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Genetic parameters of piglet survival and birth weight from a two-generation crossbreeding experiment under outdoor conditions designed to disentangle direct and maternal effects¹

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ABSTRACT: Multivariate Bayesian linear-threshold models were used to estimate genetic parameters of peri- and postnatal piglet survival and individual birth weight of piglets reared under outdoor conditions. Data of 21,835 individual piglet observations were available from a 2-generation crossbreeding experiment selected for direct and maternal genetic effects of postnatal piglet survival on piglet and dam levels, respectively. In the first generation, approximately one-half of the Landrace sires used were selected for large or average breeding values of maternal genetic effects on postnatal piglet survival, whereas in the second generation the Large White sires used were selected for direct genetic effects of the same trait. Estimates of direct and maternal heritability were 0.21 and 0.15, 0.24 and 0.14, and 0.36 and 0.28 for piglet survival at birth and during the nursing period, and individual birth weight, respectively. In particular, direct heritabilities are substantially larger than those from the literature estimated for indoor-

reared piglets, suggesting that genetic effects of these traits are substantially greater under outdoor conditions. Direct or maternal genetic correlations between survival traits or with birth weight were small (ranging from 0.06 to 0.17), indicating that peri- and postnatal survival are genetically under rather different control, and survival was only slightly positively influenced by birth weight. There were significant ($P < 0.05$) negative genetic correlations between direct and maternal genetic effects within each of the analyzed traits ranging from -0.36 to -0.45, which have to be considered when selecting for piglet survival. Adjustment of traits for litter size or inclusion of genetic groups showed insignificant effects on the magnitude of the estimated genetic parameters. The magnitude of genetic parameters suggested that there is substantial potential for genetic improvement of survival traits and birth weight in direct and maternal genetic effects, especially when piglets are kept under outdoor conditions.

Key words: Bayesian analysis, birth weight, genetic parameter, outdoor production system, piglet survival, threshold model

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INTRODUCTION

Piglet survival has been shown to be influenced by direct and maternal genetic effects (e.g., Arango et al., 2006; Su et al., 2008), which are difficult to disentangle because they are very often confounded. In the current research project a 2-generation crossbreeding experiment for piglet survival with a cross-classified mating design between direct and maternal selection groups was used to disentangle direct and maternal genetic effects. In addition, the crossbreeding experiment was carried out under outdoor conditions for which, to the best of our knowledge, no genetic parameters using a direct-

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maternal effects model are available in the literature. Birth weight has been reported to be phenotypically associated with piglet survival and has been suggested for use as an indirect trait for genetic improvement of piglet survival (Kerr and Cameron, 1995; Roehe and Kalm, 2000). Estimates of genetic correlations between piglet survival traits and birth weight using a direct-maternal effects model are rare in the literature. Moreover, litter size may influence genetic parameters of piglet survival traits and birth weight so that several studies adjust these traits for litter size (Su et al., 2008; Wolf et al., 2008). In the present crossbreeding experiment, a crossbred structure common in commercial pig production was used, in which a dam line (selected with emphasis on reproduction performance) and a sire line (selected with emphasis on growing-finishing performance) were crossed. To account for genetic differences between lines, genetic groups are often fitted in the genetic model, as described by Westell et al. (1988). Therefore, the objectives of this study were first to estimate direct and maternal genetic effects of survival traits and birth weight of piglets kept under outdoor conditions, second to examine the influence of adjustment for litter size on these genetic parameters, and third to investigate the effect of genetic groups on these genetic parameters.

MATERIALS AND METHODS

All animal care and handling procedures used in this study were reviewed and approved by the Animal Experiments Committee at the Scottish Agricultural College, Edinburgh, United Kingdom.

Animals

Data on 21,835 individual piglet observations from a 2-generation crossbreeding experiment for piglet survival under outdoor conditions were used to estimate genetic parameters. These data were recorded on piglets born from April 2005 to June 2007. In the first generation of the crossbreeding experiment, 28 Landrace boars (descending from 21 sires and 24 dams) of a dam line provided by Pig Improvement Company (PIC, Kingston Bagpuize, Oxfordshire, United Kingdom) from AI stations located in United Kingdom and Canada were mated to 384 commercial crossbred dams (Large White × Duroc) maintained at an outdoor unit. From these crosses, 514 gilts (267 and 247 were sired by high EBV and control Landrace boars, respectively, as described below) were reared and mated to 29 Large White boars (descending from 21 sires and 27 dams) of a sire line (provided by PIC AI stations in the United Kingdom). These sows were kept over 3 parities. Due to selective and involuntary culling, the number of sows was reduced to 432 (211 and 221 were sired by high EBV and control Landrace boars, respectively) and 403 (201 and 202 were sired by high EBV and control

Landrace boars, respectively) in the second and third parity, respectively. These sows were mated to 25 boars (descending from 21 sires and 25 dams) and 24 boars (descending from 18 sires and 22 dams), respectively. Some of the Large White boars were used for services over parities to achieve high genetic connectedness between these parities. In the first generation, Landrace sires (from a dam line) were selected for maternal genetic effects of postnatal survival, calculated as percentage of piglets surviving between cross-fostering to weaning. In the second generation, Large White sires (from a sire line) were selected for direct genetic effects of postnatal survival. Both direct EBV for Large White boars and maternal EBV for Landrace boars were based on postnatal survival of indoor-reared piglets. Approximately equal numbers of boars with high and average (control) EBV for direct (or maternal) genetic effects of postnatal survival were used in each generation and parity. These EBV groups will be referred to subsequently as high and control groups. In the first parity of the second generation, matched mating of high EBV or control groups for direct and maternal genetic effects was carried out. To improve the disentanglement of direct and maternal genetic effects and to identify interactions between different combinations of direct and maternal selection groups, in the second parity cross-classified mating of all 4 selection groups in direct and maternal genetic effects was designed. In the third parity, sows were mated to sires of the opposite selection group compared with their matings in the second parity. Therefore, sows of the second generation were mated at least once to 1 of the 2 EBV groups (high or control) for direct genetic effects.

Husbandry

The crossbreeding experiment was carried out on 3 different commercial outdoor units of 1 farm near Aberdeen, Scotland. The first generation animals were kept on a multiplication unit where commercial crossbred dams in their fourth and fifth parity were artificially served with Landrace boars to produce the second-generation gilts. These gilts were moved to a second unit, where they gave birth in their first parity. After weaning of their first litters, sows were moved to a third unit, at which they gave birth in their second and third parity. Sows and piglets were kept under typical commercial outdoor conditions as practiced in the United Kingdom, which were similar for all 3 units and standardized in commercial management practices. At each unit, sows were artificially inseminated in a nearby indoor facility. After mating, sows were grouped together (~20 sows) in outdoor gestation paddocks. At 4 to 5 wk after mating, sows were pregnancy tested with an ultrasound scanner. Approximately 10 d before the due date of farrowing, sows were moved to individual farrowing paddocks with double-skinned insulated huts. Piglets were weaned in weekly batches at ~26 d of

age. More detailed information about the husbandry of the animals is presented by Roehe et al. (2009).

Measurements

Farrowing huts were checked each morning. Piglets of recently farrowed sows were carried to a trailer to measure birth weight of piglets within 24 h after birth. Piglets found dead were examined for cause of death. Criteria for identification of stillbirth were placental membranes covering the face or lungs that did not float in water, or both. For piglets that died during the lactation period, the cause of piglet death was identified after postmortem examination and categorized (crushed, low vitality, starved, scour, savaged, and others). Cross-fostering of piglets took place between first handling (weighing) and 4 d after farrowing. Cross-fostering was practiced as little as possible so that only 8.2% of the piglets were transferred to foster sows. Average litter size of total piglets born (SD) was 12.8 (3.5) for the entire population (i.e., cumulated first and second generation). In the second generation data, litter size showed only a small increase with parity (12.8 to 13.1 from first to third parity).

Statistical Analysis

Traits analyzed were survival at birth (**SVB**), survival during the entire nursing period (**SVNP**), and individual birth weight including BW of stillborn piglets (**IBW**). In the genetic analyses, survival traits were coded as 1 (dead) and 2 (alive); 0 was interpreted as a missing value.

Stillborn piglets were treated as missing observations in the trait of SVNP. Multiple trait Bayesian analyses were carried out using a threshold model for survival traits and a linear Gaussian model for birth weight. The multiple trait model is as follows:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{d} + \mathbf{W}\mathbf{m} + \mathbf{U}\mathbf{c} + \mathbf{e},$$

where \mathbf{y} includes the unobservable underlying continuous variable (liability) for survival traits and the observed phenotypic observations of birth weight of each individual piglet. The underlying continuous liability was linked to the observed binary observation of piglet survival through a threshold (Sorensen et al., 1994). Vector \mathbf{b} includes the systematic effects of farm-unit-year-month-parity at farrowing (23 classes), gestation length (≤ 112 , 113, 114, 115, 116, 117, 118, 119, and ≥ 120 d), and sex of piglet. For SVNP, additionally the effect of whether piglets were fostered to nurse sows or stayed with their biological mothers was considered. The vectors \mathbf{d} , \mathbf{m} , \mathbf{c} , and \mathbf{e} represent the direct additive genetic effects, maternal additive genetic effects, common environmental litter effects, and the environmental residual effects, respectively. The common environmental litter effect was assigned by the litter of the

biological mother for all analyzed traits. For SVNP, the litter effect was, for fostered piglets, not based on the nurse sow, because of low cross-fostering (8.2% of the piglets) and the relatively long time period of up to 4 d over which the piglets were cross-fostered, which is the period during which most postnatal mortalities occur. \mathbf{X} , \mathbf{Z} , \mathbf{W} , and \mathbf{U} are incidence matrices linking the effects with \mathbf{y} .

The variance-covariance structure was as follows:

$$\mathbf{V} \begin{bmatrix} \mathbf{d} \\ \mathbf{m} \\ \mathbf{c} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_d & \mathbf{A} \otimes \mathbf{G}_{d,m} & \mathbf{0} & \mathbf{0} \\ \mathbf{A} \otimes \mathbf{G}_{m,d} & \mathbf{A} \otimes \mathbf{G}_m & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I} \otimes \mathbf{L} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} \otimes \mathbf{R} \end{bmatrix},$$

where \mathbf{G}_d , $\mathbf{G}_{d,m}$, $\mathbf{G}_{m,d}$, and \mathbf{G}_m are submatrices of the genetic variance-covariance matrix \mathbf{G} and represent the direct genetic variance-covariance matrix, the direct and maternal genetic covariances matrix, the transpose of the latter matrix, and the maternal genetic variance-covariance matrix, respectively. \mathbf{L} and \mathbf{R} represent the variance and covariance matrices of common environmental litter effects and the residual environmental effects, respectively, and \mathbf{A} and \mathbf{I} are the additive genetic relationship matrix and identity matrix, respectively.

Bayesian analyses were carried out using Gibbs sampling to estimate the variance components of survival traits and IBW. In these analyses, uniformly distributed bounded priors were assigned to the systematic effects with $\mathbf{b} \propto \text{constant}$.

The conditional prior distributions for the additive genetic, maternal litter, and residual environmental effects were sampled from multivariate normal (N) distributions with

$$\mathbf{d}, \mathbf{m} | \mathbf{A}, \mathbf{G} \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G}),$$

$$\mathbf{c} | \mathbf{I}, \mathbf{L} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{L}),$$

$$\mathbf{e} | \mathbf{I}, \mathbf{R} \sim N(\mathbf{0}, \mathbf{I} \otimes \mathbf{R}),$$

respectively.

Conjugate prior variance-covariance matrices of \mathbf{G} , \mathbf{L} , and \mathbf{R} were sampled from inverse-Wishart distributions (IW) with

$$\mathbf{G} | v_{d,m}, \mathbf{V}_{d,m} \sim IW(v_{d,m} \mathbf{V}_{d,m}, v_{d,m}),$$

$$\mathbf{L} | v_c, \mathbf{V}_c \sim IW(v_c \mathbf{V}_c, v_c),$$

$$\mathbf{R}|v_e, \mathbf{V}_e \sim IW(v_e \mathbf{V}_e, v_e),$$

respectively.

$\mathbf{V}_{d,m}$, \mathbf{V}_c , and \mathbf{V}_e are known scale parameters for the direct-maternal genetic, common environmental litter, and residual variance-covariance matrices, respectively. Corresponding $v_{d,m}$, v_c , and v_e denote the degree of freedom for the inverse-Wishart distributions and can be interpreted as the prior degree of belief. Because substantial data information were available, prior degree of belief and therefore the degrees of freedom were chosen to be low with $v_{d,m} = 24$, and $v_c = v_e = 7$.

The conditional posterior distributions of the variance-covariance matrices of \mathbf{G} , \mathbf{L} , and \mathbf{R} were also sampled from inverse-Wishart distributions, whereas the conditional posterior distributions of the effects \mathbf{d} , \mathbf{m} , \mathbf{c} , and \mathbf{e} were sampled from multivariate normal distributions.

To estimate the influence of litter size on the direct and maternal genetic parameters of survival traits and birth weight, these traits were adjusted for litter size in an additional analysis. The adjustment was for all traits based on number of piglets born in total, using linear and quadratic regression. Preliminary analysis showed that, even for piglet SVNP, the adjustment for total born piglets explained a greater proportion of the phenotypic variance than number of piglets born alive. In a further analysis, the different lines and selection groups used in the crossbreeding experiment were fitted by using genetic groups as described by Westell et al. (1988). Five genetic groups were fitted, first the crossbred foundation sows (unselected for piglet survival), second and third Landrace sires (used in the first generation) selected for high or average maternal EBV for postnatal survival, respectively, and fourth and fifth Large White sires (used in the second generation) selected for high or average direct EBV for postnatal survival, respectively.

Bayesian Inferences

Statistical inferences were derived from samples of the marginal posterior distribution obtained by using Gibbs sampling as implemented in the program THRG-IBBSF90 (Misztal et al., 2002). Posterior distributions were obtained from a Markov chain of at least 300,000 iterations using Gibbs sampling. The inspection of the series of iterations of each estimated variance component showed that a burn-in of 50,000 iterations was necessary to reach the stationary distribution of the Markov chain. To reduce autocorrelations among iterations, only every 30th iteration was considered to generate the final marginal posterior distribution. Convergence of the Markov chain was checked by the algorithm of Raftery and Lewis (1992). Posterior means of the genetic parameters were calculated from the marginal distributions of the estimated variance components. To identify the precision of the parameters, the

95% highest posterior density intervals (Bayesian confidence interval) were determined from their marginal posterior distributions.

RESULTS AND DISCUSSION

The means of the analyzed traits and their changes over generations and parities are presented in Table 1. The litter performance achieved matched the top 10% of outdoor breeding herds in the UK national recording scheme (BPEX, 2008). The average SVB was 96.4% and slightly greater than the upper level of the literature, which ranges from 82 to 95.6% as reported by Su et al. (2008) and Wolf et al. (2008), respectively. This increased perinatal survival may be due to greater activity and the better physical conditions of outdoor sows. For example, Ferket and Hacker (1985) found that sows subjected to obligatory exercise during gestation had faster farrowings. Canario et al. (2006) showed that faster farrowing duration led to greater prenatal survival, whereas the risk of stillbirth increased progressively for each supplementary hour elapsed. The sows were able to nest-build, which could facilitate parturition by reducing stress (Lawrence et al., 1992). Additionally, it may be due to the more accurate postmortem examination (as described earlier in the measurement section) of a trained researcher at the farm in comparison with standard recording systems, where stillbirths are overestimated (Edwards et al., 1994). Mean SVNP was, at 88.5%, similar to those reported by Grandinson et al. (2002), Knol et al. (2002; in this study for the dam line), Serenius et al. (2004), and Arango et al. (2006). Substantially smaller average SVNP was obtained by Knol et al. (2002) in a sire line (85%) and Su et al. (2008) in 2 dam lines (84%). Generally, mean peri- and postnatal piglet survival increased with increasing parity in generation 2, except for a slight decrease in postnatal survival in the second parity. In particular, the mean of birth weight increased from 1.5 to 1.7 kg in the first to third parity. The reduced birth weight of piglets from primiparous sows in comparison with multiparous sows could have been influenced by the farm unit effect because they are completely confounded. However, it is known from the literature (e.g., Damgaard et al., 2003) that birth weights of piglets from first-parity sows are always substantially smaller than those of later parities. Second and third parity farrowings took place on the same farm unit, and comparison is therefore independent from this farm effect. Most genetic studies analyzed populations with an average birth weight ranging between 1.3 to 1.5 kg (e.g., Roehe, 1999; Darmgard et al., 2003; Arango et al., 2006; Su et al., 2008). This is less than the average birth weight of 1.6 kg obtained in the present study. In particular, the average birth weight in the third parity was of greater magnitude, which is even as large as the reported average of the trait, maximum birth weight within litter, as analyzed by Wolf et al. (2008). This may indicate that under outdoor conditions, with the genotype typically used,

Table 1. Number of records, means, and SD of piglet survival at birth (SVB), piglet survival during the nursing period (SVNP), and individual birth weight (IBW) in the entire crossbreeding experiment, per generation and parity

Group	No.	SVB, %		SVNP, %		IBW, kg	
		Mean	SD	Mean	SD	Mean	SD
Total	21,835	96.4	18.7	88.5	31.9	1.599	0.402
First generation	5,292	93.5	24.7	83.6	37.0	1.539	0.370
Second generation/first parity	6,162	96.6	18.2	89.8	30.3	1.501	0.355
Second generation/second parity	5,239	97.6	15.4	88.5	31.9	1.654	0.415
Second generation/third parity	5,142	97.8	14.6	91.9	27.3	1.720	0.433

substantially larger average birth weights are obtained than with the genotypes and management typically used under indoor conditions.

Heritabilities

The posterior means of genetic (co)variances, heritabilities, and genetic correlations are shown in Table 2. The heritabilities of survival traits and birth weight were moderate in the range from 0.14 to 0.36. In particular, the moderate magnitudes of heritabilities for direct genetic effects on survival traits are substantially greater than those reported in the literature (e.g., Knol et al., 2002; Arango et al., 2006; Su et al., 2008), which are mostly less than 0.10. Moreover, for IBW, substantially greater direct heritability was obtained than that published in other studies (e.g., Roehe, 1999; Grandinson et al., 2002; Arango et al., 2006), which was mostly less than 0.10, but was greater than the direct heritabilities for survival traits. Maternal heritabilities of survival traits were also slightly above the greatest estimates presented by Arango et al. (2006) and Ibáñez-Escriche et al. (2009), but more than twice as large than those estimated by Su et al. (2008). The maternal heritabilities for IBW were of moderate magnitude and were in agreement with the literature cited above for the same trait.

Correlations Between Traits Within Direct or Maternal Effects

Genetic correlations between direct genetic effects of survival traits were small and not significantly different from zero ($P > 0.05$; Table 2). This indicates that postnatal piglet survival is under different genetic control to SVB. This supports research examining phenotypic traits of piglet survival under outdoor conditions (Baxter et al., 2008, 2009), where the authors showed that perinatal survival was explained by piglet shape and size, whereas postnatal survival relied heavily on piglet and maternal behavior. Thus, different biological traits relate to the different types of mortality. Using similar multiple trait threshold models, Arango et al. (2006) found moderate direct genetic correlations between SVB and SVNP, whereas Su et al. (2008) reported similar low correlations to those in the present study, which

were also not significantly different from zero ($P > 0.05$). However, both studies indicate that late postnatal survival (from d 6 to weaning) was weakly genetically associated with perinatal survival. As a consequence, perinatal survival has to be considered as a genetically different trait compared with postnatal survival. Treatment of postnatal survival into traits of early and late postnatal piglet survival may be of further advantage for the genetic evaluation of survival as suggested by Arango et al. (2006) and Su et al. (2008).

Slightly greater direct genetic correlations than between survival traits were estimated between survival traits and birth weight, which were favorable and significantly different from zero ($P < 0.05$). However, most of the survival traits were influenced by other direct genetic effects than those affecting birth weight. Between maternal genetic effects of these traits, similar weak correlations to those between direct genetic effects were obtained, and only the genetic correlation between SVNP and IBW was significantly different from zero ($P < 0.05$).

Correlations Between Direct and Maternal Effects Within or Between Traits

Direct and maternal genetic effects within survival traits or IBW showed moderate negative correlations in the range from -0.36 to -0.45 (Table 2). Generally, negative correlations between direct and maternal genetic effects within survival traits as well as IBW have been estimated, with larger negative correlations for postnatal than for perinatal survival (Arango et al., 2006; Su et al., 2008; Ibáñez-Escriche et al., 2009). Because the crossbreeding experiment was specifically structured to disentangle direct and maternal effects, and the management conditions at all farm units were similar, these negative correlations are most likely true. Biologically, the negative genetic association between direct and maternal effects within traits indicates different direct genetic control of vitality or growth of piglets in comparison with maternal genetic attributions (e.g., uterine quality, lactation ability). These negative correlations between direct and maternal effects may be due to the resource constraints of supporting piglets within litters. It may even be that these negative associations increased due to greater requirements of the

Table 2. Posterior means of genetic variances, direct and maternal heritabilities (h^2 , on diagonal), genetic correlations (above diagonal) including their 95% highest posterior density interval (in parentheses), and genetic covariances (below diagonal) for piglet survival at birth (SVB), piglet survival during the nursing period (SVNP), and individual birth weight (IBW)¹

Effect and trait	Genetic variance	Direct			Maternal		
		SVB	SVNP	IBW	SVB	SVNP	IBW
Direct							
SVB	0.3943	0.21 (0.14 to 0.28)	0.08 (-0.18 to 0.35)	0.17 (0.02 to 0.32)	-0.36 (-0.58 to -0.15)	-0.04 (-0.26 to 0.21)	-0.09 (-0.23 to 0.06)
SVNP	0.3079	0.0273	0.24 (0.14 to 0.35)	0.16 (0.01 to 0.31)	-0.01 (-0.26 to 0.25)	-0.45 (-0.62 to -0.28)	-0.06 (-0.20 to 0.08)
IBW	0.0739	0.0298	0.0249	0.36 (0.31 to 0.41)	-0.05 (-0.22 to 0.10)	-0.10 (-0.25 to 0.05)	-0.36 (-0.45 to -0.27)
Maternal							
SVB	0.2697	-0.1193	-0.0003	-0.0073	0.15 (0.10 to 0.19)	0.09 (-0.13 to 0.30)	0.06 (-0.08 to 0.20)
SVNP	0.1767	-0.0095	-0.1080	-0.0110	0.0189	0.14 (0.10 to 0.18)	0.17 (0.04 to 0.30)
IBW	0.0572	-0.0131	-0.0082	-0.0237	0.0072	0.0168	0.28 (0.24 to 0.31)

¹Estimates of genetic parameters of SVB and SVNP are based on observations transformed to the underlying scale (the normal distribution underlying the phenotypic expression of the binary survival traits observed as dead or alive) using a threshold model, whereas those of IBW are based on continuously measured observations (kg) using a linear model.

piglets caused by the selection on direct genetic effects, and these additional requirements could not be provided by the maternal genetic potential of their dams. Therefore, it is hypothesized that direct genetic effects associated with survival and growth are antagonistic to maternal genetic effects providing maternal resources for those piglets, in particular at large litter sizes.

In contrast to the direct and maternal genetic correlations within traits, the correlations between direct and maternal effects of different traits were weak and nonsignificant. As a consequence, selection for direct genetic effects of perinatal survival will negligibly change the maternal genetic effects of postnatal survival. These weak correlations are consistent with those described in the preceding section between direct or maternal effects of different traits, which confirms that peri- and postnatal survival are genetically different traits among all possible combinations of their direct and maternal effects.

Litter and Residual Environmental Effects

The phenotypic proportion of environmental variation associated with effects common to the piglets within litter for the survival traits and birth weight ranged from 0.10 to 0.17 (Table 3), which are of similar magnitude to those estimated by Su et al. (2008). The combined maternal environmental litter effect and maternal genetic effects explain 24 to 43% of the phenotypic variances of the analyzed traits, indicating the importance of the total maternal effects for piglet survival, which is consistent with results of Roehe et al. (2009) using only the first generation data of this crossbreeding experiment. Among litter effects of different traits, the correlations were slightly positive and not significantly different from zero ($P > 0.05$). In contrast, the residual correlations among these traits were moderate, reflecting larger environmental associations among traits within each individual piglet rather than due to environmental effects common to all piglets within litter.

Adjustment for Litter Size

The magnitude of litter size (12.8 to 13.1 from first to third parity) in the present study is greater than most recently presented in the literature by Arango et al. (2005) and Hellbrügge et al. (2008), but less than those reported by Su et al. (2008) and Wolf et al. (2008). Adjustment for litter size showed only a marginal change of the genetic parameters (data not shown) from those presented in Table 2. Heritabilities of SVB were reduced by 0.01, whereas those of SVNP did not change, and those of IBW increased by 0.02 for direct genetic effects and decreased by 0.02 for maternal genetic effects. The genetic correlations among traits changed only by a maximum of 0.05. Consequently, adjustment for litter size did not result in the large reduction in negative genetic correlation between direct and mater-

Table 3. Posterior means of phenotypic proportions of environmental effects common within litter (on diagonal), correlations among these litter effects (above diagonal), random residual environmental correlations (below diagonal), and their 95% highest posterior density interval (in parentheses) for piglet survival at birth (SVB), piglet survival during the nursing period (SVNP), and individual birth weight (IBW)¹

Trait	SVB	SVNP	IBW
SVB	0.17 (0.13 to 0.21)	0.21 (0.04 to 0.38)	0.14 (0.04 to 0.24)
SVNP	0.30 (0.06 to 0.53)	0.10 (0.08 to 0.12)	0.24 (0.15 to 0.34)
IBW	0.41 (0.34 to 0.46)	0.45 (0.40 to 0.50)	0.15 (0.14 to 0.16)

¹Estimates of litter effects of SVB and SVNP are based on observations transformed to the underlying scale (the normal distribution underlying the phenotypic expression of the binary survival traits observed as dead or alive) using a threshold model, whereas those of IBW are based on continuously measured observations (kg) using a linear model.

nal genetic effects from -0.41 to -0.22 as obtained by Roehle (1999) for IBW under indoor conditions. In the present study this negative correlation even slightly increased from -0.36 to -0.40 (data not shown). After adjustment for litter size, the phenotypic proportion of the common litter effect decreased by 0.01 for the survival traits and by 0.04 for IBW (data not shown). The adjustment for litter size showed slightly more influence on the correlation among litter effects of survival traits and IBW. These correlations among litter effects declined by absolute values of 0.10 to 0.14 (data not shown) from those presented in Table 3. This indicates that litter environmental correlations are influenced more by competition induced by increased litter size than the genetic correlations. Moreover, after adjustment for litter size, the residual correlations (data not shown) increased slightly to 0.34 or 0.46 between SVB and SVNP or IBW and SVNP, respectively, but did not change between SVB and IBW in comparison with the corresponding unadjusted estimates presented in Table 3. Generally, the adjustment for litter size showed little influence on the estimated genetic parameters, which may be due to the fact that differences in litter size may have been accounted for by the common litter environmental effect.

Consideration of Genetic Groups

To account for different genetic merit of selection groups and breeds, which may influence genetic parameters as shown by Kapell et al. (2009), genetic groups as described by Westell et al. (1988) were included in the analysis. Inclusion of genetic groups for selection groups and breeds showed slightly greater changes in heritabilities for survival traits and IBW (Tables 2 and 4) than those obtained without and with adjustment for litter size. Interestingly, the inclusion of genetic groups increased the maternal heritabilities, whereas it was expected that consideration of differences among lines and between selection groups by including genetic groups in the model would result in a reduction in heritabilities. The genetic correlations were even less influenced by the consideration of genetics groups than by adjustment for litter size. In contrast, Díaz et al. (2002)

reported after inclusion of genetic groups, a reduction in direct variance as well as the direct-maternal covariance for 210-d BW of beef cattle, but almost no change in the maternal genetic component. Therefore, inclusion of genetic groups can influence the genetic parameters, but this was not found to be the case in the present study. One reason may be that a cross-classified mating strategy was used among all combination of high and control selection groups for direct and maternal effects so that no biased estimates of genetic parameters were obtained when ignoring genetic groups. Furthermore, the pedigree information used in the genetic analysis may already have accounted for differences in selection.

General Discussion

Generally, the estimated heritabilities for piglet survival and birth weight, in particular those for direct genetic effects, were greater than the average estimates reported in literature reviews (e.g., Blasco et al., 1993; Rothschild and Bidanel, 1998). Potential reasons for the greater estimates of heritabilities reported in the present study include the following. First, the selection into direct and maternal selection groups may increase the genetic variance in the crossbreeding experiment. However, fitting genetic groups to account for the different genetic lines and selection groups did not reduce the heritabilities, but even slightly increased them. Moreover, it is very unlikely that 1 generation of selection in males only would substantially influence the genetic variance unless the trait under selection was highly heritable. Second, 3 different genetic lines have been crossed in the experiment so that besides additive genetic variation also nonadditive genetic variation such as dominance may have increased the estimates of heritabilities. However, it has been shown by Johansson et al. (1993) that a litter effect, as fitted in the model of the present analysis, accounts for most of the dominance variance. Third, genetic parameters of piglet survival may be affected by litter size. However, adjustment for litter size changed the heritabilities and genetic correlations only marginally. The small effect of adjustment for litter size on genetic parameters may

be due to the fitted common litter effect, which already accounts for differences in litter size as well as other factors affecting the litter environment. Fourth, the present analysis used the more appropriate threshold model for estimation of heritabilities of binary survival traits, whereas in the literature an approximate linear model has been commonly used. It is known that binary traits analyzed using linear models underestimate the heritabilities, especially in the case of low frequency of 1 of the 2 categories. Fifth, piglet survival under outdoor conditions may be subject to stronger genetic determination relative to the phenotypic variance than under indoor conditions. Piglets that are environmentally challenged under outdoor conditions may show greater genetic differences. This would result in greater direct heritabilities for survival than in an environment that protects piglets, where genetic differences in traits associated with survival are partly compensated by an improved indoor environment. An increase of genetic determination in survival traits and birth weight due to greater demands for vitality and growth under outdoor conditions would be of interest for breeding organizations to select boars more accurately for survival traits than would be possible under indoor conditions, provided no genotype \times environmental interactions are present. The realized selection response from this crossbreeding experiment, in which EBV were based on performance under indoor conditions, suggests that genotype \times environmental interactions were negligible between indoor and outdoor conditions (Roehe et al., 2008).

The crossbreeding experiment was designed to disentangle direct and maternal genetic effects using a cross-classified mating among all 4 selection groups in combination with the use of sires over parities. This results in unbiased estimation of the direct and maternal effects, which are used in the quadratic forms to estimate genetic (co)variances of these effects. These disentangled genetic effects showed negligible correlations between direct and maternal effects for different traits. For instance, selection for direct effects in perinatal survival will barely influence the genetic response in maternal genetic effects of postnatal survival. However, the correlation between direct and maternal genetic effects within survival and birth weight traits were negative at moderate magnitude, which will reduce the potential improvement of overall genetic merit in these traits compared with independent effects. A crossbreeding breeding program may be implemented to reduce the impact of negative genetic correlations between direct and maternal effects on the overall genetic response (Roehe and Kennedy, 1993).

The genetic correlations between peri- and postnatal survival traits within direct or maternal effects, or between both, were weak and not significantly different from zero. Therefore, peri- and postnatal survival would most efficiently be selected as 2 different traits. Moreover, the favorable correlations between direct or maternal genetic effects of survival traits and birth

Table 4. Posterior means of genetic variances, direct and maternal heritabilities (h^2 , on diagonal), genetic correlations (above diagonal) including their 95% highest posterior density interval (in parentheses), and genetic covariances (below diagonal) for piglet survival at birth (SVB), piglet survival during the nursing period (SVNP), and individual birth weight (IBW) fitting genetic groups for lines and their selection groups¹

Effect and trait	Genetic variance	Direct			Maternal		
		SVB	SVNP	IBW	SVB	SVNP	IBW
Direct							
SVB	0.4171	0.21 (0.14 to 0.29)	0.07 (-0.23 to 0.33)	0.18 (0.03 to 0.35)	-0.32 (-0.56 to -0.09)	-0.04 (-0.30 to 0.20)	-0.09 (-0.24 to 0.07)
SVNP	0.3352	0.0271	0.26 (0.15 to 0.38)	0.17 (0.01 to 0.34)	-0.02 (-0.27 to 0.22)	-0.41 (-0.58 to -0.24)	-0.07 (-0.22 to 0.09)
IBW	0.0764	0.0326	0.0286	0.35 (0.30 to 0.40)	-0.04 (-0.21 to 0.12)	-0.10 (-0.25 to 0.05)	-0.32 (-0.42 to -0.22)
Maternal							
SVB	0.3367	-0.1232	-0.0063	-0.0064	0.17 (0.12 to 0.23)	0.09 (-0.11 to 0.30)	0.04 (-0.10 to 0.19)
SVNP	0.2197	-0.0106	-0.1141	-0.0138	0.0255	0.17 (0.12 to 0.22)	0.19 (0.04 to 0.31)
IBW	0.0678	-0.0146	-0.0102	-0.0229	0.0065	0.0229	0.31 (0.27 to 0.35)

¹Estimates of genetic parameters of SVB and SVNP are based on observations transformed to the underlying scale (the normal distribution underlying the phenotypic expression of the binary survival traits observed as dead or alive) using a threshold model, whereas those of IBW are based on continuously measured observations (kg) using a linear model.

weight were slightly greater than those between peri- and postnatal survival and significantly different from zero. Because birth weight can be measured on a continuous scale, it contains substantially more information. Therefore, even a weak correlation will have an impact on the improvement of survival traits. In addition, it has been shown that a genetic analysis of threshold traits with continuous traits in a multiple trait model will improve the accuracy of estimation of genetic parameters of the former traits. There are also nonlinear associations between birth weight and peri- or postnatal survival (Roehe and Kalm, 2000; Canario et al., 2006), which may influence their genetic correlations. Moreover, there may be variation of birth weight within litter of importance for piglet survival (Damgaard et al., 2003) so that canalized selection of birth weight can be considered as another strategy to improve piglet survival, as found to be successful in an experiment using rabbits (Garreau et al., 2008).

Implications

The genetic parameters measured in this study suggest that there is substantial potential for genetic improvement of survival traits and birth weight in direct and maternal genetic effects, when piglets are reared under outdoor conditions. In particular, the increased genetic determination of direct genetic effects of piglet survival under outdoor conditions may be used by pig breeding organizations to identify boars of sire lines with high direct genetic potential for survival more accurately than under indoor conditions. For these boars, only the direct genetic effect of survival traits is of interest because they are producing growing-finishing pigs, which will be slaughtered. Based on the genetic parameters, selection for piglet survival is expected to reduce piglet mortality efficiently, which is a trait of great economic importance. Selection for piglet survival will enhance the environmental sustainability of outdoor production and improve the animal welfare of piglets under a production system, which also offers welfare benefits for the sow.

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