Genetic analyses of piglet survival and individual birth weight on first generation data of a selection experiment for piglet survival under outdoor conditions

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ABSTRACT

Genetic parameters of piglet survival traits and birth weight were estimated on the first generation data of a selection experiment aimed at improving piglet survival using a multiple trait linear and threshold model. Data on 5293 piglets for survival at birth, at day one after birth and during the entire nursing period, as well as individual birth weight and litter size, were recorded in an outdoor production system. Genetic effects of piglet survival traits and birth weight were estimated based on threshold and Gaussian models, respectively, using a Bayesian approach. The statistical model included as fixed effects selection group, parity, gender, fostering, gestation length and month of farrowing and, alternatively, an adjustment for litter size. Direct genetic effects (i.e. the piglet’s genetic potential) for piglet survival and birth weight were estimated separately, whereas maternal genetic and environmental effects could only be estimated for the given data structure in a combined litter effect. Posterior means of heritabilities for direct genetic effects of survival at birth, at first day after birth and the entire nursing period, as well as birth weight, were 0.08, 0.07, 0.08 and 0.20, respectively. Genetic correlations among survival traits were in the range of 0.29 to 0.40 and indicate that these traits were mainly attributable to different genetic effects. Genetic correlations between direct effects of survival traits and birth weight ranged between 0.18 and 0.23 and were reduced when weights of stillborn piglets were omitted in the analysis or the traits were adjusted for litter size. The magnitudes of direct genetic effects of survival traits are substantially higher than estimates in the literature, which may indicate that these traits have a higher genetic influence under outdoor conditions. The use of birth weight in the multiple trait estimation provided important information for the estimation of survival traits due to its favourable genetic correlations with survival, its high heritability and its high information content as a continuously measured trait.

1. Introduction

The total peri- and postnatal mortality of piglets is reported to be in the range of 14.4 to 32.1% (Knol et al., 2002; Grandinson et al., 2002; Serenius et al., 2004; Su et al., 2006) under indoor conditions. The proportion of sows which farrow under outdoor conditions differs widely between...
countries, with estimates of ≤5% in Germany and Denmark, 8% in France (EFSA, 2007) and up to 31% in the United Kingdom (Sheppard, 2004). Based on the UK recording schema, pre-weaning live born piglet mortality is on average 12.9% and 13.6% per annum in indoor and outdoor systems, respectively (MLC, 2007). As a consequence, genetic improvement in piglet survival has great potential benefits in terms of animal welfare, economics and in reducing the environmental footprint of pig production. Piglet survival is affected by two genetic components, firstly direct genetic effects on the potential of the piglet (with respect to it’s vitality, growth, resistance, etc.) for survival, and secondly maternal genetic effects on the mother’s potential to provide optimal conditions (birth conditions, milk yield, mothering ability, etc.) for piglet survival. The magnitude of direct and maternal genetic effects of piglet survival may be different under indoor compared to outdoor conditions. Under indoor conditions, the piglets are more protected by the use of farrowing crates. However, farrowing crates restrict the maternal behaviour of sows and raise substantial sow welfare concerns (Lawrence et al., 1994; Jarvis et al., 2002; Edwards, 2007). In contrast, under outdoor conditions, sows are more able to express their maternal behaviour. Genetic parameters of piglet survival under outdoor conditions are to our knowledge not available in the literature.

The estimation of genetic parameters of piglet survival has to consider the binary expression of this trait. Genetic parameters for these types of categorical data can be appropriately estimated by using a threshold model (Sorensen et al., 1994). In addition, genetic effects of piglet survival may be dependent on the stage of development of the piglet. For example, perinatal survival may be attributed to different genetic effects than postnatal survival. Genetic correlations between survival characteristics at different stages of development can be used to detect whether different or common genetic effects influence these traits (e.g. Grandinson et al., 2002).

Phenotypically, individual birth weight is closely associated with piglet survival (Kerr and Cameron, 1995; Roehe and Kalm, 2000; Canario et al., 2006). Therefore, piglet birth weight may be used to indirectly improve piglet survival. Again, genetic parameters and correlations among survival traits and birth weight may be different under outdoor than under indoor conditions. Genetic parameters for piglet survival traits and individual birth weight therefore need to be estimated under the conditions in which the piglets are kept in order to improve piglet survival efficiently. In addition, genetic parameters of piglet survival and birth weight may be affected by the often unrecorded weights of stillborn piglets. Furthermore, there have been reports that litter size is phenotypically (Kerr and Cameron, 1995; Roehe and Kalm, 2000; Canario et al., 2006) and genetically (Johnson et al., 1999; Lund et al., 2002) unfavourable associated with survival. This points to the importance of including piglet survival in those pig breeding programmes that currently only aim to increase litter size.

The first objective of the research was to estimate the heritabilities and genetic correlations of piglet survival and birth weight of pigs kept under outdoor conditions. In the genetic analysis, the binary distribution of piglet survival was considered through the use of a threshold model. The second objective was to examine the influence of considering weights of stillborn piglets on the genetic parameters of survival traits and birth weight. In the third objective, the influence of litter size on genetic parameters of survival traits and birth weight was studied.

2. Materials and methods

2.1. Animals

Data on 5293 individual piglet observations from a selection experiment for piglet survival under outdoor conditions were used in the genetic analyses. The data of piglets born during April to September 2005 were collected by a researcher with support of staff from the outdoor farm. Piglets were from 414 litters of 384 commercial crossbred dams (Large White × Duroc) from an outdoor unit and sired by 28 Landrace boars provided by PIC. Fourteen of these sires each were selected for high or average estimated breeding values (EBVs), respectively, associated with maternal genetic effects of postnatal survival, calculated as percentage of piglet surviving between cross-fostering and weaning, under indoor conditions. Only the first generation data of the selection experiment were used in the present analyses. Because selection of boars was for maternal genetic effects, the main selection response is expected to occur in the second-generation data.

2.2. Husbandry

Animals were kept on a commercial outdoor unit on a site of approximately 22 ha near Aberdeen, Scotland. Sows and piglets were kept under typical commercial conditions. All sows were artificially inseminated in a nearby indoor facility. After serving, sows were grouped together (about 20 sows) in outdoor gestation paddocks. At 4–5 weeks after serving, sows were pregnancy tested with an ultrasound scanner. Approximately 10 days before the due date of farrowing, sows were moved to individual farrowing paddocks (20 m×20 m), separated by electric fences. Farrowing occurred in sloped-wall, double insulated huts with a floor area of 3.09 m² (2.22 m×1.39 m), a roof dimension of 2.22 m×1.22 m and a height of 1.09 m. At the entrance of each hut was a fender that measured 1 m×1.07 m×0.46 m to keep the piglets within the hut during early life. Huts were initially bedded with four sections of high quality barley straw to a depth of approximately 10–12 cm. This was replenished when needed. After weaning, huts were moved to a new location and the bedding was removed from the paddocks. Once daily, pregnant sows were offered 3 kg of a diet containing 12.74% CP, 0.98% lysine, 13.32 MJ DE kg⁻¹. After farrowing, a lactation diet (17% CP, 0.99% lysine, 13.75 MJ DE kg⁻¹) was offered at a rate of 3 kg followed by 0.5 kg increments each day until 7 kg, and then followed by 1 kg increments each day up to a maximum of 12 kg until weaning. Sows had ad libitum access to water. Within 24 h after farrowing, piglets were tail docked, teeth clipped, ear tagged and weighed. Piglets are aimed to be weaned at an average age of 26 days.

2.3. Measurements

Every morning, after 8 am, all the farrowing huts were checked. Sows farrowed were lured outside the hut by feed
and piglets were collected from the back door of the hut. Piglets were carried to a trailer designed for piglet processing. In the trailer, piglet’s individual birth weight was measured within 24 h after birth using digital hanging scales with an accuracy of 10 g. Piglets were counted daily after feeding and piglets found dead were examined with respect to cause of death. In particular, it was examined on all piglets found dead during the first day, whether piglets were stillborn or died after birth. Criteria for identification of stillbirth were placental membranes covering the face and/or lungs that did not float in water. For piglets that died during the lactation period, the cause of piglet death was identified and categorised (e.g. crushed, low vitality, starved, scour, savaged). Some piglets were fostered to another sow between first handling (weighing, etc.) and four days after farrowing. In the data, 7% of the piglets born alive were fostered to nurse sows. Piglets crossfostered were taken at random as indicated by similar average weight of non-fostered and fostered piglets of 1558 g (±361 g) and 1549 g (±343 g), respectively. The corresponding means of survival during the nursing period were 83.7% and 82.9%, respectively.

2.4. Statistical analyses

2.4.1. Genetic statistical model

Traits analysed were survival at birth (complement of stillbirth), survival during the first day after birth, survival during the entire nursing period (including first day weights) and individual birth weight including or excluding weights of stillborn piglets. Survival values during the first day after birth are based on live born piglets (determined by post mortem examination of those subsequently dying) which were found alive or dead at first handling (i.e. weighing, etc.), and are therefore not influenced by crossfostering. In the genetic analyses, survival traits were coded as one (dead) and two (alive); zero was interpreted as a missing value.

Stillborn piglets were treated as missing observations in the traits of survival during the first day after birth and survival during the nursing period. 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 animal model is as follows:

\[ \mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wm} + \mathbf{e}, \]

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. Vector \( \mathbf{b} \) includes the systematic effects of the selection group (high or average EBV sire), parity (4th or 5th parity), gestation length, month of farrowing of sow and gender of piglet. For survival during the nursing period, additionally the effect of whether piglets were fostered to nurse sows or stayed with their biological mothers was considered. The vectors \( \mathbf{a}, \mathbf{m} \) and \( \mathbf{e} \) represent the direct additive genetic effects of the piglets, maternal litter effects of the dams and the environmental residual effects, respectively. Because no pedigree information for the commercial crossbred dams was available, maternal genetic effects could not be estimated separately, and were therefore estimated in combination with maternal environmental effects within the litter effects. \( \mathbf{X}, \mathbf{Z} \) and \( \mathbf{W} \) are incidence matrices linking the effects with \( \mathbf{y} \). In further analyses, birth weights of stillborn piglets were excluded or traits were additionally adjusted for number of piglets born in total.

The variance–covariance structure was:

\[
\begin{bmatrix}
\mathbf{a} \\
\mathbf{m} \\
\mathbf{e}
\end{bmatrix}
= 
\begin{bmatrix}
\mathbf{A} \otimes \mathbf{G}_0 & 0 & 0 \\
0 & \mathbf{I} \otimes \mathbf{M}_0 & 0 \\
0 & 0 & \mathbf{I} \otimes \mathbf{R}_0
\end{bmatrix}
\]

where \( \mathbf{A} \) and \( \mathbf{I} \) are the additive genetic relationship matrix and identity matrix, respectively. \( \mathbf{G}_0, \mathbf{M}_0 \) and \( \mathbf{R}_0 \) represent the variance and covariance matrices of direct additive genetic effects of the piglets, the maternal litter effects and the residual environmental effects, respectively.

Bayesian analyses were carried out using Gibbs sampling in order to estimate the variance components of survival traits and individual birth weight. In these analyses uniformly distributed bounded priors were assigned to the systematic effects with:

\[ \mathbf{b} \sim \text{constant}. \]

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

\[ \mathbf{a} | \mathbf{A}, \mathbf{G}_0 \sim \mathcal{N}(0, \mathbf{A} \otimes \mathbf{G}_0), \]

\[ \mathbf{m} | \mathbf{M}_0 \sim \mathcal{N}(0, \mathbf{I} \otimes \mathbf{M}_0), \]

\[ \mathbf{e} | \mathbf{R}_0 \sim \mathcal{N}(0, \mathbf{I} \otimes \mathbf{R}_0), \]

respectively.

Conjugate prior variance–covariance matrices of \( \mathbf{G}_0, \mathbf{M}_0 \) and \( \mathbf{R}_0 \) were sampled from inverse-Wishart distributions (\( \mathcal{IW} \)) with:

\[ \mathbf{G}_0 | \mathbf{V}_g, \mathbf{V}_a \sim \mathcal{IW}(\mathbf{V}_g \mathbf{V}_a, \mathbf{v}_g), \]

\[ \mathbf{M}_0 | \mathbf{V}_m, \mathbf{V}_m \sim \mathcal{IW}(\mathbf{V}_m \mathbf{V}_m, \mathbf{v}_m), \]

\[ \mathbf{R}_0 | \mathbf{V}_e, \mathbf{V}_e \sim \mathcal{IW}(\mathbf{V}_e \mathbf{V}_e, \mathbf{v}_e), \]

\[ \mathbf{V}_g, \mathbf{V}_m, \mathbf{V}_e \] and \( \mathbf{V}_a \) are known scale parameters for the additive genetic, maternal litter and residual variance–covariance matrices, respectively. Corresponding \( \mathbf{v}_g, \mathbf{v}_m, \mathbf{v}_e \) 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 degree of freedom were chosen to be low with \( \mathbf{v}_g = \mathbf{v}_m = \mathbf{v}_e = 7 \).

The conditional posterior distributions of the variance–covariance matrices of \( \mathbf{G}_0, \mathbf{M}_0 \) and \( \mathbf{R}_0 \) were also sampled from inverse-Wishart distributions, whereas the conditional posterior distributions of the effects \( \mathbf{b}, \mathbf{a}, \mathbf{m} \) and \( \mathbf{e} \) were sampled from multivariate normal distributions.
2.4.2. Bayesian analyses and inferences

Statistical inferences were derived from samples of the marginal posterior distribution obtained by using Gibbs sampling as implemented in the program THRGIBBSF90 (Misztal et al., 2002). The posterior distributions were obtained from a Markov chain of 300,000 iterations using Gibbs sampling. The inspection of the series of iterations of each estimated variance component showed that a “burn in” of 10,000 iterations was necessary to reach the stationary distribution of the Markov chain. To reduce autocorrelations among iterations, only every 25th 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). The heritabilities and genetic correlations of the traits were calculated as posterior means from the marginal distributions of these parameters. In order to identify the precision of the parameters, the 95% highest posterior density (HPD) intervals (Bayesian confidence intervals) were determined from their marginal posterior distributions. In addition, the marginal distributions of the genetic and environmental parameters were drawn in order to inspect their accuracy under consideration of skewness and kurtosis of these distributions.

3. Results

3.1. Descriptive statistics

The mean birth weight, including stillborn piglets, was 20 g less and showed 11 g higher standard deviation than those excluding weights of stillborn piglets (Table 1). Stillbirth occurred at a level of 6.5% of the piglets born, whereas postnatal mortality was 16.3% of the number of piglets born alive. The major cause of postnatal mortality at 61% was crushing, including the combination of crushing with other causes of death. Starvation, low vitality and their combination with other causes explained in total 10% of the losses (Table 2). Differences in survival traits between selection groups (high and control) were small (≤1% points) and non-significantly different from zero. This was expected because selection in the first generation took place on maternal genetic effects, which are expected to be expressed in the second generation. Maximum differences in piglet survival among months of farrowing within the recording period from April to September were significant (P<0.01) and 4.2%, 4.3% and 5.7% points for survival at birth, day one and the entire nursing period, respectively.

Table 2

<table>
<thead>
<tr>
<th>Cause</th>
<th>Single cause</th>
<th>Multiple causes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Incidence</td>
<td>Percentage</td>
</tr>
<tr>
<td>Crushed</td>
<td>469</td>
<td>58.0</td>
</tr>
<tr>
<td>Low vitality</td>
<td>16</td>
<td>2.0</td>
</tr>
<tr>
<td>Starved</td>
<td>44</td>
<td>5.4</td>
</tr>
<tr>
<td>Scour</td>
<td>7</td>
<td>0.9</td>
</tr>
<tr>
<td>Savaged</td>
<td>3</td>
<td>0.4</td>
</tr>
<tr>
<td>Others</td>
<td>220</td>
<td>27.2</td>
</tr>
</tbody>
</table>

Based on the available data (no maternal pedigree) only direct heritabilities representing the genetic contributions of the piglets to their survival and birth weight could be estimated. The posterior means of heritabilities for peri- and postnatal piglet survival ranged from 0.07 to 0.08, whereas the corresponding estimate for individual birth weight was almost three times as high at 0.20 (Table 3). These heritabilities of survival traits and individual birth weight were significantly different from zero as indicated by their 95% HPD intervals in the range of 0.03 to 0.15 and 0.13 to 0.28, respectively (Fig. 1). The posterior distributions of heritabilities of piglet survival traits showed a positive skewness and therefore resulted in relation to their means, in larger HPD intervals than expected under a normal distribution. In contrast, the posterior distribution of the heritability of individual birth weights showed almost a Gaussian distribution and resulted relative to its mean, in a substantially lower HPD interval than those obtained for survival traits. Excluding weights of stillborn piglets changed the heritability of survival traits and birth weight only marginally (Tables 3 and 4). A slightly higher heritability of survival at birth was obtained.

Table 1

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th>Mean/Percentage</th>
<th>S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual birth weight (kg)</td>
<td>5103</td>
<td>1.54</td>
<td>0.370</td>
</tr>
<tr>
<td>(including stillborn piglets)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual birth weight (kg)</td>
<td>4774</td>
<td>1.56</td>
<td>0.359</td>
</tr>
<tr>
<td>(excluding stillborn piglets)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual birth weight (kg)</td>
<td>329</td>
<td>1.27</td>
<td>0.402</td>
</tr>
<tr>
<td>of stillborn piglets</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of piglets born per litter</td>
<td>414</td>
<td>12.8</td>
<td>3.2</td>
</tr>
<tr>
<td>Number of piglets born alive per litter</td>
<td>414</td>
<td>12.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Number of piglets weaned per litter</td>
<td>414</td>
<td>10.0</td>
<td>2.7</td>
</tr>
<tr>
<td>Total piglet born (%)</td>
<td>5293</td>
<td>100</td>
<td>–</td>
</tr>
<tr>
<td>Survival at birth (%)</td>
<td>4948</td>
<td>93.48</td>
<td>–</td>
</tr>
<tr>
<td>Survival at first day after birth (%)</td>
<td>4668</td>
<td>94.34</td>
<td>–</td>
</tr>
<tr>
<td>Survival during entire nursing period (%)</td>
<td>4139</td>
<td>83.65</td>
<td>–</td>
</tr>
</tbody>
</table>

a Number piglets born alive as proportion of total number piglets born.

b Number piglets at the first day after birth as proportion of number piglets born alive.

c Number piglets weaned as proportion of number piglets born alive.

### Table 3

<table>
<thead>
<tr>
<th>Trait</th>
<th>(SVB)</th>
<th>(SVD1)</th>
<th>(SVNP)</th>
<th>(IBW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival at birth (SVB)</td>
<td>0.08 (0.03)</td>
<td>0.29 (0.25)</td>
<td>0.36 (0.26)</td>
<td>0.18 (0.19)</td>
</tr>
<tr>
<td>Survival at first day after birth (SVD1)</td>
<td>0.75 (0.08)</td>
<td>0.07 (0.03)</td>
<td>0.40 (0.23)</td>
<td>0.15 (0.18)</td>
</tr>
<tr>
<td>Survival during the nursing period (SVNP)</td>
<td>0.76 (0.07)</td>
<td>0.78 (0.03)</td>
<td>0.08 (0.03)</td>
<td>0.23 (0.17)</td>
</tr>
<tr>
<td>Birth weight (IBW; incl. stillborn piglet's weight)</td>
<td>0.34 (0.03)</td>
<td>0.36 (0.03)</td>
<td>0.38 (0.03)</td>
<td>0.20 (0.04)</td>
</tr>
</tbody>
</table>

Standard deviation in parentheses.

a Direct genetic effects with respect to the piglets.
after its adjustment for litter size at birth (0.08 vs. 0.10, Tables 3 and 5).

3.3. Genetic correlations

Genetic correlations among direct genetic effects of survival at birth, at first day and during the entire nursing period were low to moderate (0.29 to 0.40, Table 3). Posterior distributions of these estimates indicate that the maximum values of the 95% Bayesian confidence intervals were less than or equal to 0.84, so that these correlations among survival traits are significantly different from one (Fig. 2). On the other side, the correlations among survival traits were, with a probability of 0.86 to 0.95, greater than zero and therefore most likely favourable. Moreover, direct genetic effects of birth weight were positively genetically associated with survival traits, whereby the highest genetic correlation (0.23) was found with survival during the entire nursing period. The probabilities that these correlations were greater than zero ranged from 0.78 to 0.91 (Fig. 2). In particular, the posterior distributions of correlations among peri- and postnatal survival were negatively skewed and resulted in large HPD intervals.

Excluding weights of stillborn piglets reduced the genetic correlations of survival traits with individual birth weight by 13 to 33% of their original values (Tables 3 and 4). These reductions in correlations with individual birth weight influenced the correlations among survival traits, which also declined. Therefore, the highest absolute reduction in genetic correlation after excluding weights of stillborn piglets was

![Fig. 1. Marginal posterior distributions, means ($h^2$), and highest posterior density intervals (in parentheses) of heritabilities for direct genetic effects of piglet survival traits and individual birth weight including weights of stillborn piglets.](image)

<table>
<thead>
<tr>
<th>Table 4</th>
<th>Posterior means of heritabilities (diagonal), genetic correlations (above diagonal) of direct genetic effects and residual environmental correlations (below diagonal) for traits and individual birth weight excluding weights of stillborn piglets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trait</td>
<td>(SVB)</td>
</tr>
<tr>
<td>Survival at birth (SVB)</td>
<td>0.08 (0.04)</td>
</tr>
<tr>
<td>Survival at first day after birth (SVD1)</td>
<td>0.73 (0.08)</td>
</tr>
<tr>
<td>Survival during the nursing period (SVNP)</td>
<td>0.74 (0.08)</td>
</tr>
<tr>
<td>Birth weight (IBW; excl. stillborn piglet's weight)</td>
<td>0.32 (0.05)</td>
</tr>
</tbody>
</table>

Standard deviation in parentheses.

Direct genetic effects with respect to the piglets.

<table>
<thead>
<tr>
<th>Table 5</th>
<th>Posterior means of heritabilities (diagonal), genetic correlations (above diagonal) of direct genetic effects and residual environmental correlations (below diagonal) for piglet survival traits and individual birth weight after adjustment for litter size at birth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trait</td>
<td>(SVB)</td>
</tr>
<tr>
<td>Survival at birth (SVB)</td>
<td>0.10 (0.04)</td>
</tr>
<tr>
<td>Survival at first day after birth (SVD1)</td>
<td>0.73 (0.08)</td>
</tr>
<tr>
<td>Survival during the nursing period (SVNP)</td>
<td>0.74 (0.08)</td>
</tr>
<tr>
<td>Birth weight (IBW; incl. stillborn piglet's weight)</td>
<td>0.34 (0.03)</td>
</tr>
</tbody>
</table>

Standard deviation in parentheses.

Direct genetic effects with respect to the piglets.
found for the association between survival at birth and during the entire nursing period.

Adjustment of survival traits as well as birth weight for litter size also resulted in a reduction in correlations among the analysed traits, except for the correlation between survival at day one and during the entire nursing period (Tables 3 and 5). The greatest decrease in genetic correlation after adjustment for litter size was detected between survival at birth and during the entire nursing period. Moreover, the associations between survival traits and birth weight declined.

3.4 Litter effects

The phenotypic fractions of the variances common to all piglets within a litter were for piglet survival traits (0.11 to 0.22, Table 6), substantially higher than the phenotypic fraction of the direct genetic variances (i.e. heritabilities) of the same traits (Table 3). However, it has to be considered that these litter effects include both maternal genetic and maternal environmental effects. Furthermore, correlations among litter effects of survival traits were of higher magnitude than corresponding correlations among direct genetic effects. Individual birth weight also had higher correlations with survival traits as a result of litter effects (Table 6) rather than due to direct genetic effects (Table 3). Excluding weights of stillborn piglets resulted in almost no change in magnitude of the litter effects and their correlations of all analysed traits and therefore these results have not been presented. In contrast, adjustment for litter size decreased the phenotypic fractions of the litter variances in particular those of birth weight (Table 6 and 7). Moreover, the correlations among litter effects of the analysed traits were reduced by adjustment for litter size, in particular all correlations with survival at birth.

3.5 Residual correlations

The residual environmental correlations among survival traits were of very high magnitude in the range of 0.75 to 0.78.

<table>
<thead>
<tr>
<th>Trait</th>
<th>(SVB)</th>
<th>(SVD1)</th>
<th>(SVNP)</th>
<th>(IBW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival at birth</td>
<td>0.22</td>
<td>0.46</td>
<td>0.53</td>
<td>0.27</td>
</tr>
<tr>
<td>Survival at first day</td>
<td>0.16</td>
<td>0.77</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>Survival during the</td>
<td></td>
<td></td>
<td>0.11</td>
<td>0.43</td>
</tr>
<tr>
<td>nursing period</td>
<td></td>
<td></td>
<td>(SVNP)</td>
<td>(0.09)</td>
</tr>
<tr>
<td>Birth weight</td>
<td></td>
<td></td>
<td></td>
<td>0.21</td>
</tr>
<tr>
<td>(IBW; incl.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stillborn piglet’s</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>weight)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation in parentheses.

Litter variance is a combination of maternal genetic and maternal environmental variances.
Table 7

<table>
<thead>
<tr>
<th>Trait</th>
<th>(SVB)</th>
<th>(SVD1)</th>
<th>(SVNP)</th>
<th>(BW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival at birth (SVB)</td>
<td>0.17</td>
<td>(0.04)</td>
<td>0.28</td>
<td>(0.16)</td>
</tr>
<tr>
<td>Survival at first day after</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>birth (SVD1)</td>
<td>0.13</td>
<td>(0.03)</td>
<td>0.73</td>
<td>(0.07)</td>
</tr>
<tr>
<td>Survival during the</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>nursing period (SVNP)</td>
<td>0.09</td>
<td>(0.02)</td>
<td>0.25</td>
<td>(0.10)</td>
</tr>
<tr>
<td>Birth weight (BW; incl.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stillborn piglet's weight)</td>
<td>0.16</td>
<td>(0.02)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Standard deviation in parentheses.

* Litter variance is a combination of maternal genetic and maternal environmental variances.

(Table 3). Substantially lower residual correlations were estimated between survival traits and birth weight (0.34 to 0.38). Exclusion of stillborn piglets slightly reduced the residual correlations of all traits, especially those between survival traits and birth weight. Adjustment for litter size showed hardly any influence on the residual correlations among traits.

4. Discussion

Mean birth weight for piglets born, born alive and stillborn are reported in the range of 1.27 to 1.46 kg, 1.30 to 1.54 kg and 1.07 to 1.20 kg, respectively, in breeds of Large White, Landrace and Yorkshire (Roehe and Kalm, 2000; Kaufmann et al., 2000; Knol et al., 2002; Grandin et al., 2002; Damgaard et al., 2003; Su et al., 2006). The birth weights obtained in the present study are for all corresponding categories of piglet above those reported in the literature. The reduction in mean piglet birth weight after including weights of stillborn piglets showed that stillborn piglets had substantially lower weights (1.27 vs. 1.56 kg). Interestingly, the standard deviation of piglet birth weight increased after inclusion of stillborn piglets, which supports suggestions that variation of birth weight is associated with pre-term mortality of piglets (Ashworth et al., 1996; Damgaard et al., 2003).

In the present study, survival at birth was, at 93.5%, at the upper level of the literature, which is in the range of 82 to 95% (see literature above cited for mean birth weight and Lund et al., 2002; Serenius et al., 2004; Arango et al., 2005). This higher perinatal survival may be due to the higher activity of outdoor in comparison to indoor sows, suggesting that outdoor sows are physically in better condition for farrowing than those kept indoors. There is a significant amount of data to show that stillbirth rate is reduced in indoor loose farrowing systems in comparison with gestation crates, and that sows subjected to obligatory exercise during gestation have faster farrowings (Perket and Hacker, 1985). However, it may also be an effect of the more accurate post mortem examination to determine stillbirth in the present study than used in standard recording systems of data from outdoor farms, where stillbirths are over-estimated (Edwards et al., 1994). Generally, collection of good records on piglet mortality under outdoor conditions is more difficult than in controlled housing. It has been shown that dead piglets may be overlooked and that causes of mortality may be misclassified, with over-emphasis on stillbirths (Edwards et al., 1994). In the current study, a trained researcher worked in addition to farm staff, used specially designed mobile facilities for data collection and carried out post mortem investigations to accurately determine the cause of death. Under these conditions, a reliable data set was obtained for the analysis. Data from national statistics comparing performance of sows in indoor and outdoor herds do not always show this trend, but this may well be attributable to the incorrect over-assignment of early mortality to the stillbirth category (Edwards et al., 1994).

The survival during the nursing period was, at 84%, below the median of 88% for the same literature cited for survival at birth (range from 77 to 92%). This lower postnatal survival is consistent with findings of Edwards et al. (1994) that there is a higher proportion of piglets being crushed under outdoor than indoor (farrowing crate) conditions.

Whilst a number of studies have been estimated genetic parameters of survival of piglets raised under controlled indoor conditions (e.g. Grandinson et al., 2002; Lund et al., 2002; Serenius et al., 2004; Su et al., 2006), this is to our knowledge the first time that those parameters are estimated on records from outdoor raised piglets. The methodology used in the present analyses accounted for the binary expression of survival traits using a threshold model and the continuously measured birth weight, was fitted using a linear model. Using a Bayesian technique, it was possible to estimate genetic correlations among threshold traits as well as their correlations with a trait fitted using a linear model (Arango et al., 2005).

Genetic parameters for piglet survival traits have mainly been estimated by treating survival as a trait of the dam using, for example, number of piglets stillborn or its proportion of the number of piglets born (see reviews of Blasco et al., 1993; Rothschild and Bidanel, 1998). In the present analysis, piglet survival was regarded as a trait of the piglet in order to estimate direct genetic effects of piglet survival. Therefore, in the following discussion only studies which also estimated genetic effects of survival at the piglet level will be reviewed. Using a linear model, van Arendonk et al. (1996) estimated direct heritabilities for total peri- and postnatal piglet survival of 0.11. Derived from the sire and dam genetic contributions, including all genetic relationships, Lund et al. (2002) obtained direct heritabilities for survival at birth and survival during the nursing period of 0.01 (0.05) and 0.04 (0.02), respectively, in Landrace (Yorkshire). Knol et al. (2002) fitted in a linear model the direct genetic and the litter effects and estimated for a dam (sire) line direct heritabilities of survival at birth and during the nursing period of 0.04 (0.05) and 0.05 (0.05), respectively. Similarly to the present study, Su et al. (2006) used a threshold model for survival traits and a Gaussian model for birth weight. They estimated heritabilities of the direct genetic effects of survival at birth, survival from birth to day 5 and survival from day 6 to weaning of 0.04 (0.01), 0.06 (0.03) and 0.03 (0.03), respectively, in Landrace (Yorkshire). In the present analysis, the heritabilities of the piglet’s direct genetic effects were substantially higher than those reported by Su et al. (2006). One reason may be that under outdoor conditions piglets have a higher genetic contribution to their survival than under indoor conditions. It might be expected that, in the absence of artificial
 aids to reduce risk of crushing and hypothermia, the genetic predisposition for survival would be of greater importance.

For birth weight, direct heritabilities are reported in the range from 0.02 to 0.11 (van Arendonk et al., 1996; Roehe, 1999; Kaufmann et al., 2000; Knol et al., 2002; Grandinson et al., 2002; Chimonyo et al., 2006; Su et al., 2006). The estimates of the present analysis were higher than those in the literature. This may be partly due to the fact that a direct-maternal effects model could not be fitted for the present data and maternal genetic and environmental effects were estimated in a combined litter effect. In a simulation, Rohe and Kennedy (1993) showed that the direct genetic and litter effects model can be efficiently used to estimate direct genetic effects independent of maternal genetic effects, when maternal genetic and maternal environmental effects cannot be disentangled or not enough pedigree information is available. Piglets of the present study were from a three-way cross so that heterosis caused by dominance effects may influence the estimation of direct genetic effects. However, Johansson et al. (1993) showed that litter effects account for dominance effects and therefore no significant bias in estimation of additive genetic effects occurred. Consequently, estimated direct genetic effects may not be over-estimated by maternal genetic and dominance effects, which are expected to be estimated within the litter effects.

The genetic correlations (0.29 to 0.40) among direct genetic effects of survival traits were significantly different from one (upper level of HPD intervals < 0.85). Consequently, these perinatal and postnatal survival traits are recommended to be treated genetically as different traits. In agreement with the present study, Lund et al. (2002) estimated low genetic correlations between direct effects of piglet survival at birth and during the nursing period of 0.20 and 0.05 in Landrace and Yorkshire, respectively. Su et al. (2006) estimated similar direct genetic correlations among survival traits in the range of 0.12 to 0.44.

The genetic correlations between birth weight and survival traits were estimated by Su et al. (2006) to be between 0.15 and 0.60. Their highest correlation is even higher than those estimated in the present study, which may be partly due to the use of differently defined perinatal survival traits. For example, for similar survival traits such as survival at birth, both studies showed similar genetic correlations with birth weight 0.15 vs. 0.18, whereas for survival from birth to day 5 Su et al. (2006) estimated a much higher correlation than those obtained in our study. Grandinson et al. (2002) estimated an unfavourable genetic correlation between stillbirth and birth weight; but a favourable correlation between postnatal crushing of piglets and birth weight. One difficulty of estimation of genetic correlations, in particular for those of stillbirth and birth weight, may be nonlinear genetic associations between these traits. The methodology used in the referenced studies and in the present study assumes linear associations between those traits. However, at least on the phenotypic level, the association between birth weight and survival has been shown to be nonlinear (e.g. Rohe and Kalm, 2000; Canario et al., 2006). Generally, selection for birth weight should be to an optimal birth weight in order to avoid a potential increase in stillbirth due to heavy piglets. In addition, the reduction in variation of birth weight around this optimum birth weight may further improve piglet survival (Damgaard et al., 2003; Rohe, 2003; Canario et al., 2006).

5. Conclusions

The results of the present study showed that piglet survival at birth, at day 1 and during the entire nursing period can be attributed to genetic effects of the piglets, which can be efficiently used to improve their survival. These direct genetic effects explained a substantial higher proportion on the phenotypic variation of piglet survival under outdoor conditions than expected based on studies using data from indoor herds. Genetically, peri-and postnatal survival traits seem to be affected by different genes or gene effects, as indicated by correlations of less than or equal to 0.4. Therefore, a multiple trait model treating at least peri- and postnatal survival as different traits is recommended. The substantial direct genetic effects of birth weight are of great interest to be exploited for correlated improvement of piglet survival. The correlations of direct genetic effects of piglet survival traits and birth weight were all favourable but low. However, even low genetic correlations will have a substantial effect on piglet survival because birth weight showed an almost three times higher heritability and can be measured on the continuous scale. Its inclusion will therefore result in considerably more response to selection than the less informative categorical survival traits (Meuwissen et al., 1999). Recording of weights of stillborn piglets is shown to be informative because it increased the favourable correlation among survival traits as well as their correlations with birth weight. Furthermore, the use of birth weight together with survival traits in the multiple trait model provided important information for the estimation of survival traits.

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References


