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Including crossbred pigs in the genomic relationship matrix through utilization of both linkage disequilibrium and linkage analysis[1]

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ABSTRACT

In pig breeding, the final product is a crossbred (CB) animal, while selection is performed at the purebred (PB) level using mainly PB data. However, incorporating CB data in genetic evaluations is expected to result in greater genetic progress at the CB level. Currently, there is no optimal way to include CB genotypes into the genomic relationship matrix. This is because, in single-step genomic BLUP, which is the most commonly used method, genomic and pedigree relationships must refer to the same base. This may not be the case when several breeds and CB are included. An alternative to overcome this issue may be to use a genomic relationship matrix (G matrix) that accounts for both linkage disequilibrium (LD) and linkage analysis (LA), called $\mathbf{G}_{\mathbf{LDLA}}$. The objectives of this study were to further develop the $\mathbf{G}_{\mathbf{LDLA}}$ matrix approach to utilize both PB and CB genotypes simultaneously, to investigate its performance, and the general added value of including CB genotypes in genomic evaluations. Data was available on Dutch Landrace, Large White, and the F1 cross of those breeds. In total, 7 different G matrix compositions (PB alone, PB together, each PB with the CB, all genotypes across breeds, and $\mathbf{G}_{\mathbf{LDLA}}$) were tested on 3 maternal traits: total number born (TNB), live born (LB), and gestation length (GL). Results show that $\mathbf{G}_{\mathbf{LDLA}}$ gave the greatest prediction accuracy of all the relationship matrices tested, and that including CB genotypes in general also increased prediction accuracy. However, in some cases, these increases in prediction accuracy were not significant (at $P < 0.05$). To conclude, CB genotypes increased prediction accuracy for some of the traits and breeds, but not for all. The $\mathbf{G}_{\mathbf{LDLA}}$ matrix had significantly greater prediction accuracy than the other G matrix with both PB and CB genotypes, except in one case. However, computation time was high for $\mathbf{G}_{\mathbf{LDLA}}$, and research will be needed to reduce its computational costs to make it feasible for use in routine evaluations.

Key words: crossbreds, genomic relationship matrix, linkage analysis, linkage disequilibrium, maternal traits, pigs

INTRODUCTION

In pig breeding, the final product is the crossbreds (**CB**) animal. However, selection is performed at the purebred (**PB**) level using mainly PB data, which may result in a reduced genetic progress at the CB level (Dekkers, 2007; Toosi et al., 2010; Bloemhof et al., 2012; Bijma and Bastiaansen, 2014; Esfandyari et al., 2015). Hence, the inclusion of CB data in the breeding value estimation of PB is expected to improve genetic progress of CB animals. Currently, there is no optimal way to include CB genotypes in the genomic relationship matrix (Misztal et al., 2014) or in single-step GBLUP (**ssGBLUP**) (Christensen et al., 2014). In ssGBLUP, an **H** matrix (combination of pedigree-based and genomic-based relationships) is used, assuming that both relationships refer to the same base (Legarra et al., 2015). However, this assumption does not hold when several breeds and CB are included. Using breed-specific allele frequencies from genomic information may alleviate this problem, but this is not possible in ssGBLUP (Lourenco et al., 2016). An alternative option is to use the **G**$^{\textbf{LDLA}}$ relationship matrix, which utilizes both linkage disequilibrium (**LD**) and linkage analysis (**LA**), making use of genotypes, genotype probabilities and pedigree relationships (Meuwissen et al., 2015). Genetic groups can be accounted for so that the base animals of different breeds can be entered as alternative genetic groups, and thus use allele frequencies according to breed rather than across all animals. This would accommodate CB because they are linked to the PB through the pedigree. The **G**$^{\textbf{LDLA}}$ matrix has shown promising results analyzing PB data (Meuwissen et al., 2015), but has not yet been applied to CB data. Therefore, the aim of this study was to further develop the **G**$^{\textbf{LDLA}}$ matrix approach to combine PB and CB genotypes simultaneously, to investigate its performance, and the general added value of including CB genotypes in genomic evaluations.

MATERIALS AND METHODS

Care and Use of Animals

Data recording and sample collection were conducted strictly in line with the laws given by Dutch animal research authorities on the protection of animals (Gezondheids- en welzijnswet voor dieren). The data was obtained as part of routine data recording in commercial breeding programs. Samples collected for DNA extraction were only used for the routine diagnostic purpose of the breeding program.

Animals and Data

Data was available on 2 PB populations (Dutch Landrace and Large White) and their F1 cross, hereafter referred to as **A**, **B**, and **X**, respectively. The traits evaluated in this study were total number born (**TNB**, sum of alive and dead piglets), live born (**LB**, number of piglets born alive) and gestation length (**GL**, number of days between insemination and farrowing). Phenotypic observations were available on 11,491 sows, and genotypes were available on 8,350 animals. Both males and females were genotyped in the PB, but in the F1 population, only females were genotyped. All animals were genotyped using the Illumina Porcine SNP60 Beadchip (Illumina Inc., San Diego, CA). Quality control consisted of excluding SNP with GenCall < 0.15, call rate < 0.95, minor allele frequency < 0.01, and strong deviations from Hardy-Weinberg equilibrium ($\chi^2 > 600$). The SNP located on sex chromosomes and unmapped SNP were also excluded. Positions of the SNP were based on the Sscrofa10.2 assembly of the reference genome (Groenen et al., 2012). All genotyped animals had a frequency of missing genotypes above the threshold of 0.05 for excluding poorly-genotyped animals. After quality control, SNP not segregating in all breeds were excluded, leaving 36,778 SNP common to all breeds for further analysis. An overview of phenotypic and genotypic data can be found in Table 1 and 2.

Statistical Analysis

The Linkage Disequilibrium Multilocus Iterative Peeling (**LDMIP**) program (Meuwissen and Goddard, 2010) was used to get genotype probabilities for the genotyped animals and their ungenotyped ancestors. It is a method for imputation of phase and missing genotypes, and sets up the linkage analysis part of the identity by descent (**IBD**) matrix (Meuwissen and Goddard, 2010). There is an option in LDMIP to run both with (genetic) groups and without groups. Here the base animals of the two PB were entered into different genetic groups according to breed. With this, LDMIP accounts for differences in allele frequencies according to which breed(s) the animals originate from (Meuwissen et al., 2015). This will also apply to CB because they are linked to the PB through the pedigree. The option to run without genetic groups was also used to determine the importance of including genetic groups when having a multi-breed dataset. Information from neighboring loci was not used when running LDMIP because Meuwissen et al. (2015) found better accuracies of genomic selection when not using information from neighboring loci.

This estimation of genotype probabilities was followed by setting up the $\mathbf{G}_{\mathbf{LDLA}}$ matrix. The genotype probabilities from LDMIP were used to set up the gametic relationship matrix:

$$\mathbf{G} = \mathbf{WW'} / \sum_j \mathbf{p_j}(1 - \mathbf{p_j}),$$

where **G** was a ($2n$ x $2n$) matrix of gametic relationships (n = number of animals); and **W** was a ($2n$ x m) matrix of standardized genotypes (m = number of markers). Element W_{ij} is obtained by taking the probability of a '1' allele of gamete i at marker j and subtracting the appropriate allele frequency, p_j (Meuwissen et al., 2015). The expectation is that the diagonal of **G** is 1, because the relationship of a gamete with itself is 1. Off-diagonals represent inbreeding because; non-zero off-diagonals indicate that the maternal and paternal gamete is related. However, the diagonal of **G** may deviate from 1, either due to sampling or because

genotype probabilities have lower variance than actual genotypes (Meuwissen et al., 2015). This may lead to underestimated relationships, and **G** was adjusted for this through the following formula:

$$\mathbf{G_{LDLA}} = [\mathbf{S(DGD} + \Delta\tilde{\mathbf{A}}\Delta)\mathbf{S'}]/2,$$

where **D** was a diagonal matrix with elements $\sqrt{(1/G_{ii})}$ when G_{ii} is greater than 1, or 1 elsewhere, Δ was a diagonal matrix with elements $\sqrt{(1-G_{ii})}$ when G_{ii} was less than 1, or 0 elsewhere, **Ã** was the pedigree-based gametic relationship matrix, and **S** was the design matrix that indicated which gametes belong to which animals, which reduces the size of the gametic relationship matrix to number of animals squared. For further details, and an example, see Meuwissen et al. (2015). Ungenotyped descendants of the genotyped animals were added to the relationship matrix according to Henderson's rules.

In addition to the $\mathbf{G_{LDLA}}$ matrix, 7 other relationship matrices were built for comparison. These were; the pedigree-based A matrix (**PED**), G matrix for breed A ($\mathbf{G_A}$, i.e. a G matrix with breed A genotypes), breed B ($\mathbf{G_B}$), breed A and B together (including marker-based relationships between breeds, $\mathbf{G_{AB}}$), each of the PB with the CB ($\mathbf{G_{AX}}$ and $\mathbf{G_{BX}}$), and a G matrix including all of the genotypes across breeds ($\mathbf{G_{ABX}}$). The G matrices (except $\mathbf{G_{LDLA}}$) were built with the Gmatrix program (Su and Madsen, 2014) that is part of the DMU package. After building the different G matrices, ssGBLUP was used as implemented in DMU (Madsen and Jensen, 2008) for analyzing the full dataset for all of the matrices using a multitrait model. The G-ADJUST option in DMU (adjusts genomic relationships so that they correspond to average relationships in the A matrix (Gao et al., 2012)) was used for all G matrices except $\mathbf{G_{LDLA}}$ when building the **H** matrix used in ssGBLUP. The full pedigree (including all breeds) was used for building the A matrix in all analyses.

The focus was on maternal traits, and the majority of the sows had more than one observation per trait. Consequently, a repeatability model was used to account for the effect of permanent maternal environment. The model was:

$$\mathbf{y = Xb + Zu + Wm + Vv + e},$$

where **y** was a vector of observations (TNB, LB, and GL), **X**, **Z**, **W**, and **V**, known incidence matrices, **b** a vector of fixed effects, **u** a vector of random additive genetic effects, with $\mathbf{u \sim N(0, A\sigma_u^2}$ or $\mathbf{G\sigma_u^2)}$, where $\boldsymbol{\sigma_u^2}$ was the additive genetic variance, **m** a vector of permanent maternal environmental effects, with $\mathbf{m \sim N(0, I_m\sigma_m^2)}$, where $\boldsymbol{\sigma_m^2}$ was the non-genetic maternal environmental variance, **v** a vector of herd-year-season effects, with $\mathbf{v \sim N(0, I_v\sigma_v^2)}$, where $\boldsymbol{\sigma_v^2}$ was the variance of herd-year-season effects, and **e** a vector of residuals with $\mathbf{e \sim N(0, I_e\sigma_e^2)}$, where $\boldsymbol{\sigma_e^2}$ was the residual variance. $\mathbf{I_m}$, $\mathbf{I_v}$, and $\mathbf{I_e}$ were identity matrices of the appropriate dimensions, **A** was a matrix of pedigree-based, additive genetic relationships (**PED**) and **G** a matrix of genomic relationships between all individuals. Here, **G** represents the aforementioned G matrices ($\mathbf{G_A}$, $\mathbf{G_B}$, $\mathbf{G_{AB}}$, $\mathbf{G_{AX}}$, $\mathbf{G_{BX}}$, $\mathbf{G_{ABX}}$, or $\mathbf{G_{LDLA}}$). Variance components ($\boldsymbol{\sigma_u^2}$, $\boldsymbol{\sigma_m^2}$, $\boldsymbol{\sigma_v^2}$, $\boldsymbol{\sigma_e^2}$) were estimated by DMU from the data. Fixed effects were breed, parity, farm, and farrowing quarter for TNB and LB, and breed, farm, and farrowing quarter for GL. Random effects were genetic effects of animal, permanent environmental effect (non-genetic maternal effects), and herd-year-season effects. The same model was used with all of the relationship matrices.

The analysis was performed using the entire dataset, and the solutions for fixed and random effects were extracted from this analysis for each of the relationship matrices. The dataset was then modified to mask phenotypes for the validation animals (1000 animals) and their offspring (both PB and CB offspring if applicable), for either breed A or breed B. Thus, validation was either in the A or B animals, not in both at the same time. Two validation sets

were used for each breed (2 x 1000 animals), where validation animals were different between the validation sets. The training set was the remaining animals after validation animals had been removed. Validation was done in PB animals, and not in CB, because selection is in PB animals. Thus, the aim is to produce the best CB animals by selecting the PB animals best suited to produce commercial CB. Therefore, PB animals need accurate EBV for CB performance. To create the validation sets, the first (oldest) 1000 animals in the list of genotyped animals in each breed were chosen, and then the next 1000 animals in the next validation set for that breed. Thus, there were 2 validation sets with 1000 animals each for each breed (A or B) (~4790 observations per validation dataset). The youngest animals with genotypes did not have sufficient phenotypes to make a large enough validation set, and were not used for validation. Only animals that had both genotypes and phenotypes were included in the validation set. Matrices $\mathbf{G_A}$ and $\mathbf{G_{AX}}$ were only used in the validation of breed A animals, and likewise matrices $\mathbf{G_B}$ and $\mathbf{G_{BX}}$ were only used in the validation of breed B animals. After analyzing with the reduced dataset, fixed and non-genetic random effects from the full analysis (for each matrix) were included before predicting phenotypes of validation animals to avoid altering the precision of estimates of fixed and non-genetic random effects by using a smaller dataset. The prediction accuracy of the cross-validation was estimated by the following formula: $\mathbf{r} = \frac{corr(EBV, AdjPheno)}{\sqrt{h^2}}$, where EBV was estimated breeding value, **AdjPheno** was phenotype (of validation animal) adjusted for fixed and (non-genetic) random effects, and $\mathbf{h^2}$ was the heritability of the trait. Regression coefficients between EBV and adjusted phenotypes were estimated by fitting a linear model with adjusted phenotype as response variable and EBV as the explanatory variable. Standard deviations of estimated breeding values were also estimated. Except when the pedigree-based relationship matrix (**PED**) was used, EBV were genomic EBV (GEBV).

In addition, accuracy was also estimated when using fixed and random effects from the analysis using the full dataset with the **PED** matrix. Thus, **AdjPheno** was adjusted for fixed and random effects from **PED**, and not from each matrix. This reduces the accuracy for each method, but makes methods comparable when testing for significant differences. This does not however, change the EBV from the methods.

Bootstrapping was used to test whether accuracies of the different genomic prediction methods were significantly different from each other. This was done on the results from using the fixed and random effects from **PED**. The EBV from two methods at a time were compared against each other (pair-wise comparison), to see which was best to predict the adjusted phenotypes (of the validation animals) from the **PED** evaluation. The Bootstrap procedure randomly samples with replacement data point triplets: the adjusted phenotype and their predictions (EBV) using two methods. It estimates which of the methods yields a greater correlation with the adjusted phenotype in each Bootstrap sample. A total of 10,000 Bootstrap samples were constructed. If one of the methods had a greater correlation in at least 97.5% of Bootstrap samples, the two methods (matrices) were considered to be significantly different (at a P-value of 5% due to the two-sided nature of the test).

The relationships that were common to both $\mathbf{G}_{\mathbf{LDLA}}$ and $\mathbf{G}_{\mathbf{ABX}}$ were plotted against each other to see if these would differ between the two matrices. The average relationship within and across breeds were estimated for $\mathbf{G}_{\mathbf{LDLA}}$ and $\mathbf{G}_{\mathbf{ABX}}$.

RESULTS

Trait means, standard deviations, number of observations and other trait statistics are presented in Table 3. Heritability estimates are across all breeds. The mean number of parities for sows with observations was 5.85.

In terms of prediction accuracy (Table 4), the $\mathbf{G}_{\mathbf{LDLA}}$ matrix had the greatest accuracy for all traits and breeds, followed by $\mathbf{G}_{\mathbf{ABX}}$. Mean gain (in accuracy) from using $\mathbf{G}_{\mathbf{LDLA}}$ over $\mathbf{G}_{\mathbf{ABX}}$ was 1.0 and 1.1 percentage points across traits for A and B, respectively. Including CB in the genomic relationship matrix ($\mathbf{G}_{\mathbf{AX}}$, $\mathbf{G}_{\mathbf{BX}}$, $\mathbf{G}_{\mathbf{ABX}}$, $\mathbf{G}_{\mathbf{LDLA}}$) always gave a greater accuracy than not including CB genotypes ($\mathbf{G}_{\mathbf{A}}$, $\mathbf{G}_{\mathbf{B}}$, $\mathbf{G}_{\mathbf{AB}}$). Including both PB in the same genomic relationship matrix ($\mathbf{G}_{\mathbf{AB}}$) increased accuracy compared to not including both PB in the same matrix. The increase in accuracy was larger for Dutch Landrace (A) than for Large White (B). Overall, breed A benefitted more from including more animals in the genomic relationship matrix than breed B. In terms of individual traits, GL had the lowest increase in accuracy by including more animals in the genomic relationship matrix, but had the largest initial and overall accuracy.

When using fixed and random effects from **PED** for all matrices, the accuracies reduced with 3.8 to 15.4 percentage points. In terms of differences in accuracies between matrices, not all of these were significant (Table 5). For breed A, $\mathbf{G}_{\mathbf{LDLA}}$ had a significantly greater accuracy than all other matrices for traits TNB and GL. For TNB, also $\mathbf{G}_{\mathbf{ABX}}$ had a significantly greater accuracy than the other matrices, except $\mathbf{G}_{\mathbf{LDLA}}$. For LB, $\mathbf{G}_{\mathbf{LDLA}}$ was not significantly more accurate than $\mathbf{G}_{\mathbf{ABX}}$ and $\mathbf{G}_{\mathbf{AB}}$. Nor was $\mathbf{G}_{\mathbf{ABX}}$'s accuracy significantly different from that of $\mathbf{G}_{\mathbf{A}}$. For breed B, $\mathbf{G}_{\mathbf{LDLA}}$ had a significantly greater accuracy than all other matrices except $\mathbf{G}_{\mathbf{BX}}$ for TNB and GL. For LB, $\mathbf{G}_{\mathbf{LDLA}}$ only had a significantly greater accuracy than $\mathbf{G}_{\mathbf{AB}}$ and $\mathbf{G}_{\mathbf{ABX}}$. All pairwise comparisons are found in Table 5.

Regression coefficients between EBV and adjusted phenotypes were close to 1 and similar across methods and no relationship matrix was clearly better than the others (Table 6).

Within trait, $\mathbf{G}_{\mathbf{LDLA}}$ always had the greatest standard deviation of estimated breeding values (for validation animals) (Table 7). This was followed by including genotypes from all breeds ($\mathbf{G}_{\mathbf{ABX}}$), and for TNB and LB, by including CB with the PB ($\mathbf{G}_{\mathbf{AX}}$ and $\mathbf{G}_{\mathbf{BX}}$). For GL, including CB had the third greatest standard deviation for B ($\mathbf{G}_{\mathbf{BX}}$), but for A, $\mathbf{G}_{\mathbf{AB}}$ produced the third greatest standard deviation.

There was very little difference in terms of accuracy (<0.01 percentage points) and regression coefficients (0.01 increase for $\mathbf{G}_{\mathbf{LDLA}}$ for TNB), and no difference for standard deviations of EBV in analyzing without genetic groups compared to with groups, and therefore these results are not presented here.

The correlation between allele frequencies of A and B was 0.25. The correlations between allele frequencies of PB and CB were 0.77 and 0.76 for A and B, respectively.

When plotting relationships common to $\mathbf{G}_{\mathbf{LDLA}}$ and $\mathbf{G}_{\mathbf{ABX}}$ against each other, there was some discordance between the matrices (Fig. 1). This was especially true for low relationships (<0.4). Some animals were seemingly unrelated in one of the matrices, but had relationships as strong as 0.6 in the other. This type of discordance went both ways. This led to the discovery of some pedigree errors, although not all could be corrected because not all of the animals in the pedigree had genotypes. Self-relationships were generally larger in $\mathbf{G}_{\mathbf{LDLA}}$ than in $\mathbf{G}_{\mathbf{ABX}}$. Note: this was before $\mathbf{G}_{\mathbf{ABX}}$ was adjusted for pedigree relationships with G-ADJUST, while $\mathbf{G}_{\mathbf{LDLA}}$ is already adjusted for pedigree relationships (as this is part of the method).

Average relationships within and across breeds for $\mathbf{G}_{LDLA}$ and $\mathbf{G}_{ABX}$ are shown in Table 8 and 9, respectively. In general, mean relationships were greater in $\mathbf{G}_{LDLA}$ than in $\mathbf{G}_{ABX}$, except between A and B. The greatest relationship between individuals within A was between two inbred full-sibs, whose parents were also full-sibs. The greatest relationship within B is a sire-offspring relationship. The greatest relationship between A and B seems unreasonable, and is likely due to some animals being assigned the wrong breed and therefore seeming unrelated in the pedigree even though that is not the case.

The computation time for building the G matrices was not the same between matrices. Computation time for LDMIP (pre-program for $\mathbf{G}_{LDLA}$) was from 11.5 h to 14.0 h (18 parallel jobs on the Abel computer cluster, dual Intel E5-2570 based, 2.6 GHz per node, (UiO, 2017)) and for building $\mathbf{G}_{LDLA}$ from 11.5 h to 12.5 h (on the Abel computer cluster). In comparison, computation time for building the other G matrices was a couple of minutes (on a 46 bit physical Intel Core i7, 3.40 GHz core processor running Linux). Computation time for DMU5 (on a 46 bit physical Intel Core i7, 3.40 GHz core processor running Linux) increased with the size of the G matrix, thus $\mathbf{G}_{LDLA}$ was the slowest, with a computation time of about 1 h, and $\mathbf{G}_{ABX}$ second slowest with approximately 40 min.

DISCUSSION

Including CB genotypes in the genomic relationship matrix, whether based on markers only ($\mathbf{G}_{AX}$, $\mathbf{G}_{BX}$, $\mathbf{G}_{ABX}$) or through using $\mathbf{G}_{LDLA}$, increased prediction accuracy for PB. However, not all of these increases were significantly different from not including CB. Depending on trait and breed, prediction accuracy increased with between 0.9 and 11.6 percentage points compared to using a PB G matrix ($\mathbf{G}_{A}$ or $\mathbf{G}_{B}$). This also led to a larger standard deviation of estimated breeding values (increase of 0.005 to 0.244). The increase in accuracy from

including CB genotypes was larger for total number born (TNB) (4.0 to 11.6 percentage points) and live born (LB) (5.1 to 10.0 percentage points) than for gestation length (GL) (0.9 to 4.7 percentage points). The increase was also greater for Dutch Landrace (A) than for Large White (B), except for the trait GL.

Accuracy

The greater prediction accuracy with $\mathbf{G}_{\mathbf{LDLA}}$ could be a result of this matrix utilizing more information than the other matrices. The increase in accuracy compared to using only one breed or both PB is probably mainly due to the utilization of across breed information. However, when comparing $\mathbf{G}_{\mathbf{LDLA}}$ to the G matrix that also utilizes all the genotypes across all breeds ($\mathbf{G}_{\mathbf{ABX}}$), $\mathbf{G}_{\mathbf{LDLA}}$ still has a significantly greater accuracy. An exception exists for the trait LB for breed A, although the difference is small. This might suggest that $\mathbf{G}_{\mathbf{LDLA}}$ is a more appropriate relationship matrix when dealing with crosses between breeds. Often, marker and QTL linkage phases will be different between different breeds (Zhou et al., 2014), which supports this notion. In theory, it should not be possible to include CB in ssGBLUP, because pedigree and genomic relationships will not refer to the same base and due to differences in allele frequencies between breeds (Legarra et al., 2015; Lourenco et al., 2016). However, in practice, $\mathbf{G}_{\mathbf{ABX}}$ yields quite accurate predictions (at least in the current dataset). Nonetheless, $\mathbf{G}_{\mathbf{ABX}}$ is not significantly better than only including the PB ($\mathbf{G}_{\mathbf{A}}$, $\mathbf{G}_{\mathbf{B}}$, or $\mathbf{G}_{\mathbf{AB}}$), except for GL in breed B and TNB in breed A. An explanation for this could be that the genotyped animals make up 52.4% of the animals in the pedigree and 56.6% of the animals with phenotypes, i.e. the proportion of genotyped animals was rather large. It is therefore likely, that if a smaller proportion of the animals were genotyped, the relative difference between $\mathbf{G}_{\mathbf{LDLA}}$ and $\mathbf{G}_{\mathbf{ABX}}$ might increase.

It is expected that using population-specific allele frequencies (as in $\mathbf{G}_{\mathbf{LDLA}}$ for example) can accurately predict breeding values across populations (Wientjes et al., 2015). If the allele frequencies between the two PB were highly correlated (correlation close to 1), there would be little difference between these matrices, but this was not the case here. In addition, the $\mathbf{G}_{\mathbf{LDLA}}$ matrix also uses identity by descent (IBD) information, whereas the other G matrices use only identity by state (IBS) information. However, as seen here, this might be problematic if there is discordance between the pedigree and the genotypes. Pedigree errors led to some strange relationships between individuals for $\mathbf{G}_{\mathbf{LDLA}}$ that were not in agreement with the genotypes. On the other hand, this approach may be a useful tool to detect pedigree errors that are not detected by comparison of genotypes of parents and their offspring. For example, it could detect errors in the relationships between genotyped and un-genotyped individuals that cannot be detected by comparing genotypes. Possibly, the $\mathbf{G}_{\mathbf{LDLA}}$ approach is more sensitive to pedigree errors, and it may be expected that without pedigree errors, $\mathbf{G}_{\mathbf{LDLA}}$ will yield greater accuracies relative to $\mathbf{G}_{\mathbf{ABX}}$ than the results shown here.

Combining genotypes from the two PB in the G matrix ($\mathbf{G}_{\mathbf{AB}}$) seemed to increase prediction accuracy over using single-breed matrices, although this increase was not statistically significant. This increase is in agreement with findings by Esfandyari et al. (2016), who did not test for its significance. However, Hidalgo et al. (2015), found that including two PB in the G matrix reduced accuracies for all four traits under study. Relationships between the breeds will contribute to this increase in accuracy, even though the breeds are assumed unrelated. The mean relationship between animals of these breeds would indicate unrelatedness, but there were some notable relationships that could have influenced the results. It is also possible that this increase would be insignificant with larger population sizes for the PB as these are relatively small in the current study.

Regression Coefficients

Regression coefficients did not really differ between the different relationship matrices and no particular matrix was clearly best. These results are in agreement with Xiang et al. (2016), who did not find differences in regression coefficients between different scenarios either. This indicates that all models are unbiased and that the heritability estimates are reasonable.

Traits

There were differences between traits in terms of accuracy and standard deviations, although the overall trend was that $\mathbf{G}_{\mathbf{LDLA}}$ and $\mathbf{G}_{\mathbf{ABX}}$ performed the best across traits. More was gained in TNB and LB than in GL in terms of accuracy by adding CB genotypes to the relationship matrix. This could be because the proportion of CB animals with phenotypes for GL was lower than for the other two traits. In addition, GL had a greater initial accuracy, which could be due to greater heritability for GL than for TNB and LB. It is also possible that the purebred-crossbred correlation (r_{pc}) for GL is greater than for TNB and LB, and thus adding CB data does not really add more information than just adding more animals in general (i.e. if $r_{pc} = 1$, CB data equals PB data). A r_{pc} of 0.70 to 0.78 has been reported for TNB in Landrace and 0.57 to 0.68 for Yorkshire (Xiang et al., 2016), and Lopes et al. (2016) found an r_{pc} of 0.90 for both TNB and GL. Thus, adding the CB genotypes would not be much different than adding more animals in general when PB and CB performance is considered as the same trait, and it is difficult to conclude whether the increase is due to adding CB specifically or just adding more information. If r_{pc} is low, PB and CB performance should be considered as different traits, and it would be more important to use CB data to predict CB-GEBV for PB animals.

Whether to consider PB and CB performance as the same or different traits depends on several factors. However, in most cases, it is the genetic correlation between PB and CB performance (r_{pc}) that is taken into consideration, both in terms of whether to include CB data

at all, but also in terms of whether to consider PB and CB performance as different, but genetically correlated traits. The exact size of r_{pc} at which CB data is beneficial is debated, but most studies recommend inclusion of CB data when r_{pc} is below 0.7 or 0.8 (Dekkers, 2007; Bloemhof et al., 2012; Hidalgo et al., 2015; Tusell et al., 2016). Differences in r_{pc} is affected by several factors such as non-additive effects (dominance, heterosis etc.), genotype by environment interactions, breed of origin effects, differences in allele frequencies between breeds, etc. (Dekkers and Chakraborty, 2004; Christensen et al., 2014; Van Grevenhof and Van der Werf, 2015; Lopes et al., 2016). If the r_{pc} is low, it would make sense to consider PB and CB performance as different traits. This makes it possible to select for animals that have a better breeding value for CB performance. The traits could also be weighed differently in the breeding goal, ensuring genetic progress in both PB and CB performance. A limitation to viewing PB and CB performance as different traits might be data availability. If there are few observations on either PB or CB, it might not be enough data available for analysis. Considering PB and CB performance as the same trait would result in more available data, but if r_{pc} is low, this would result in poor prediction. A benefit of considering PB and CB performance as the same trait is that one can have observations on both parents and offspring, or other close relationships such as half-sib PB and CB, increasing prediction accuracy. In the current study, PB and CB performance was analyzed as the same trait. This is mainly because other studies have found reasonably high r_{pc} for the traits in this study (0.68-0.90) (Lopes et al., 2016; Xiang et al., 2016).

Breeds

Dutch Landrace (breed A) gained more in accuracy by using CB genotypes, or even just by adding genotypes from the other PB, than Large White (breed B). One reason might be that breed A had lower accuracy to start with, thus more to gain in general. Esfandyari et al. (2016) also found greater prediction accuracies in one breed (Yorkshire) over another

(Landrace). They suggested that this may be due to a larger variance in genomic relationships for the Yorkshire animals (Esfandyari et al., 2016), but this does not agree with the results in the current study, where larger variation in relationships was found in breed A. It is possible that the correlation between PB and CB performance is greater for some breeds than others, and may need to be assessed in each case to find the best approach for evaluation of animals. An increase in accuracy when including more than one breed could be explained by relatively close relationships between the breeds (Zhou et al., 2014), but this was not the case in the current study, although there were some high relationships between the breeds. The average relationship between individuals of A and B was -0.15 and -0.14 for $\mathbf{G}_{LDLA}$ and $\mathbf{G}_{ABX}$, respectively. According to Lourenco et al. (2016), using breed-specific allele frequencies will pull across-breed relationships closer to zero, but no such effect was seen when using $\mathbf{G}_{LDLA}$ compared to $\mathbf{G}_{ABX}$ in the current study. When the correlation between allele frequencies of two breeds is low, this may lead to negative relationships between breeds (Lourenco et al., 2016), which is in agreement with the findings of the current study.

Computation Time

The computation time for $\mathbf{G}_{LDLA}$ was considerable longer than for the other G matrices. In part this is because computations for $\mathbf{G}_{LDLA}$ have not been optimized as is the case for DMU routines, but still the calculation of genotype probabilities for all animals in the pedigree and all SNP on the chip implies substantial computational costs. Possibly, in the future the calculation of genotype probabilities for ungenotyped animals may become an integral part of the genotype imputation algorithms, which are routinely used to impute missing genotypes. In any case, more research is needed to reduce the computational costs of the $\mathbf{G}_{LDLA}$ approach, especially when applied to larger data sets than the current one.

Grouping

The $\mathbf{G}_{\mathbf{LDLA}}$ matrix only outperforms $\mathbf{G}_{\mathbf{ABX}}$ by a small amount across traits (1.0 to 1.1 percentage points), but unlike $\mathbf{G}_{\mathbf{ABX}}$, it keeps track of which breed each animal comes from, or at least which genetic group it belongs to. Thus, for estimation of genetic trends or levels of genetic groups, it might be more accurate, although this was not attempted in this study. It is possible that to get a marked difference between grouping strategies, groups may need to be more detailed than simply using breeds as genetic groups. It is likely that a year-effect within-breed may more accurately reflect the genetic differences, because not all animals with unknown parents will be base animals, and will thus have different genetic levels to start with.

Breed Composition

Crossbred (CB) data make up a relatively large part of the genotypes (almost 16.5%) and phenotypes (11.4%) in this study, which may not be the case in routine evaluations where PB data dominate. For most breeding organizations, most the available data is on PB, although this is likely to change in the future. Thus, it is possible that the gain from including CB genotypes would be less in routine situations than in the current study, but the genotyping and phenotyping of CB individuals will improve this situation. The proportion of CB phenotypes for GL (7.0%) was less than for TNB and LB, and may be one of the reasons that the gain in accuracy by adding CB is less for GL.

Conclusions

Including CB genotypes is beneficial for prediction accuracies of PB animals when these are parents of the CB for some traits, but not for all. Prediction accuracies increase with 0.9 to 11.6 percentage points by including CB genotypes. The $\mathbf{G}_{\mathbf{LDLA}}$ matrix gave a significantly greater accuracy than $\mathbf{G}_{\mathbf{ABX}}$ in all but one scenario (LB for breed A), although the gain in accuracy was less than 2 percentage points. Computation time for $\mathbf{G}_{\mathbf{LDLA}}$ was much longer

than for the other relationship matrices. Thus, research on how to reduce computational costs will be needed to make the **GLDLA** approach feasible in large scale routine evaluations.

LITERATURE CITED

Bijma, P., and J. W. M. Bastiaansen. 2014. The Standard Error of the Estimated Purebred-Crossbred Genetic Correlation. In: Proc. 10th World Congr. Genet. Appl. Livest. Prod., Vancouver, Canada.

Bloemhof, S., A. Kause, E. F. Knol, J. A. M. Van Arendonk, and I. Misztal. 2012. Heat stress effects on farrowing rate in sows: genetic parameter estimation using within-line and crossbred models. J. Anim. Sci. 90(7):2109-2119. doi: 10.2527/jas.2011-4650

Christensen, O. F., P. Madsen, B. Nielsen, and G. Su. 2014. Genomic evaluation of both purebred and crossbred performances. Genet. Sel. Evol. 46(1):23-32. doi: 10.1186/1297-9686-46-23

Dekkers, J. C. M., and R. Chakraborty. 2004. Optimizing purebred selection for crossbred performance using QTL with different degrees of dominance. Genet. Sel. Evol. 36(3):297-324. doi: 10.1051/gse:2004003

Dekkers, J. C. M. 2007. Marker-assisted selection for commercial crossbred performance. J. Anim. Sci. 85(9):2104-2114. doi: 10.2527/jas.2006-683

Esfandyari, H., A. C. Sørensen, and P. Bijma. 2015. Maximizing crossbred performance through purebred genomic selection. Genet. Sel. Evol. 47(1):16. doi: 10.1186/s12711-015-0099-3

Esfandyari, H., P. Bijma, M. Henryon, O. F. Christensen, and A. C. Sørensen. 2016. Genomic prediction of crossbred performance based on purebred Landrace and Yorkshire data using a dominance model. Genet. Sel. Evol. 48(1):1. doi: 10.1186/s12711-016-0220-2

Gao, H., O. F. Christensen, P. Madsen, U. S. Nielsen, Y. Zhang, M. S. Lund, and G. Su. 2012. Comparison on genomic predictions using three GBLUP methods and two single-step blending methods in the Nordic Holstein population. Genet. Sel. Evol. 44(1):8. doi: 10.1186/1297-9686-44-8

Groenen, M. A., A. L. Archibald, H. Uenishi, C. K. Tuggle, Y. Takeuchi, M. F. Rothschild, C. Rogel-Gaillard, C. Park, D. Milan, and H.-J. Megens. 2012. Analyses of pig genomes provide insight into porcine demography and evolution. Nature 491(7424):393-398. doi: 10.1038/nature11622

Hidalgo, A. M., J. W. M. Bastiaansen, M. S. Lopes, B. Harlizius, M. A. M. Groenen, and D.-J. de Koning. 2015. Accuracy of Predicted Genomic Breeding Values in Purebred and Crossbred Pigs. G3 (Bethesda) 5(8):1575-1583. doi: 10.1534/g3.115.018119

Legarra, A., O. F. Christensen, Z. G. Vitezica, I. Aguilar, and I. Misztal. 2015. Ancestral relationships using metafounders: finite ancestral populations and across population relationships. Genetics 200(2):455-468. doi: 10.1534/genetics.115.177014

Lopes, M. S., H. Bovenhuis, A. M. Hidalgo, J. A. van Arendonk, E. F. Knol, and J. W. Bastiaansen. 2016. Genomic selection for crossbred performance accounting for breed-specific effects. PhD Diss. Wageningen University, Wageningen, The Netherlands.

Lourenco, D., S. Tsuruta, B. Fragomeni, C. Chen, W. Herring, and I. Misztal. 2016. Crossbreed evaluations in single-step genomic best linear unbiased predictor using adjusted realized relationship matrices. J. of Anim. Sci. 94(3):909-919. doi: 10.2527/jas2015-9748

Madsen, P., and J. Jensen. 2008. DMU: a user's guide. A package for analysing multivariate mixed models, Version 6. http://dmu.agrsci.dk/DMU/Doc/Current/dmuv6_guide.5.2.pdf (Accessed 04.05.2016).

Meuwissen, T., and M. Goddard. 2010. The use of family relationships and linkage disequilibrium to impute phase and missing genotypes in up to whole-genome sequence density genotypic data. Genetics 185(4):1441-1449. doi: 10.1534/genetics.110.113936

476 Meuwissen, T. H., M. Svendsen, T. Solberg, and J. Ødegård. 2015. Genomic predictions
477 based on animal models using genotype imputation on a national scale in Norwegian
478 Red cattle. Genet. Sel. Evol. 47(1):1-9. doi: 10.1186/s12711-015-0159-8
479 Misztal, I., A. Legarra, and I. Aguilar. 2014. Using recursion to compute the inverse of the
480 genomic relationship matrix. J. Dairy Sci. 97(6):3943-3952. doi: 10.3168/jds.2013-
481 7752
482 Su, G., and P. Madsen. 2014. User's Guide for Gmatrix Ver2. A program for computing
483 Genomic relationship matrix. http://dmu.agrsci.dk/Gmatrix/Doc/Current/GmatrixV2-
484 User-Guide.pdf (Accessed 26.09. 2016).
485 Toosi, A., R. L. Fernando, J. C. M. Dekkers, and R. L. Quaas. 2010. Genomic selection in
486 admixed and crossbred populations. J. Anim. Sci. 88(1):32-46. doi: 10.2527/jas.2009-
487 1975
488 Tusell, L., H. Gilbert, J. Riquet, M.-J. Mercat, A. Legarra, and C. Larzul. 2016. Pedigree and
489 genomic evaluation of pigs using a terminal-cross model. Genet. Sel. Evol. 48(1):1.
490 doi: 10.1186/s12711-016-0211-3
491 UiO. 2017. The Abel computer cluster.
492 http://www.uio.no/english/services/it/research/hpc/abel/more/index.html (Accessed
493 27.02 2017).
494 Van Grevenhof, I. E. M., and J. H. J. Van der Werf. 2015. Design of reference populations
495 for genomic selection in crossbreeding programs. Genet. Sel. Evol. 47(1):1-9. doi:
496 10.1186/s12711-015-0104-x
497 Wientjes, Y. C., R. F. Veerkamp, P. Bijma, H. Bovenhuis, C. Schrooten, and M. P. Calus.
498 2015. Empirical and deterministic accuracies of across population genomic
499 prediction. Genet. Sel. Evol. 47(5). doi: 10.1186/s12711-014-0086-0

Xiang, T., B. Nielsen, G. Su, A. Legarra, and O. F. Christensen. 2016. Application of single-step genomic evaluation for crossbred performance in pig. J. Anim. Sci. 94(3):936-948. doi: 10.2527/jas.2015-9930

Zhou, L., M. S. Lund, Y. Wang, and G. Su. 2014. Genomic predictions across Nordic Holstein and Nordic Red using the genomic best linear unbiased prediction model with different genomic relationship matrices. J. Anim. Breed. Genet. 131(4):249-257. doi: 10.1111/jbg.12089

511 ***Tables and Figures***

512 **Table 1.** Number of genotyped animals, individuals in pedigree and, phenotypic observations

Breeds	Nr. of genotyped animals	Nr. of animals in pedigree
Dutch Landrace (A)	3,238	6,620
Large White (B)	3,735	7,240
F1 crosses (X)	1,377	1,377
Total	**8,350**	**15,932**[1]

Traits	Nr. of observations	Nr. of phenotyped animals
Total number born (TNB)	67,063	11,491
Live born (LB)	66,958	11,491
Gestation length (GL)	61,015	10,768
Total		**11,491**

513 [1]Includes pseudoparents for animals with one missing parent.

514 **Table 2.** Number of animals with phenotypes per breed, and number of animals for each

515 breed with both genotype and phenotype information

Breed	Phenotypes[1]		Genotype and phenotype[2]
	TNB and LB	GL	
Dutch Landrace (A)	4,802	4,792	2,377
Large White (B)	5,377	5,217	2,859
F1 crosses (X)	1,312	759	1,312

516 [1]Phenotypes: TNB = total number born, LB = live born, GL = gestation length.

517 [2]Number of genotyped animals with at least one phenotype.

518 **Table 3.** Descriptive statistics

Traits[1]	Mean	SD	Minimum	Maximum	h^2
TNB	15.34	3.46	1	32	0.10
LB	14.02	3.23	1	28	0.07
GL, d	115.48	1.65	105	124	0.34

519 [1]TNB = Total number born, LB = Live born, GL = Gestation length in days.

520 **Table 4.** Accuracy estimates of the relationship matrices (mean accuracy between 2
521 validation sets of 1000 animals each per breed). Bold numbers indicate the largest accuracy
522 within each column

	Total number born		Live born		Gestation length	
Matrix[1]	Breed A[2]	Breed B[2]	Breed A	Breed B	Breed A	Breed B
PED	0.446	0.434	0.411	0.425	0.562	0.587
G_A	0.521	-	0.508	-	0.706	-
G_B	-	0.575	-	0.569	-	0.713
G_{AB}	0.567	0.593	0.552	0.593	0.712	0.716
G_{AX}	0.596	-	0.559	-	0.715	-
G_{BX}	-	0.615	-	0.619	-	0.750
G_{ABX}	0.632	0.626	0.599	0.633	0.726	0.755
G_{LDLA}	**0.637**	**0.640**	**0.608**	**0.647**	**0.743**	**0.760**

523 [1]PED = pedigree-based relationship matrix, G_A = genomic relationship matrix for breed A,
524 G_B = genomic relationship matrix for breed B, G_{AB} = genomic relationship matrix for breed A
525 and B combined, G_{AX} = genomic relationship matrix for breed A and crossbreds (X), G_{BX} =
526 genomic relationship matrix for breed B and crossbreds (X), G_{ABX} = genomic relationship
527 matrix for both purebreds and crossbreds combined, G_{LDLA} = genomic relationship matrix for
528 both purebreds and crossbreds utilizing linkage disequilibrium and linkage analysis.

529 [2]A = Dutch Landrace, B = Large White.

530

Table 5. Accuracies (mean accuracy between 2 validation sets of 1000 animals each per breed) of the different relationship matrices when using fixed and random effects from **PED** to create adjusted phenotype

	Total number born		Live born		Gestation length	
Matrix[1]	Breed A[2]	Breed B[2]	Breed A	Breed B	Breed A	Breed B
PED	0.446^{a,b}	0.434^{a}	0.411^{a}	0.425^{ab}	0.562^{a}	0.587^{a}
G_A	0.455^{a}	-	0.451^{a,b,c}	-	0.668^{b}	-
G_B	-	0.466^{a}	-	0.460^{a,b}	-	0.645^{b}
G_{AB}	0.480^{a,b}	0.472^{a}	0.473^{b,d}	0.460^{a}	0.656^{b}	0.639^{b}
G_{AX}	0.486^{b}	-	0.462^{a,b}	-	0.668^{b}	-
G_{BX}	-	0.482^{a,b}	-	0.474^{a,b}	-	0.672^{c,d}
G_{ABX}	0.511^{c}	0.488^{a}	0.489^{c,d}	0.479^{a}	0.663^{b}	0.671^{c}
G_{LDLA}	0.524^{d}	0.506^{b}	0.496^{d}	0.498^{b}	0.684^{c}	0.684^{d}

[1]PED = pedigree-based relationship matrix, G_A = genomic relationship matrix for breed A, G_B = genomic relationship matrix for breed B, G_{AB} = genomic relationship matrix for breed A and B combined, G_{AX} = genomic relationship matrix for breed A and crossbreds (X), G_{BX} = genomic relationship matrix for breed B and crossbreds (X), G_{ABX} = genomic relationship matrix for both purebreds and crossbreds combined, G_{LDLA} = genomic relationship matrix for both purebreds and crossbreds utilizing linkage disequilibrium and linkage analysis.

[2]A = Dutch Landrace, B = Large White.

[a-d]Accuracies within column with different superscript letters are significantly different ($P < 0.05$).

Table 6. Regression coefficients between estimated breeding values and adjusted phenotypes, across traits and breeds (i.e. mean across traits and breeds), for the different relationship matrices

Matrix[1]	Mean	Minimum	Maximum
PED	0.99	0.95	1.02
G_A[2]	1.00	0.97	1.02
G_B[2]	0.92	0.91	0.94
G_{AB}	0.98	0.91	1.05
G_{AX}[2]	1.00	1.00	1.01
G_{BX}[2]	0.96	0.93	0.99
G_{ABX}	0.99	0.92	1.05
G_{LDLA}	0.97	0.92	1.00

[1]PED = pedigree-based relationship matrix, G_A = genomic relationship matrix for breed A, G_B = genomic relationship matrix for breed B, G_{AB} = genomic relationship matrix for breed A and B combined, G_{AX} = genomic relationship matrix for breed A and crossbreds (X), G_{BX} = genomic relationship matrix for breed B and crossbreds (X), G_{ABX} = genomic relationship matrix for both purebreds and crossbreds combined, G_{LDLA} = genomic relationship matrix for both purebreds and crossbreds utilizing linkage disequilibrium and linkage analysis.

[2]Based on fewer validation sets due to validating in only one breed.

553 **Table 7.** Standard deviations of breeding values for the different relationship matrices (mean
554 over 2 validation sets of 1000 animals each per breed). Bold numbers indicate the largest
555 standard deviation within each column

	Total number born		Live born		Gestation length	
Matrix[1]	Breed A[2]	Breed B[2]	Breed A	Breed B	Breed A	Breed B
PED	0.454	0.406	0.333	0.321	0.472	0.448
G_A	0.524	-	0.390	-	0.561	-
G_B	-	0.607	-	0.480	-	0.611
G_{AB}	0.544	0.600	0.412	0.484	0.571	0.613
G_{AX}	0.582	-	0.434	-	0.566	-
G_{BX}	-	0.614	-	0.499	-	0.626
G_{ABX}	0.608	0.621	0.608	0.510	0.582	0.635
G_{LDLA}	**0.634**	**0.636**	**0.634**	**0.527**	**0.598**	**0.644**

556 [1]PED = pedigree-based relationship matrix, G_A = genomic relationship matrix for breed A,
557 G_B = genomic relationship matrix for breed B, G_{AB} = genomic relationship matrix for breed A
558 and B combined, G_{AX} = genomic relationship matrix for breed A and crossbreds (X), G_{BX} =
559 genomic relationship matrix for breed B and crossbreds (X), G_{ABX} = genomic relationship
560 matrix for both purebreds and crossbreds combined, G_{LDLA} = genomic relationship matrix for
561 both purebreds and crossbreds utilizing linkage disequilibrium and linkage analysis.

562 [2]A = Dutch Landrace, B = Large White.

563

564 **Table 8.** Off-diagonal relationship coefficients within and across breeds for G_{LDLA}

Relationship[1]	Mean	Minimum	Maximum	Median	Variance
Within A	0.183	-0.227	1.229	0.178	0.012
Within B	0.164	-0.062	0.977	0.155	0.004
Within X	0.019	-0.136	0.819	0.015	0.003
Between A-B	-0.155	-0.281	0.595	-0.156	0.001
Between A-X	0.014	-0.167	0.676	0.009	0.004
Between B-X	-0.002	-0.208	0.680	-0.003	0.001

565 [1]A = Dutch Landrace, B = Large White, X = F1 Crossbreds.

566

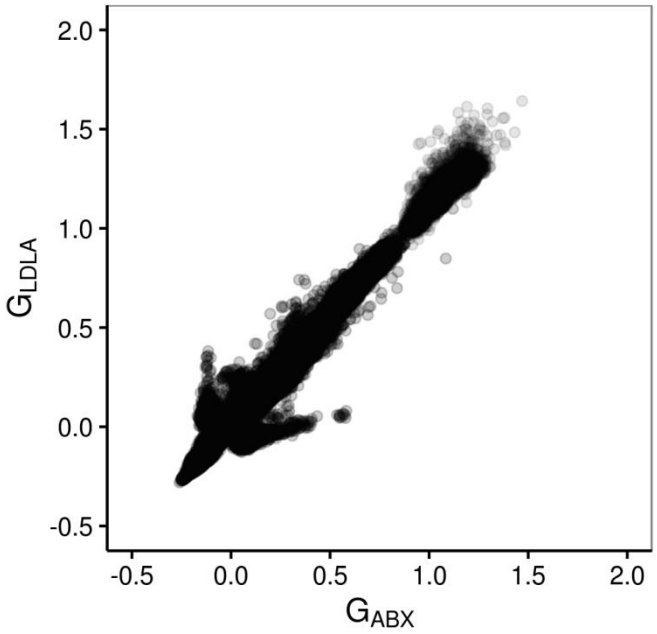
567 **Table 9.** Off-diagonal relationship coefficients within and across breeds for G_{ABX}

Relationship[1]	Mean	Minimum	Maximum	Median	Variance
Within A	0.162	-0.215	1.149	0.157	0.010
Within B	0.129	-0.210	0.833	0.123	0.003
Within X	0.010	-0.133	0.660	0.006	0.002
Between A-B	-0.144	-0.259	0.603	-0.146	0.001
Between A-X	0.009	-0.188	0.760	0.004	0.003
Between B-X	-0.012	-0.226	0.544	-0.014	0.001

568 [1]A = Dutch Landrace, B = Large White, X = F1 Crossbreds.

569

570 ***Figures***



571

572 **Figure 1.**

573 ***Figure captions***

574 **Figure 1.** Common matrix elements of $\mathbf{G}_{\mathbf{ABX}}$ and $\mathbf{G}_{\mathbf{LDLA}}$ plotted against each other. Matrix
575 $\mathbf{G}_{\mathbf{ABX}}$ is the genomic relationship matrix for both purebreds and crossbreds combined, and
576 matrix $\mathbf{G}_{\mathbf{LDLA}}$ is the genomic relationship matrix for both purebreds and crossbreds utilizing
577 linkage disequilibrium and linkage analysis.

578

579