**Conceptus competition for uterine space: Different strategies exhibited by the Meishan and Yorkshire pig**

**K. A. Vonnahme**, **M. E. Wilson**, and **S. P. Ford**

Department of Animal Science, Iowa State University, Ames 50011

**ABSTRACT:** Our laboratory has demonstrated that Yorkshire placenta increase in size and surface area during the final third of gestation. In contrast, Meishan placental size remains constant during late gestation, but the density of blood vessels at the placental-endometrial interface increases markedly. Preliminary observations from our laboratory suggest that if one of two adjacent Meishan fetuses dies, the placenta of the remaining Meishan conceptus fails to increase its length of implantation or its placental weight or surface area. In contrast, if one of two adjacent Yorkshire fetuses dies, the adjacent conceptus accelerates its placental growth. The objective of this experiment was to document that Yorkshire, but not Meishan, conceptuses accelerate placental growth when adjacent fetuses are experimentally destroyed on d 40 of gestation. Straight-bred Meishan \((n = 5)\) and Yorkshire \((n = 5)\) females were laparotomized and one uterine horn was randomly assigned to receive fetal crushing (treated horn); the other uterine horn served as a within-animal control. In the treated horn, every other fetus was then crushed through the uterine wall and the animals were allowed to recover. On d 111, animals were killed, uteri were recovered, and fetal weight, crown-rump length (CRL), placental weight, implantation site length, and placental surface area were recorded. Although there were no statistically significant differences in fetal weight or CRL observed between treated or control horns of females of either breed, there was a tendency for the fetuses in the treated uterine horn to be longer and heavier in both breeds. There were no differences in placental weight, placental surface area, or implantation site length between conceptuses in Meishan treated and control horns, which averaged \(173.8 \pm 6.4\) g, \(1,162.7 \pm 35.9\) cm\(^2\), and \(19.0 \pm 0.4\) cm, respectively. In contrast, placental weight, placental surface area, and implantation site length were increased \((P < 0.05)\) in Yorkshire treated horns compared to Yorkshire control horns \((306.1 \pm 26.0\) g, \(1,835 \pm 93.9\) cm\(^2\), and \(33.4 \pm 1.5\) cm vs \(253.7 \pm 13.4\) g, \(1,474.3 \pm 50.4\) cm\(^2\), and \(27.2 \pm 0.8\) cm; respectively). These data confirm that Yorkshire conceptuses, but not Meishan conceptuses, accelerate placental growth when adjacent littermates perish as late as d 40 of gestation. These data indicate that differences exist in the strategies employed by Meishan and Yorkshire conceptuses in the competition for nutrients during gestation.

Key Words: Gestation, Pigs, Placental Growth

©2002 American Society of Animal Science. All rights reserved.

Introduction

Reproductive efficiency in the pig is greatly influenced by the highly variable loss of potential piglets during the course of gestation (Dzuik, 1987; Lawrence, 1993; Pope, 1994). Fifteen to 20% of fetuses are lost between d 30 and 50 of gestation (Dzuik, 1968; Fenton et al., 1972; Webel and Dzuik, 1974), and an additional 5 to 10% fetal loss occurs from d 90 to 114 (Christenson et al., 1987). In order to supply the rapidly growing fetus with enough nutrients and oxygen during this second period of fetal loss, the placenta either increases in surface area of attachment with the endometrium (e.g., Yorkshire placenta) or increases vascular density (e.g., Meishan placenta; Biensen et al., 1998). As uterine space becomes limiting after d 30 (Christenson et al., 1987; Wilson et al., 2000), the ability of a conceptus to increase its placental size may be limited. Increasing the density of blood vessels at the placental-endometrial interface could facilitate nutrient uptake per unit area without requiring any additional uterine space.

We have routinely observed large, unoccupied spaces in the gravid Meishan uterus on d 110 of gestation that...
are equal to or exceed the spaces occupied by viable littermates (S. P. Ford, unpublished observations). In contrast, we have rarely observed significant unoccupied spaces in the uterus of the late-pregnant Yorkshire female. We hypothesized that due to their ability to increase placental vascular density, Meishan conceptuses may not increase their placental size near term, even after an adjacent littermate dies. In contrast, the apparent inability of the Yorkshire conceptus to increase placental vascular density near term may drive an increase in placental size after the death of an adjacent littermate. Therefore, it was our objective to document any placental growth differences of Meishan or Yorkshire conceptuses resulting from the crushing of an adjacent conceptus on d 40 of gestation.

Meishan (n = 5) and Yorkshire (n = 5) females, exhibiting two to four postpubertal estrous cycles, were checked daily for the onset of estrus with intact boars of the same breed. Females were bred at estrus and 18 to 24 h later. On d 40 of gestation, Yorkshires and Meishans were laparotomized as previously described (Anderson et al., 1993) and one uterine horn (treated horn) was randomly assigned to have every other fetus crushed through the uterine wall using digital pressure. No fetuses were crushed in the other horn (control horn). The first fetus nearest the ovarian end of the treated uterine horn was left intact and every other conceptus was crushed in situ. We chose to reduce fetal number on d 40 for three primary reasons: 1) the chorio-allantoic fluid levels in the placenta are decreasing, thus reducing intraluminal pressure and allowing easy location and crushing of fetuses, 2) the size of the fetus is large enough to easily locate, but early enough in development to allow for ease in crushing, and 3) d 40 is a time point during gestation when conceptus loss naturally occurs as a result of limitations of uterine capacity. Conceptus number in both horns was recorded. After recovery from surgery, females were returned to their pen until slaughter on d 111 of gestation. At slaughter, gravid uteri were collected and immediately placed on ice for transport to the laboratory. At the laboratory, the mesometrium was trimmed from each uterine horn and its length was determined along the antimesometrial border using a cloth-type measure. After the chorio-allantoic fluid was drained from each conceptus, the horn was opened along its antimesometrial border. Each fetus had its umbilical cord double-ligated and transected and its location, weight, and crown-rump length were recorded. For each uterine horn, the distances between all adjacent umbilical attachment sites were measured and within each interfetal space areas occupied by placentae and the unoccupied area were determined (Figure 1). Individual placentae were then manually separated from the endometrium. After weighing, placentae were then spread out on plastic-coated paper ("butcher's paper") and their outer perimeters were traced for later determination of placental surface area using a compensating planimeter (Compensating Polar Planimeter, Keufel and Esser Co., New York) as previously described (Biensen et al., 1998). In order to estimate placental efficiency, fetal weight was divided by the weight of its placenta. All procedures outlined above were approved by the Iowa State University Committee on Animal Care.

### Statistics

Statistical analyses were performed using the general linear models procedures of SAS (SAS Inst. Inc., Cary, NC). Because there was no effect of gilt, gilt was removed from the model. The females were used as the experimental units for analysis (Steel et al., 1997) because fetal weights, crown-rump lengths, placental weights, placental efficiencies, uterine horn length, conceptus number, implantation site lengths, and length of the unoccupied spaces were averaged within a litter. Model statements included the effect of uterine horn (treated or control) and breed on measurements of fetal weight, placental weight, placental efficiency, conceptus number, uterine horn length, implantation site length, and the length of the unoccupied uterine space. Mean separation was performed by LSMEANS. A significance level of $P < 0.05$ or less was considered statistically significant.

### Results

The number of conceptuses did not differ in the control and treated uterine horns of Yorkshire vs Meishan females on d 40, before alternate fetal crushing was accomplished (Yorkshire control and treated uterine horns: $7.0 \pm 1.0$ and $8.4 \pm 0.9$ vs Meishan control and treated uterine horns: $7.0 \pm 0.7$ and $7.4 \pm 0.8$, respectively). At slaughter on d 111, no difference in uterine horn length was observed between Meishan and Yorkshire females (Table 1). Further, although there was an appropriately reduced number of fetuses in the treated vs the control horns (approximately half that of the control) of each breed, there was no difference...
between Yorkshire and Meishan females. Additionally, the range of viable conceptus numbers within a breed was similar (range = two to eight conceptuses/horn). Percentage survival (calculated as the number of viable conceptuses at slaughter on d 111 vs the number remaining after fetal crushing on d 40) was not different between the control or treated horns, or between the Yorkshire and Meishan females, averaging 88.94 ± 3.25%.

Although fetal weights and crown-rump length did not differ between the control and treated uterine horns of either the Yorkshire or Meishan breeds (Table 2), there was a tendency for the fetuses in the treated uterine horn to be longer and heavier than the conceptuses in the control uterine horn in both breeds. There were marked differences in the weight (P < 0.001) and surface area (P < 0.0001) of the placentae between the two breeds (Figure 2). Meishan placentae were markedly smaller and lighter than the Yorkshire placenta on d 111. There was no difference in placental weight or placental surface area between the control and treated horns in the Meishan females. In contrast, however, there were marked increases not only in placental weight (P < 0.05) but also in placental surface area (P < 0.001) compared to the implantation site length in the Meishan conceptuses in either the control or treated horn (Figure 3), whereas the implantation site length of the Meishan conceptuses gestated in the treated horn was increased ∼27% (P < 0.05) compared to the implantation site lengths in the control horn. In contrast, there was an increase (P < 0.05) in the average length of unoccupied spaces in the Meishan treated horn compared to the Meishan control horn, whereas there was no difference (P > 0.1) in the length of the average unoccupied spaces in the control and treated horns of Yorkshire females (Figure 3).

Although there was a significant difference (P < 0.05) in the average interfetal distance between the Yorkshire control and treated horns, there was no significant difference in the percentage of unoccupied space of these horns (Table 3). Similarly, the percentage of the space within a uterine horn occupied by placenta was similar between the Yorkshire control and treated horns. The Meishan females also had a significant difference (P < 0.001) in the average interfetal space on d 111 between the control and treated horns. However, in contrast to the Yorkshire females, the percentage of unoccupied space was significantly reduced (P < 0.001) in the control horn of Meishan females compared to the treated horn. Similarly, the percentage uterine space occupied by placentae was significantly greater (P < 0.001) in the Meishan control horn than in the treated horn. When comparing across breeds, the unoccupied space of both Yorkshire horns and the Meishan control horn was similar, averaging ∼21% of the interfetal space; however, the unoccupied space of the Meishan treated horn was twofold greater.

**Discussion**

In this study, Meishan conceptuses did not differ in fetal or placental size on d 111 in the control uterine horn.
horn vs the treated uterine horn in which every other conceptus was crushed on d 40 of gestation. In contrast, the remaining conceptuses in the treated horn of Yorkshire females exhibited an acceleration in placental growth, placental surface area, and implantation site length compared to the conceptuses in the control horn. Further, although the percentage of unoccupied space increased in the treated uterine horn of Meishan females compared to that in the control uterine horn, there was no effect of fetal crushing on the percentage of unoccupied space in the treated uterine horn of the Yorkshire females. These data demonstrate that a distinct difference exists between the Meishan and Yorkshire breeds in the response of their conceptuses to the loss of a littermate during midgestation.

In this study, both Yorkshire and Meishan litters had less space between neighboring fetuses in the control uterine horn than in the treated uterine horn on d 111.

However, if we take a closer look at the composition of the uterine area between the fetuses we see a distinct difference between the breeds. In the Yorkshire females, there was no difference in the percentage of unoccupied interfetal space or the space occupied by placentae in the control and treated uterine horns. However, Meishan females exhibited an increase in the unoccupied space and a decrease in the space occupied by placentae as a percentage of the interfetal distances in the treated uterine horn compared to the control uterine horn. These data demonstrate that although conceptuses in both Yorkshire and Meishan treated uterine horns have an increase in interfetal distances on d 111 compared to those in control horns, the Yorkshire uses more of the existing interfetal space for placental tissue development than does the Meishan.

Throughout gestation and at farrowing, Meishan conceptuses are smaller and lighter than conceptuses of U.S. or European pig breeds (Lee et al., 1995; Biensen et al., 1998). Further, Meishan placental weight and surface area do not increase from d 70 of gestation to term (≅114 d; Biensen et al., 1998; Wilson et al., 1998). In contrast, placental growth, as measured by weight and surface area, has been reported to increase from d 90 through the end of gestation in U.S. and European pig breeds (Knight et al., 1977; Wigmore and Strickland, 1985; Biensen et al., 1998). In the occidental pig breeds, placental surface area increases rapidly (four-fold increase) from d 35 to 70 (Knight et al., 1977), achieving a plateau in size on ≅100, when there is another marked increase in placental surface area to accommodate increasing fetal nutrient and oxygen demands (Wigmore and Strickland, 1985; Biensen et al., 1998, 1999). Knight et al. (1977) demonstrated that conceptuses in control pigs had markedly heavier and larger placentae than those of unilateral hysterectomized (UHO) animals from d 20 through d 100. The UHO gilt has been a model for investigating uterine capacity because the ovulation rate is similar to intact gilts with only half the uterine space available for conceptus growth. Along with the current study, the UHO data imply that placental growth in U.S. and European pig breeds is prevented from obtaining an optimal rate when the uterine conditions are crowded compared to a uterus in which more space is available for conceptus expansion. It appears that U.S. and European pig breeds increase placental size and surface area (Biensen et al., 1998) during the last third of gestation in order to optimally nourish their rapidly developing fetuses in preparation for birth. If placental growth is hindered when uterine conditions are crowded, piglet viability may be compromised. A greater than average litter size in U.S. and European pig breeds often results in decreased piglet birth weights, leading to reduced neonatal survivability (Fahmy, 1971; Johnson et al., 1999). In contrast, Meishan placentae fail to increase in size or surface area when there is extra uterine space for placental growth (this study) or when placed in a more permissive uterine...
Might have resulted from an accelerated placental d of the surviving conceptuses in the treated horn. It is possible that the increased placental size observed on d 111 in the treated uterine horn of Yorkshire females (but not Meishan females) compared to the control uterine horn. This was evidenced by increases in placental weight, surface area, and implantation site length of Yorkshire conceptuses in the treated vs the control horn. It is possible that the increased placental size observed on d 111 of the surviving conceptuses in the treated horn may have resulted from an accelerated placental growth between d 40 and 50, although confirmation of this cannot be derived from the current study.

The uterus of U.S. and European pigs elongates in response to embryo stimulation (Knight et al., 1977; Wu et al., 1987; Chen and Dzuik, 1993), especially when the length of space per conceptus is restricted (Chen and Dzuik, 1993). Likewise, a segment of uterus has been reported to shorten when not occupied by a conceptus (Chen and Dzuik, 1993; Lamberson and Eckardt, 1996). Chen and Dzuik (1993) demonstrated that the loss of conceptuses between d 3 and 41 of gestation in U.S. or European pig breeds resulted in a decrease in uterine length. Lamberson and Eckardt (1996) performed an experiment in which uterine horns were initially ligated on d 2 to 4 after the onset of estrus, and on d 28 of gestation serosal sutures were placed to mark the placental boundaries and every third embryo was crushed. Unfortunately, they slaughtered their animals on d 100, a time period just prior to the documented secondary growth phase of the placenta. As a result, there was no evidence of accelerated fetal or placental growth of the surviving conceptuses in the crushed horn compared to the control horn. They also reported that in response to conceptus crushing on d 28 of gestation, the uterus shortened in those areas that had previously been occupied by a conceptus. Because we could not obtain a meaningful estimate of initial uterine length at surgery on d 40, we are unable to refute or confirm the shrinkage of unoccupied spaces in these studies.

As previously stated, we have observed that placental size was approximately 30% greater for the surviving Yorkshire conceptuses of the treated horn than those present in the control horn, and that no similar difference in placental size was observed in the Meishan. We observed no difference in the length of the control and treated horns, the number of viable conceptuses in a uterine horn (treated or control), or the number of viable conceptuses in the Yorkshire or Meishan females. Therefore, if any uterine shortening had occurred in unoccupied interfetal spaces in response to conceptus loss, this shortening must have been compensated for by a matching increase in uterine size in segments occu-

<table>
<thead>
<tr>
<th>Uterine horn</th>
<th>Average interfetal distance, cm</th>
<th>Unoccupied space (% of interfetal space)</th>
<th>Space occupied by placenta (% of interfetal space)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yorkshire control horn (n = 5)</td>
<td>34.5 ± 3.5a</td>
<td>19.4 ± 5.2%a</td>
<td>80.6 ± 5.2%a</td>
</tr>
<tr>
<td>Yorkshire treated horn (n = 5)</td>
<td>48.4 ± 2.8b</td>
<td>29.2 ± 3.1%a</td>
<td>70.8 ± 3.1%a</td>
</tr>
<tr>
<td>Meishan control horn (n = 5)</td>
<td>23.0 ± 3.6c</td>
<td>15.4 ± 7.2%a</td>
<td>84.6 ± 7.2%a</td>
</tr>
<tr>
<td>Meishan treated horn (n = 5)</td>
<td>36.7 ± 3.0a</td>
<td>46.2 ± 3.9%b</td>
<td>53.8 ± 3.9%b</td>
</tr>
</tbody>
</table>

*a,b,cMeans ± SE (%) within a column with different superscripts differ (P < 0.05).
plied by an adjacent viable conceptus. Unlike the other studies described above (Chen and Dzuik, 1993; Lamberson and Eckardt, 1996), we allowed gestation to continue until a few days prior to expected farrowing (d 111). As has been documented by several researchers (Wigmore and Strickland, 1985; Biensen et al., 1998, 1999; Wilson et al., 1998), placental growth increases dramatically during the last 2 wk of gestation. This period is a particularly critical time in conceptus growth and development that is required to prepare the fetus for birth. The failure of Lamberson and Eckardt (1996) to slaughter their pigs after d 100 may have prevented them from observing compensatory placental growth when a more roomy uterine environment was created through the removal of selected conceptuses.

**Implications**

Understanding the biological differences between the highly prolific Chinese Meishan and the less prolific Yorkshire breed may give us some insight into the mechanisms influencing uterine capacity, a major limitation to litter size in the pig. In contrast to the surviving Yorkshire conceptuses in the treated uterine horn, which had increased placental size and surface area of attachment, surviving Meishan conceptuses in the treated uterine horn failed to exhibit similar compensatory increases in placental size in response to the loss of an adjacent littermate. This failure of surviving Meishan conceptuses to accelerate their placental growth may be due to its documented ability to increase the density of blood vessels at the placental:endometrial interface in response to increasing fetal demands. A similar strategy of reduced placental growth may exist in selected piglets of U.S. pig breeds; we have shown that selection of gilts for greater than average placental efficiency at birth results in marked increases in litter size by these selected females.

**Literature Cited**


