

ANIMAL GENETICS AND GENOMICS

Investigating pig survival in different production phases using genomic models

Natália Galoro Leite,^{†,1} Egbert Frank Knol,[‡] André Luiz Seccatto Garcia,[†] Marcos Soares Lopes,^{||} Louisa Zak,[‡] Shogo Tsuruta,[†] Fabyano Fonseca e Silva,^{\$} and Daniela Lourenco[†]

[†]Department of Animal and Dairy Science, University of Georgia, Athens, GA 30602, USA, [‡]Topigs Norsvin Research Center, Beuningen, GE 6641 SZ, The Netherlands, ^{||}Topigs Norsvin, Curitiba, PR 80420-210, Brazil, ^{\$}Departamento de Zootecnia, Universidade Federal de Viçosa, Viçosa, MG 36570-900, Brazil

¹Corresponding author: nataliagaloro@uga.edu

ORCID numbers: 0000-0001-9327-426X (N. G. Leite); 0000-0001-9778-7978 (A. L. S. Garcia); 0000-0002-6897-6363 (S. Tsuruta); 0000-0001-9536-1113 (F. F. e. Silva).

Abstract

Pig survival is an economically important trait with relevant social welfare implications, thus standing out as an important selection criterion for the current pig farming system. We aimed to estimate (co)variance components for survival in different production phases in a crossbred pig population as well as to investigate the benefit of including genomic information through single-step genomic best linear unbiased prediction (ssGBLUP) on the prediction accuracy of survival traits compared with results from traditional BLUP. Individual survival records on, at most, 64,894 crossbred piglets were evaluated under two multi-trait threshold models. The first model included farrowing, lactation, and combined postweaning survival, whereas the second model included nursery and finishing survival. Direct and maternal breeding values were estimated using BLUP and ssGBLUP methods. Furthermore, prediction accuracy, bias, and dispersion were accessed using the linear regression validation method. Direct heritability estimates for survival in all studied phases were low (from 0.02 to 0.08). Survival in preweaning phases (farrowing and lactation) was controlled by the dam and piglet additive genetic effects, although the maternal side was more important. Postweaning phases (nursery, finishing, and the combination of both) showed the same or higher direct heritabilities compared with preweaning phases. The genetic correlations between survival traits within preweaning and postweaning phases were favorable and strong, but correlations between preweaning and postweaning phases were moderate. The prediction accuracy of survival traits was low, although it increased by including genomic information through ssGBLUP compared with the prediction accuracy from BLUP. Direct and maternal breeding values were similarly accurate with BLUP, but direct breeding values benefited more from genomic information. Overall, a slight increase in bias was observed when genomic information was included, whereas dispersion of breeding values was greatly reduced. Combined postweaning survival presented higher direct heritability than in the preweaning phases and the highest prediction accuracy among all evaluated production phases, therefore standing out as a candidate trait for improving survival. Survival is a complex trait with low heritability; however, important genetic gains can still be obtained, especially under a genomic prediction framework.

Key words: pig welfare, post-weaning mortality, prediction accuracy, pre-weaning mortality

Abbreviations

BLUP	best linear unbiased prediction
EBV	estimated breeding value
FAS	farrowing survival
FIS	finishing survival
GEBV	genomic estimated breeding value
LAS	lactation survival
LR	linear regression
MCMC	Markov chain Monte Carlo
NUS	nursery survival
POS	postweaning survival
ssGBLUP	single-Step genomic best linear unbiased prediction

Introduction

Pig survival can be understood as the success of animal adaptation to different challenges throughout the production system. About one-third of pigs do not survive or are culled by the end of the finishing phase (Arango et al., 2006; Dufresne et al., 2014); thus, highlighting the economic and social welfare relevance of piglet survivability for the current pig industry. The most challenging periods for pig survival are the first few days after birth and after weaning. Newborn piglets experience a drop of 15 to 20 °C in body temperature and an abrupt change from a continuous glucose supply from the placenta to an intermittent supply from colostrum (Herpin et al., 2002). After weaning, the rearrangement of litters and the new feed, management, and environment are big stressors that piglets may have to face (Campbell et al., 2013). The beginning of both phases requires fast physiological, environmental, and social adaptation which undoubtedly challenges pig survivability. Numerically, most deaths occur during the parturition expulsion period and right after birth, and, as a result, the risk factors and the potential genetic variation surrounding survival before weaning are more frequently studied (Knol et al., 2002a; Grandinson et al., 2005; Arango et al., 2006). Although the number of animals dying after weaning is not big as before weaning, the economic loss is much significant in this phase due to the larger rearing costs per animal lost, therefore encouraging further research for improving both preweaning survival and postweaning survival.

Survival is typically measured as a binary response (i.e., dead or alive), although it is commonly evaluated with linear models with the assumption of a continuous distribution (van Arendonk et al., 1996; Knol et al., 2002a; Grandinson et al., 2005), or evaluated at the litter level, excluding piglet individual information (i.e., piglets birth weight, sex, and genetic contribution; Lund et al., 2002; Guo et al., 2015; Aldridge et al., 2020). When survival is evaluated at the piglet level, the use of nonlinear models, such as threshold models, is statistically more suitable. Those models accommodate the natural distribution of such binary responses and allow for better capturing of the genetic variance (Gianola, 1982). Regardless of models and trait definitions, studies investigating the genetic basis of survival have indicated that there might be an opportunity to improve pig survivability through selection (Leenhouders et al., 2001; Knol et al., 2002a; Dufresne et al., 2014). Despite the low heritability, genetic improvement may be achieved in the long-term selection.

One way to further the genetic improvement, with primary benefits for lowly heritable traits, is including genomic information (García-Ruiz et al., 2016). Genomics can improve selection response by increasing the breeding values accuracy of young animals, which speeds up selection decisions,

consequently reducing the generation interval (Meuwissen et al., 2001). Genomic information from single nucleotide polymorphism (SNP) marker panels has been incorporated and successfully used for whole-genome prediction in pig breeding programs (Knol et al., 2016). Such information can be incorporated into genetic evaluations through the single-step genomic best linear unbiased prediction (ssGBLUP) method (Legarra et al., 2009; Aguilar et al., 2010; Christensen and Lund, 2010), which simultaneously uses information from phenotypes, pedigree, and genotypes in a single run, simplifying routine evaluations and allowing the implementation of complex models, such as threshold models.

In the present study, we used threshold models to estimate (co)variance components for crossbred pig survival in different production phases. We also investigated the benefits of including genomic information through ssGBLUP on the prediction accuracy, bias, and dispersion of direct and maternal survival breeding values compared with their counterpart obtained through traditional BLUP.

Materials and Methods

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

Data

The dataset used for this study was obtained as part of the routine data collection in a research farm in the Netherlands. The studied population resulted from a three-way crossbreeding scheme based on a synthetic sire line (Large White-based) and two crossbred F1 dam populations (Dutch Landrace or Norwegian Landrace × Large White). Survival records were available for, at most, 64,894 piglets born from a total of 4,236 litters, between August 2012 and September 2019, out of 1,249 dams and 589 sires. Pedigree information was available for 70,507 animals, out of which 10,022 were genotyped for 50,689 SNP (Geneseek custom 50K SNP chip, Lincoln, NE, USA). Information on litter size, birth weight, sex, and dam parity order was available for each animal. For cross-fostered piglets, which represented 21.1% of the studied population, nurse litter and parity order of nurse dam were also recorded. A summary of the data is presented in Table 1.

Pig survival was defined as a binary trait (1 = dead and 2 = alive) and was recorded in four different production phases. Farrowing survival (FAS) was recorded within 12 h of farrowing and was defined as the complement of stillborn (i.e., non-mummified dead piglets, found close to the dam's vagina and covered by

Table 1. Population means and standard deviations

Information	Number	Mean ^(SD)
Birth weight, kg	64,894	1.31 ^(0.35)
Weaning weight, kg	48,823	7.25 ^(1.62)
Litter size	4,236	15.33 ^(3.75)
Parity order of biological dam	4,236	3.66 ^(2.28)
Parity order of nurse dam	5,114	3.70 ^(2.28)
Sex, % males	64,894	50.84 ^(49.99)
Farrowing survival, %	64,894	93.57 ^(24.53)
Lactation survival, %	60,068	88.63 ^(31.75)
Nursery survival, %	48,823	97.72 ^(14.93)
Finishing survival, %	35,862	98.42 ^(12.46)
Postweaning survival, %	36,975	95.46 ^(20.82)

placental membranes). Lactation survival (LAS) was defined as the survivability of liveborn piglets from 12 h of life to weaning; nursery survival (NUS) was defined as the survival of piglets from weaning to the transferring day to the finishing barns, and finally, finishing survival (FIS) was defined as the survivability of pigs from the end of the nursery phase to the transferring day to the slaughterhouse. Further, we defined combined postweaning survival (POS), which merged NUS and FIS, representing the total pig survival from weaning to the end of the finishing phase. Animals with score 1 (dead) for NUS or FIS were coded as 1 for POS, the ones scored as 2 (alive) for both NUS and FIS were scored as 2 for POS, and animals following a different rule (i.e., with missing information for NUS or FIS) had their phenotype for POS set to missing.

Data editing and quality control

Animals that died or were removed from the farm before slaughter had their survival information on subsequent phases set to missing since such animals did not have the chance to further express their phenotype. Contemporary groups were formed by year and month of birth. Observations from parity greater than seven or litter size less than 6 or more than 22 were grouped to avoid classes with a low incidence of records. The phenotypes of animals with birth or weaning weight out of a range of 4 standard deviations greater or smaller than the population mean were classified as outliers and removed from the dataset.

Quality control of the genomic data was performed using PREGSF90 (Misztal et al., 2014). The chromosomal positions were determined based on the Sscrofa11.1 genome reference assembly (Warr et al., 2020) and only SNPs located on autosomal chromosomes were kept. Markers with call rate <0.95 or minor allele frequency <0.05 were excluded. No genotyped animals were excluded due to the low call rate. Imputation of missing genotypes after quality control was performed using FImpute (Sargolzaei et al., 2014), which considers pedigree and genomic data to increase imputation accuracy. Imputation of missing genotypes of the purebred population was performed within the population, whereas crossbred genotypes were imputed using both crossbred and purebred data to increase the reference population. After imputation, the consistency of genotypes between parents and offspring was checked with SEEKPARENTF90 (Misztal et al., 2014), and the pedigree and genotypes of parent-progeny pairs with more than 1% mismatching SNP were removed. After quality control and imputation steps, 9,916 animals genotyped for 45,116 SNPs were available for analysis.

Statistical models

Two Bayesian threshold models were used for the estimation of variance components without the inclusion of genomic information. Systematic effects were previously evaluated by a generalized linear model using a probit regression implemented in the R software (R Development Core Team, 2020), and the significant effects ($P < 0.05$) were kept in the models. Model 1 was a three-trait model, including FAS (equation 1), LAS (equation 2), and POS (equation 3), with respective liability vectors given by \mathbf{l}_{t1} , \mathbf{l}_{t2} , and \mathbf{l}_{t3} , whereas model 2 was a two-trait model combining NUS (equation 4) and FIS (equation 5), with liabilities represented by \mathbf{l}_{t4} and \mathbf{l}_{t5} , respectively. A first attempt to construct a model combining both preweaning (FAS and LAS) and postweaning phases (NUS and FIS) into a four-trait model did not reach convergence, likely because of the instability of

traits with low incidence (i.e., NUS and FIS). Therefore, NUS and FIS were combined into POS in model 1, and NUS and FIS were evaluated separately in model 2. The description of both models follows below:

Model 1:

$$\mathbf{l}_{t1} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_a + \mathbf{Z}_2\mathbf{u}_m + \mathbf{Z}_3\mathbf{u}_{ys} + \mathbf{Z}_4\mathbf{u}_{li} + \mathbf{e}, \quad (1)$$

$$\mathbf{l}_{t2} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_a + \mathbf{Z}_2\mathbf{u}_m + \mathbf{Z}_3\mathbf{u}_{ys} + \mathbf{Z}_4\mathbf{u}_{li} + \mathbf{e}, \quad (2)$$

$$\mathbf{l}_{t3} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_a + \mathbf{Z}_3\mathbf{u}_{ys} + \mathbf{Z}_4\mathbf{u}_{li} + \mathbf{e}. \quad (3)$$

Model 2:

$$\mathbf{l}_{t4} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_a + \mathbf{Z}_3\mathbf{u}_{ys} + \mathbf{Z}_4\mathbf{u}_{li} + \mathbf{e}, \quad (4)$$

$$\mathbf{l}_{t5} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_a + \mathbf{Z}_3\mathbf{u}_{ys} + \mathbf{Z}_4\mathbf{u}_{li} + \mathbf{e}, \quad (5)$$

where: \mathbf{l}_{t1} , \mathbf{l}_{t2} , \mathbf{l}_{t3} , \mathbf{l}_{t4} , and \mathbf{l}_{t5} are the vector of survival records in the liability scale for FAS, LAS, POS, NUS, and FIS, respectively; β is the vector of systematic effects of overall mean (equations 1–5), birth (equations 1 and 2) and weaning weight (equations 3–5) as linear covariables, parity order of the biological (equations 1 and 2) and nurse dam (equation 2), litter size (equations 1 and 2), and sex (equations 1–5); \mathbf{u}_a , \mathbf{u}_m , \mathbf{u}_{ys} , and \mathbf{u}_{li} are the vectors of random effects of additive direct, additive maternal, contemporary group, and biological/nurse common litter environment, respectively; \mathbf{e} is the vector of random residuals; \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , \mathbf{Z}_3 , and \mathbf{Z}_4 , and are incidence matrices for the effects contained in β , \mathbf{u}_a , \mathbf{u}_m , \mathbf{u}_{ys} , and \mathbf{u}_{li} , respectively. Due to confounding between line and contemporary groups, only the contemporary group effect, which takes into account the crossbred lines, was kept in the models.

Cross-fostering is a common practice to increase homogeneity and to improve the survival of litters. In this process, piglets might be transferred from the biological dam to a nurse dam within the first days of age. This is important for the modeling of the common litter environmental effect, as cross-fostered piglets experience a different common environment than their non-cross-fostered siblings. In our study, except for the modeling of FAS, the effect of the common litter environment took into account the nurse litter rather than the biological litter of piglets.

A general description of the models (assuming only two random effects common to equations 1 and 2) is given by:

$$\begin{bmatrix} \mathbf{l}_{t1} \\ \mathbf{l}_{t2} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{t1} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_{t2} \end{bmatrix} \begin{bmatrix} \beta_{t1} \\ \beta_{t2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{1t1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{1t2} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{at1} \\ \mathbf{u}_{at2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{2t1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{2t2} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{mt1} \\ \mathbf{u}_{mt2} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{t1} \\ \mathbf{e}_{t2} \end{bmatrix},$$

where: \mathbf{l}_{t1} and \mathbf{l}_{t2} are the liability vectors for the two traits (t_1 and t_2), being the other terms of the model a simple generalization of the effects presented in equations 1–5. Additionally, we defined:

$$\mathbf{l} = \begin{bmatrix} \mathbf{l}_{t1} \\ \mathbf{l}_{t2} \end{bmatrix}, \beta = \begin{bmatrix} \beta_{t1} \\ \beta_{t2} \end{bmatrix}, \mathbf{u}_a = \begin{bmatrix} \mathbf{u}_{at1} \\ \mathbf{u}_{at2} \end{bmatrix}, \mathbf{u}_m = \begin{bmatrix} \mathbf{u}_{mt1} \\ \mathbf{u}_{mt2} \end{bmatrix}, \mathbf{u} = \begin{bmatrix} \mathbf{u}_a \\ \mathbf{u}_m \end{bmatrix}, \text{ and } \mathbf{e} = \begin{bmatrix} \mathbf{e}_{t1} \\ \mathbf{e}_{t2} \end{bmatrix}.$$

The general data distribution based on the liability scale was assumed as $\mathbf{1}|\mathbf{y}, \tau, \text{else} \sim N(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u}, \mathbf{I} \otimes \boldsymbol{\Sigma}_e)$, where $\boldsymbol{\Sigma}_e$ is the residual covariance matrix. The prior distribution for $\boldsymbol{\beta}$ was assumed to follow a uniform distribution (i.e., non-informative prior) and $\mathbf{u}|\boldsymbol{\Sigma}_u \sim N(\mathbf{0}, \mathbf{A} \otimes \boldsymbol{\Sigma}_u)$ in BLUP, and $\mathbf{u}|\boldsymbol{\Sigma}_u \sim N(\mathbf{0}, \mathbf{H} \otimes \boldsymbol{\Sigma}_u)$ in ssGBLUP, where $\boldsymbol{\Sigma}_u$ is the additive genetic covariance matrix (assuming direct and maternal effects), \mathbf{A} is the pedigree relationship matrix, and \mathbf{H} is a matrix combining pedigree and genomic relationships to simultaneously accommodate genotyped and non-genotyped animals. The Wishart distribution was adopted as prior for the covariance matrices $\boldsymbol{\Sigma}_u$ and $\boldsymbol{\Sigma}_e$. For simplicity, additive and maternal covariances across traits and additive-maternal covariances within traits were estimated, but all the other effects were assumed to be uncorrelated. The inverse of the \mathbf{H} matrix (\mathbf{H}^{-1}) was defined as in (Aguilar et al., 2010):

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

where \mathbf{A}^{-1} is the inverse of the pedigree relationship matrix, \mathbf{A}_{22}^{-1} is the inverse of the pedigree relationship matrix for genotyped animals, accounting for pedigree-based inbreeding, and \mathbf{G}^{-1} is the inverse of the type 1 genomic relationship matrix (\mathbf{G}) as in VanRaden (2008):

$$\mathbf{G} = \frac{\mathbf{M}\mathbf{M}'}{2\sum p_j(1-p_j)},$$

where \mathbf{M} is a matrix of SNP and p_j is twice the across-breed allele frequency of the j th locus computed from the current genotyped population. To avoid singularity problems, \mathbf{G} was blended with 5% of \mathbf{A}_{22} .

Statistical analyses

Variance components based on pedigree and phenotypes were estimated using THRGIBBS1F90b, a program from the BLUPF90 suite programs that allow the use of threshold models for binary responses (Misztal et al., 2014). According to Aldridge et al. (2020), the inclusion of genomic information for variance components estimation should increase the computational time; however, it might not result in substantial changes compared with estimates from non-genomic models. Moreover, Cesarani et al. (2019) showed that in the presence of selective genotyping (i.e., when only survivors are genotyped), genomic variance components are expected to be biased.

For both models, 250,000 Markov chain Monte Carlo (MCMC) samples were generated, with a burn-in of 50,000 and thinning interval of 10. Convergence was checked by several criteria such as graphical inspection of both samples and posterior distribution of the parameters, the effective number of samples available after burn-in, and the Geweke criterion (Geweke, 1992).

All of these are implemented on the software POSTGIBBSF90 from the BLUPF90 family of programs (Misztal et al., 2014). Further, posterior means of the variance components were obtained based on the final 20,000 and were employed to generate breeding values through BLUP and ssGBLUP using THRGIBBS1F90b (Misztal et al., 2014) based on 10,000 MCMC samples.

Validation of traditional and genomic predictions

Validation of the direct effect was performed on purebred sires, whereas the validation of the maternal effect was performed on F1 dams (two-way crossbred). The validation set was composed of genotyped animals with progeny born in 2019 that had their progeny phenotypes removed from the data. The distribution of genotypes and progeny records is presented in Table 2. The linear regression (LR) method (Legarra and Reverter, 2018) was used to validate breeding values from BLUP and ssGBLUP. In this method, once a set of validation or focal animals is defined, several statistics can be computed to compare evaluations with the partial data (progeny phenotypes of the validation animals not included) and with the whole data (progeny phenotypes of the validation animals included). The LR prediction accuracy is given by:

$$\rho_{\text{cov}_{w,p}} = \sqrt{\frac{\text{cov}((\mathbf{G})\text{EBV}_p, (\mathbf{G})\text{EBV}_w)}{(1-F)\sigma_u^2}},$$

where $(\mathbf{G})\text{EBV}_w$ and $(\mathbf{G})\text{EBV}_p$ are the vectors of estimated breeding value (G)EBV calculated with the whole and partial data, respectively, F is the average inbreeding coefficient of validation animals, and σ_u^2 the additive genetic variance of the trait. The LR bias is calculated as:

$$\hat{\Delta}_p = \bar{\hat{u}}_p - \bar{\hat{u}}_w,$$

where $\bar{\hat{u}}_p$ is the average of the predicted (G)EBV with the partial data and $\bar{\hat{u}}_w$ with the whole data, and finally, the LR dispersion is estimated from the regression of \hat{u}_w on \hat{u}_p as follows:

$$\hat{b}_p = \frac{\text{cov}(\hat{u}_w, \hat{u}_p)}{\text{var}(\hat{u}_p)},$$

with parameters defined as above.

Results and Discussion

Descriptive statistics

The total mortality from farrowing to finishing summed up to 26.4% in the evaluated population. The preweaning phase, which included FAS and LAS, had a mortality rate (% mortality)

Table 2. Number of validation sires/dams and number of progeny phenotypes removed from the partial data

Information/effect ¹	Direct					Maternal	
	FAS	LAS	NUS	FIS	POS	FAS	LAS
Item/trait ²							
N	75	75	62	45	60	33	33
Mean ^(SD)	101.3 ^(59.6)	86.3 ^(62.5)	37.4 ^(42.2)	35.1 ^(35.6)	28.0 ^(34.0)	20.8 ^(7.2)	18.1 ^(7.4)

¹Direct effect (validated on purebred sires); maternal effect (validated on F1 dams).

²N, number of validation animals; Mean, mean progeny phenotypes; FAS, farrowing survival; LAS, lactation survival; NUS, nursery survival; FIS, finishing survival; POS, postweaning survival.

3.8 times higher than after weaning. Among the preweaning phases, lactation was the most challenging, accounting for 62.1% of the total mortality. The distribution of piglet mortality by age for preweaning and postweaning is shown in Figure 1. Around 85.2% of the preweaning mortality occurred in the first 3 d of the piglet's life and was later identified as stillborn (37.9%), crushed/bitten by the dam (28.6%), weak/light piglet (13.0%), and others (20.5%). Postweaning mortality was more distributed across age, although almost half (49.7%) of the animals died within the first 30 d after weaning.

Birth weight was the most important explanatory variable for the survivability of piglets in the preweaning phases ($P < 0.001$; Figure 2A). Survivor piglets were, on average, 20.4% and 27.1% heavier than those that died during farrowing and lactation, respectively. From the farrowing moment up to the first few hours of life, birth weight plays an important role in the newborn's thermoregulation, and lighter piglets might be more prone to hypothermia (Herpin et al., 2002). After farrowing, besides thermoregulation, birth weight may also be relevant for litter hierarchy establishment and colostrum uptake (Leenhouwers et al., 2001; Rootwelt et al., 2013).

There was a negative and linear effect of parity of biological dams over survivability from the second to the seventh or later parities, while a slightly deviant behavior was observed for primiparous dams (Figure 2B). The negative effect of first parity might be associated with a reduced piglet birth weight due to the ongoing body development of dams (Solanes and Stern, 2001; Bunter et al., 2010). As shown in Figure 2C, first parity dams produced the lightest piglets ($P < 0.01$) in the studied population.

Litter size had a negative effect on FAS and LAS, with a regression coefficient of -0.4% and -0.7% on survivability per piglet born, respectively. This may be because larger litters prolong the farrowing process and have a negative effect on piglet birth weight (Rutherford et al., 2013). For instance, in the studied population, for each piglet born, there was a 31-g reduction in the average birth weight of the litter.

Weaning weight was the most important factor for POS ($P < 0.001$). Piglets weaned with at least 4 kg were, on average, 9.6% more likely to survive up to the end of the finishing stage. As pointed out by Melotti et al. (2011), during hierarchy establishment, heavier piglets have an advantage over lighter ones, giving them more access to feed and less chance of getting injured by others.

Variance components and genetic parameters

Posterior means of variance components and heritabilities are presented in Table 3. Direct and maternal heritabilities for

survival in all phases and both models ranged from 0.02 to 0.09, indicating that genetic variability for pig survival exists in all phases of the production system.

Farrowing survival

The direct heritability of FAS was 0.02, whereas its maternal counterpart was higher, at 0.09 (Table 3). This indicates that both piglet and dam have an additive genetic contribution to piglet survival during farrowing, although the maternal contribution is more relevant. For piglets, the direct effect of FAS might be associated with the piglet's vitality and ability to maintain the homeothermic balance right after birth (Leenhouwers et al., 2001; Herpin et al., 2002), whereas the dams may have a bigger contribution through the quality of uterus and farrowing process.

Arango et al. (2006) and Ibáñez-Escriche et al. (2009), using a similar approach to our current study, found similar results with statistically significant direct (from 0.02 to 0.05) and maternal heritabilities (from 0.10 to 0.13) for stillborn (complement of FAS). Roehe et al. (2009) also looked at FAS using a threshold animal model excluding the dam genetic contribution and found direct heritabilities ranging from 0.08 to 0.10. The heritability estimates in the literature for FAS might vary depending on the model assumptions and trait definition. For instance, using linear models, Knol et al. (2002a)—in their model 4 (including direct and maternal effects)—and Grandinson et al. (2005) found a nonstatistical significant genetic contribution of piglets and smaller maternal heritability (0.02 to 0.05), whereas Lund et al. (2002) found a statistical significant contribution of piglets with a heritability ranging from 0.01 to 0.05 and a constant maternal heritability at 0.06.

The common litter environment explained the highest proportion of the total phenotypic variance for FAS (14%) (Table 3), suggesting that important early life experiences related to the dam (i.e., dam immunization) may influence the survival of the piglets, but those are independent of the genetic component. Differently, the variance due to the contemporary groups was very low (1%) (Table 3), indicating a small difference between the two crossbred lines or between the environment experienced by late gestating dams and their newborn litters. This difference, however, might increase when more than one farm is evaluated or when dams and piglets are subjected to commercial conditions.

Lactation survival

The direct heritability of LAS was higher (0.05) than for FAS, whereas the maternal contribution had the same magnitude for both traits (0.08 and 0.09; Table 3). Arango et al. (2006)

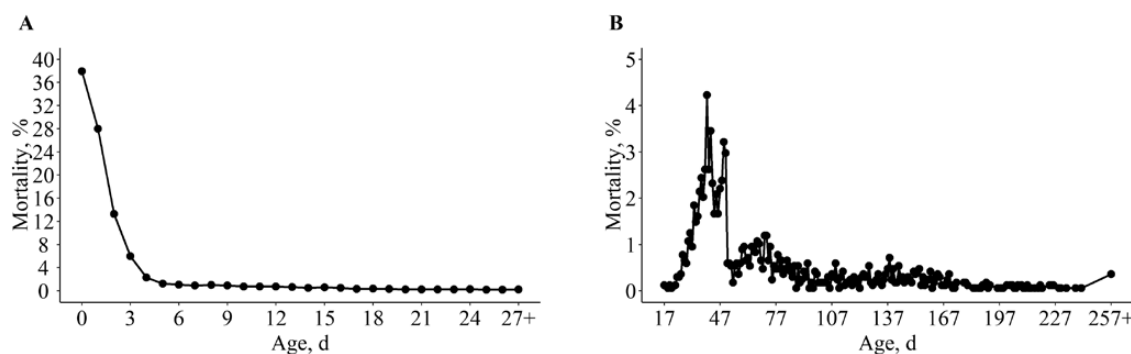


Figure 1. Mortality by piglet age during preweaning (A) and postweaning (B) phases. Dots in (A) and (B) represent the percentage of the total mortality (y-axis) in preweaning and postweaning phases given the age of the pig (x-axis), respectively.

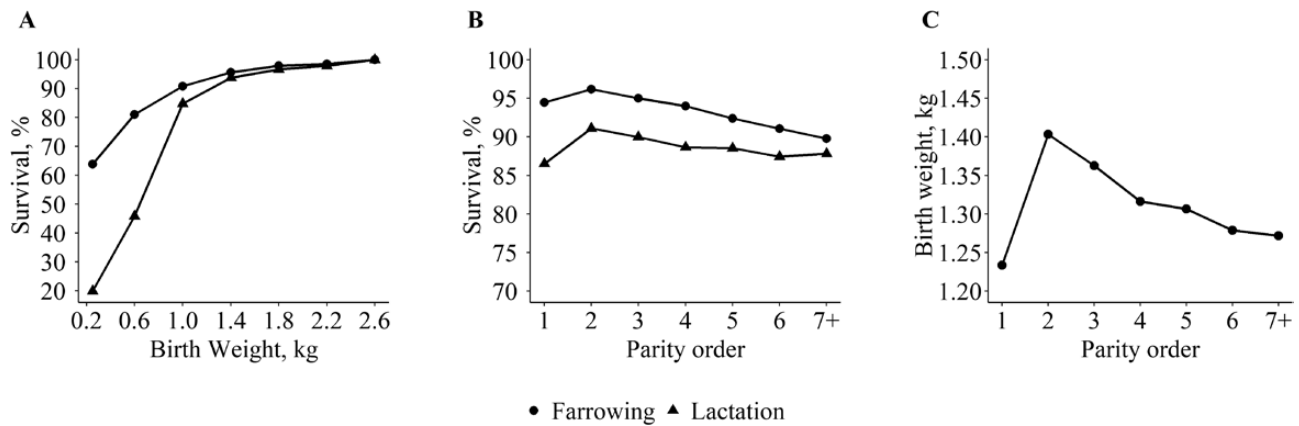


Figure 2. Average survival by birth weight (A) and by parity order of biological dam (B) during farrowing and lactation, and average birth weight by parity order of biological dam (C). Dots represent, in (A), the total survivability of piglets through farrowing and lactation (y-axis) given their birth weight (x-axis); in (B), the survivability of piglets through farrowing and lactation (y-axis) given the parity order of the biological dam (x-axis); and in (C), the birth weight of piglets (y-axis) given the parity order of the biological dam (x-axis).

Table 3. Estimates of heritabilities and proportions of the phenotypic variance explained by common environmental effects for survival traits in models 1 and 2

Model	Parameter ^t	h^2_a		h^2_m		prop(li)		prop(ys)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	FAS	0.02	0.01	0.09	0.01	0.14	0.01	0.01	0.00
	LAS	0.05	0.01	0.08	0.01	0.10	0.01	0.07	0.02
	POS	0.06	0.01	—	—	0.12	0.01	0.30	0.04
2	NUS	0.08	0.02	—	—	0.16	0.02	0.19	0.03
	FIS	0.04	0.02	—	—	0.09	0.02	0.05	0.02

^t h^2_a , direct heritability; h^2_m , maternal heritability; prop(li), proportion of the total phenotypic variance explained by common litter environment; prop(ys), proportion of the total phenotypic variance explained by the contemporary group; FAS, farrowing survival; LAS, lactation survival; NUS, nursery survival; FIS, finishing survival; POS, postweaning survival.

found the same direct (0.05) and maternal (0.08) heritabilities for lactation mortality using a multiple-trait threshold model with stillborn and birth weight. Studies using linear models have also found low direct and maternal heritabilities ranging from nearly zero to 0.04 and from 0.02 to 0.08, respectively (Knol et al., 2002a; Lund et al., 2002; Grandinson et al., 2005). The increase in the additive genetic variance of LAS compared with FAS indicates that the importance of piglets' genes increases as they age, whereas maternal contribution is kept constant. During lactation, piglet survival depends on a larger number of factors, such as disease resistance, hierarchical establishment, milk intake, thermoregulation, and growth rate (Nowak et al., 2000; Herpin et al., 2002). Such a variety of factors require piglets to express their genetic merit for survival over a larger variety of environmental stressors in comparison to the moment of birth.

The phenotypic variation of LAS explained by the common litter environment was 10% (Table 3), which might be related to infectious diseases, nurse litter size, and maternal ability of nurse dams. The genetic effect of nurse dams can also be considered for LAS (Knol et al., 2002a); however, in our study, the effect of nurse dams for cross-fostered piglets was assumed to be fully environmental.

Differences in contemporary groups explained 7% of the total phenotypic variance for LAS (Table 3). Compared with the moment of birth, when contemporary group differences were shown to be less influential (1% of phenotypic variation), the

sucking period is when piglets are more exposed to differences in temperature, management, and herd pathogens, which might explain the increase in contemporary group variation. When exposed to such factors, a possible higher genetic differentiation between the two crossbred lines could also be observed.

Nursery, finishing, and postweaning survival

The postweaning phase can be divided into two separate phases: nursery and finishing. In our study, we evaluated survival in these phases combined (POS) in model 1 and separately in model 2. The heritability of NUS and FIS was 0.08 and 0.04, respectively. When both traits were combined into POS, the heritability assumed an intermediate value of 0.06 (Table 3). While many studies investigated the genetic variability for survival in preweaning phases, to our knowledge, only one study exploited the genetics of survival for the nursery and finishing phases (Dufresne et al., 2014), and no studies have evaluated the overall survivability from weaning to the end of the finishing phase. Dufresne et al. (2014) evaluated a crossbred population using sire threshold models and found a direct heritability of 0.14 for culling during the nursery phase and 0.10 for culling during the finishing phase. When going from the nursery to the finishing phase, the authors observed a similar slight decrease in heritability as observed herein; however, our heritability estimates had a lower magnitude.

The common litter environment represented 16% and 9% of the total phenotypic variance of NUS and FIS, respectively.

When both traits were combined into POS, the common litter environment explained 12% of the phenotypic variation (Table 3). Postweaning mortality is known as a complex trait that involves multiple contributing factors as the animal itself, the environment, and potential infectious diseases (see Gebhardt et al. (2020) for a review). According to the USDA (2012), respiratory diseases are responsible for 47.3% and 75.1% of mortality in the nursery and finishing phases, respectively. Therefore, the high variation that is explained by the common litter environmental effect in these phases might be likely associated with differences in antibodies and metabolites that are transferred through colostrum/milk from the dams to their litters, particularly in the earlier phase (i.e., NUS) (Madec et al., 2008; Opriessnig et al., 2010; Picone et al., 2018). Moreover, different pathogen exposure during lactation may also contribute to an increase in common litter environmental variance after weaning.

The contemporary group explained the highest proportion of the phenotypic variance of NUS (19%) and POS (30%), while only 6% of FIS (Table 3). A proper contemporary group definition is important because it accounts for factors as penstock density, stocking period, pathogen load, and social interaction among individuals, which might directly affect pig survivability. Moreover, in our models, contemporary groups should also account for crossbred line variation, which is expected to get bigger as piglets become independent of their dams after weaning.

Genetic correlations

Covariance components and genetic correlations for both models are presented in Table 4. The direct genetic correlation for all studied survival combinations was positive and ranged from 0.36 to 0.90, suggesting no antagonist behavior of survival traits in different production phases.

Farrowing and lactation survival

The direct genetic correlation between the FAS and LAS was strong (0.90) (Table 4), indicating that the genes responsible for increasing farrowing survivability are also associated with survival during lactation. The positive sign of our estimate was in agreement with the results from multi-trait threshold models reported by Arango et al. (2006) (0.45) and by Roehe et al. (2009) (0.24 to 0.53), even though our estimate had a higher magnitude. FAS and LAS are commonly evaluated at the litter level, thus ignoring the piglet's contribution. For such models, the genetic correlation between farrowing and lactation was shown to be around 0.81, as summarized in a literature review by Rothschild and Bidanel (1998).

Mortality during lactation is mostly caused by chilling, starvation, and crushing, which are underlying factors of piglet's poor vitality and thermoregulation just after birth (Herpin et al.,

2002; Edwards and Baxter, 2015). Therefore, a strong genetic correlation between those two phases seems to agree with this biological relationship. However, the strong genetic correlation found in our study could be also due to a level of confounding between FAS and LAS; some piglets might be born alive but be scored as stillborn (i.e., liveborn piglets crushed just after vaginal expulsion). This confounding was confirmed by Leenhouders et al. (2003) who performed postmortem examination in piglets classified as stillborn and observed that 16.4% of them in fact died after farrowing. Although clinical differentiation between FAS and LAS is possible, it remains a challenge in practical applications.

The direct-maternal correlations for FAS (0.02) and LAS (−0.04) were weak and not statistically different from zero (i.e., highest posterior density interval at 95% included 0), indicating that the selection for the direct effect of survival may not affect the dam's maternal ability. Therefore, selection for both direct and maternal effects might be performed to increase the overall piglet survival. Results from the literature are very diverse; whereas some studies found nonsignificant or positive correlations (Knol et al., 2002a; Lund et al., 2002; Grandinson et al., 2005), others have found moderate negative correlations between FAS and LAS (Lund et al., 2002; Arango et al., 2006). This is likely due to trait definitions, model fitting, and the complexity of estimating (co)variance components for survival traits.

The maternal correlation between FAS and LAS was 0.19. Although positive, it was not significantly different from zero, meaning that a correlated selection response for the maternal ability in these two phases is not likely to occur in this population. Arango et al. (2006) found a moderate (0.43) maternal correlation, and the significance of their estimate suggests that a positive correlated response might be achieved in the long-term selection.

According to our study, the selection for the direct effect of survival in one of the preweaning phases could improve the other through correlated response to selection. However, if the selection is only based on direct effect, the increase in the genetic ability of piglets to survive will be likely mitigated phenotypically by the difficulty of dams in taking care of the litter or be associated with a higher cost of intervention during farrowing or lactation (i.e., high level of cross-fostering).

Farrowing, lactation, and postweaning survival

The genetic correlation between FAS and POS was 0.69, whereas it was reduced to 0.36 between LAS and POS (Table 4). These positive estimates suggest that selection for piglet survival could have a positive effect on pig survivability from weaning up to the finishing phase. Interestingly, a positive, stronger genetic correlation between LAS and POS would be expected because they are more related in time compared with FAS and POS. However, Dufresne et al. (2014) showed that a negative correlation between preweaning mortality (i.e., excluding culled animals) and culling during the nursery phase might exist. In our study, POS was defined as the combination of NUS and FIS; therefore, a potential negative correlation between LAS and NUS might have reduced the correlation between LAS and POS. Such a topic deserves further investigation.

Nursery and finishing survival

The direct genetic correlation between NUS and FIS was strong and positive (0.83; Table 4). This result indicates that genes affecting survivability during nursery may also be associated with FIS. Moreover, such a strong positive correlation suggests that a combination of both traits into POS in model 1 is

Table 4. Estimates of genetic correlation for survival traits in models 1 and 2

Model	Parameter ¹	$\sigma_{a1,a2}$		$r_{a,a}$	
		Mean	SD	Mean	SD
1	FAS–LAS	0.04	0.01	0.90	0.05
	FAS–POS	0.04	0.01	0.69	0.10
	LAS–POS	0.03	0.01	0.36	0.16
2	NUS–FIS	0.07	0.02	0.83	0.12

¹ $\sigma_{a,a}$, direct genetic covariance; $r_{a,a}$, direct genetic correlation; FAS, farrowing survival; LAS, lactation survival; NUS, nursery survival; FIS, finishing survival; POS, postweaning survival.

reasonably supported. [Dufresne et al. \(2014\)](#) found a correlation of 0.59 between culling during nursery and finishing phases (0.59) using a sire threshold model. The close relationship between NUS and FIS is reasonable since the main factors affecting the survivability in both phases are similar. According to the [USDA \(2012\)](#), 56.7% and 78.7% of the nursery and finishing mortality can be similarly attributed to respiratory diseases or scours, respectively.

Validation of traditional and genomic predictions

The main objective of pig breeding programs is to predict crossbred future performance. With genomic selection, cross-validation became popular in animal breeding, and prediction accuracy has been commonly used to evaluate models for genetic evaluations. Prediction accuracy or predictability is typically defined as the correlation between (G)EBV from a reduced data (i.e., when phenotypes of validation animals are not included in the model), and phenotypes adjusted by fixed effects estimated from complete data. Although adjusted phenotypes serve as a convenient benchmark for most traits, it relies on factors, for instance, precise estimation of fixed effects, the heritability of the trait, and accuracy of EBV ([Legarra and Reverter, 2017](#)). Further, obtaining adjusted phenotypes may be challenging for categorical traits, because, in such a case, the fixed effects and the observed phenotypes are from different distributions, sometimes leading to nonsensical predictability results ([Silva et al., 2019](#)).

To avoid such limiting factors, [Legarra and Reverter \(2018\)](#) proposed the LR method as an alternative method of validation. Such a method can be applied to many types of models and traits, including categorical and low heritability traits, and models with maternal effects ([Legarra and Reverter, 2018](#)). The ability to validate maternal effects is one of the main advantages of using the LR validation method. As pointed out by [Lourenco et al. \(2015\)](#), calculating predictability for maternal effects based on adjusted phenotypes is difficult because the expression of such effects has a lag of one generation, being hard to access.

Results for the LR prediction accuracy, bias, and dispersion of breeding values based on the LR validation method are presented in [Table 5](#). Overall, compared with BLUP, the ssGBLUP evaluation increased prediction accuracy, slightly increased bias, and reduced the dispersion of breeding values. The prediction accuracy of the direct effect in different production phases ranged from 0.19 to 0.30 with BLUP, and from 0.28 to 0.36 with ssGBLUP, whereas the accuracy of the maternal effect ranged from 0.22 to 0.24 with BLUP and from 0.27 to 0.30 with ssGLUP ([Table 5](#)).

The direct effect of NUS and FIS was overall more accurate than for FAS and LAS in BLUP (0.26 and 0.24 vs. 0.19 and 0.24, respectively); however, with the inclusion of genomic information, the preweaning phases benefited more and

became overall more accurate (0.28 and 0.32 vs. 0.24 and 0.35, respectively). Such an increase represented a relative gain that ranged from 31.8% to 43.5% for FAS and LAS and from 15.7% to 17.7% for NUS and FIS. The higher accuracy for the direct effect among all traits was observed when NUS and FIS were combined into POS, either with BLUP (0.30) or with ssGBLUP (0.36). The accuracy for POS might have been increased because of the correlation structure with preweaning phases in model 1 and the better stability of the model (i.e., overall lower SD) when compared with NUS and FIS evaluated separately in model 2.

A similar relative increase as found herein was observed by [Guo et al. \(2015\)](#) for the direct effect of pig mortality rate up to day 5 (from 14.9% to 30.3%) in two purebred populations, whereas a greater relative gain in accuracy of 100% was observed by [González-Recio et al. \(2008\)](#) for the direct effect for mortality in broilers. In fact, with the inclusion of genomic information, the Mendelian sampling and the relationships among animals are better estimated, which leads to an expected increase in prediction accuracy and consequently higher genetic gains.

The maternal effect of FAS and LAS was as accurate as of the direct effect in BLUP (0.22 and 0.24 vs. 0.24 and 0.19, respectively) but benefited less from the inclusion of genomic information (0.27 and 0.30 vs. 0.35 and 0.34, respectively). This might be explained by the already higher amount of information used for calculating maternal breeding values due to the dam's multiple parities and large progeny size. Although the estimates of accuracy in our study are encouraging, they are based on a small number of validation animals. Validation studies for the same traits in larger populations could help to confirm the present results.

Not only accuracy but bias and dispersion of breeding values may also impact selection decisions and should be taken into account in genetic evaluations ([Legarra and Reverter, 2017](#)). The estimated bias for all traits and effects was close to zero with BLUP ([Table 5](#)), but it increased in genomic models. Such an increase might be due to the difference in allele frequencies among lines, which was not taken into account in the construction of **G** in ssGBLUP. The use of metafounders ([Legarra et al., 2015](#)) can help to reduce bias (and also dispersion) of GEBV by adjusting A_{22} to match **G**. This can be useful in multi-breed or crossbred populations because it does not rely on allele frequencies estimated in the admixed population, but uses 0.5 instead, increasing the compatibility between the pedigree and the genomic relationship matrices in ssGBLUP. Unfortunately, the metafounders approach has not been implemented yet in the THRIGIBSF90 programs.

With the genomic models, the dispersion of all traits and effects was closer to the unit. The direct and maternal breeding values for LAS were the most overdispersed/underdispersed in BLUP (0.54 and 1.85, respectively), and although they were closer to the unit with the inclusion of genomic information (0.80 and

Table 5. Prediction accuracy, bias, and dispersion of breeding values for BLUP and ssGBLUP evaluations

	Direct										Maternal			
	FAS ¹		LAS		NUS		FIS		POS		FAS		LAS	
	BLUP	ssGLUP	BLUP	ssGLUP	BLUP	ssGLUP	BLUP	ssGLUP	BLUP	ssGLUP	BLUP	ssGLUP	BLUP	ssGLUP
Accuracy	0.24	0.35	0.19	0.34	0.26	0.32	0.24	0.28	0.30	0.36	0.22	0.27	0.24	0.30
Bias	0.01	0.07	0.03	0.15	0.05	0.11	0.01	0.03	0.07	0.07	-0.01	0.01	0.07	0.06
Dispersion	0.81	0.93	0.54	0.80	1.17	1.11	0.93	0.95	1.18	1.17	0.98	0.78	1.81	0.72

¹BLUP, best linear unbiased prediction; FAS, farrowing survival; LAS, lactation survival; NUS, nursery survival; FIS, finishing survival; POS, postweaning survival; ssGBLUP, single-step genomic BLUP.

0.72, respectively), breeding values were still overdispersed. Dispersion of LAS direct and maternal breeding values may be due to the previously discussed confounding between FAS and LAS and the difficulty in modeling cross-fostering. For survival traits, bias and dispersion of breeding values may also arise from selective genotyping (i.e., only survivors are genotyped) and from the lack of parent phenotype variation (i.e., only survivors have the chance to become parents), which might reduce predictability and increase standard errors of breeding values (Grandinson et al., 2005; Garcia et al., 2018). Those topics deserve great attention for survival evaluations.

Selection for survival traits

Substantial genetic variability exists for survival in all phases of the production system. Although lowly heritable, sustained genetic progress can be achieved if survival is selected as a long-term breeding goal. Moreover, a known negative genetic correlation between survival and other important traits under current selection in the pig industry, such as litter size (Högberg and Rydhmer, 2000; Sorensen et al., 2000; Lund et al., 2002), leanness (Knol, 2001; Arango et al., 2005), and growth rate (Högberg and Rydhmer, 2000; Arango et al., 2005), makes efforts to improve survivability even more important.

Lowly heritable traits might greatly benefit through indirect selection for correlated traits. Increased birth weight (Arango et al., 2006), carcass weight (Dufresne et al., 2014), and reduced litter weight variation (Knol, 2001) were shown to positively affect pig survivability. However, given the multifactorial and complex nature of survival, the magnitude of such genetic correlations is rarely high. Moreover, some discussion might exist regarding the use of such traits for survival improvement (see Knol et al., 2002b, for a review). The inclusion of genomic information might also increase possibilities for survival selection. As shown herein, relative gains of up to 43.5% might be expected. In fact, traits with low heritability and that are hard to measure may benefit the most from genomic selection (Meuwissen et al., 2001; García-Ruiz et al., 2016), especially under ssGBLUP in which phenotypes of ungenotyped animals are linked to genotyped animals through the **H** matrix (Guo et al., 2015; Garcia et al., 2018).

We showed that survival should become more heritable as piglets age. The combination of the postweaning stages into POS produced similar or higher direct heritability than in the preweaning phases, the highest prediction accuracy among all evaluated production phases, and was positively correlated with the direct effect of preweaning phases. Moreover, we observed that a high contemporary group variation (30% of phenotypic variation) exists for POS, which we hypothesize could be associated with the social interaction among animals. Important factors that affect POS, such as tail/ear-biting and cannibalism, are directly influenced by the social behavior of animals. This generates further opportunities to explore social genetic effects for increasing pig survival (Bijma et al., 2007a, 2007b).

Based on the results of our study, the yearly average response to selection, in the observed scale, assuming a generation interval of 1 yr and intensity of selection corresponding to the selection of the 20% top animals, is expected to be 0.6% and 1.3% with BLUP and of 0.9% and 1.7% with ssGBLUP, for the direct and maternal effects, respectively. Although it might be a simplification of the pig selection scheme (i.e., multi-trait and/or multi-breed selection), we illustrate that the genetic progress for survival traits should be, although small, highly relevant given the economic importance of the trait.

Conclusions

Survivability before weaning shows a considerable genetic variation, hidden by the environment, resulting in low, but statistically significant direct and maternal heritabilities. From farrowing to the lactation phase, the direct contribution of the piglet to its survivability increases with age, whereas the impact of the maternal ability remains constant. A nonsignificant correlation exists between direct and maternal effects within traits; thus, both should be considered in the selection index to maximize genetic gains for preweaning survival. Postweaning phases have similar or higher heritabilities compared with preweaning phases. The genetic correlations between survival traits within preweaning and postweaning phases are favorable and strong, but correlations between preweaning and postweaning phases are moderate. The prediction accuracy of breeding values for survival traits, as well as the dispersion, can be improved with the use of genomic information through ssGBLUP. The similar heritability of POS compared with preweaning phases, its higher prediction accuracy, and positive genetic correlation with preweaning phases highlights this trait as a potential candidate trait for improving pig survival. Although survival is a complex trait with low heritability, important genetic gains can be obtained, especially under a genomic prediction framework.

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Conflict of interest statement

The authors declare no conflicts of interest.

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