Genetic and phenotypic relationships of farrowing and weaning survival to birth and placental weights in pigs

H. Mesa, T. J. Safranski, K. M. Cammack, R. L. Weaber, and W. R. Lamberson

Division of Animal Sciences, University of Missouri, Columbia 65211

ABSTRACT: Data obtained during 4 generations of divergent selection for placental efficiency were used to determine factors influencing survival at farrowing and weaning in litters produced by first-parity females. Data were collected from 193 litters and included records on 2,053 individuals. Farrowing survival (FS) and weaning survival (WS) were considered traits of the piglet and were scored 1 if the individual was alive at a time point or 0 if dead. Estimates of (co)variance components for direct and maternal additive genetic effects for FS and WS were obtained using an animal model and computed with the MTDFREML program. Estimates of direct heritability were 0.16 for FS and 0.18 for WS. Estimates of maternal heritability were 0.14 for FS and 0.10 for WS. Genetic correlation estimates between direct and maternal effects were high and negative for both traits. The direct genetic correlation between FS and WS was 0.92. Variables associated with FS and WS were determined using logistic regression procedures. Birth weight (BRW), placental weight, their interaction, and total born can be used as predictors of survival at farrowing in the absence of estimates of genetic merit for survival. The same model, excluding total number born, was the best model for predicting WS. In the presence of BRW information, placental efficiency did not improve the prediction of survival. While it was clearly disadvantageous for a piglet to be below the litter mean in BRW, being above the mean did not provide a substantial advantage in survival. Results from this analysis suggest that it is possible to select for increased survival at farrowing and at weaning. Information on a piglet’s BRW, placental weight, litter average BRW, and deviation from litter average BRW can be used to optimize those values at levels resulting in high survival probability.

Key words: birth weight, genetic parameter, pig, survival

INTRODUCTION

Litter size at weaning is a trait of major economic importance to swine producers (Tess et al., 1983). It may be possible to effectively increase litter size by selection (Lamberson et al., 1991; Bidanel et al., 1994; Johnson et al., 1999), although its heritability is low. A correlated response to selection for increased litter size has been decreased birth weight (BRW; Johnson et al., 1999; Mesa et al., 2003). Low BRW, and particularly low BRW within a litter, has been linked to high piglet mortality (Damgaard et al., 2003). A survey of US swine producers in 2000 revealed that average litter size was 10.9 pigs, of which 10.0 were born alive and 8.9 survived to weaning. Thus, of those pigs born alive, average preweaning mortality was 11%; more than 50% of preweaning deaths resulted from being crushed by the sow (USDA, 2002). Previous results have suggested that direct selection for increased preweaning survival may not be effective because the heritability seems to be very low (Lamberson and Johnson, 1984; Grandinson et al., 2002), although the heritability of stillbirths may be somewhat greater (Grandinson et al., 2002).

These traits are, in part, connected by prenatal growth of the piglet, which in turn is influenced by the placenta. Emphasis on placental efficiency, defined as the ratio of BRW to placental weight (PW) at birth, may be a mechanism through which litter size can be increased while maintaining adequate BRW (Wilson et al., 1999). Data for the current study were collected during 4 generations of divergent selection for placental efficiency (PE; Mesa et al., 2005). The objectives of this study were to determine the relationships between BRW and PW and factors influencing survival at farrowing and weaning in swine.

MATERIALS AND METHODS

Selection procedures and results of the selection experiment that provided the data for this study have

1Research supported by the Missouri Agricultural Experiment Station and National Pork Producers Council.
2Corresponding author: LambersonW@missouri.edu
Received December 17, 2004.
Accepted September 13, 2005.
been reported previously (Mesa et al., 2005). Briefly, divergent selection was performed on an index that included total number born (TB), BRW, and PW. Animals were ranked based on an index (index = 0.073 TB + 0.003 BRW − 0.012 PW), and the greatest and lowest ranking individuals were selected to produce divergent lines with either high or low PE, calculated as the ratio of BRW to PW. Selection produced significant genetic and phenotypic divergence between lines in PW and PE. The divergence in PW caused differences in PE to result from piglets of similar weight being associated with smaller placentas in the high line than in the low line.

**Animal Management**

Data were collected from only 193 litters produced by 68 sires over 5 generations. Due to the intensive nature of data collection, they were not available from larger populations. To facilitate data collection, each farrowing group was limited to a 7-d period. The generation interval was 1 yr, and females produced only 1 litter. Animals were fed a diet based on corn-soybean meal and formulated to meet or exceed NRC requirements at every stage (NRC, 1998). At 107 d of pregnancy, females were transferred to the Animal Sciences Research Center farrowing facility, where parturition was supervised 24 h/d. In the morning of the fifth day of the 7-d farrowing period, parturition was induced in females that had not already farrowed with 2 i.m. injections of 10 mg of dinoprost (5 mg/mL; Lutalyse; Pharmacia and Upjohn Co., Kalamazoo, MI) given 12 h apart.

To match each piglet to its placenta at birth, the umbilical cord of each fully formed piglet was double-tagged with identically numbered mouse ear tags (Gey Band & Tag Co., Norristown, PA). One tag was placed approximately 10 cm from the piglet, and the umbilical cord was severed so the first tag retracted into the birth canal with the cord stump. The second tag was placed on the piglet’s umbilical cord stump approximately 5 cm from the abdomen. Piglets were weighed immediately after birth, before suckling began, and all placentas were collected and individually weighed at delivery. Approximately 21% of the placentas were not tagged because the umbilical cord broke during the tagging process or the piglet was already detached from it at birth.

Piglets were processed and ear-notched within 24 h of farrowing. Fostering was minimal. Thus, the natural mother and nurse effects were confounded in all analyses. Piglets were weaned when the oldest litter was 21 d of age (average 18 d) and subsequently maintained in environmentally controlled nursery facilities. Farrowing survival (FS) and weaning survival (WS) were each considered a binary trait of the piglet and scored 1 if the individual was alive or 0 if it was dead at the respective time points. Stillborn piglets were accurately differentiated from early postnatal deaths as a result of the constant farrowing supervision. Piglets were considered born alive even if they died within minutes after being born. Unthrift piglets killed before weaning were classified as dead even if they might have survived until just before weaning.

Analyses of survival traits in this study were retrospective. Consequently, management practices were not designed to facilitate the interpretation of such analyses. For example, obstetric assistance was provided to those females having difficulty at farrowing, and this might have increased a piglet’s ability to survive at farrowing. Similarly, the cause and time of death of piglets that were dead at weaning was not recorded. However, because of these data collection protocols, the results from this study could be extrapolated to swine herds where obstetric assistance is routine.

**Statistical Analyses**

The relationship between BRW and PW was explored by fitting segmented and nonlinear regression curves to the data. A quadratic regression with plateau and a nonlinear model (Brody curve) describing changes in BRW dependent on PW were fitted by using PROC NLIN (SAS Inst., Inc., Cary, NC).

Estimates of (co)variance components for FS and WS for direct and maternal additive genetic effects were obtained using an animal model and computed with the multiple-trait, derivative-free REML program (Boldman et al., 1995). This program was also used to estimate heritabilities and genetic and phenotypic correlations. The basic univariate model was:

\[ y = Xb + Z_a a + Z_c c + e, \]

in which \( y \) is a vector of observations corresponding to the trait(s) in the analysis, \( b \) is a vector of fixed effects (contemporary group and sex) for the trait, \( a \) is a vector of random animal genetic effects, \( c \) is a vector of random litter effects, \( e \) is a vector of random residual effects, \( X \) is an incidence matrix relating observations to fixed effects, \( Z_a \) is an incidence matrix relating observations to random animal genetic effects, and \( Z_c \) is an incidence matrix relating observations to random litter effects. Assumptions for the univariate model were:

\[
E[y] = Xb \text{ and } \]

\[
\text{Var}[y] = \begin{bmatrix} a & 0 \\ c & \end{bmatrix} \begin{bmatrix} \sigma_a^2 & 0 \\ 0 & \sigma_c^2 \end{bmatrix},
\]

in which matrix \( A \) is the numerator relationship matrix and \( I \) is the identity matrix of appropriate order. Birth weight and TB were additionally included as linear covariates. Two-trait analyses performed for FS and WS, FS and PW, FS and PE, WS and BRW, WS and PW, and WS and PE excluded the linear adjustment...
Table 1. Models used to test the association of trait combinations with farrowing survival (FS) and weaning survival (WS)

<table>
<thead>
<tr>
<th>Set number</th>
<th>Model Effect tested</th>
<th>FS Log likelihood</th>
<th>Effect tested</th>
<th>WS Log likelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>I 1</td>
<td>BRW, PW, BRW × PW, TB</td>
<td>-206.65</td>
<td>BRW, PW, BRW × PW, TB</td>
<td>-498.11</td>
</tr>
<tr>
<td>I 2</td>
<td>PW, PE, TB</td>
<td>-221.57</td>
<td>PW, PE, TB</td>
<td>-489.34</td>
</tr>
<tr>
<td>I 3</td>
<td>BRW, PE, TB</td>
<td>-211.75</td>
<td>BRW, PE, TB</td>
<td>-488.89</td>
</tr>
<tr>
<td>II 4</td>
<td>mBRW, dBRW, TB</td>
<td>-216.51</td>
<td>mBRW, dBRW, mBRW × TB</td>
<td>-492.26</td>
</tr>
<tr>
<td>II 5</td>
<td>mPW, dPW, TB</td>
<td>-221.57</td>
<td>mPW, dPW, TB</td>
<td>-514.59</td>
</tr>
<tr>
<td>II 6</td>
<td>mPE, dPE, TB</td>
<td>-221.57</td>
<td>mPE, dPE, TB</td>
<td>-511.49</td>
</tr>
</tbody>
</table>

1 Each model tested included all possible linear interactions of its components.
2 BRW = birth weight, PW = placental weight, PE = placental efficiency, mBRW = litter mean BRW, mPW = litter mean PW, mPE = litter mean placental efficiency, dBRW = deviation from litter mean BRW, dPW = deviation from litter mean PW, dPE = deviation from litter mean placental efficiency, and TB = total born.
3 Log likelihood values refer to the model with all significant effects entered.
4 Denotes effects selected for inclusion in a model of FS.
5 Denotes effects selected for inclusion in a model of WS.

for BRW. Threshold models fit binary data better than linear mixed models. However, both approximations perform equally well for the estimation of variance components over a range of different incidence levels (Mäntysaari et al., 1991). The pedigree file represented 7 generations (including parents and grandparents at the base generation) and included 2,236 individuals.

Variables associated with FS and WS were determined using logistic regression procedures (PROC LOGISTIC, SAS Inst., Inc.). Farrowing survival and WS were defined as binary-dependent variables with survival coded as 1 and death as 0. Multiple linear regression techniques were not chosen for analysis of this data because they focus on prediction of a continuously distributed dependent variable. Rather, logistic regression was chosen because most of the other assumptions required for a typical linear multiple regression were violated here. The assumptions required for multiple linear regression include a linear relationship between independent and dependent variables, homoscedasticity of error terms, and a normal distribution of error terms. Logistic regression only assumes a linear relationship between the log of the odds ratio (logit) and independent variables. In fact, the logit is a transformation of the dependent variable such that the typical regression assumptions of linearity, normality, and homoscedasticity are closely met. The independent variables of BRW, PW, PE, and an individual piglet’s deviations from litter means for these 3 traits were treated as continuous variables.

A detailed description of the models evaluated is presented in Table 1. Each trait was fitted to 2 sets of models exploring different combinations of explanatory variables. Set I (Models 1 to 3) tested the effects of BRW, PW, and PE. Set II (Models 4 to 6) tested the effects of litter average for BRW, PW, PE, and the individual’s deviation from its litter mean for each trait. All models also included the effect of TB. Main effects and their interactions were entered into a model one at a time using the FORWARD model selection option. After all variables with significant effects in each model had been entered, the best model from each set was selected for goodness of fit. Model selection was based on log likelihood ratio tests after the data were trimmed to ensure that models were compared using the same number of observations.

Probabilities of FS and WS were predicted using logistic regression estimates obtained from Models 1 and 4. The probabilities of survival at birth and at weaning were calculated for deviations from the mean for significant effects in a model by using the inverse link function

\[ p_i = \frac{e^{X_i\beta}}{1 + e^{X_i\beta}}, \]

in which \( p_i \) is the probability estimate, \( X \) is the coefficient matrix, and \( \beta \) is the solution vector (Kaps and Lamberson, 2004).

RESULTS

Descriptive statistics for litter traits and for traits tested for association with FS and WS are presented in Table 2.

A Brody curve and a segmented regression curve describing the relationship between BRW and PW are plotted in Figure 1.

The Brody curve was of the form:

\[ BW_i = A - (A - BW_{100})e^{-k(PW_i - PW_{100})}, \]

in which

\[ A = 1,893 \text{ g} \quad \text{(asymptotic BRW)}, \]
\[ BW_{100} = 661.3 \text{ g} \quad \text{(estimated BRW at PW}_{100}). \]
Table 2. Numbers of observations and descriptive statistics for litter traits, farrowing survival (FS) and weaning survival (WS), and associated traits\(^1\)

<table>
<thead>
<tr>
<th>Variable</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>FS</td>
<td>2,053</td>
<td>0.96</td>
<td>0.18</td>
<td>0</td>
<td>1.0</td>
</tr>
<tr>
<td>WS</td>
<td>1,981</td>
<td>0.89</td>
<td>0.31</td>
<td>0</td>
<td>1.0</td>
</tr>
<tr>
<td>FS EBV, %</td>
<td>2,053</td>
<td>-0.30</td>
<td>2.47</td>
<td>-15.8</td>
<td>11.4</td>
</tr>
<tr>
<td>WS EBV, %</td>
<td>2,053</td>
<td>2.11</td>
<td>4.69</td>
<td>-20.2</td>
<td>18.0</td>
</tr>
<tr>
<td>BRW, g</td>
<td>2,050</td>
<td>1,390</td>
<td>334</td>
<td>75</td>
<td>2,530</td>
</tr>
<tr>
<td>mBRW, g</td>
<td>193</td>
<td>1,421</td>
<td>236</td>
<td>808</td>
<td>2,173</td>
</tr>
<tr>
<td>Deviation from mBRW, g</td>
<td>2,050</td>
<td>0.0</td>
<td>248</td>
<td>-1,000</td>
<td>988</td>
</tr>
<tr>
<td>PW, g</td>
<td>1,630</td>
<td>305</td>
<td>99.3</td>
<td>54</td>
<td>714</td>
</tr>
<tr>
<td>mPW, g</td>
<td>189</td>
<td>311</td>
<td>67.9</td>
<td>135</td>
<td>569</td>
</tr>
<tr>
<td>Deviation from mPW, g</td>
<td>1,630</td>
<td>0.0</td>
<td>76.1</td>
<td>-241</td>
<td>315</td>
</tr>
<tr>
<td>PE, g</td>
<td>1,630</td>
<td>4.9</td>
<td>1.27</td>
<td>1.7</td>
<td>15.9</td>
</tr>
<tr>
<td>mPE, g</td>
<td>189</td>
<td>4.9</td>
<td>0.74</td>
<td>3.37</td>
<td>7.84</td>
</tr>
<tr>
<td>Deviation from mPE, g</td>
<td>1,630</td>
<td>0.0</td>
<td>1.07</td>
<td>-3.6</td>
<td>8.9</td>
</tr>
<tr>
<td>Total born</td>
<td>193</td>
<td>11.0</td>
<td>3.3</td>
<td>2.0</td>
<td>18.0</td>
</tr>
<tr>
<td>Born alive</td>
<td>193</td>
<td>10.4</td>
<td>3.3</td>
<td>2.0</td>
<td>17.0</td>
</tr>
<tr>
<td>Stillborn</td>
<td>193</td>
<td>0.6</td>
<td>1.2</td>
<td>0.0</td>
<td>9.0</td>
</tr>
<tr>
<td>Mummies</td>
<td>193</td>
<td>0.8</td>
<td>1.2</td>
<td>0.0</td>
<td>8.0</td>
</tr>
<tr>
<td>Number weaned</td>
<td>193</td>
<td>9.5</td>
<td>3.3</td>
<td>0.0</td>
<td>17.0</td>
</tr>
</tbody>
</table>

1\(^1\)EBV = estimated breeding value, BRW = birth weight, mBRW = litter mean BRW, PW = placental weight, mPW = litter mean PW, PE = placental efficiency, and mPE = litter mean placental efficiency.

PW\(_{100} = 100\) g (lower PW associated with a fully formed piglet), and

\(k = 0.00515\) (growth rate index).

The segmented regression curve was of the form

\[
BW_i = a + (b \times PW_i) + c \times PW_i^2 \quad \text{for} \ PW_i \leq X_0
\]

\[
BW_i = a + (b \times X_0) + (c \times X_0^2) \quad \text{for} \ PW_i > X_0,
\]

in which

\(a = 213.4\) g (intercept),

\(b = 5.76\) (linear regression coefficient),

\(c = -0.005\) (quadratic regression coefficient),

\(X_0 = 529.2\) g [point on the X axis at which the plateau begins (knot)], and

BRW plateau = 1,738 g for all PW \(\geq X_0\).

The segmented regression analysis of BRW on PW showed that BRW increased to a plateau of 1,738 g with increasing PW up to 529 g. This indicated that within the range of PW observed in most populations, a heavier placenta will always allow the expression of growth potential to produce a heavier piglet. Although the Brody curve predicted a greater plateau for BRW, the 2 curves were very similar in the range over which PW were densely represented.

Estimates of variance components and genetic parameters from single-trait models are presented in Table 3. The direct and maternal heritability for FS and WS showed substantial additive genetic variation for these 2 traits. The correlations between direct and maternal effects for both traits were high and negative. There was a significant common litter environmental effect for FS, but the estimate for WS was not significantly different from 0.

Estimates of direct and maternal genetic correlations between FS and WS, BRW, PW, and PE are presented in Table 4. Both direct and maternal correlations between FS and WS were close to 1, which indicated that essentially the same genetic effects influenced both traits. The direct genetic correlation was positive and high between BRW and FS, and positive and moderate between BRW and WS. Placental weight had the lowest direct and maternal correlations with FS and WS. The

Figure 1. Scatter plot of the relationship between birth weight (BRW) and placental weight (PW), and fitted Brody curve and segmented regression curve with plateau.
Table 3. Estimates of (co)variance components and genetic parameters with SE from single-trait models for farrowing survival (FS) and weaning survival (WS)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\sigma^2_p$</th>
<th>$h^2_a$</th>
<th>$h^2_m$</th>
<th>$r_{am}$</th>
<th>$l^2$</th>
<th>$e^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>FS</td>
<td>0.03075</td>
<td>0.16 (0.12)</td>
<td>0.14 (0.08)</td>
<td>-1.0 (0.16)</td>
<td>0.15 (0.05)</td>
<td>0.70 (0.08)</td>
</tr>
<tr>
<td>WS</td>
<td>0.08763</td>
<td>0.18 (0.10)</td>
<td>0.10 (0.06)</td>
<td>-0.77 (0.19)</td>
<td>0.00 (0.02)</td>
<td>0.83 (0.07)</td>
</tr>
</tbody>
</table>

1$\sigma^2_p$ = phenotypic variance, $h^2_a$ = additive heritability (SE), $h^2_m$ = maternal heritability (SE), $r_{am}$ = correlation between additive and maternal genetic effects (SE), $l^2$ = proportion of phenotypic variance due to litter effect (SE), and $e^2$ = proportion of phenotypic variance due to environmental effects (SE).

direct and maternal correlations between PE and FS were positive, but the direct correlation between PE and WS was negative.

Of the models describing FS in terms of BRW, PW, PE, and TB (set I), the greatest log likelihood was obtained when BRW, PW, BRW \times PW, and TB were included (Model 1). When FS was modeled in terms of litter mean BRW (mBRW), litter mean PW (mPW), litter mean PE (mPE), and the individual’s deviation from each mean (dBRW, dPW, and dPE, respectively; set II), mPW, mPE, dPW, and dPE had no predictive value. Therefore, Model 4 (mBRW, dBRW, and their interaction) was selected for further analyses.

Of the models describing WS in terms of BRW, PW, PE, and TB (set I), the greatest log likelihood was obtained when BRW, PW, and BRW \times PW were included (Model 1). When WS was modeled in terms of mBRW, mPW, mPE, and the individual piglet’s deviations from their respective litter means (set II), Model 4 (mBRW, dBRW, and their interaction) had the greatest log likelihood.

Logistic regression coefficients and their significance for effects included in Models 1 and 4 are presented for both survival traits in Table 5. A response surface describing the probability of FS predicted by model 1 is presented in Figure 2a. The probability of FS is dramatically reduced when BRW drops below the population average (1,390 g), but it was not substantially increased for piglets weighing more than average. For piglets with BRW in the range from 800 to 1,000 g, increasing PW has a slight positive effect on FS. Conversely, if an individual’s BRW was >1,500 g, the greatest FS resulted when PW was <350 g.

A response surface describing the probability of FS predicted by using Model 4 is presented in Figure 2b. Individuals from litters with an average BRW at and above the population mean (1,421 g) and that did not deviate negatively from their litter’s mean had the greatest FS probability. If both litter and individual weight were above the average, FS was not substantively increased, but reduction of both values drastically reduced the probability of FS.

The probability of WS predicted by using Model 1 is presented in Figure 2c. There was an interaction between BRW and PW in their effect on WS. The greatest WS occurred when BRW was above the mean and when PW was below the mean, but WS was reduced in all other quadrants of the survival surface plot. Increasing BRW above the population mean did not produce a substantial increment in WS. Interestingly, when both BRW and PW were in the higher end of the range, WS fell below 80%.

Weaning survival predicted by Model 4 is presented in Figure 2d. Similar to the trend already described, WS was maximized when mBRW was at the population average and individuals within that litter were at or above the average. Reducing any of those variables to values below their average rapidly reduced the probability of WS.

**DISCUSSION**

The proportion of stillborn piglets in this study (3.5%) was significantly lower than the average 8.3% reported for the US swine industry (USDA, 2002) and is likely the result of constant supervision at farrowing and ob-

Table 4. Estimates of direct and maternal genetic correlations from 2-trait analyses involving farrowing survival (FS) and weaning survival (WS)

<table>
<thead>
<tr>
<th></th>
<th>WS</th>
<th>Birth weight</th>
<th>Placental weight</th>
<th>Placental efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>FS</td>
<td>Direct</td>
<td>0.92</td>
<td>0.83</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>0.99</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>WS</td>
<td>Direct</td>
<td>-</td>
<td>0.32</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>Maternal</td>
<td>-</td>
<td>0.01</td>
<td>0.00</td>
</tr>
</tbody>
</table>

1Standard errors of estimates were not available from multiple-trait, derivative-free REML procedures due to missing values in the data sets.
Table 5. Logistic regression coefficients (±SE) and their significance for effects included in models used for predicting survival traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Model number</th>
<th>Effect</th>
<th>Logistic regression coefficient</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Farrowing survival</td>
<td>1</td>
<td>Intercept</td>
<td>$-2.7678 \pm 1.1802$</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BRW</td>
<td>$0.00443 \pm 0.00088$</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PW</td>
<td>$0.00469 \pm 0.00383$</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BRW × PW</td>
<td>$-6.28 \times 10^{-6} \pm 2.45 \times 10^{-6}$</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TB</td>
<td>$0.1393 \pm 0.0493$</td>
<td>0.0047</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Intercept</td>
<td>$-1.3138 \pm 1.2212$</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mBRW</td>
<td>$0.00219 \pm 0.00068$</td>
<td>0.0013</td>
</tr>
<tr>
<td></td>
<td></td>
<td>dBRW</td>
<td>$0.00181 \pm 0.00066$</td>
<td>0.0013</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TB</td>
<td>$0.1606 \pm 0.0494$</td>
<td>0.0012</td>
</tr>
<tr>
<td>Weaning survival</td>
<td>1</td>
<td>Intercept</td>
<td>$-2.6267 \pm 0.8320$</td>
<td>0.0016</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BRW</td>
<td>$0.00422 \pm 0.00067$</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PW</td>
<td>$0.00602 \pm 0.00299$</td>
<td>0.044</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BRW × PW</td>
<td>$-6.3 \times 10^{-6} \pm 1.98 \times 10^{-6}$</td>
<td>0.0015</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Intercept</td>
<td>$0.5887 \pm 0.5736$</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mBRW</td>
<td>$0.00121 \pm 0.00041$</td>
<td>0.0034</td>
</tr>
<tr>
<td></td>
<td></td>
<td>dBRW</td>
<td>$0.00715 \pm 0.00231$</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mBRW × dBRW</td>
<td>$-3.5 \times 10^{-6} \pm 1.65 \times 10^{-6}$</td>
<td>0.032</td>
</tr>
</tbody>
</table>

$^{1}$BRW = birth weight, PW = placental weight, mBRW = litter mean BRW, dBRW = deviation from litter mean BRW, and TB = total born.

Figure 2. Response surface of the effect of birth weight (BRW) and placental weight (PW; panels a and c) or litter mean BRW (mBRW) and individual deviation from the mean (panels b and d) on the probability of farrowing survival (FS) and weaning survival (WS).
gestic assistance. This indicates that benefits to the swine industry could be achieved initially by changes in management practices that provide an environment conducive to survival. Management practices can then be supplemented with selection strategies that produce piglets with a high potential for survival.

A study of Meishan-White crossbred gilts on d 105 of gestation after unilateral ovariohysterectomy suggested that there is no relationship between fetal weight and PW for placentas weighing >200 g (Vallet, 2000). Our results using segmented regression analysis indicate that the positive relationship between BRW and PW holds up to a PW of 529 g. Similarly, segmented regression analysis of the relationship between BRW and PW in the Nebraska index lines studied by Mesa et al. (2003) showed that BRW increases to a plateau of 1,520 g when PW reaches 454 g (unpublished data). Calculation of segmented regression parameters based on the regression equation reported by Vallet (2000) shows that BRW plateaus at 1,066 g when PW reaches 350 g. Differences among data sets most likely reflect differences in the genetic composition of the populations used and to a lesser degree the gestational age of the evaluation.

Previous estimates of direct and maternal heritability of WS were low (Lamberson and Johnson, 1984). Similarly, estimates of direct and maternal heritability for FS and WS obtained in a within-line analysis were consistently low (Knol et al., 2002). On the other hand, the results presented here agree well with estimates of direct and maternal heritability and their correlation for weaning survival of 0.11, 0.09, and −0.56, respectively, from a study involving >50,000 piglets (van Aren donk et al., 1996).

Survival traits are often categorized as FS and total survival, the latter encompassing survival from the onset of parturition to weaning. In this type of analysis, the heritabilities of farrowing survival and total survival were estimated to be 0.15 and 0.05, respectively, with no discrimination between direct and maternal effects (Grandinson et al., 2002).

The results of our study indicate that selection for increased WS may be effective. Because maternal heritability is of similar magnitude to direct heritability, and maternal and direct effects are negatively correlated, a genetic evaluation and selection program will need to include both types of effects to be successful. The high direct genetic correlation between FS and WS ($r_g = 0.92$) and the magnitude of the heritability of FS (0.16) indicate that selection for increased FS can result in positive correlated responses in WS. Birth weight, PW, and their interaction provide a model that could be used to help in the prediction of probability of survival traits. In the presence of BRW information, inclusion of PW data does not improve the prediction of the probability of survival.

In agreement with the results of the present report, a study including litters from gilts and sows found that increased BRW and PW positively influenced the probability of WS, but BRW has a greater effect on survival than either PW or PE (van Rens et al., 2005). Similarly, PW has a larger effect on survival than PE, and this effect is most likely mediated through effects on BRW; therefore, PE has little value as a predictor of piglet survival.

In the present study, the effect of total born on both survival traits in all models in which this effect was included was always positive, which contradicts the hypothesis that the environmental effect of increasing litter size will decrease survival directly. This result conflicts with the negative association between WS and the number of piglets born alive found by van Rens et al. (2005).

Piglets in litters with high variation in BRW, especially if the litter’s mean was low, have a lower probability of WS (Milligan et al., 2002). Similarly, the average BRW of the litter and the variation in BRW within the litter decreased when the maternal estimated breeding value for FS increased (Leenhouwers et al., 2003). Our results indicate that low BRW, and especially low BRW relative to the litter mean, negatively affects the probability of survival. Selection for a sow’s ability to produce uniform litters might be possible. Damgaard et al. (2003) obtained a heritability estimate of 0.08 for within-litter variation in a data set that had >2,000 litters. Here, the heritability estimate for the SD of piglet weights produced by a sow was 0.03 ± 0.34 (data not shown).

In a study focused on the physiological components of increased ability of a piglet to survive from the onset of parturition to weaning, pigs with greater genetic merit for total survival had lower BRW, and their high genetic merit was not related to differences in the progress of farrowing, early postnatal behavior, or rectal temperature 24 h after birth (Leenhouwers et al., 2001). Their results contradict those reported in our study. Larger BRW always increased the probability of survival as long as both BRW and PW were not in the high end of the range (Figure 2a and 2c). The difference could reflect the fact that Leenhouwers et al. (2001) did not provide obstetrical assistance in their experiment, whereas in the present study heavy pigs experiencing difficulty passing through the birth canal were always assisted.

In late gestation, litters with high genetic merit for total survival had lower average PW and lower variation in this trait, although PE tended to be greater. On the other hand, average fetal weight and variation in this trait were not correlated to genetic merit for survival (Leenhouwers et al., 2002). Fetal cortisol levels were greater in fetuses with high genetic merit for survival and most likely were associated with the maturity differences observed (Leenhouwers et al., 2002). Those results mark a sharp contrast between pre- and postnatal life. Placental weight and PE account for differences in survival potential before birth, but after birth, BRW becomes the major factor in a piglet’s ability to survive.
There has been much discussion in the literature of the fetal wastage that occurs between d 30 of gestation and term. Likewise, considerable wastage occurs between the onset of parturition and weaning. Variation in piglet weight at birth results in suboptimal litter size and weight at weaning. Within a litter, piglet survival is highly dependent on BRW in part because light piglets have to compete with heavier littermates for colostrum and weight at weaning. Within a litter, piglet survival is highly dependent on BRW in part because light piglets have to compete with heavier littermates for colostrum (English and Wilkinson, 1982; Fraser, 1990). However, across lines or breeds, greater preweaning survival is associated with litter uniformity and a greater physiological maturity at birth (Leenhouwers et al., 2002). Below 1 kg BRW, >11% of piglets are stillbirths and subsequently >17% die within the first 24 h; above 1 kg BRW, 4% are stillbirths and 3% die within 24 h (Quiniou et al., 2002). The proportion of piglets below 1 kg BRW increases from 14 to 23% if litter size increases from 15 to ≥16 (Quiniou et al., 2002).

Based on our results for FS and WS, BRW of around 1,400 g would be satisfactory, but beyond this level it would not result in substantial benefits in piglet survival. This means that allocation of extra fetal mass to piglets of high BRW would be inefficient.

Our results suggest that it is possible to select for increased genetic merit for piglet survival that would increase survival beyond that gained by crossfostering. Additionally, information on a piglet’s BRW and PW can be used to assist in this effort. Conceivably, litters with more homogeneous BRW would have acceptable individual piglet survival at even lower weights. We suggest that at current uterine capacity levels, it might be possible to produce 13 to 14 viable piglets at birth that survive to weaning by selecting for uniformity and low BRW. This alone would benefit the swine industry without the need to select for increased uterine capacity.

In conclusion, the results from this experiment suggest that it is possible to select for increased FS and WS, provided that both the direct and maternal effects are taken into account in the estimation of breeding values. Information on a piglet’s BRW, PW, mBRW, and the individual’s deviation from that mean can be used to optimize those values at levels resulting in high probability of survival.

**IMPLICATIONS**

The probability of piglet survival from birth to weaning has a large environmental component. Most rapid progress in number of piglets weaned can be achieved through application of improved management practices. Then long-term improvements can be achieved by genetically enhancing a piglet’s ability to survive, and that effort can be facilitated by the use of information on the piglet’s birth and placental weight.

**LITERATURE CITED**


