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Bayesian threshold analysis of direct and maternal genetic parameters for piglet mortality at farrowing in Large White, Landrace, and Pietrain populations¹

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ABSTRACT: A Bayesian threshold model was fitted to analyze the genetic parameters for farrowing mortality at the piglet level in Large White, Landrace, and Pietrain populations. Field data were collected between 1999 and 2006. They were provided by 3 pig selection nucleus farms of a commercial breeding company registered in the Spanish Pig Data Bank (BDporc). Analyses were performed on 3 data sets of Large White (60,535 piglets born from 4,551 litters), Landrace (57,987 piglets from 5,008 litters), and Pietrain (42,707 piglets from 4,328 litters) populations. In the analysis, farrowing mortality was considered as a binary trait at the piglet level and scored as 1 (alive piglet) or 0 (dead piglet) at farrowing or within the first 12 h of life. Each breed was analyzed separately, and operational models included systematic effects (year-season, sex, litter size, and order of parity), direct and maternal additive genetic effects, and common litter effects. Analyses were

performed by Bayesian methods using Gibbs sampling. The posterior means of direct heritability were 0.02, 0.06, and 0.10, and the posterior means of maternal heritability were 0.05, 0.13, and 0.06 for Large White, Landrace, and Pietrain populations, respectively. The posterior means of genetic correlation between the direct and maternal genetic effects for Landrace and Pietrain populations were -0.56 and -0.53 , and the highest posterior intervals at 95% did not include zero. In contrast, the posterior mean of the genetic correlation between direct and maternal effects was 0.15 in the Large White population, with the null correlation included in the highest posterior interval at 95%. These results suggest that the genetic model of evaluation for the Landrace and Pietrain populations should include direct and maternal genetic effects, whereas farrowing mortality could be considered as a sow trait in the Large White population.

Key words: Bayesian analysis, farrowing mortality, genetic parameter, piglet mortality, threshold model, variance component

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INTRODUCTION

Litter size at weaning is an important economic trait in prolific species (Tess et al., 1983). Even though heritability estimates of pig litter size are usually low, several studies have reported a successful response by direct selection (Bidanel et al., 1994; Johnson et al., 1999; Noguera et al., 2002). However, experimental evidence suggests that litter size selection could increase piglet mortality (Johnson et al., 1999; Sorensen et al., 2000).

Both prolificacy and piglet mortality are the main determinants of litter size at weaning.

Farrowing mortality has traditionally been considered as a maternal trait (Grandinson et al., 2002; Arango et al., 2005; Su et al., 2007), ignoring the genetic background of piglets. Nevertheless, it can also be considered as a piglet trait (Knol et al., 2002; Serenius et al., 2003; Mesa et al., 2006). Most of these research reports have assumed linear models, which ignore the categorical nature of this trait and probably lead to biased estimates (Gianola, 1982). Threshold models account for the nonlinear nature of categorical traits, but few studies (Grandinson et al., 2002; Arango et al., 2006; Su et al., 2006) have used these models to analyze farrowing mortality at the piglet level. Moreover, only 2 of them (Arango et al., 2006; Su et al., 2006) have considered maternal components.

Available estimates of genetic parameters from all these studies showed a high degree of variability, which,

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to a certain extent, was related to differences in population abilities. In this context, it should be interesting to estimate and compare the genetic parameters in pig populations selected with different objectives. The aim of this study was to estimate (co)variance components of piglet mortality at farrowing for 3 purebred pig populations with different selection objectives: Large White, Landrace, and Pietrain. A threshold model with maternal effects was applied to ascertain the possibility of reducing piglet mortality by selection.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database.

Populations and Data Source

Field data were recorded between 1999 and 2006 at 3 nucleus pig farms belonging to a commercial breeding company (COPAGA SCCL, Lleida, Spain) registered in the Spanish Pig Data Bank (BDporc, <http://www.bdporc.irta.es>; last accessed Nov. 17, 2008). Sows belonged to 3 specialized purebred pig lines: 2 commercial dam lines (Large White and Landrace) and 1 sire line (Pietrain). The complete data set consisted of farrowing mortality data on 60,535 (Large White), 57,987 (Landrace), and 42,707 (Pietrain) piglets collected from 4,551, 5,008, and 4,328 litters, respectively. For the analyses, farrowing mortality was considered at the individual level as a binary trait. It was coded as 1 if the piglet was alive and 0 if the piglet was dead at farrowing (stillbirth) or died within the first 12 h after farrowing (early neonatal mortality). This trait was routinely registered by the nucleus farms.

In the 3 lines, the pedigree dated back at least 3 generations and no selection for survival traits was performed. Sows were kept under commercial conditions, and farrowing occurred in individual crates and standard confinement facilities. Registration of the litter characteristics and the individual data corresponded to the current registration protocol for farrowing on the nucleus farms: description of litter size (identification, size, and parity number) and information about each individual record, which included state at birth (12 h after farrowing), sex, and birth date. No data were available on BW at birth.

Statistical Analysis

A threshold animal model with maternal genetic effects was fitted to analyze the farrowing mortality of piglets. Statistical analyses were performed separately for the 3 populations. The assumed model for the liability $\mathbf{T}$ of piglet mortality at farrowing was

$$\mathbf{T} = \mathbf{X}\mathbf{b} + \mathbf{Z}_d\mathbf{a}_d + \mathbf{Z}_m\mathbf{a}_m + \mathbf{W}_l\mathbf{c}_l + \mathbf{e},$$

Table 1. Number of piglets, sows, sires, and litters in the study

Population	Piglets	Sows	Boars	Litters
Large White	61,827	1,082	209	4,553
Landrace	59,822	1,890	194	5,008
Pietrain	43,398	888	269	4,328

where $\mathbf{b}$ represents the systematic effects of sex (male or female), year-season (31 levels), litter size (12 levels, from 5 to 17 or more piglets), and order of parity (7 levels, first to seventh parity or greater), $\mathbf{a}_d$ is the vector of direct additive genetic effects, $\mathbf{a}_m$ is the vector of maternal additive genetic effects, $\mathbf{c}_l$ is the vector of common litter effects, $\mathbf{e}$ is the vector of residuals, and $\mathbf{X}$, $\mathbf{Z}_d$, $\mathbf{Z}_m$, and $\mathbf{W}_l$ are known incidence matrices that relate the fixed and random sources of variation to the liability, respectively. The number of levels for the direct and maternal additive effect and common litter effect are shown in Table 1.

The response in piglet mortality at farrowing ($\mathbf{y}$) was modeled as

$$f(\mathbf{y}|\mathbf{T}) = \prod_{i=1}^n f(y_i|T_i) = \prod_{i=1}^n 1(T_i < t_i)1(y_i = 0) + 1(T_i > t)1(y_i = 1),$$

and

$$f(\mathbf{T}|\mathbf{b}, \mathbf{G}, \sigma_e^2) = N(\mathbf{X}\mathbf{b} + \mathbf{Z}_d\mathbf{a}_d + \mathbf{Z}_m\mathbf{a}_m + \mathbf{W}_l\mathbf{c}_l, \mathbf{I}\sigma_e^2),$$

where y_i ($i = 1, 2, \dots, n$) is the i th phenotypic observation (categories 0 or 1), n is the total number of observations, T_i is its corresponding liability, and t is the threshold arbitrarily fixed at 0 that defines the categories of the response.

The following prior assumption was made for vector $\mathbf{c}_l$:

$$p(\mathbf{c}_l|\sigma_{cl}^2) \sim N(\mathbf{0}, \mathbf{I}_l\sigma_{cl}^2),$$

where σ_{cl}^2 is the common litter variance and $\mathbf{I}_l$ is the identity matrix with dimensions equal to the number of litters. The prior distribution assumed for $\mathbf{a}_d$ and $\mathbf{a}_m$ was

$$p\left(\begin{bmatrix} \mathbf{a}_d \\ \mathbf{a}_m \end{bmatrix} \middle| \mathbf{G}\right) \sim N\left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{G} \otimes \mathbf{A}\right) \quad \mathbf{G} = \begin{bmatrix} \sigma_{ad}^2 & \sigma_{ad,m} \\ \sigma_{ad,m} & \sigma_{am}^2 \end{bmatrix},$$

where $\mathbf{A}$ is the additive genetic relationship matrix and $\mathbf{G}$ is the genetic (co)variance matrix. The residual variance was arbitrarily fitted to 1, and the following uni-

form bounded priors were assigned for $\mathbf{b}$, σ_{cl}^2 , and to the elements of matrix $\mathbf{G}$:

$$p(b) \sim U[-100, 100],$$

$$p(\sigma_{cl}^2) \sim U[0, 10],$$

$$p(\sigma_{ad}^2),$$

$$p(\sigma_{am}^2) \sim U[0, 10], \text{ and}$$

$$p(\sigma_{ad,m}^2) \sim U\left[-\sqrt{\sigma_{ad}^2 \sigma_{am}^2}, \sqrt{\sigma_{ad}^2 \sigma_{am}^2}\right].$$

Bayesian analysis was implemented with a data augmentation step for the liability, following Sorensen et al. (1995). Marginal posterior distributions of all unknowns were estimated by using the Gibbs sampling algorithm (Geman and Geman, 1984). After exploratory analyses, we used a total of 500,000 samples for each analysis, with a burn-in period of 50,000. Convergence was separately tested for all dispersion parameters by using the algorithm of Raftery and Lewis (1992) and the Z criterion of Geweke (1992). Effective sample size was evaluated by using the algorithm of Geyer (1992), and Monte Carlo sampling errors were computed by using the time-series procedures described by Geyer (1992).

To validate the statistical analysis applied and discard any bias attributable to the extreme category problem, we used simulation data with the same pedigree structure and prevalence as those for the target populations. In all simulations, the direct and maternal heritabilities for the liability underlying the categorical phenotype were set as 0.05 and 0.10, respectively. The value set for the proportion of phenotypic variance attributable to a common litter effect was 0.10, and the rank value of systematic effects was $[-2, 2]$. The simulated genetic model and the analysis approach in this simulation study were the same as mentioned. The highest posterior densities at 95% (**HPD95%**) of variance components (not shown) included the true values in every simulation performed.

RESULTS

Means and coefficients of variation for the total number of piglets born and mortality rates at farrowing of the 3 analyzed populations are shown in Table 2. The Large White population had the largest prolificacy and mortality rates at farrowing, followed by the Landrace and Pietrain populations. However, the coefficient of variation for total number of piglets born was similar for the 3 populations.

Table 2. Mean and CV for total number of piglets born and percentage of mortality

Item	Large White	Landrace	Pietrain
Mean	13.29	11.58	9.96
CV, %	27.10	30.05	26.61
Mortality, %	14.30	9.45	8.23

A plot of mortality rate at farrowing across order of parity is shown in Figure 1 (top). Evolution of farrowing mortality differed according to the population ability. Hence, farrowing mortality was almost constant across parities in the sire line (Pietrain), with small increases in the first and last parities, whereas regular increases in mortality rate after the second parity occurred in the dam lines (Large White and Landrace). Figure 2 (top panel) shows the relationships between mortality rates at farrowing and litter size (total number of piglets born). Here, the evolution was similar for the 3 populations, showing a substantial increase in mortality rate for as many as 13 piglets per litter. From this point onward, the Pietrain line showed a faster increase in farrowing mortality than the dam lines. A plot of the posterior means for the parity number and litter size effects on the farrowing mortality liability after the Bayesian threshold analyses are also shown in Figures 1 and 2 (bottom panel), respectively. Observed trends of the posterior means across parities and litter sizes match with those of phenotypic rates of mortality presented in the top panels.

Estimates of the marginal posterior distributions of the variance components for individual farrowing mortality in 3 populations are shown in Table 3. They had a Monte Carlo error of less than 0.0005, and the Geweke test did not detect any lack of convergence. The maternal lines (Large White and Landrace) provided larger posterior means for maternal additive genetic variance than for direct additive genetic variance, whereas the opposite was observed in the paternal line (Pietrain). Moreover, the common litter variance showed the largest posterior mean in this line (0.61).

Features of the estimated marginal posterior distributions of heritabilities, the genetic correlation between direct and maternal effects, and the proportions of the phenotypic variance attributable to common litter effects are presented in Table 4. As for variance components, they exhibited only a very small Monte Carlo error, and the Geweke test did not detect any lack of convergence. Direct heritability was low for the 3 populations, being particularly negligible for the Large White population, where the HPD95 provided values close to zero (from 0.01 to 0.04). The Pietrain population provided the posterior mean of direct heritability, with a value of 0.10, followed by the Landrace population (0.06). The posterior mean of maternal heritability corresponded to the Landrace population (0.13). Regarding the additive genetic correlation between direct and maternal effects, Landrace and Pietrain popula-

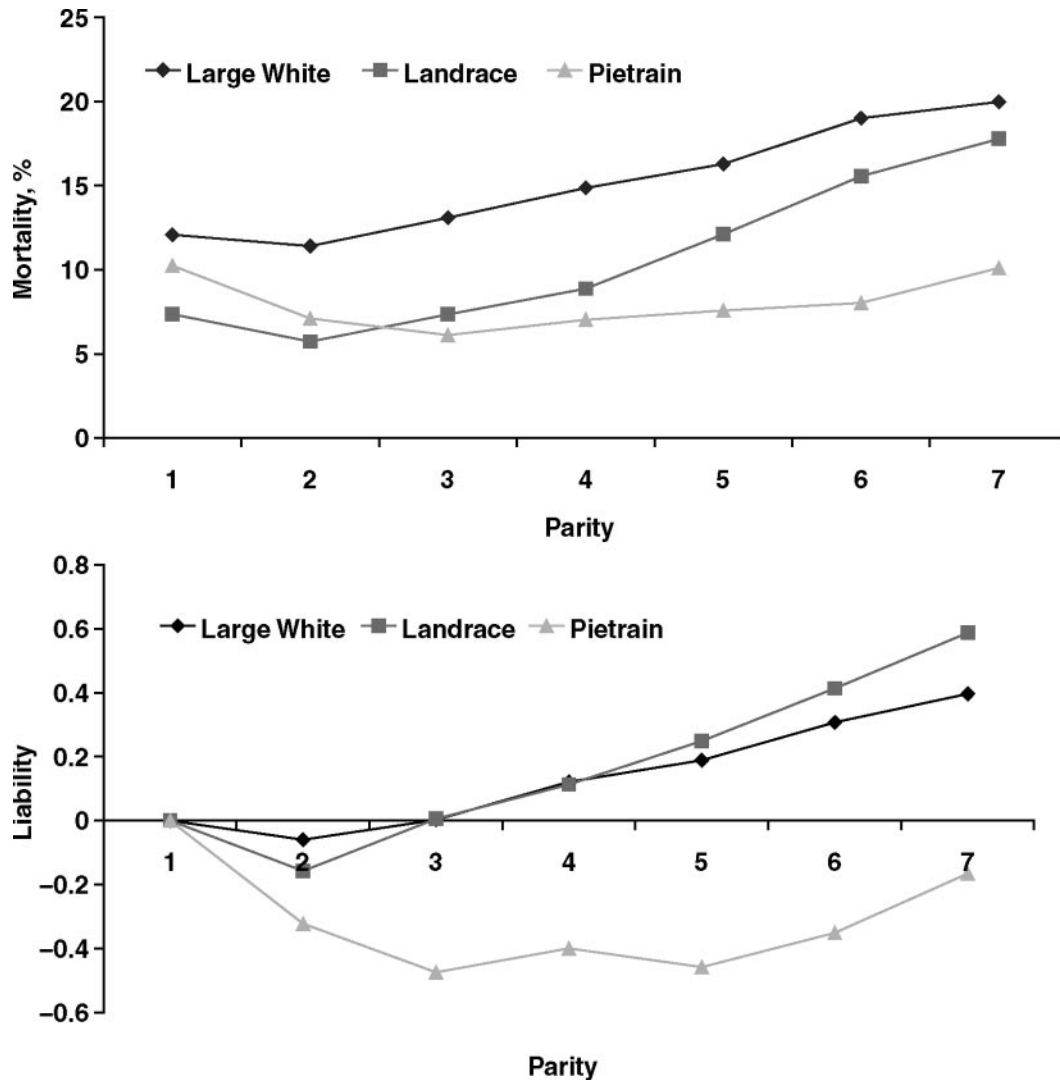


Figure 1. Top panel: Mortality rate at farrowing across parity order for the Large White, Landrace, and Pietrain populations. Bottom panel: Posterior means of parity order effects on liability for the Large White, Landrace, and Pietrain populations.

tions had negative correlations and their HPD95% did not include zero. In contrast, the Large White population had a positive correlation (0.15); although its HPD95% included zero, the posterior probability over zero was 75%. The proportion of phenotypic variance attributable to the common litter effect was moderate for the Large White and Landrace populations and was high for the Pietrain population, which presented a narrow HPD95%, with a posterior 90% probability of being greater than 0.33.

DISCUSSION

The present study showed a very different pattern of mortality rates at farrowing for each population. Dam lines (Large White and Landrace) showed greater mortality rates than the sire line (Pietrain). The mortality rate at farrowing in the Pietrain population (8.2%) was similar to that published by the Spanish Pig Data Bank (8.3%; BDPorc, 2006), that by Knol et al. (2002) for dam and sire lines (8.0 and 6.8%, respectively), and

that by Moeller et al. (2004) for commercial dam lines (7.7%). The Landrace population presented a mortality rate at farrowing slightly superior to (9.4%), but smaller than, those reported by Serenius et al. (2003) and Su et al. (2007) for, respectively, Finnish (12.1%) and Danish (18.4%) Landrace. Finally, the Large White population showed the greatest farrowing mortality rate (14.3%), but was less than the value reported by Arango et al. (2006) in the same breed (17.6%). On one hand, this variability between studies could be explained by genetic and environmental differences between populations and, on the other, could be explained by differences in the method of recording. The recording procedure affects the ability to distinguish between stillborn piglets and those that died in the first hours of life.

In the present study, the rate of mortality at farrowing increased with litter size in all 3 populations, reaching its maximum when litter size was close to the upper biological limit of each population. These results are consistent with the positive relationship between farrowing mortality and litter size reported by Sorensen

Table 3. Estimates of (co)variance components for individual piglet mortality at farrowing

Item ¹	Large White ²			Landrace ²			Pietrain ²		
	Mean (SD)	HPD95%	MCse	Mean (SD)	HPD95%	MCse	Mean (SD)	HPD95%	MCse
σ_{ad}^2	0.02 (0.01)	0.00, 0.04	0.000099	0.08 (0.02)	0.04, 0.13	0.000036	0.17 (0.03)	0.11, 0.23	0.000051
σ_{am}^2	0.06 (0.01)	0.05, 0.08	0.000024	0.18 (0.03)	0.13, 0.23	0.000025	0.10 (0.03)	0.04, 0.16	0.000031
σ_{cl}^2	0.15 (0.01)	0.13, 0.17	0.000062	0.19 (0.01)	0.15, 0.21	0.000033	0.61 (0.04)	0.54, 0.68	0.000019

¹ σ_{ad}^2 = direct additive genetic variance; σ_{am}^2 = maternal additive genetic variance; σ_{cl}^2 = common litter variance.

²HPD95% = highest posterior density interval (95%); MCse = Monte Carlo error.

et al. (2000) and Robinson and Quinton (2002). On the other hand, the increase in mortality at farrowing across order of parity was more striking in the dam lines. Some authors (Leenhouders et al., 1999; Knol et al., 2002; Damgaard et al., 2003) attribute this event to the fact that greater parities could be associated with larger litter sizes. As mentioned by these authors, larger litter sizes are related to crowded and prolonged farrowing and to a decrease in uterus quality. Neverthe-

less, the Large White and Landrace populations exhibited increases in liability associated with greater parity numbers, although litter size was accounted for by the model.

To date, only a small number of studies (Grandinson et al., 2002; Arango et al., 2006; Su et al., 2006) have obtained (co)variance estimates for farrowing survival under a nonlinear model. Individual piglet mortality at farrowing has traditionally been analyzed by applying

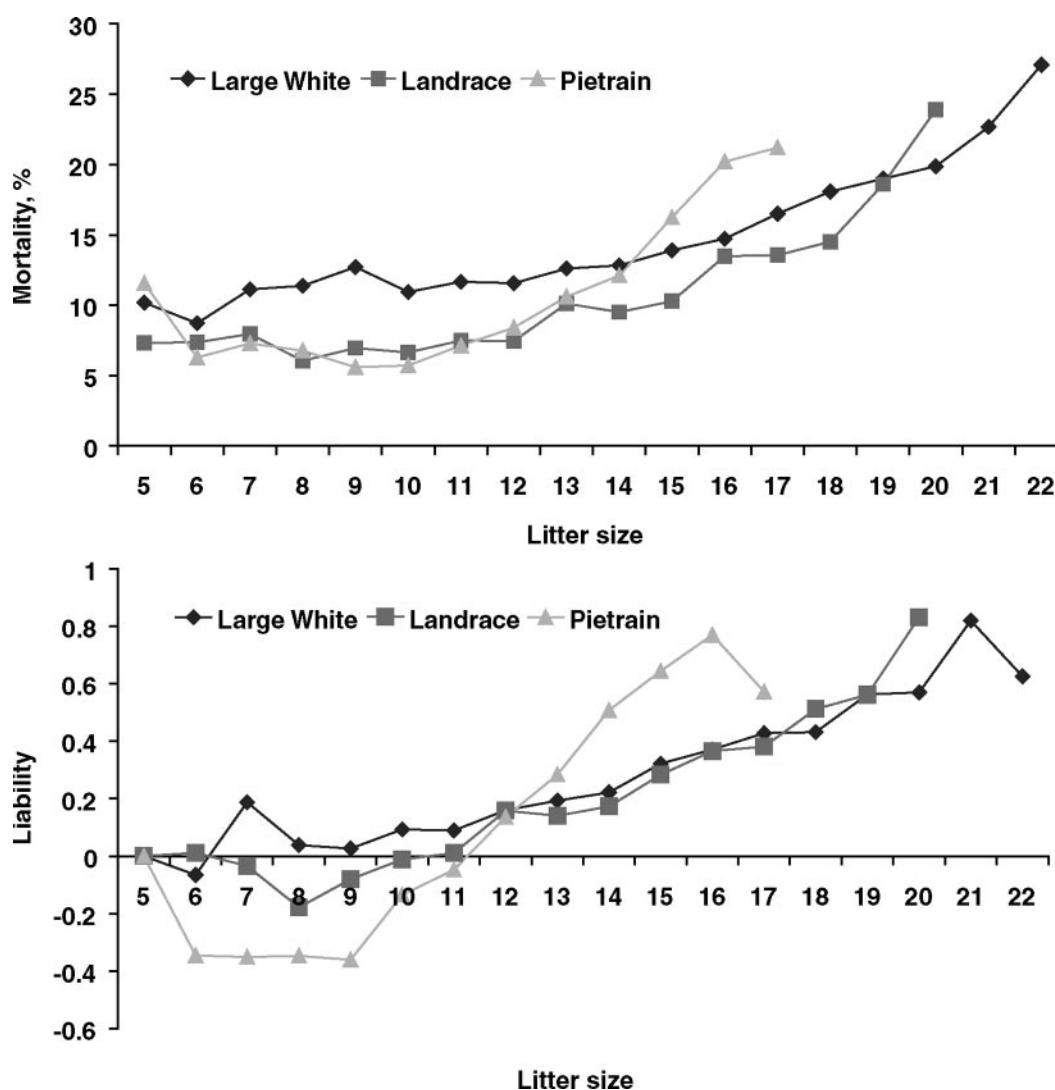


Figure 2. Top panel: Mortality rate at farrowing across litter size for the Large White, Landrace, and Pietrain populations. Bottom panel: Posterior means of litter size effects on liability for the Large White, Landrace, and Pietrain populations.

Table 4. Estimates of (co)variance components and genetic parameters for individual piglet mortality at farrowing

Item ¹	Large White ²			Landrace ²			Pietrain ²		
	Mean (SD)	HPD95%	MCse	Mean (SD)	HPD95%	MCse	Mean (SD)	HPD95%	MCse
h_d^2	0.02 (0.02)	0.01, 0.04	0.000034	0.06 (0.01)	0.03, 0.09	0.000018	0.10 (0.01)	0.07, 0.13	0.000024
h_m^2	0.05 (0.01)	0.04, 0.08	0.000073	0.13 (0.02)	0.10, 0.17	0.000023	0.06 (0.01)	0.03, 0.08	0.000015
c_1^2	0.12 (0.01)	0.11, 0.13	0.000065	0.14 (0.01)	0.12, 0.16	0.000087	0.35 (0.01)	0.32, 0.38	0.000010
r_{dm}	0.15 (0.13)	-0.11, 0.38	0.000551	-0.56 (0.12)	-0.32, -0.80	0.000140	-0.53(0.16)	-0.27, -0.79	0.000275

¹ h_d^2 = direct heritability; h_m^2 = maternal heritability; c_1^2 = proportion of phenotypic variance attributable to common litter effect; r_{dm} = genetic correlation between additive direct and maternal effects.

²HPD95% = highest posterior density interval (95%); MCse = Monte Carlo error.

the classical linear model (e.g., van Arendonk et al., 1996; Knol et al., 2002; Mesa et al., 2006). However, it is well known that the use of linear models with categorical data ignores their nonlinear distribution and tends to produce underestimates of heritability and residual correlations (Gianola, 1982). Therefore, it is especially important to use threshold models to estimate variance components for categorical data. Abdel-Azim and Berger (1999) showed a great loss of accuracy for the heritability and, as a result, for the genetic predictions when linear models were used for categorical data. Nevertheless, use of a threshold model may cause severe bias when no statistical information at the systematic effects level is available (Moreno et al., 1997). To avoid these problems, we analyzed individual mortality at farrowing by using a threshold model and checked the ability of the model to identify systematic effects by simulating data with the same structure as those for the target populations, discarding any bias attributable to the extreme category problem.

As mentioned above, direct heritability of individual piglet mortality at farrowing (or individual farrowing survival) reported in previous studies was rather variable (from 0.00 to 0.16). Here, direct heritability in the Large White population was low (0.02), in agreement with the estimates reported by Arango et al. (2006) in another Large White population. Low estimates for direct heritability of farrowing survival were also obtained by Su et al. (2006) in Landrace and Yorkshire populations (0.03 and 0.01, respectively), and by Knol et al. (2002) in a sire line by using linear models (0.01). On the other hand, the direct heritabilities for the Landrace and Pietrain populations in the present study were moderate, close to the results reported by Roehe and Kalm (2000) with a nonlinear model that ignored maternal effects (0.07). Far from these estimates, Mesa et al. (2006) reported a direct heritability of 0.16 when using linear models in a sire line, but with very low accuracy.

The maternal heritability of individual farrowing mortality for the Large White and Pietrain was consistent with the estimates reported by Knol et al. (2002) in a dam line (0.05) and a sire line (0.03) and by Su et al. (2006) in Landrace and Yorkshire populations

(0.05). Nevertheless, some studies have provided larger estimates of maternal heritability (Arango et al., 2006; Mesa et al., 2006), in agreement with the maternal heritability for the Landrace population obtained here. In our study, dam lines (Large White and Landrace) showed a maternal genetic variance larger than the direct additive variance, whereas the sire line (Pietrain) revealed the opposite.

We also found strong negative direct-maternal genetic correlations in Landrace and Pietrain populations, in agreement with previous research (Van Arendonk et al., 1996; Knol et al., 2002; Arango et al., 2006; Mesa et al., 2006). In contrast, the Large White population showed a positive correlation with a posterior probability of 0.75. However, the posterior distribution of this genetic correlation was very wide, caused by the low magnitude of the direct additive genetic variance. Negative estimates of genetic correlation between direct and maternal effects have often been obtained in animal breeding. The biological interpretation of this phenomenon is still not clear, and the possibility of an environmental source of bias has been pointed out by several authors (e.g., Robinson, 1996; Meyer, 1997; Quintanilla et al., 1999). This strong negative estimate could be explained by the existence of environmental covariances between dam and offspring records, or by misidentification of the systematic effects structure (Bijma, 2006). However, a model that considers these (co)variances is not available under a population with multiple litters and multiple offspring per litter (Bijma, 2006).

The results of this study showed substantial genetic variability at the piglet level in Landrace and Pietrain populations, but with a negative relationship between direct and maternal genetic effects. These results suggest the existence of genetic determinism from both the piglet and its dam, affecting piglet survival at farrowing in these populations. In contrast, individual genetic variability was noticeably low in the Large White population. In conclusion, results support the feasibility of reducing farrowing mortality by selection, although it should be based on different models of evaluation depending on the population. According to these results, the evaluation model for the Landrace and Pietrain populations must consider farrowing mortality

as a piglet trait, in which direct and maternal effects have to be taken into account, whereas in the Large White population, farrowing mortality can be considered a sow trait.

It must be underlined that the dam lines (Large White and Landrace) showed smaller direct heritability for farrowing mortality, which can be associated with the greater degree of prolificacy. One possible explanation for this could be the difficulty involved in expressing the genetic ability of piglets to survive at farrowing, given the stressful environment in the uterus caused by large litter size (Knol et al., 2002). Moreover, greater litter sizes could be related to smaller BW at birth, which is considered a very important factor in piglet survival (Högberg and Rydhmer, 2000; Damgaard et al., 2003). In the present study, BW at birth was not included in the model because it was not always recorded by the nucleus. Several authors have suggested selecting for BW at birth as a way of increasing piglet survival (Kerr and Cameron, 1995; Roehe and Kalm, 2000). The purported advantages of applying this strategy are not so clear because Knol et al. (2002) found a negative effect of BW at birth on farrowing mortality. Additionally, other studies have indicated that extreme selection based on BW at birth could produce a considerable increase in farrowing mortality, partly because of dystocia and prolonged parturition (Grandinson et al., 2002; Damgaard et al., 2003; Holm et al., 2004). This fact could also explain the large common litter variance observed in the sire line. Populations with low prolificacies tend to produce litters that include some heavy-weighted piglets, with a subsequent increase in the frequency of dystocia, which affects the chance of survival for the whole litter.

Prewaning mortality after farrowing has the most relevant economic weight in pig production. Nevertheless, while taking into account the difficulty involved in correctly identifying cross-fostered pigs on commercial farms, the present study was conducted on farrowing mortality. The genetic correlations between mortality at farrowing and preweaning mortality were positive and high with both the linear and threshold models (Arango et al., 2006; Mesa et al., 2006). This should make it possible to select populations for farrowing mortality with the objective of reducing total preweaning mortality via correlated genetic response.

The final conclusion from this study is that farrowing mortality can be modified by genetic selection. However, these results could be affected by the selection process applied to litter size; further studies are therefore required to examine the relationship between farrowing mortality and litter size. One interesting approach would be to implement a recursive model including a linear or nonlinear relationship with litter size (Gianola and Sorensen, 2004). Another possibility would be to consider a threshold reaction norm model associated with litter size, in which the phenotype would be described as a continuous function of an environmental

variable (Kolmoding and Bijma, 2004). Such a model would be useful for studying the genotype $\times$ environmental interaction when phenotype changes gradually over an environmental scale such as production level (de Jong, 1995). Moreover, it would be interesting to fit a heteroscedastic model that assumes environmental variance is heterogeneous and partly under genetic control (SanCristobal-Gaudy et al., 1998). This last approach seems particularly interesting for the Pietrain population, which showed an important degree of phenotypic variance attributable to common litter effects (σ_{cl}^2). On this subject, Gutiérrez et al. (2006) pointed out that large estimates for the permanent environmental variance decreased considerably when this heteroscedastic model was fitted, because it captured the genetic variance of the additive genes relating to environmental variability from the common environmental component.

In light of these results, farrowing mortality is genetically determined by direct and maternal additive effects. Use of selection procedures could therefore help to reduce farrowing mortality. However, considerable variability between estimates was observed among the populations analyzed. As a consequence, before implementing any particular selection strategy, it would be advisable to conduct a genetic parameter estimation for each population.

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