A whole genome scan to detect quantitative trait loci for gestation length and sow maternal ability related traits in a White Duroc × Erhualian F2 resource population

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Gestation length and maternal ability are important to improve the sow reproduction efficiency and their offspring survival. To map quantitative trait loci (QTL) for gestation length and maternal ability related traits including piglet survival rate and average body weight of piglets at weaning, more than 200 F2 sows from a White Duroc × Erhualian resource population were phenotyped. A genome-wide scan was performed with 194 microsatellite markers covering the whole pig genome. QTL analysis was carried out using a composite regression interval mapping method via QTL express. The results showed that total number of born piglets was significantly correlated with gestation length ($r = -0.13$, $P < 0.05$). Three QTL were detected on pig chromosome (SSC)2, 8 and 12 for gestation length. The QTL on SSC2 achieved the 5% genome-wide significant level and the QTL on SSC8 was consistent with previous reports. Four suggestive QTL were identified for maternal ability related traits including 1 QTL for survival rate of piglets at weaning on SSC8, 3 QTL for average body weight of piglet at weaning on SSC3, 11 and 13.

**Keywords:** gestation length, maternal ability related traits, QTL, resource population

**Implications**

Sow reproduction ability is important to economics of pig industry. A shorter gestation length means higher reproduction efficiency. With an increased litter size, good maternal ability is required to sows to improve the survival rate of their offspring. In this study, a whole genome scan was conducted to identify the chromosome regions influencing the sow maternal ability and gestation length. This is an important step to identify causative genes for sow maternal ability and gestation length, and then to genetic improvement of sow reproduction ability.

**Introduction**

Reproduction traits are the important economic traits for the pig industry. It has profound effects on economical interest of pig production. Besides some well-known reproduction traits, such as litter size and age at puberty, gestation length and maternal ability are also important to sow reproduction. It is important for commercial pig farms to predict the starting time of farrowing. Producers can supervise the farrowing and treat sows at the appropriate time to induce farrowing and give assistance to sows and piglets to reduce piglet mortality during the perinatal periods (Holyoake et al., 1995). The selection for increased litter size brings problems with increasing piglet mortality and decreasing piglet growth (Johnson et al., 1999). Sows are required for good maternal ability to take care of their litters, because maternal effects are more important than any other single factor in determining early offspring growth and survival (Lee et al., 1991). Variation among sows in their gestation length and maternal ability is caused by both genetic and environmental effects. Gestation length varies in both purebred sows (Kennedy and Moxley, 1978) and crossbred sows (Sasaki and Koketsu, 2007). Sasaki and Koketsu (2007) showed that shorter gestation length was associated with more piglets born and dead piglets. An increase in gestation length has been related with improved piglet vitality at birth and reduced stillbirths (Knol et al., 2002). Variation in maternal ability also exists in different breeds. The Meishan breed shows good maternal abilities with resulting in heavier piglets at weaning than European white sows (Sinclair et al., 1998). Meishan piglets have 5% advantage in survival rate than large white piglets due to good maternal behavior (van der Steen and de Groot, 1992).
As a complex trait, maternal ability is considered to have a relatively low additive genetic variance and low heritability (Gäde et al., 2008). The heritability of gestation length in pigs ranges from 0.47 (Leigh, 1981; Hanenberg et al., 2001) to 0.13 (Casellas et al., 2008). The moderate-to-high values of heritability estimated have increased its importance as a potential breeding goal to improve the reproduction efficiency of sow per year (Casellas et al., 2008). Until now, no quantitative trait loci (QTL) were reported for maternal ability related traits in pigs. In mice Peripato et al. (2002) mapped two QTL for maternal performance for offspring (Gaede et al., 2008). The heritability of gestation length in a three-generation Meishan cross was described in detail by Chen et al. (2008) and no QTL for maternal performance for offspring (Gaede et al., 2008). The heritability of gestation length in a three-generation Meishan cross was described in detail by Chen et al. (2008) and no QTL for maternal performance for offspring (Gaede et al., 2008).

In this study, a whole genome scan was performed to identify QTL for gestation length and maternal ability related traits in a White Duroc × Erhualian intercross resource population.

Material and methods

Animals and phenotype recording

Experimental animals were from a three-generation White Duroc × Erhualian intercross. Erhualian is a Chinese indigenous pig breed well known for its excellent reproductive performance, and Duroc is a popular Western pig breed. Two White Duroc boars and 17 Erhualian sows were crossed as founder animals to produce F1 animals, and 59 F1 sows were randomly mated with 9 F1 boars to produce 1912 F2 individuals in six batches. Two hundred and thirty-seven sows were raised in three pig farms including Shangyou (n = 112), Dongxiang (n = 52) and Nanchang (n = 73). Animal management was described in detail by Chen et al. (2008) and Li et al. (2009). In brief, gilts were observed for signs of standing estrus for 30 min twice a day in the interval of 8 to 10 h at the age of 7 to 10 months. All sows were naturally mated to Western purebred boars or F2 boars after 24 h detecting standing estrus, and the second natural service was given in the interval of 12 h (Li et al., 2009). From the 1st week after mating to 1 month before the expected farrowing day, two sows were housed in a pen of 2 × 2.5 meters with a concrete floor. After that, each pen accommodated only one sow. The straw was provided when sows were near to giving birth. The room temperatures were uncontrolled with natural lighting. Animals were floor fed three times a day and were offered the formula feed for lactation diet from gestation through lactation. In the last 3 weeks of gestation, the amount of diet was increased in moderation. All sows gave birth naturally.

Gestation length, litter size related traits and maternal ability related traits were measured in 237 F2 sows. The gestation length was defined as the number of days from the date of second natural service to the date of farrowing completed. Litter size related traits included total number born (TNB), number born alive (NBA), number of stillborn (NSB) piglets, number of mummies and piglet birth weight per litter were recorded as described previously (Li et al., 2009). No piglet was cross fostered in all 237 F2 sows. Piglets were weaned at 45 days after birth. Litter size at weaning and piglet body weight at weaning was also recorded. The survival rate of piglet at weaning was defined as the percentage of the all-living piglets at weaning in total NBA.

Marker genotyping

Genomic DNA was extracted from porcine ear or spleen tissues using a phenol/chloroform extraction method and diluted to a final concentration of 20 ng/µl. A total of 194 informative microsatellite markers covering all 18 porcine autosomes and the X chromosome at approximate intervals of 20 cM were selected according to the USDA-MARC linkage map (Rohrer et al., 1996). Primers were labeled with fluorescent dye (HEX, NED or FAM). All founder animals, F1 individuals and 280 F2 sows were genotyped for the 194 markers as described previously in Guo et al. (2009). The linkage map was constructed with CRIMAP version 2.4 (Green et al., 1990) as described by Guo et al. (2009). The PROC GLM procedure of SAS version 9.0 (SAS Institute Inc., Cary, NC, USA) was used to determine factors affecting the gestation length and maternal ability related traits. Factors above 5% significance level were included as fixed effects or covariates in the subsequent QTL mapping model. Correlation coefficients (r) between gestation length and traits related to litter size were analyzed by PROC CORR procedure of SAS version 9.0.

The presence of potential QTL and their relative positions were determined by a composite interval mapping based on the least-squares regression analysis (Haley et al., 1994). All analyses were carried out with QTL express (Seaton et al., 2002). Family and farm was included as fix effects for both gestation length and maternal ability related traits. TNB was kept as a covariate in the QTL model for gestation length. For maternal ability related traits, average body weight of piglet at birth was included as a covariate. Litter size showed no significant effect on survival rate of piglets at weaning, so it was not included into the QTL model. The phenotypic data were regressed onto the additive and dominance effects of putative QTL. The QTL analysis was carried out at 1 cM intervals along each chromosome and the F-value for the QTL effect was calculated at each point. The detected QTL was fixed as the genetic background for next round QTL identification. Empirical threshold values for QTL mapping were determined by using the genome-wide permutation test with 1000 random data shuffles as described by Churchill and Doerge (1994). The suggestive, 5% and 1% genome-wide threshold values were used. The 5% chromosome-wide threshold obtained following de Koning et al. (2001) was considered as the suggestive significance level. The empirical 95% CIs were estimated by the bootstrapping approach with 2000 iterations (Vischer et al., 1996).
Results

Phenotypic data and correlation of gestation length with litter size related traits

The valid data number of gestation length, survival rate of piglet at weaning and average body weight of piglet at weaning in the current population was 237, 212 and 216, respectively (Table 1). The phenotypic mean, standard error, standard deviation and range of gestation length, and maternal ability related traits are listed in Table 1. The F2 gilts from the White Duroc $\times$ Erhualian resource population showed considerably large variation and segregation in all traits measured. The correlation coefficients ($r$) between gestation length and litter size related traits are shown in Table 2. Gestation length was significantly correlated with TNB ($r = -0.13$; $P < 0.05$). Sows with more total number of born piglets had shorter gestation length. There was no correlation of gestation length with NBA, NSB, mummies and the means of piglet birth weight per litter ($P > 0.05$).

QTL mapping of gestation length and sow maternal ability related traits

Separate significance thresholds were determined for each trait via experiment-wide permutations. The average of the suggestive, 5% and 1% genome-wide threshold values and their s.d. were $5.39$ (0.021), $8.70$ (0.262) and $11.08$ (0.535), respectively. Three QTL were detected on SSC2, 8 and 12 for gestation length. The QTL at 82 cM on SSC2 achieved 5% genome-wide significance level. It accounted for 5.4% of phenotypic variance and had a 95% CI of 41.0 to 120.0 cM (Figure 1a). The additive effect of this QTL was 0.72 ± 0.16 for this QTL indicated that sows receiving both alleles from their Meishan granddames had a gestation length of 1.44 days longer than the average of the mean of piglets per litter. The QTL for survival rate of piglet at weaning was mapped at 86 cM on SSC8, which explains 6.42% of phenotypic variance. The additive effect of 0.05 ± 0.01 for this QTL showed that sows inheriting two alleles from Erhualian granddames had 10% advantage in their offspring survival than sows receiving both alleles from White Duroc grandsires. Three suggestive QTL for average body weight of piglet at weaning were found at 87 cM on SSC3, 55 cM on SSC11 and 32 cM on SSC13, explaining 3.96%, 5.86% and 4.72% of the phenotypic variance, respectively. The alleles from the Erhualian breed at the two loci on SSC11 and SSC13 were associated with increased average body weight of piglet at weaning, but the QTL on SSC3 acted in the opposite directions with the favorable allele derived from the White Duroc breed.

Discussion

In this study, the mean of gestation length in the White Duroc $\times$ Erhualian F2 sows was 113.84 days at their first farrowings. The value was comparable with the mean gestation length in a naturally mated West-type population (113.5 to 114.5 days) (Leenhouwers et al., 1999; Cassady et al., 2002), but longer than in Iberian $\times$ Meishan F2 sows (112.16 days), which were mated with artificial insemination (Casellas et al., 2008). Just as the results reported by Sasaki and Koketsu (2007), gestation length had a negative correlation with total number of born piglets. The possible explanation for this observation is that large litter size may have a larger placental unit, which release more oxytocin and prostaglandin (Dziuk, 1991). The moderate-to-high heritability estimates for gestation length (Hanenberg et al., 2001; Nguyen et al., 2006) have

Table 1: Phenotypic data of gestation length and maternal ability related traits at the first parity in the White Duroc $\times$ Erhualian resource population

<table>
<thead>
<tr>
<th>Traits</th>
<th>Number</th>
<th>Mean ± s.e.</th>
<th>STD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gestation length (day)</td>
<td>237</td>
<td>113.84 ± 0.13</td>
<td>2.04</td>
<td>106</td>
<td>125</td>
</tr>
<tr>
<td>Survival rate of piglets at weaning (%)</td>
<td>212</td>
<td>0.90 ± 0.01</td>
<td>0.14</td>
<td>0.38</td>
<td>1.00</td>
</tr>
<tr>
<td>Average body weight of piglet at weaning (kg)</td>
<td>216</td>
<td>4.93 ± 0.07</td>
<td>1.00</td>
<td>2.93</td>
<td>7.70</td>
</tr>
</tbody>
</table>

STD = standard deviation.

Table 2: Correlation coefficients ($r$) between gestation length and litter size related traits in the F2 sows

<table>
<thead>
<tr>
<th></th>
<th>TNB</th>
<th>NBA</th>
<th>NSB</th>
<th>NM</th>
<th>Means of PBW</th>
</tr>
</thead>
<tbody>
<tr>
<td>r</td>
<td>$-0.13$</td>
<td>$-0.08$</td>
<td>$-0.10$</td>
<td>$-0.04$</td>
<td>$0.07$</td>
</tr>
<tr>
<td>$P$</td>
<td>$0.04*$</td>
<td>$0.23$</td>
<td>$0.11$</td>
<td>$0.58$</td>
<td>$0.28$</td>
</tr>
</tbody>
</table>

$r$ = correlation coefficients; $P = P$ value; TNB = total number born; NBA = number born alive; NSB = number stillborn; NM = number of mummies; PBW = piglet birth weight.

* $P < 0.05$ significant level.

QTL for gestation length and sow maternal ability related traits

Showing two F-value peaks at 28 cM and 49 cM of this genome. A suggestive QTL was identified on SSC8, indicating that sows receiving both alleles from their Meishan grandsires. Three suggestive QTL for average body weight of piglet at weaning were found at 87 cM on SSC3, 55 cM on SSC11 and 32 cM on SSC13, explaining 3.96%, 5.86% and 4.72% of the phenotypic variance, respectively. The alleles from the Erhualian breed at the two loci on SSC11 and SSC13 were associated with increased average body weight of piglet at weaning, but the QTL on SSC3 acted in the opposite directions with the favorable allele derived from the White Duroc breed.
increased the potential of this trait as a breeding goal to improve the sow reproduction efficiency. Three QTL were detected for gestation length in this study and the QTL on SSC2 and SSC12 were detected for the first time. Several peaks of F-value curve were shown on SSC8, suggesting that there might be more than one QTL for gestation length on this chromosome (Figure 1b). The peak at 49 cM was consistent with the previous QTL found in a Meishan × Large white population (Jiang et al. 2002). In this region, Jiang et al. (2002) found that estrogen sulfotransferase gene showed overdominance effects on gestation length. The peak near the 110 cM was overlapped with QTL region for gestation length reported by Casellas et al. (2008) in the Iberian × Meishan F2 sows, although it did not achieve 5% genome-wide significance.

![Figure 1](https://www.cambridge.org/core/nginx/res/01751736.png)

**Figure 1**: The statistic F-curves showing quantitative trait loci (QTL) for gestation length, survival rate of piglets at weaning and average body weight of piglets at weaning. Markers and distance in cM are given on the x-axis; F-values are shown on the y-axis. (a) 5% genome-wide significant QTL for gestation length on SSC2; (b) suggestive QTL for gestation length and survival rate of piglets at weaning on SSC8; and (c) suggestive QTL for average body weight of piglets at weaning on SSC11.

Table 3 Details of quantitative trait loci for gestation length and sow maternal ability related traits in the White Duroc × Erhualian F2 resource population

<table>
<thead>
<tr>
<th>Trait</th>
<th>Chr</th>
<th>Position (cM)</th>
<th>95% CI position (cM)</th>
<th>F-ratio</th>
<th>LRT</th>
<th>LOD</th>
<th>Additive effect ± s.e.</th>
<th>Dominant effect ± s.e.</th>
<th>Variance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gestation length</td>
<td>2</td>
<td>82</td>
<td>41.0 to 120.0</td>
<td>11.25</td>
<td>21.61</td>
<td>4.69</td>
<td>−0.72 ± 0.16</td>
<td>−0.09 ± 0.26</td>
<td>5.40</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>49</td>
<td>22.0 to 114.0</td>
<td>5.89</td>
<td>11.54</td>
<td>2.51</td>
<td>0.50 ± 0.15</td>
<td>−0.32 ± 0.21</td>
<td>3.22</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>86</td>
<td>7.0 to 86.0</td>
<td>8.41</td>
<td>16.31</td>
<td>3.54</td>
<td>0.15 ± 0.17</td>
<td>0.96 ± 0.27</td>
<td>3.16</td>
</tr>
<tr>
<td>Maternal ability</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survival rate of piglet before weaning</td>
<td>8</td>
<td>86</td>
<td>0 to 105.0</td>
<td>8.50</td>
<td>16.33</td>
<td>3.55</td>
<td>0.05 ± 0.01</td>
<td>0.04 ± 0.02</td>
<td>6.42</td>
</tr>
<tr>
<td>Average body weight of piglet at weaning</td>
<td>3</td>
<td>87</td>
<td>32.5 to 136.0</td>
<td>5.80</td>
<td>11.29</td>
<td>2.45</td>
<td>−0.18 ± 0.06</td>
<td>0.15 ± 0.09</td>
<td>3.96</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>55</td>
<td>6.5 to 79.5</td>
<td>8.11</td>
<td>15.61</td>
<td>3.39</td>
<td>0.21 ± 0.06</td>
<td>−0.20 ± 0.10</td>
<td>5.86</td>
</tr>
<tr>
<td></td>
<td>13</td>
<td>32</td>
<td>0.0 to 115.0</td>
<td>6.74</td>
<td>13.05</td>
<td>2.83</td>
<td>0.11 ± 0.08</td>
<td>0.44 ± 0.13</td>
<td>4.72</td>
</tr>
</tbody>
</table>

Chr = chromosome; LRT = likelihood ratio test; LOD = log odds score. *5% genome-wide significant level.
such as a at 80 cM for test number (Ding et al., 2009), at 77 cM for age at puberty (Yang et al., 2008), at 84 cM for NSB (Li et al., 2009), at 86 cM for survival rate of piglets at weaning and at 49 cM for gestation length detected in this study. According to the porcine QTL database (Hu et al., 2005), QTL influencing ovulation rate (Rathje et al., 1997), TNB and NBA (King et al., 2003) have also been mapped to this chromosome. This further confirms that the pig chromosome 8 plays very important roles to porcine female reproduction.

In summary, a whole genome scan was conducted to detect the QTL for gestation length and maternal ability related traits in the White Duroc × Erhualian resource population. Three QTL for gestation length were detected on SSC2, 8 and 12, and the QTL on SSC2 achieved 5% genome-wide significance level. A suggestive QTL was identified on SSC8 for survival rate of piglets at weaning, and three suggestive QTL for average body weight of piglets at weaning were found on SSC3, 11 and 13.

QTL for gestation length and sow maternal ability related traits

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