A Decreased Placental Size and Increased Vascular Density Results in Increased Prolificacy in the Meishan Pig

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Summary and Implications

The Chinese Meishan pig farrows 3 to 5 more pigs per litter than U.S. pig breeds. When Meishan and Yorkshire embryos are co-transferred to a Yorkshire recipient, Meishan fetuses and placentae are smaller than Yorkshire fetuses and placentae through day 90 of gestation. At farrowing, Meishan placentae are still smaller than Yorkshire placentae; however, Meishan fetuses are born at the same weight as their Yorkshire littermates. This tremendous growth of the Meishan fetus between day 90 and term is the result of an increased vascularization of the Meishan placenta. In this experiment we investigated the time course of placental vascular development of Meishan and Yorkshire conceptuses during late gestation. Our results demonstrate that Yorkshire fetuses increase the potential for nutrient extraction from the maternal blood by increasing the size of their placentae; however, Meishan fetuses achieve the same end by increasing the density of placental blood vessels while maintaining a constant placental size. The increased vascular density of the Meishan placenta then allows the conceptus to occupy less space in the uterus, allowing more fetuses to survive to term.

Introduction

For approximately seven years we have been investigating Chinese Meishan pigs in an attempt to understand why this breed farrows three to five more pigs per litter than our U.S. breeds. Both the Meishan and U.S. pig breeds ovulate 15 to 16 ova, but U.S. pig breeds exhibit markedly higher rates of conceptus loss. There are two periods of gestation to which almost all the prenatal loss have been attributed. First is a period of early embryo mortality, which occurs between days 12 and 18 post-mating. This is believed to result from the largest, most advanced embryos in a litter, producing large quantities of a steroid hormone, estradiol-17β, which alters the uterine environment (i.e., the composition of uterine milk) in a manner that is detrimental to their less developed littermates. The second period of loss occurs after day 30 of gestation, when the size of the uterus begins to be limiting which will dictate the number of conceptuses that can survive. We have previously shown that the Meishan embryo has a slower rate of cell division as early as five to six days of gestation when compared to similar age Yorkshire embryos. This decreased mitotic rate of the Meishan embryo occurs in the cell layer responsible for the production of steroids and leads to a markedly lower estradiol-17β secretion into the uterine environment. Therefore, the Meishan strategy of a decreased growth rate, when compared with the Yorkshire embryo, ultimately results in a greater percentage of Meishan as compared with Yorkshire embryos surviving the period of early embryo mortality. However, simply increasing the number of embryos that survive beyond about day 18 of gestation is not sufficient to increase litter size, as the capacity of the uterus begins to limit litter size around day 30 of gestation. In U.S. pig breeds, each viable fetus appears to require a placenta of a certain size for adequate nutrient and oxygen exchange. Further, as the size of the placenta increases, there is a corresponding increase in fetal size. Therefore the only way to increase litter size is to adjust the functional capacity of the uterus, either by selecting for a larger uterus or a smaller placenta. Work done at the USDA Meat Animal Research Center, Clay Center, NE, over the past nine years has demonstrated that uterine capacity as measured by uterine size is lowly heritable and therefore unlikely to be increased through standard selection techniques.

Early work on the Meishan pig demonstrated that there was no difference between the size of their uterus and that of a domestic pig. In previous experiments in our lab and others, the Meishan fetus has consistently been observed to develop with a smaller placenta than the Yorkshire or Large White fetus throughout gestation. By having a reduced placental size, as compared with domestic breeds, each Meishan conceptus occupies less space in the uterus, ultimately allowing more smaller piglets to survive to term. These smaller piglets are not runts, however, as the Meishan neonate is vigorous and active, indicating that although the Meishan placenta is small, it allows the Meishan fetus to receive adequate nutrition throughout gestation. In a recent experiment, in which Meishan and Yorkshire embryos were co-transferred into a Yorkshire recipient, we found that Meishan piglets had significantly smaller placentae than their Yorkshire littermates as expected; however, to our surprise both breeds of piglet were born at an identical weight. This further indicated to us that the Meishan piglet, although attached to a smaller placenta, was able to not only extract adequate nutrients via its small placenta, but as many nutrients as did the much larger Yorkshire placenta.

To better understand the differences in placental development between the Meishan and Yorkshire pig we undertook an experiment to investigate the pattern of placental growth, and the development of the placental and endometrial vasculature, with regard to both fetal and maternal breed.

Materials and Methods

Six Meishan and six Yorkshire females were mated to a boar of the same breed at the onset of estrus and again 24 hours later, to provide tissues from Meishan fetuses gestated in Meishan uteri or Yorkshire fetuses gestated in

Yorkshire uteri. An additional six Meishan and six Yorkshire females received embryos from donor females of the opposite breed on days two to three of gestation, to provide tissues from Yorkshire fetuses gestated in Meishan uteri or Meishan fetuses gestated in Yorkshire uteri. Females in each group were then slaughtered, two each day, at 70, 90, or 110 days of gestation. Each fetus was identified, removed from the uterus and weighed. The sex and crown-rump length of each fetus was also determined. Individual placentae then had a small section of the utero-placental interface collected and fixed for histologic evaluation of the density of blood vessels in the placenta and adjacent endometrium. Once all the histologic sections had been removed, the individual placentae were peeled away from the endometrium, and each placenta's weight, length, volume, and surface area of attachment were determined. The sections taken for histologic evaluation were stained to allow visualization of the blood vessels, and using a video camera attached to a microscope, were projected onto a TV monitor. The image on the TV monitor was then traced so that the percentage of placental and endometrial tissue occupied by blood vessels could be quantitated. This measurement is referred to as vascular density and gives a relative estimation of the amount of blood flowing through each tissue.

Results and Discussion

Regardless of uterine type (i.e., Meishan or Yorkshire), the surface area of the Yorkshire placenta increased from days 70 to 110 of gestation, paralleling the increase in fetal weight (fig. 1). The Meishan placenta, however, did not increase in surface area between days 70 and 110 of gestation, in the face of an ever increasing fetal weight throughout this time interval (fig. 2). The concentration of blood vessels along with the size of the placenta together will determine the total amount of exchange between a fetus and its dam. Coincident with the increase in Yorkshire placental size, the concentration of blood vessels in that placenta did not change. This indicates that as the nutrient demands of the Yorkshire fetus increase near term, the response of the fetus to increase nutrient and gas exchange is to simply increase the size of the placenta with no change in its efficiency. However, as the Meishan placenta remains relatively constant throughout days 70 to 110, the increased nutrient demand of the fetus is satisfied by increasing the density of blood vessels in its placenta an astonishing 2.5-fold.

Figure 1. Yorkshire fetal weight (g., solid line) and placental surface area (cm.^{2}, dashed line) on days 70, 90, and 110 of gestation.

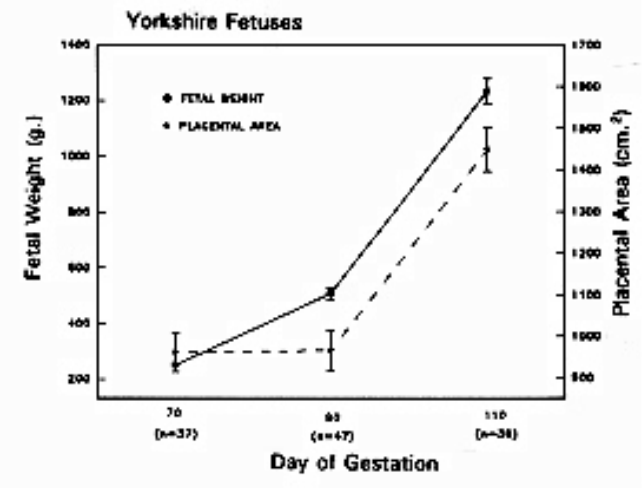
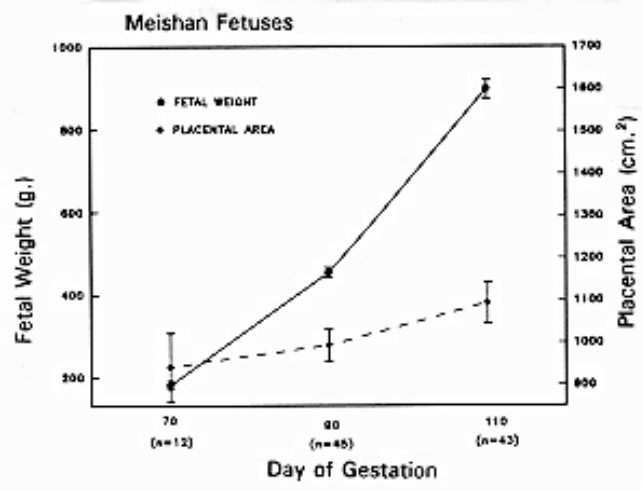
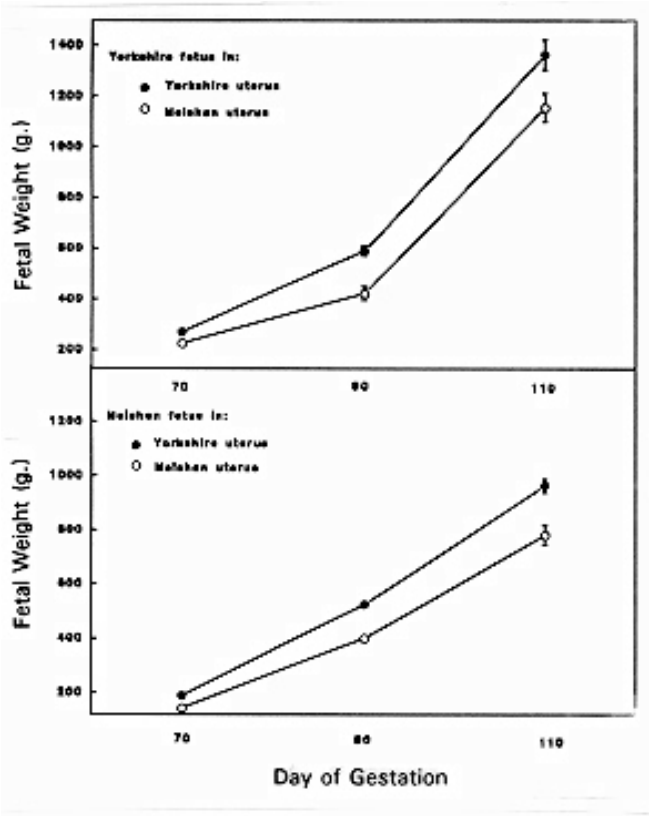


Figure 2. Meishan fetal weight (g., solid line) and placental surface area (cm.^{2}, dashed line) on days 70, 90, and 110 of gestation.



Each fetal breed exhibited a specific pattern of growth from days 70 to 110, regardless of recipient breed. The Yorkshire fetuses increased in weight in an exponential manner from days 70 to 110, growing faster between days 90 and 110 than 70 and 90. The Meishan fetuses, however, exhibited a linear pattern of growth from days 70 to 110. Further, each fetal breed was heavier by day 110 if gestated in a Yorkshire uterus than the same fetal breed gestated in a Meishan uterus (fig. 3). To our surprise, we also found that the Yorkshire endometrium had a markedly greater density of blood vessels, when compared with the Meishan endometrium, indicating the potential for a greater delivery of nutrients to the fetal-maternal interface.

Figure 3. ***Top panel.*** **Yorkshire fetal weight in either a Yorkshire (●) or Meishan (○) uterus on days 70, 90, and 110 of gestation.** ***Bottom panel.*** **Meishan fetal weight in either a Yorkshire (●) or Meishan (○) uterus on day 70, 90 and 110 of gestation.**



As a result of increasing the efficiency of extraction over each square inch of its placenta, the Meishan conceptus is able to develop a viable fetus with a much smaller placenta than is found in U.S. pig breeds. Since the real limitation to litter size is the available space in the uterus, conceptuses that occupy less space will have room for additional littermates. The results of this experiment also explain the unexpected similarity in birth weight of Meishan and Yorkshire littermate piglets gestated in a Yorkshire uterus. The richly vascularized Yorkshire endometrium would be expected to deliver more oxygen and nutrients to the fetal-maternal interface, than would the Meishan endometrium. Additionally, the increased extraction efficiency of the Meishan placenta, as compared with Yorkshire placenta, should allow maximal utilization of the nutrients and oxygen delivered.

The Meishan pig therefore has two separate yet complimentary mechanisms operating to allow it to farrow more pigs per litter than our domestic breeds of swine at the same ovulation rate. First, the Meishan embryo develops from fewer cells in the early stages of embryonic development than does the Yorkshire embryo, resulting in less estradiol-17β production and a less drastic change in the composition of uterine milk, allowing more embryos to survive beyond day 18 of gestation. Second, the Meishan conceptus develops a smaller placenta than does the Yorkshire conceptus, and increases the density of vasculature on that placenta in lieu of increasing its size. This results in each Meishan conceptus taking up less space and so the increased number of Meishan embryos surviving beyond day 18, as compared to our U.S. breeds, can continue to survive to term.

Little progress has been made over the last twenty years in increasing the number of pigs per litter per female. Increasing litter size is widely believed to be the best way to decrease the cost of piglet production, thereby increasing producer profits. It has been estimated that increasing litter size by one pig per litter would be worth approximately $2 billion annually to the swine industry. Understanding the mechanisms that result in the Meishan fetus developing a smaller more efficient placenta, will eventually allow selection of U.S. pigs that exhibit the same phenotype, potentially increasing litter size in U.S. pig breeds.