I. Abstract:

One of the factors that influences litter size in swine is the ability of the mother to gestate to term the major possible proportion of viable embryos. This ability has been termed uterine capacity and is considered dependent on the physical capacity of the uterus, fetal demand for nutrients, and the efficiency of the placenta to supply them. A selection index (SI) including litter size (LS), birth weight (BW), and placental weight (PW) was designed to increase or decrease the efficiency of the placental function. Divergent selection was practiced with two replicates per line. The SI, the three components of SI, and placental efficiency (PE) measured as the ratio BW: PW, were compared between the upward (H) and downward (L) selected lines following two and three of selection. The GLM procedure of SAS was used to calculate and compare least-squares means for all variables.

At generation two, PW tended to be lower in H than L (281 g vs. 345 g, respectively; P = .07), PE was higher in H than L (5.2 vs. 4.5, respectively; P = .02), and SI tended to be higher in H than L (2.01 vs. 1.69, respectively; P = .09). At generation three, divergence between lines was not significant for PW, PE or SI (P = .99, .45 and .84, respectively). Divergence between lines was not significant for LS or BW at any generation (P > .70). Heritability, calculated by doubling the regression of offspring on dam, was not significantly different from zero for BW. Heritability of LS was negative and thus assumed to be zero. Heritability estimates (se) for SI, PW, and PE were .27 (.07), .25 (.06), and .28 (.07), respectively. Realized heritability (se) for SI, calculated as the ratio of cumulative response to cumulative selection differential, was .02 (.03). Involuntary culling reduced the selection differential for SI from 2.6 at generation one to 1.5 at generation two. This and sampling error are probable causes of the non-significant divergence for the traits studied at generation three. Information obtained from this experiment will allow the computation of genetic parameters among components of litter size. Those parameters can be used to design a selection index that maximizes response.
II. Introduction

Increasing litter size in swine would tremendously enhance sow productivity (Tess et al., 1983). Significant efforts have, therefore, been devoted towards developing novel methods to achieve this result. Litter size in swine is a natural index of ovulation rate, fertilization rate, embryo survival and fetal survival; accordingly, selection strategies to increase this trait have been directed to these components or physiological traits correlated with them (Johnson et al., 1985). Fetal survival is affected by, among other factors, uterine capacity defined as the maximum number of fetuses a female can carry to term; uterine capacity is considered to be the most limiting component of litter size (Bennett and Leymaster, 1989). Uterine capacity includes the volume of the uterus, nutrient and gaseous exchange efficiency, placental surface (Webel and Dziuk, 1974) and placental size (Lamberson and Eckardt, 1996). Wilson et al. (1999) propose that uterine capacity is better described as the total amount of placental mass or surface area that a female can carry to term. Consequently, uterine capacity is affected by the absolute surface area available and both endometrial and placental transfer efficiency.

Current strategies to increase litter size are difficult to apply by the average pork producer since they require either big centralized sets of performance records or complicated surgical procedures to measure components of litter size. The weight ratio between the fetus and its placenta has been used as a measurement of placental efficiency in a selection experiment (Wilson et al., 1998; 1999). An understanding of the physiological components of litter size is needed if this trait is going to be modified through selection directed to the most critical and malleable components.

III. Objective:

The objective of the present study was to evaluate the response to index selection for reproductive components and its effect on litter size in swine.

IV. Procedures:

Divergent selection for reproductive components was initiated in the summer of 1998 using University of Missouri Duroc x (Landrace-Yorkshire rotational) pigs (generation 0). The base population was composed of litters from 20 sows in each of two farrowing groups (replicates) separated by one month. Litter size (LS), birth weight (BW), and placental weight (PW) were recorded and this information used to construct a selection index (SI). Within each replicate the 24 highest and lowest indexing female progeny and the seven highest and lowest indexing male progeny were chosen to create divergent lines with either high or low placental efficiency. This selection scheme was continued in the upward (H) and the downward (L) selected lines for high and low index values, respectively. Generation interval was one year.

For detection of estrus, gilts were exposed to direct contact with a mature, intact boar for 10 minutes daily beginning at 160 days of age. After at least 75% of selected gilts had expressed their first estrus, a breeding period of 2 weeks was initiated with the intention of synchronizing estrous cycles. Synchronization was accomplished with two Lutalyse® (Pharmacia and Upjohn Co., Kalamazoo, MI) injections of 2 mL each, 12 hours apart, 14 days after finalization of the breeding period. Two breeding groups were created in this way in generation 1 and three in generations 2 and 3.

After estrus synchronization, females were artificially inseminated with fresh diluted semen from males in the same line and replicate, avoiding half- and full-sibling matings. Breeding took place between the months of May and July of 1999 and 2000. Due to poor pregnancy rates a third group was mated and farrowed in January, 2002. Females were bred 12 and 24 hours after the first signs of behavioral estrus. At 107 days of pregnancy, females were transferred to the Animal Sciences Research Center.
farrowing facility where parturition was supervised 24-hours per day. In the morning of
the fifth day of the seven-day farrowing period, parturition was induced in remaining
females with a 2 mL intramuscular injection of Lutalyse®.

The umbilical cord of each piglet was double tagged with identically numbered
mouse ear tags (Gey Band & Tag Co. Norristown, PA) at birth. One tag was placed
approximately 10 cm from the piglet and the cord severed allowing it to retract into the
birth canal with the tag. The second tag was placed in the umbilical cord stump
approximately 5 cm from the piglet. Piglets were weighed immediately after birth before
suckling began. All placentas were collected and weighed at delivery.

The selection index developed includes LS in which the piglet was born and BW
and PW adjusted for differences in litter size and gestation length. In the base
population, BW and PW were adjusted also for parity number. The rationale behind the
construction of the index was to obtain equal response in each trait by giving the
components equal weight; thus keeping those in balance. Equal weight for each
component was achieved by dividing the trait value by its standard deviation to remove
the effect of the units used and the inherent differences in variability. Litter size was
further adjusted to take into account that it has a heritability estimated to be half of the
other two traits, and that individual selection for litter size using the dam’s record halves
the effective heritability. The sign given to each component represents the aim of
obtaining bigger litters of heavier piglets but carried by smaller and more efficient
placentas in the H line and the opposite in the L line.

The index was calculated as:

\[
\text{Index} = \frac{(0.25 \times \text{LS})}{\sigma_{\text{LS}}} + \frac{\text{BW}}{\sigma_{\text{BW}}} - \frac{\text{PW}}{\sigma_{\text{PW}}}
\]

The resulting index was:

\[
\text{Index} = 0.073(\text{LS}) + 0.003(\text{BW}) - 0.012(\text{PW}).
\]

The only selection criterion in generations 0 and 1 was the high or low selection
index value. With the intention of avoiding selection of runts in the second and third
generations, all piglets weighing less than one-third of their litter average at birth and
less than 1000 g were culled.

After three generations of selection, SI, the three components of SI, and
placental efficiency (PE), measured as the ratio BW: PW, were compared among the H
and L lines. Least-squares means were calculated for all variables, and statistical
analyses performed using the GLM procedure of SAS (SAS, 1999). The model
included the effects of generation, line within generation and replicate within line on SI
\(n = 1491\), BW \(n = 1859\), PW \(n = 1772\), PE \(n = 1491\), and LS \(n = 165\). Replicate
within line was used as the error term to test all line effects. Multiple comparisons were
performed using the Tukey-Kramer method (SAS, 1999). Heritabilities were estimated
by regression of progeny on dam (Falconer and Mackay, 1996). Additional analyses
were performed to identify line differences on the number of mummified fetuses (NMF),
number of weaned piglets (NWP), number born alive (NBA), number of stillborns
(NSB), and preweaning survival (PWS) calculated as (NBA/NWP)*100.
V. Results:

No significant differences were observed between replicates of the same line; therefore, reported values are the average of two replicates. Least-squares means for BW, PW, PE, LS and SI by line and generation are shown in Table 1. At generation two, PW tended to be lower in H than L (P = .07), PE was higher in H than L (P = .02), and SI tended to be higher in H than L (P = .09). At generation three, divergence between lines was not significant for PW, PE or SI (P = .99, .45 and .84, respectively). Divergence between lines was not significant for LS or BW at any generation (P > .70). Inclusion of LS as a covariate did not affect the magnitude of line effects on BW, PW, or PE. Means for each line and the selected individuals within line at each generation for BW, PW, PE, LS, and SI are presented in Figures 1 through 5, respectively. Least-squares means and the magnitude and significance of the divergence at generation 2 are summarized in Table 2.

None of the litter traits examined was significantly different between lines at any generation. Weighted overall least-squares means (sem) at generation 3 for NMF, NWP, NBA, NSB, and LS were .98 (.14), 9.89 (.86), 10.67 (.97), .75 (.12), and 11.42 (.82) piglets, respectively. Least-squares mean (sem) for PWS at generation 3 was 88.97% (4.74). Realized heritability for the index (se), estimated as the ratio of corrected cumulative response to corrected cumulative selection differential, was .02 (.03). Heritability estimates by regression of progeny on dam are shown in Table 3. This estimate was not significantly different from zero for BW. Heritability of LS was negative and thus assumed to be zero.

At generation two placental weight and efficiency were modified without affecting birth weight. This indicates that the index, or a refinement of it, could be an effective way of achieving increased placental efficiency and probably correlated responses in litter size without decreasing birth weight.

Involuntary culling reduced the corrected selection differential for SI from 2.6 at generation one to 1.5 at generation two. This and sampling error are probable causes of the non-significant divergence for the traits studied at generation three. Trait values in line H remained constant from generation two to three, but these values in line L approached the values of line H during the same period.

If placental efficiency is in fact one key component of the increased uterine capacity and fetal survival observed in the prolific Meishan pig, subsequent divergence in placental weight and efficiency would be expected to result in populations with ability to support different litter sizes to term. Considering survival of an individual fetus a binary trait, the lack of a correlated response in litter size at generation two could mean that the space vacated by smaller placentas in H is not sufficient to support one extra piglet. Alternatively, the extra space occupied by larger placentas in L has not been enough to have detrimental effects on piglet survival.

The observed response in the index value shows that index selection based on placental efficiency may be a useful tool to improve litter size in swine herds of any size by using technology and procedures that are relatively simple and inexpensive. Results suggest that the level of response may not be expected to be as great as previously reported from one generation of similar selection (Wilson et al, 1998). Using the information obtained from the current experiment to determine the genetic parameters among components of litter size will allow the design of a selection index to maximize response. Subsequent generations of divergent index selection are likely to result in significant differences in litter size through a physiological mechanism that involves changes in placental efficiency. The population resulting from this selection experiment should be useful in understanding the physiological factors contributing to variation in litter size in swine.
The complexity of the interactions among the component traits of litter size makes the manipulation of this trait difficult. Comparison of the results of the present experiment and the literature available on the Meishan breed and other selection experiments leads to the conclusion that in any given population, prolificacy can be increased through different physiological mechanisms. Additional comparisons of litter size components (including ovulation rate, embryo survival, uterine capacity and placental efficiency) in those populations would allow a better understanding of their relationships. This knowledge can be used to optimize selection strategies, leading to a more profitable swine industry.
Table 1. Least-squares means (sem) by line and generation for the base population (BP) and high (H) and low (L) select lines.

<table>
<thead>
<tr>
<th></th>
<th>Index (se)</th>
<th>Birth wt (se)</th>
<th>Placental wt (se)</th>
<th>Placental Efficiency (se)</th>
<th>Litter Size (se)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BP</td>
<td>1.97 (0.04)</td>
<td>1448.90 (14.41)</td>
<td>304.61 (4.49)</td>
<td>4.99 (0.04)</td>
<td>11.73 (0.46)</td>
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<tr>
<td>H Gen 1</td>
<td>2.01 (0.05)</td>
<td>1453.38 (17.97)</td>
<td>305.04 (5.47)</td>
<td>5.02 (0.05)</td>
<td>12.13 (0.60)</td>
</tr>
<tr>
<td>L Gen 1</td>
<td>1.78 (0.05)</td>
<td>1445.94 (19.01)</td>
<td>303.83 (5.81)</td>
<td>4.91 (0.05)</td>
<td>10.69 (0.59)</td>
</tr>
<tr>
<td>H Gen 2</td>
<td>2.09 (0.05)</td>
<td>1414.71 (19.46)</td>
<td>281.05 (5.93)</td>
<td>5.20 (0.05)</td>
<td>10.50 (0.60)</td>
</tr>
<tr>
<td>L Gen 2</td>
<td>1.70 (0.07)</td>
<td>1510.11 (25.68)</td>
<td>345.58 (7.95)</td>
<td>4.54 (0.07)</td>
<td>11.10 (0.82)</td>
</tr>
<tr>
<td>H Gen 3</td>
<td>2.10 (0.05)</td>
<td>1472.83 (34.29)</td>
<td>302.83 (7.30)</td>
<td>5.20 (0.06)</td>
<td>10.96 (0.77)</td>
</tr>
<tr>
<td>L Gen 3</td>
<td>2.00 (0.06)</td>
<td>1429.32 (36.98)</td>
<td>307.61 (7.93)</td>
<td>5.02 (0.06)</td>
<td>12.02 (0.87)</td>
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<tr>
<td>Coefficient of Variation</td>
<td>49.6%</td>
<td>19.8%</td>
<td>29.8%</td>
<td>24.7%</td>
<td>27.3%</td>
</tr>
</tbody>
</table>
Table 2. Least-squares means (sem) at generation 2. Average of two replicates.

<table>
<thead>
<tr>
<th>Trait</th>
<th>n</th>
<th>H Line (se)</th>
<th>L Line (se)</th>
<th>Divergence (% of the higher value)</th>
<th>Divergence Significance (P value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selection Index</td>
<td>333</td>
<td>2.09 (0.05)</td>
<td>1.70 (0.07)</td>
<td>18.7</td>
<td>0.09</td>
</tr>
<tr>
<td>Birth Weight (g)</td>
<td>396</td>
<td>1414.71 (19.5)</td>
<td>1510.1 (25.7)</td>
<td>6.3</td>
<td>0.70</td>
</tr>
<tr>
<td>Placental Weight (g)</td>
<td>377</td>
<td>281.1 (5.9)</td>
<td>345.6 (7.8)</td>
<td>18.7</td>
<td>0.07</td>
</tr>
<tr>
<td>Placental Efficiency</td>
<td>333</td>
<td>5.20 (0.05)</td>
<td>4.54 (0.07)</td>
<td>12.7</td>
<td>0.02</td>
</tr>
<tr>
<td>Litter Size</td>
<td>37</td>
<td>10.5 (0.60)</td>
<td>11.1 (0.8)</td>
<td>5.4</td>
<td>0.97</td>
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</table>

Table 3. Heritability estimates after three generations of divergent selection.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>Probability &gt; 0 (P value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter Size</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Birth Weight</td>
<td>.02</td>
<td>.05</td>
<td>.59</td>
</tr>
<tr>
<td>Placental Weight</td>
<td>.25</td>
<td>.06</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>Placental Efficiency</td>
<td>.28</td>
<td>.07</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>Index</td>
<td>.27</td>
<td>.07</td>
<td>&lt; .001</td>
</tr>
</tbody>
</table>
Figure 1. Line and selected individuals mean birth weight by generation.

Figure 2. Line and selected individuals mean placental weight by generation.
Figure 3. Line and selected individuals mean placental efficiency by generation.

Figure 4. Line and selected individuals mean litter size by generation.
Figure 5. Line and selected individuals mean index value by generation.
LITERATURE CITED


