Relationship between litter size and perinatal and pre-weaning survival in pigs

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Abstract

The objective of this study was to analyse the relationship between direct and maternal genetic effects on litter size and piglet survival. The analyses were performed on records from 26 564 Landrace litters and 15 103 Yorkshire litters from first parity dams in Finnish herds. The trivariate model fitted total number of piglets born, proportion alive at birth and proportion survived from birth until 3 weeks as traits of the litter. The model included direct genetic and maternal genetic effects for all traits. In Landrace pigs, maternal heritabilities were estimated to be 0.11 for total number born, 0.06 for proportion alive at birth, and 0.08 for proportion survived from birth until 3 weeks. The corresponding estimates for the Yorkshire breed were 0.14, 0.06 and 0.01. All heritability estimates of direct effects were below 0.05. In the Landrace breed, there was a negative correlation of –0.39 between maternal genetic effects on total number born and maternal genetic effects on proportion survived from birth until 3 weeks and a negative correlation of –0.41 between direct and maternal genetic effects on proportion survived from birth until 3 weeks. These correlations were not significant in the Yorkshire breed. The results show that selection for number born in total alone will lead to a deterioration in the maternal ability of sows. Selection for pre-weaning survival could be achieved by selecting on direct and maternal components jointly.

Keywords: genetic correlation, litter size, mortality, piglets, sows.

Introduction

The number of piglets weaned per sow is a trait of major economic importance in pig production. The main components of this trait are the ovulation rate of the sow, early embryonic survival, foetal survival until and around farrowing and survival of piglets from birth until weaning. The number of piglets weaned can be increased by improving any of these components. However, the traits are not uncorrelated and research with mice (Bradford, 1969; Land and Falconer, 1969) and swine (Cunningham et al., 1979; Lambertson et al., 1991) demonstrated that ovulation rate responded to selection but correlated responses in litter size were small. On the other hand, Bradford (1969) selected for prenatal survival in mice and litter size increased significantly. Johnson et al. (1999) selected on an index for ovulation rate and embryonic survival in swine and found a genetic improvement in both traits. Even though the selection increased litter size they found an increase in foetal loss late in gestation and they also found a decline in number of piglets weaned in the selection line. These results indicate that there are unfavourable correlations between the maternal genetic contributions to litter size, foetal survival rate and pre-weaning survival rate of piglets. This is intuitively in conflict with other field studies which suggest that there is a high positive correlation between total number born, number of piglets born alive, and number of piglets alive after 3 weeks (Strang and King, 1970; Johansson and Kennedy, 1985). However, these high correlations are expected due to the high part-whole relationship between the variables that are analysed jointly. In analogy, Lobke
et al. (1983) found that the genetic correlation between litter size and number of piglets lost until weaning was 0.54, which also can be expected by the part-whole relationship. The part-whole relationship arises because number born alive (NBA) is the product of total number born (TB) and the proportion alive at birth (PAB, NBA = TB × PAB). Consequently, the variance of NBA is largely a function of the variance of TB, and the correlation between the two traits is largely just a function of the correlation between TB with itself. Therefore, if the aim is to estimate covariances between TB and a piglet survival trait it is more appropriate to analyse TB and PAB.

Litter size is usually considered a trait of the dam. However, both maternal genetic factors in the sows as well as direct genetic effects in the piglets may influence litter size and the survival traits. Indeed, the effect of crossbred litters (Hill and Webb, 1982) and an early estimate of sire variances (Strang, 1970) show that the progeny genotype has an influence, possibly due to embryonic and early foetal survival. For pre-weaning survival, an early study on pigs from the Nebraska Gene Pool population suggested that the piglets’ own genetic contribution to survival is negligible (Lambertson and Johnson, 1984), while the heritability of maternal contributions was estimated to be between 0.01 and 0.07. In contrast to these results, van Arendonk et al. (1996) analysed two lines (Large White and Pietrain) simultaneously, and estimated the direct heritability to be 0.11. They estimated the maternal heritability to be 0.09 and a negative genetic correlation of -0.56 between direct and maternal genetic effects. This suggests that survival is a trait of the piglets but with an important maternal component.

Therefore, the aim for this study was to estimate direct and maternal genetic variation in total number born, proportion alive at birth, and proportion of liveborns alive at 3 weeks, and genetic correlations between direct and maternal genetic effects on these traits.

Material and methods
Data were available on 36,769 Landrace and 23,179 Yorkshire litters, all purebred first parity litters born in the period 1985 to 1998 from Finnish commercial farms. Records were discarded due to missing pedigree information, small herd-year and sire groups (less than four), and usage of cross fostering. The requirement for no cross fostering deleted only very few records. After editing, records for the analysis included 26,564 Landrace litters from 2408 herd × year groups and 999 artificial insemination (AI) sires, and 15,103 Yorkshire litters from 1347 herd × year groups and 542 AI sires. For these records assessments were available for TB, NBA and number of piglets alive after 3 weeks (NA3W). According to the instructions from the national Finnish breeding organization, NBA is defined as the number of piglets alive the first time the litter is recorded (i.e. if the litter was born during the night; the piglets that died before recording in the morning were defined as still born piglets). NA3W was recorded as the number of piglets alive at 21 days of age.

The three traits in the analyses were TB, proportion alive at birth (PAB = NBA/TB) and proportion of live born alive at 3 weeks (PAW = NA3W/NBA).

Because we only have records on the litters and not individual piglets, it is not possible to use an animal model for piglets with the usual assumptions. Instead we use the model below with contributions from sires and dams of the piglets.

\[
\begin{bmatrix}
TB \\
PAB \\
PAW
\end{bmatrix}
\begin{bmatrix}
X_{TB} & 0 & 0 \\
0 & X_{PAB} & 0 \\
0 & 0 & X_{PAW}
\end{bmatrix}
\begin{bmatrix}
\beta_{TB} \\
\beta_{PAB} \\
\beta_{PAW}
\end{bmatrix}
\end{equation}
\]

where \(X_{TB}, X_{PAB}\) and \(X_{PAW}\) are design matrices for fixed effects in \(\beta\), which only includes a season effect. \(X_{TB}, X_{PAB}\) and \(X_{PAW}\) are design matrices for the random herd year effects \(\mathbf{h}_{TB}, \mathbf{h}_{PAB}\) and \(\mathbf{h}_{PAW}\). \(Z\)'s are design matrices for sire effects, and dam effects.

Random effects were assumed to follow a normal distribution with mean zero and the following variances.

\[
\operatorname{Var}[\mathbf{h}_{TB}, \mathbf{h}_{PAB}, \mathbf{h}_{PAW}] = \mathbf{G}_0 \otimes \mathbf{I}_v \quad \operatorname{Var}[\mathbf{d}_{TB}, \mathbf{d}_{PAB}, \mathbf{d}_{PAW}] = \mathbf{G}_0 \otimes \mathbf{I}_v
\]

where \(\mathbf{H}_0, \mathbf{G}_0\) and \(\mathbf{R}_0\) are variance-covariance matrices of random effects over the three traits.

The (co)variance components were estimated using the average information restricted maximum likelihood (AI-REML) procedure (Jensen et al., 1997) in the DMU package (Madsen and Jensen, 2000).
In this model the sire effect is half the sire direct genetic effect and the dam effect is half the dam direct genetic effect plus the maternal genetic effect. As a result the variances and covariances estimated will be a mixture of direct and maternal effects. Within a trait the relationships are: $\sigma_s^2 = \sigma_{a,m}^2 + \sigma_{a,m} + 1/4\sigma_d^2$, $\sigma_d^2 = 1/4\sigma_s^2$, and $\sigma_{a,d} = 1/2\sigma_{a,m} + 1/4\sigma_d^2$. Covariances between traits are: $\sigma_{a1,d2} = \sigma_{m1,m2} + \sigma_{a1,m2} + 1/4\sigma_{s1,s2}$, $\sigma_{s1,d2} = 1/4\sigma_{s1,s2}$, and $\sigma_{s1,d2} = 1/2\sigma_{s1,m2} + 1/4\sigma_{s1,s2}$. These relationships were used to transform results from the analysis into a variance covariance matrix between direct and maternal effects. For the transformed components a Taylor series expansion was used to calculate the standard errors of the estimates.

**Results**

Landrace and Yorkshire pigs had similar means in TB (10.2 (s.e. 2.7) and 10.4 (s.e. 2.9)), PAB (0.92 (s.e. 0.13) and 0.93 (s.e. 0.15)), and PAW (0.89 (s.e. 0.14) and 0.92 (s.e. 0.15)). Table 1 shows the residual variances and correlations between the three traits for the Landrace and Yorkshire breeds. Sire and dam variances and covariances were transformed to obtain estimates of direct and maternal variances. These estimates were used to calculate direct and maternal heritabilities and correlations, which are shown in Tables 2 and 3. For the Landrace breed, all direct and maternal variances were estimated to be significantly larger than zero. For the Yorkshire breed, maternal heritabilities for TB and direct and maternal variances for PAB were estimated to be significantly larger than zero. Most correlations were small and not significantly different from zero. However, maternal genetic effects on TB show consistently negative correlations with direct effects on TB (significant in both breeds), maternal genetic effects on PAB (significant in Landrace), maternal genetic effects on PAW in the Landrace breed and direct effects on PAW in the Yorkshire breed. The correlation between maternal genetic effects on TB and PAW was not significant in the Yorkshire breed of pig because there was very low genetic variation.

### Table 1  Residual variances (diagonals) and correlations under the diagonals (with s.e.), for Landrace and Yorkshire pigs

<table>
<thead>
<tr>
<th></th>
<th>Landrace</th>
<th></th>
<th>Yorkshire</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_{TB}$</td>
<td>$r_{PAB}$</td>
<td>$r_{PAW}$</td>
<td>$r_{TB}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r_{TB}$</td>
<td>6.427</td>
<td>0.006</td>
<td>7.103</td>
<td>0.123</td>
</tr>
<tr>
<td>$r_{PAB}$</td>
<td>-0.015</td>
<td>0.066</td>
<td>-0.097</td>
<td>0.010</td>
</tr>
<tr>
<td>$r_{PAW}$</td>
<td>0.170</td>
<td>0.055</td>
<td>0.069</td>
<td>0.005</td>
</tr>
</tbody>
</table>

### Table 2  REML estimates of direct and maternal heritabilities (diagonal) and correlations between direct and maternal effects (with s.e.) for Landrace pigs

<table>
<thead>
<tr>
<th></th>
<th>$m_B$</th>
<th>$a_B$</th>
<th>$m_{PAB}$</th>
<th>$a_{PAB}$</th>
<th>$m_{PAW}$</th>
<th>$a_{PAW}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m_B$</td>
<td>0.11</td>
<td>0.003</td>
<td>0.09</td>
<td>0.004</td>
<td>0.005</td>
<td>0.001</td>
</tr>
<tr>
<td>$a_B$</td>
<td>-0.20</td>
<td>0.094</td>
<td>0.21</td>
<td>0.116</td>
<td>0.33</td>
<td>0.161</td>
</tr>
<tr>
<td>$m_{PAB}$</td>
<td>-0.05</td>
<td>0.028</td>
<td>0.09</td>
<td>0.010</td>
<td>0.09</td>
<td>0.010</td>
</tr>
<tr>
<td>$a_{PAB}$</td>
<td>0.05</td>
<td>0.139</td>
<td>0.33</td>
<td>0.161</td>
<td>0.25</td>
<td>0.186</td>
</tr>
<tr>
<td>$m_{PAW}$</td>
<td>-0.05</td>
<td>0.059</td>
<td>-0.22</td>
<td>0.126</td>
<td>0.20</td>
<td>0.075</td>
</tr>
<tr>
<td>$a_{PAW}$</td>
<td>0.05</td>
<td>0.093</td>
<td>-0.22</td>
<td>-0.126</td>
<td>-0.41</td>
<td>0.086</td>
</tr>
</tbody>
</table>

### Table 3  REML estimates of direct and maternal heritabilities (diagonal) and correlations between direct and maternal effects (with s.e.) for Yorkshire pigs

<table>
<thead>
<tr>
<th></th>
<th>$m_B$</th>
<th>$a_B$</th>
<th>$m_{PAB}$</th>
<th>$a_{PAB}$</th>
<th>$m_{PAW}$</th>
<th>$a_{PAW}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m_B$</td>
<td>0.14</td>
<td>0.019</td>
<td>0.01</td>
<td>0.001</td>
<td>0.01</td>
<td>0.001</td>
</tr>
<tr>
<td>$a_B$</td>
<td>-0.47</td>
<td>0.231</td>
<td>0.09</td>
<td>0.008</td>
<td>0.06</td>
<td>0.001</td>
</tr>
<tr>
<td>$m_{PAB}$</td>
<td>-0.15</td>
<td>0.128</td>
<td>-0.60</td>
<td>0.104</td>
<td>-0.07</td>
<td>0.005</td>
</tr>
<tr>
<td>$a_{PAB}$</td>
<td>0.01</td>
<td>0.222</td>
<td>0.13</td>
<td>0.026</td>
<td>-0.48</td>
<td>-0.19</td>
</tr>
<tr>
<td>$m_{PAW}$</td>
<td>-0.48</td>
<td>0.427</td>
<td>-0.04</td>
<td>0.123</td>
<td>0.05</td>
<td>0.032</td>
</tr>
<tr>
<td>$a_{PAW}$</td>
<td>0.01</td>
<td>0.413</td>
<td>0.04</td>
<td>0.075</td>
<td>0.01</td>
<td>0.060</td>
</tr>
</tbody>
</table>
in PAW. In the Landrace breed there was a positive genetic correlation between direct and maternal effects on PAB and a negative genetic correlation between direct and maternal effects on PAW. Further, there was a positive genetic correlation between maternal effects on PAB and PAW.

**Discussion**

This study established that genetic variation exists for direct and maternal effects for litter size (TB), perinatal survival (PAB), and pre-weaning survival (PAW), and that important correlations exist between these effects.

The maternal heritabilities for TB were in close agreement with estimates from previous studies where the trait was measured as a trait of the sow (Rothschild and Bidanel, 1998). The direct heritability for TB was smaller, which is in agreement with results of Brandt and Grandjot (1998) who analysed litter size with the effect of litter sire in the model and found a heritability of 0.01. However, the direct heritability was significantly different from zero in the Landrace and our results therefore indicate that there may be a direct genetic contribution of progeny in some breeds. This direct effect probably includes both fertility of individual eggs and sperms and individual embryo survival.

In the Yorkshire breed, direct and maternal heritabilities were higher for PAB than for PAW, while in the Landrace it was the other way around. According to Rothschild and Bidanel’s review (1998) prenatal survival rate has a higher heritability than piglet survival to weaning, when regarded as traits of the sow. However, using that model will underestimate the maternal genetic contribution if it is negatively correlated to a significant direct genetic component. Another difference between the analyses is that we only used records from litters where crossfostering (which is not common in Finland) had not been practised. Maternal effect on survival after farrowing is more difficult to measure when crossfostering is used. The maternal heritabilities were higher than the direct heritabilities for PAB in both breeds and for PAW in the Landrace, which is in agreement with results from van Arendonk et al. (1996) who measured the total survival of each piglet during farrowing and lactation and included individual piglet weight at birth.

Genetic correlations were generally small but two important results were found. First, the maternal genetic effects on TB were in general negatively correlated with direct effects on TB and direct and maternal effects on PAB and PAW, especially with a negative correlation of −0.39 with maternal effects on PAW in the Landrace. Therefore, selecting for sows with high litter size may lead to deterioration in mothering ability of sows and other components associated with piglet survival. This could be one explanation why selection for TB in a composite population of Landrace and Large White pigs did not show a correlated response in number of piglets weaned, in the selection experiment of Johnson et al. (1999). Second, the genetic correlation between direct and maternal genetic effects on PAW was unfavourable (−0.41) in the Landrace. Thus, to improve piglet survival it may be necessary to select for both direct and maternal effects. We analysed prenatal and pre-weaning survival as two different traits. Without post-mortem examination it is difficult to distinguish between stillborn piglets and piglets dying during the first hours after birth (Vaillancourt et al., 1990). However, based on the low genetic and residual correlations between PAB and PAW they seem to be very different traits.

There were some differences between estimates from the two breeds. This could be a general difference between the Yorkshire and Landrace but the difference between populations within a breed could be equally important. In this study, Yorkshire litters tended to be larger, both in total number born and number born alive. In data from the Swedish litter recording scheme, total number born was higher in the Yorkshire than in the Landrace but perinatal survival was lower, resulting in less piglets born alive (9.72 v. 9.92 for first prenatal survival; Tummaruk et al., 2000). This shows that variances and covariances of direct and maternal components of survival must be estimated in the actual population before an effective breeding programme can be designed. In the Finnish populations studied here selection for perinatal survival seems possible in both the Landrace and the Yorkshire. For the Landrace, selection for pre-weaning survival should be achieved by selecting on direct and maternal components jointly, while very little genetic variance seems to exist for pre-weaning survival in the Yorkshire breed.

Current selection programmes focus on genetic improvement in TB. When larger litters are selected for it increases the demands on the mothering ability of sows if the piglets are to survive until weaning. The strategy to cope with this has been to crossfoster piglets in order to spread the burden. However, when decreased mothering ability is inadvertently selected for, as indicated by results from these analyses, even crossfostering is not enough to maintain the survival rate. In France, an effective selection for TB has resulted in large genetic progress in the Hyperprolific Large White (Bidanel et al., 1994). When 25% of the sows produce 15 or more
Genetic effects on litter size and piglet survival

piglets per litter, as reported by Orgeur et al. (1998), sows’ demands on the environment and management routines increases dramatically. Fostering, followed by weaning 1 week after birth is a method currently used to save surplus piglets (Orgeur et al., 2000). This shows that selection for TB alone is not optimal. However, genetic improvement of piglet survival is possible and should be initiated. Indeed the most efficient way to increase number of weaned piglets may be to concentrate selection on improving the survival rate.

The selection criteria should be chosen based on the relevant variances and covariances in a given population. It is not necessary to include all six genetic effects in the evaluation. If, for example, direct variances are negligible for TB and prenatal survival, it might be sufficient to model events until after farrowing using maternal effects on number born alive. In most populations crossfostering is a common practice. This means that it is not necessarily the biological mother that has the maternal effect on a given piglet’s survival, since the maternal effect for the piglet is the environmental effect of the sow that nurses it. If assessments of maternal genetic effects on piglet survival are aimed for, it is therefore important to know which sow affected the relevant trait for each piglet. This makes it difficult to define one trait (e.g. number of piglets weaned) that can be selected for directly. Because most crossfostering are completed within the first 2 days after farrowing it is convenient to define different survival traits before and after e.g. day 2 after farrowing. If direct or maternal genetic variance exists in survival from day two to weaning this trait should be included as a selection criteria.

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References


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