *J. Anim. Sci.* 83:1241–1246. doi:10.2527/2005.8361241x
- Ask, B., O. F. Christensen, M. Heidaritabar, P. Madsen, and H. M. Nielsen. 2020. The predictive ability of indirect genetic models is reduced when culled animals are omitted from the data. *Genet. Sel. Evol.* 52:8. doi:10.1186/s12711-020-0527-x
- Bergsma, R., E. Kanis, E. F. Knol, and P. Bijma. 2008. The contribution of social effects to heritable variation in finishing traits of domestic pigs (*Sus scrofa*). *Genetics* 178:1559–1570. doi:10.1534/genetics.107.084236
- Berry, D. P., A. R. Cromie, and M. M. Judge. 2017. Rapid Communication: Large exploitable genetic variability exists to shorten age at slaughter in cattle. *J. Anim. Sci.* 95:4526–4532. doi:10.2527/jas2017.2016
- Bijma, P. 2010. Multilevel selection 4: modeling the relationship of indirect genetic effects and group size. *Genetics* 186:1029–1031. doi:10.1534/genetics.110.120485
- Bijma, P. 2014. The quantitative genetics of indirect genetic effects: a selective review of modelling issues. *Heredity (Edinb)*. 112:61–69. doi:10.1038/hdy.2013.15
- Bijma, P., W. M. Muir, and J. A. Van Arendonk. 2007. Multilevel selection 1: quantitative genetics of inheritance and response to selection. *Genetics* 175:277–288. doi:10.1534/genetics.106.062711
- Canario, A., and P. Bijma. 2010. Pig growth is affected by social genetic effects and social litter effects that depend on group size. In: *Proceedings of the 9th World Congress on Genetic Applied to Livestock Production (WCGALP)*; August 1 to 6, 2010; Leipzig, Germany; p. 87.
- Carabaño, M. J., A. Moreno, P. López-Romero, and C. Díaz. 2004. Comparing alternative definitions of the contemporary group effect in Avilena Negra Iberica beef cattle using classical and Bayesian criteria. *J. Anim. Sci.* 82:3447–3457. doi:10.2527/2004.82123447x
- Christensen, O. F., P. Madsen, B. Nielsen, and G. Su. 2014. Genomic evaluation of both purebred and crossbred performances. *Genet. Sel. Evol.* 46:23. doi:10.1186/1297-9686-46-23
- Crump, R., N. Wray, R. Thompson, and G. Simm. 2010. Assigning pedigree beef performance records to contemporary groups taking account of within herd calving patterns. *Anim. Sci.* 65:193–198. doi:10.1017/S1357729800016490
- Gao, H., B. Nielsen, G. Su, P. Madsen, J. Jensen, O. F. Christensen, T. Ostersen, and M. Shirali. 2019. Use of repeated group measurements with drop out animals for variance component estimation and genetic evaluation: a simulation study. *G3 (Bethesda)*. 9:2935–2940. doi:10.1534/g3.119.400484
- Heidaritabar, M., P. Bijma, L. Janss, C. Bortoluzzi, H. M. Nielsen, P. Madsen, B. Ask, and O. F. Christensen. 2019. Models with indirect genetic effects depending on group sizes: a simulation study assessing the precision of the estimates of the dilution parameter. *Genet. Sel. Evol.* 51:24. doi:10.1186/s12711-019-0466-6
- Legarra, A., and A. Reverter. 2018. Semi-parametric estimates of population accuracy and bias of predictions of breeding values and future phenotypes using the LR method. *Genet. Sel. Evol.* 50:53. doi:10.1186/s12711-018-0426-6
- Legarra, A., C. Robert-Granié, E. Manfredi, and J. M. Elsen. 2008. Performance of genomic selection in mice. *Genetics* 180:611–618. doi:10.1534/genetics.108.088575
- Lutaaya, E., I. Misztal, J. W. Mabry, T. Short, H. H. Timm, and R. Holzbauer. 2001. Genetic parameter estimates from joint evaluation of purebreds and crossbreds in swine using the crossbred model. *J. Anim. Sci.* 79:3002–3007. doi:10.2527/2001.79123002x
- Misztal, I., S. Tsuruta, D. Lourenco, I. Aguilar, A. Legarra, and Z. Vitezica. 2014. *Manual for BLUPF90 family of programs*. Athens: University of Georgia.

- Santos, V. S., S. Martins Filho, M. D. Resende, C. F. Azevedo, P. S. Lopes, S. E. Guimarães, L. S. Glória, and F. F. Silva. 2015. Genomic selection for slaughter age in pigs using the Cox frailty model. *Genet. Mol. Res.* 14:12616–12627. doi:10.4238/2015.October.19.5
- Shull, C. 2013. *Modeling growth of pigs reared to heavy weights* [dissertation]. University of Illinois at Urbana-Champaign. Available from <https://www.ideals.illinois.edu/handle/2142/44329>
- Torres Filho, R. d. A., R. d. A. Torres, P. S. Lopes, R. F. Euclides, C. V. d. Araújo, C. S. Pereira, and M. d. A. e. Silva. 2004. Avaliação de modelos para estimação de componentes de (co)variância em características de desempenho e reprodutivas em suínos. *Revista Brasileira de Zootecnia* 33: 350–357. doi:10.1590/S1516-35982004000200011
- Vasconcelos, J., F. Santos, A. Bagnato, and J. Carvalheira. 2008. Effects of clustering herds with small-sized contemporary groups in dairy cattle genetic evaluations. *J. Dairy Sci.* 91:377–384. doi:10.3168/jds.2007-0202
- Wei, M., and J. H. J. van der Werf. 1994. Maximizing genetic response in crossbreds using both purebred and crossbred information. *Anim Sci* 59:401–413. doi:10.1017/S0003356100007923