JOURNAL OF ANIMAL SCIENCE
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J Anim Sci 2002. 80:553-559.

Impacts on conceptus survival in a commercial swine herd[1,2]

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ABSTRACT: An estimated 30 to 40% of potential piglets are lost before farrowing in U.S. or European pig breeds. Because these studies were conducted in limited numbers of university research herds, we decided to characterize the timing, pattern, and extent of conceptus loss in a commercial swine herd in Iowa (Pig Improvement Company; Camborough Line). Sows (parities 2 to 14) were slaughtered on d 25 (n = 83), 36 (n = 78), or 44 (n = 83) of gestation. These days coincide with periods before, during, and after uterine capacity becomes limiting to conceptus survival. At slaughter, numbers of corpora lutea (CL) and uterine horn length were determined, and conceptuses were removed and evaluated. Uterine horn length and CL number did not differ among these days of gestation, averaging 217 cm and 26.6 CL, respectively. In contrast, numbers of conceptuses decreased ($P < 0.05$) from 15.8 on d 25 to 12.9 on d 36, then remained relatively constant through d 44 (12.1). Thus, conceptus survival averaged 60.2% on d 25, 50.1% on d 36, and 46.3% on d 44, based on numbers of CL present. There was a positive correlation ($P < 0.001$; r = 0.50) between numbers of viable conceptuses on d 25 and ovulation rate, but this association was completely lost by d 36 ($P > 0.10$) when uterine capacity becomes limiting. In agreement with this premise, uterine horn length and conceptus number were not associated on d 25 but exhibited positive correlations ($P < 0.05$) on d 36 (r = 0.36) and d 44 (r = 0.40). On all 3 d examined, the numbers of viable conceptuses were not associated with fetal weight but were negatively correlated ($P < 0.05$) with placental weight. Compared with the commonly reported values for ovulation rate and percentage conceptus loss in university research herds, values from these production animals were extremely high. Data suggest that throughout this period, larger litters were associated with conceptuses exhibiting small placentae. These data lend support to the concept that increased placental efficiency (fetal weight/placental weight) may contribute to increased litter size in the pig.

Key Words: Abortion, Commercial Farming, Placenta

 J. Anim. Sci. 2002. 80:553–559

Introduction

Litter size is an important component of profitability for U.S. swine producers (Lawrence, 1993). Over the last 87 yr, litter size has increased modestly in U.S. pig herds from seven to eight pigs/litter in 1914 (Hammond, 1914) to current values averaging eight to nine pigs/litter in the overall industry (NASS, 2001) and 10 to 11 pigs/litter in selected maternal lines (NPPC, 2001). This litter size is not optimal; published values for ovulation rate average 14 to 16 ova, 95% are fertilized, and sows have 12 to 14 functional teats (Christenson, 1993).

To understand the constraints on litter size, the limitations of ovulation rate (Johnson et al., 1999), uterine capacity (Christenson et al., 1989), and placental size and efficiency (Wilson et al., 1999) have been investigated. Although ovulation rate can be increased by selection, it has variable effects on increasing litter size in the pig (Lamberson et al., 1991). Superovulation (Dzuik, 1968) or superfetation (Fenton et al., 1972) increase embryo numbers to d 30 of gestation. However, these extra embryos were soon lost due to limitations of uterine capacity. Although selection for increased uterine capacity has resulted in modest and variable increases in litter size (Gama and Johnson, 1993), selec-

[1]Journal paper no. J-19317 of the Iowa Agric. and Home Econ. Exp. Sta., Ames. Project nos. 0239, 3505, and 3900, and supported by Hatch Act and State of Iowa Funds.

[2]Technical and financial support was also provided by Gene Gourley, Swine Graphics Enterprises, Webster City, IA; Teddi Wolff, Roche Vitamins, Kansas City, MO; and Michelle Quirk-Thomas, Pig Improvement Company, Franklin, KY.

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Received July 5, 2001.

Accepted September 28, 2001.

tion for reduced placental size shows greater promise (Wilson et al., 1999).

To date, an understanding of the limitations of litter size are based on data from limited numbers of university herds. Commercial swine producers have continuously accessed dam lines intensively selected for prolificacy. However, the biologic characteristics of these lines are not known. Selection for prolificacy may have indirectly increased ovulation rate with important implications for patterns of prenatal loss (Foxcroft, 1997) and for early placental growth and development (Almeida et al., 2000). Our objective was to characterize the reproductive phenotype of a commercial swine herd from d 25 to 44 of gestation, when uterine capacity becomes limiting.

Materials and Methods

Pig Improvement Company Camborough sows from a commercial breeding unit (Dayton Pork, Dayton, Iowa; Swine Graphic Enterprises, Inc., Webster City, Iowa) were made available for this study as part of a herd depopulation exercise. The semen used was from Dayton Pork's boar stud and was Pig Improvement Company (northern pyramid) 337, which was mostly a Duroc line. Sows (n = 244) of differing parities (1 to 14; with 58.0% of the sows in parity 1 to 4; 36.7% of the sows in parity 5 to 8, and 5.3% of the sows in parity 9 to 14) were weaned (18.7 ± 0.1 d average lactation length) in groups of 30 once per week (on Wednesdays) and artificially inseminated at the subsequent estrus, which occurred 3 to 7 d after weaning ($\bar{x}$ = 4.99 ± 0.06 d to estrus). Animals were randomly slaughtered (10/d) at a local abattoir (Iowa Pack, Des Moines, IA) on d 30 (n = 83), 40 (n = 78), or 50 (n = 83) after weaning, which averaged 25.05 ± 0.03, 36.02 ± 0.05, and 44.02 ± 0.03 d of gestation, respectively. At slaughter, the gravid uteri were identified and placed on ice for immediate transport back to the laboratory at Iowa State University. Upon arrival in the laboratory, the mesometrium was trimmed away at its junction with each uterine horn, and the length of each horn was determined by measuring along the antimesometrial border using a cloth tape measure. Two of the 10 gravid uteri each day were randomly chosen for measurement of total conceptus volumes. For these animals, the uterine wall was opened over each conceptus without puncturing the chorioallantoic membrane. The entire conceptus (fetus, placental membranes, and contained placental fluids) was then peeled from the endometrium and its volume was determined by placing the intact conceptus in a graduated cylinder partially filled with a known volume of water. After recording conceptus volume, placental membranes were punctured to allow the draining of placental fluids, and individual fetal weights and crown-rump lengths and placental weights were determined. For the remaining eight gravid uteri on each day, the uterine wall and chorioallantoic membrane was cut over each conceptus, and the fetal and placental weights were determined. Conceptus viability was determined by visual observation. Placental efficiency was then calculated by dividing the fetal weight by the weight of its placenta. The number of corpora lutea was also determined on the right and left ovaries of each sow via blunt dissection.

Statistical analyses were performed using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). Because there was no effect of parity of the sow on any of the variables measured, parity was dropped from the analyses. Model statements included the effect of day of gestation on fetal weight, placental weight, placental efficiency, total conceptus volume, number of corpora lutea, and uterine horn length. Correlations within gestational age between fetal weight, placental weight, placental efficiency, number of corpora lutea, uterine horn length, and total conceptus volume were also analyzed using the PROC CORR procedure. There was no effect of sow within a day (P = 0.40) on fetal weight or placental weight of the conceptuses. In order to determine a measure of variation of fetal and placental weights among conceptuses on d 25, 36, and 44, the percentage variation around mean fetal and placental weight was calculated per day. Effect of day on percentage variation around the mean was analyzed by the homogeneity of variance test using the Brown and Forsythe's variation of Levene's test. Percentage variation around the mean was calculated by subtracting mean fetal weight per day from an individual's fetal weight and dividing this by the individual's fetal weight. This value was then put on a percentage basis. The same calculation was performed for percentage variation of placental weights.

Results

Of the 244 sows slaughtered, 190 were confirmed pregnant by the presence of viable conceptuses, for an overall conception rate of 77.9 ± 2.7%. Further, there was no effect of day of gestation or parity at slaughter on conception rate (d 25, 75.9 ± 4.7%; d 36, 76.9 ± 4.8%; d 44, 80.7 ± 4.4%). Similarly, there were no day of gestation or parity differences in the number of corpora lutea dissected from the ovaries of each animal, which averaged 26.6 ± 0.4 (Figure 1). Likewise, there was no effect of parity on the number of viable conceptuses per sow (P = 0.53). Uterine horn length increased (P < 0.001) from d 25 (206.8 ± 3.8 cm) to d 36 (226.7 ± 3.9 cm) then remained relatively constant through d 44 (218.1 ± 3.7 cm); however, there was no significant association between the length of uterine horns and the parity of the sow on any day examined.

Conceptus number decreased (P < 0.005) from 15.8 ± 0.6 fetuses on d 25 to 12.9 ± 0.5 on d 36, then remained relatively constant through d 44 (Table 1). As a result, conceptus survival (number of conceptuses/ number of corpora lutea) declined (P < 0.05) from 60.2 ± 0.1% on d 25 to only 50.1 ± 0.1% on d 36, and 46.3 ± 0.1% by d 44. There were marked and progressive increases in

Table 1. Effect of day of gestation on conceptus measurements

Measurement	Day of gestation 25	36	44	SE
Viable conceptus/litter, no.	15.8[d]	12.9[e]	12.1[e]	0.6
Conceptus survival, %[a]	60.2[d]	50.1[e]	46.3[e]	0.1
Fetal wt, g	0.56[d] (n = 994)	4.95[e] (n = 769)	19.03[f] n = 811)	0.03
Placental wt, g	5.95[d] (n = 994)	46.94[e] (n = 769)	65.5[f] (n = 811)	0.1
Crown-rump length, cm	2.77[d] (n = 994)	4.95[e] (n = 769)	8.26[f] (n = 811)	0.02
Placental efficiency[b]	0.12[d] (n = 994)	0.13[d] (n = 769)	0.33[e] (n = 811)	0.005
Total conceptus volume, mL[c]	75.4[d] (n = 330)	201.5[e] (n = 253)	155.0[f] (n = 253)	6.6

[a]Conceptus survival is the total number of viable fetuses divided by the number of corpora lutea on the ovaries.
[b]Placental efficiency is the fetal weight:placental weight ratio.
[c]Total conceptus volume is the volume of water displaced from the entire conceptus (placental membranes, fetus and conceptus fluids; see text for more detail).
[d,e,f]Means ± SEM within a row with different superscripts differ ($P< 0.05$).

both fetal (P < 0.0001) and placental (P < 0.0001) weights and crown-rump lengths (P < 0.0001) from d 25 to d 44 of gestation (Table 1). In contrast, placental efficiencies remained constant from d 25 to d 36, before increasing (P < 0.05) by d 44. In the subset of sows in which the volumes of each conceptus in their litters were determined by volume displacement, conceptus volume increased (P < 0.0001) markedly from d 25 to 36 of gestation, then declined (P < 0.01) to intermediate levels by d 44 (Table1).

Table 2 depicts the associations between selected reproductive measurements and the number of viable conceptuses recovered from gravid uteri on d 25, 36, and 44 of gestation. There was a highly significant positive correlation (r = 0.50; P < 0.001) between numbers of viable conceptuses in a litter and ovulation rate on d 25, but this association was absent on d 36 and 44. On all 3 d of gestation examined, placental weight exhibited significant negative correlations, whereas placental efficiency exhibited significant positive correlations with the numbers of viable conceptuses recovered from a gravid uterus. In contrast, no association (P = 0.58) was observed between fetal weight and the number of viable conceptuses on any of the 3 d of gestation examined. Placental efficiency was unrelated to fetal weight but was negatively correlated (P < 0.001) with placental weight on d 25 (Figure 2), 36 (Figure 3), and 44 (Figure 4). Total conceptus volume was positively correlated with placental weight (r = 0.67; P < 0.001) and negatively correlated with placental efficiency (r = –0.54; P < 0.001) throughout this interval of gestation.

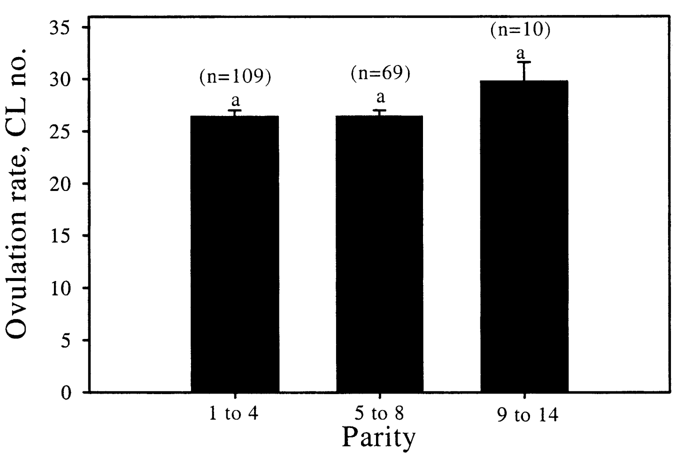

Figure 1. The average ovulation rate of females in this study divided into groups by parity. Means (± SEM) with different superscripts differ (P < 0.05). (n = the number of observations per group).

Figure 5 depicts the percentage variation around the mean in fetal (A) and placental (B) weights on d 25, 36, and 44 of gestation. The percentage variation in both fetal and placental weight decreased markedly (P < 0.001) from d 25 to 36 through d 44 of gestation, largely as a result of the disappearance of a group of conceptuses with larger than average placental sizes.

Discussion

These data demonstrate that the ovulation rate exhibited by the intensively selected sows in this commercial herd (≅26 ovulations) was markedly greater than has been reported previously for university/government herds, which averaged 12 to 18 ovulations (Wrathall, 1971; Christenson, 1993; Ford, 1997). Of interest was the observation that neither ovulation rate nor uterine horn length was affected by the parity of the sows,

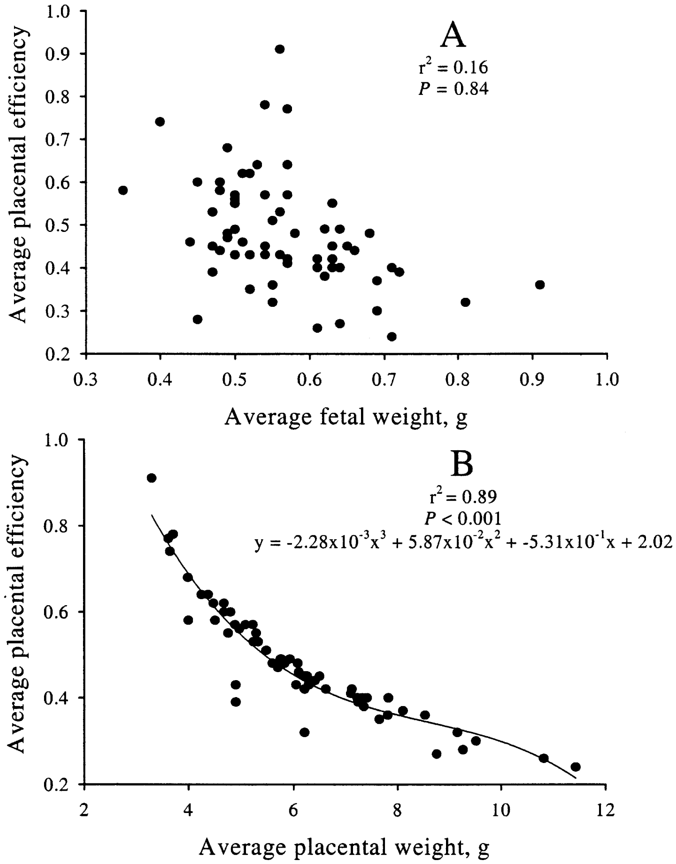

Figure 2. Associations between average within-litter placental efficiencies and average within-litter fetal weights (A) or placental weights (B) on d 25. Placental efficiency is the fetal weight:placental weight ratio.

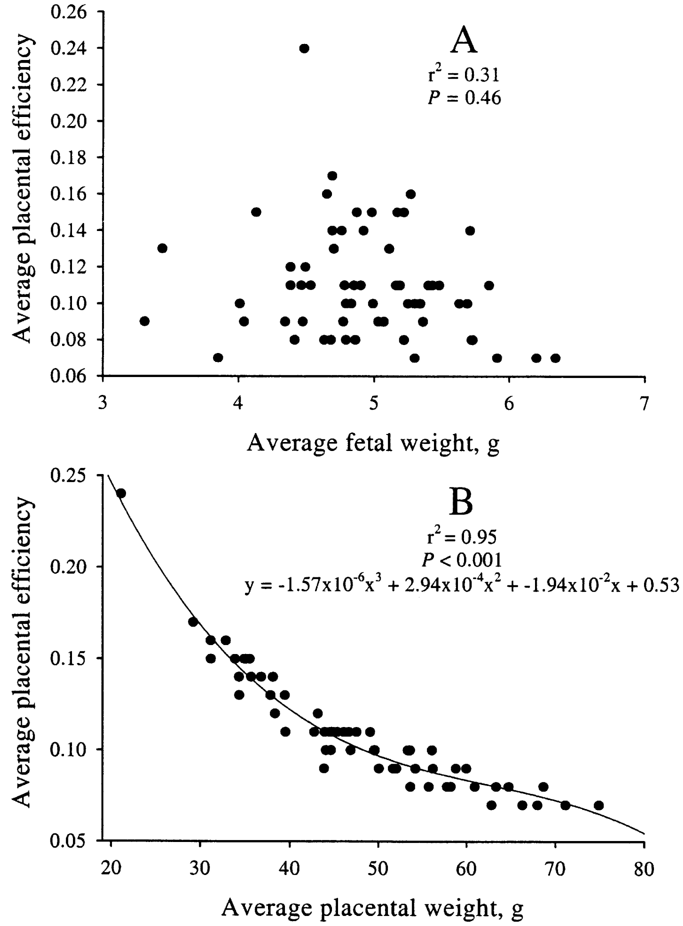

Figure 3. Associations between average within-litter placental efficiencies and average within-litter fetal weights (A) or placental weights (B) on d 36. Placental efficiency is the fetal weight:placental weight ratio.

which ranged from 2 to 14 in this study. Johnson et al. (1999) increased ovulation rate from 14 to 20.5 in his research population after 10 generations of selection for this trait. Although this selection increased survival by 3.3 fetuses up to d 50 of gestation, he only realized an increase of 1.1 live piglets/litter by the 11th generation. By the 14th generation, he obtained an increase of 1.4 live piglets/litter in his selected line; however, numbers of stillborn piglets increased and birth weights decreased. As a result, the number of piglets weaned in his selected line actually declined compared with his unselected control line. Blichfeldt and Almlid (1982) reported that ovulation rates up to 18.1 in Norwegian Landrace sows resulted in increasing numbers of embryos surviving to d 34, but no advantage was seen at higher ovulation rates. Further, Blasco et al. (1996) reported no further increase in litter size for French Large White sows whose ovulation rate exceeded 20.9. Thus, there appears to be an upper limit on the number of conceptuses that can be accommodated by the uterus, regardless of the numbers of ova shed. This limitation in uterine space may have resulted in the greater than expected conceptus losses (40 to 54%) observed in this study and suggests that ovulation rate in this population of commercial sows is not limiting to litter size.

Unilateral hysterectomy-ovariectomy has been proposed as a technique that allows a true estimate of uterine capacity (i.e., the maximal number of conceptuses that can be successfully accommodated per uterine horn) of female swine, in the absence of any possible limitation in ovulation rate (Christenson et al., 1987). Whereas Spruill and Eisen (1985) reported that selection for litter size resulted in longer uteri in cyclic and pregnant mice, no similar finding has been reported for the pig. In an experiment by Gama and Johnson (1993), no significant changes were found in uterine dimensions after a multigeneration selection for increased litter size in the pig. Further, these researchers reported no significant differences in uterine capacity as estimated after unilateral hysterectomy-ovariectomy between the line of pigs selected for increased litter size and unselected controls. The lack of a direct association between uterine size and litter size is consistent with previous reports demonstrating that uterine dimensions of cyclic and pregnant Meishan gilts were smaller than (Bazer et al., 1988) or not different from (Ford, 1997) those of U.S. or European pig breeds, but the

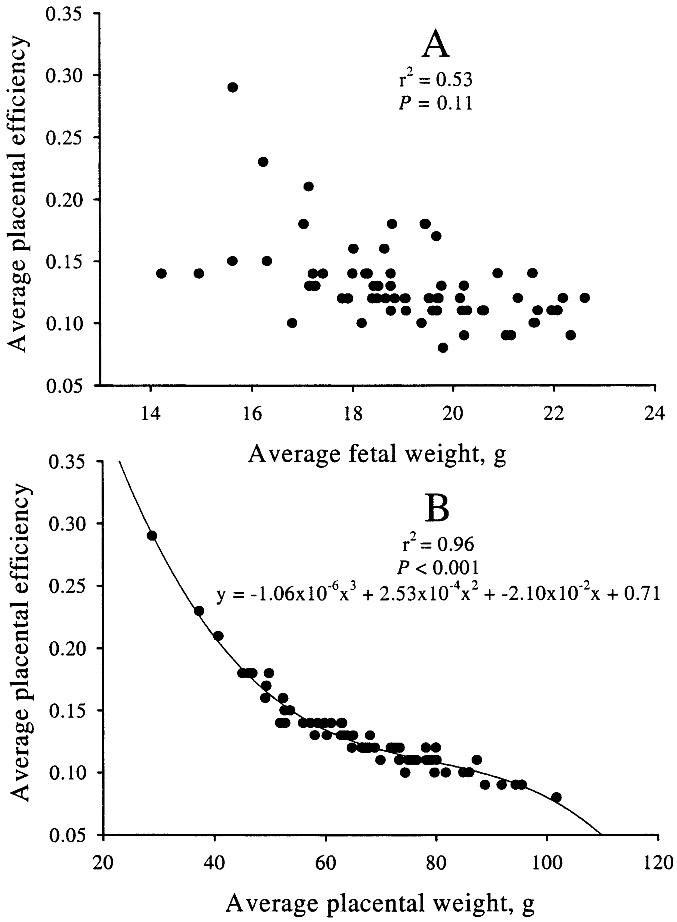

Figure 4. Associations between average within-litter placental efficiencies and average within-litter fetal weights (A) or placental weights (B) on d 44. Placental efficiency is the fetal weight:placental weight ratio.

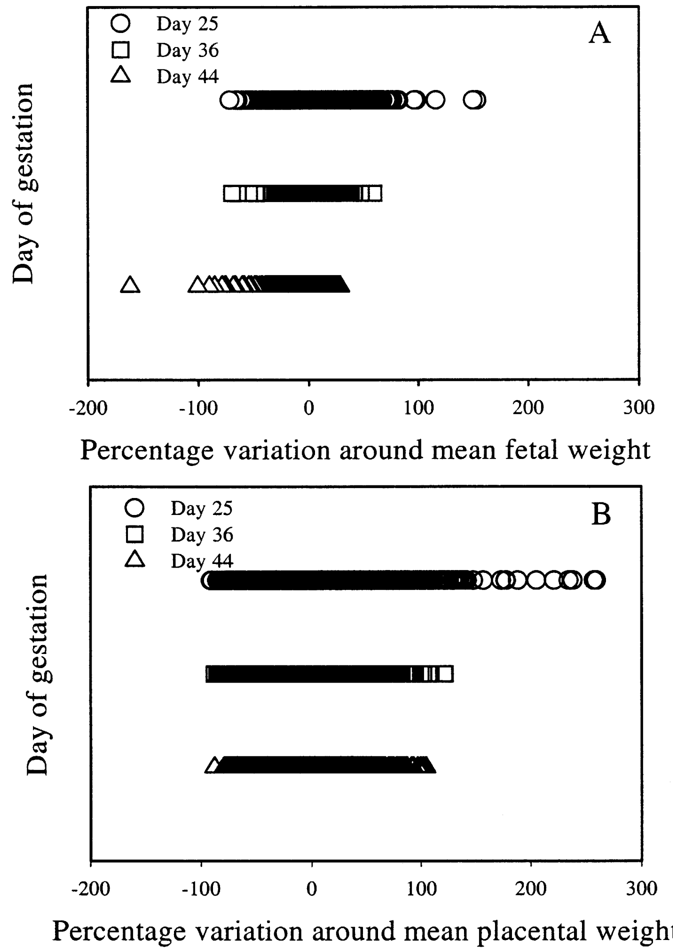

Figure 5. Percentage variation around the fetal (A) or placental (B) weight on d 25, 36, and 44 of gestation (d 25 > d 36 = d 44; $P < 0.001$).

Meishan females farrowed three to four more live pigs/litter.

In contrast, data in this study demonstrate a highly significant positive correlation between the number of viable conceptuses found and uterine horn length on d 36 and 44. These are the days when uterine capacity has been shown by numerous groups to exert a negative effect on conceptus numbers (Dziuk, 1968; Pope et al.,

Table 2. Correlation coefficients of selected reproductive measurements with numbers of viable conceptuses on d 25, 36, and 44 of gestation

	Day of gestation		
Measurement	25	36	44
Ovulation rate	0.50[a] (< 0.0001)	0.02 (= 0.98)	0.10 (= 0.41)
Uterine length, cm	0.03 (= 0.83)	0.36 (< 0.0001)	0.40 (< 0.0001)
Placental wt, g	–0.36 (< 0.005)	–0.27 (< 0.05)	–0.33 (< 0.01)
Fetal wt, g	–0.04 (= 0.74)	0.09 (= 0.51)	–0.09 (= 0.49)
Placental efficiency[b]	0.44 (< 0.001)	0.28 (< 0.05)	0.28 (< 0.05)

[a]Values are r (P-value).
[b]Placental efficiency is the fetal weight:placental weight ratio.

1972; Monk and Erb, 1974). It appears that due to the extremely high ovulation rate and increased embryo numbers produced by females in this commercial herd, uterine horn length may indeed impose a restriction on the numbers of conceptuses surviving to term. Dzuik (1985) reported that it required eight or more fetuses per uterine horn in the sow to stimulate an increased length of the horn after d 35 of gestation, which may suggest a crowded uterine environment. These data are consistent with several studies reporting that in U.S. and European pig breeds, an average of seven fetuses could be supported in a single uterine horn (Dzuik, 1968; Webel and Dziuk, 1974; Knight et al., 1977). Further, Holness (1982) and Wu et al. (1987) reported that when the number of ovulations exceeds the maximum uterine capacity of a female, the number of live fetuses is correlated with uterine horn length, but not with the number of corpora lutea, as reported in the present study. Of interest, however, is the fact that placental efficiency was positively associated ($r = 0.44$; $P < 0.001$) with the number of viable conceptuses present on d 25 of gestation, a day that precedes any evidence of uterine crowding, and a time by which 40% of the potential embryos have already been lost. These data suggest that increased placental efficiency is not a result of the limitations in uterine space per conceptus, but rather is a conceptus-associated trait.

These data are consistent with evidence suggesting that another major limitation on uterine capacity is indeed placental size, and that this trait is heritable (Wilson et al., 1999). Our data established significant negative correlations between the number of viable conceptuses recovered on d 25, 36, and 44 and the average placental weight of the litter but no association between the number of viable conceptuses and fetal weight. These results are consistent with the data of Almeida et al. (2000) and support the concept that placental efficiency is a critical factor in maintaining embryonic development. Wilson et al. (1999) reported that selection of Yorkshire breeding stock (boars and gilts) from piglets gestated on smaller than average placentae farrowed three more piglets/litter than those piglets gestated on larger than average placentae over multiple farrowings (12.8 ± 0.7 vs 9.5 ± 0.6, respectively). These researchers selected piglets of similar birth weight for inclusion in both the smaller than average placental group and the larger than average placental group. Thus, it was only differences in placental size and weight, and not differences in piglet size and weight, that resulted in marked differences in placental efficiency and litter size between groups in their study. These data suggested that selection on placental size and weight alone can affect uterine capacity and litter size. In agreement with this concept, there were no associations found between the number of viable conceptuses in a uterine horn on d 25, 36, or 44 and fetal weight in the present study. Vallet et al. (2001), utilizing the unilateral hysterectomy-ovariectomy model, reported that placental efficiency was elevated in a line of pigs selected for increased ovulation rate and litter size. Of interest is the heritability of 0.29 ± 0.08 for placental efficiency reported by Vallet et al. (2001) for the 422 litters utilized in their study. When compared with the reported heritabilities of 0.09 for uterine capacity (Young et al., 1996) and 0.16 for litter size (Hertzer et al., 1940), the heritability of placental efficiency is noteworthy.

Implications

These data suggest that the reproductive biology of commercially reared swine may differ substantially from that of swine being studied at university/government facilities. It is imperative to conduct an evaluation of the reproductive phenotypes of production animals to confirm the relevance of our findings. The extremely high ovulation rate of animals in this study suggests that it is not limiting to litter size in this herd. In fact, the excessively high ovulation rate of these animals may result in uterine crowding and excessive competition for nutrients and oxygen, which may negatively afect the growth rate and body composition of the survivors. Both increased uterine length and decreased placental size were associated with increases in the number of viable conceptuses recovered in this study. Because uterine capacity and placental size have been shown to be moderately heritable, selecting on one or both of these components may have potential for increasing litter size in this commercial herd.

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