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Growth and compositional changes of fetal tissues in pigs¹

R. L. McPherson*, F. Ji*, G. Wu†, J. R. Blanton, Jr.*, and S. W. Kim*²

*Texas Tech University, Department of Animal and Food Sciences, Lubbock 79409; and

†Texas A&M University, Department of Animal Science, College Station 77843

ABSTRACT: Three hundred twenty fetuses were obtained from 33 pregnant gilts (Camborough-22, Pig Improvement Co.) to determine rates of nutrient deposition in fetal tissues and to estimate nutrient requirements for fetal growth. Pregnant gilts were fed an equal amount of a gestation diet (2.0 kg/d; as-fed basis), and were slaughtered at d 0, 45, 60, 75, 90, 102, or 110 of gestation (n = 3 to 6 per day). Fetuses were dissected into carcass and individual tissues (including gastrointestinal tract, liver, lung, heart, kidney, spleen [\geq d 75]), and partial placental collection was made for chemical analysis. Fetal tissues were weighed and analyzed for DM, ash, CP, and crude fat. Regression equations were obtained to explain the weight and compositional changes of individual tissues during gestation. Weights of the fetus, carcass, gastrointestinal tract, liver, heart, lung, and kidney increased cubically ($P < 0.001$),

whereas brain weight increased linearly ($P < 0.001$) as gestation progressed. Fetal protein and fat contents increased quadratically ($P < 0.001$) as gestation progressed ($R^2 = 0.906$ and 0.904 , respectively). Changes in fetal protein and fat contents fit a multiphasic regression that consisted of two linear equations ($P < 0.001$, $R^2 = 0.988$ and $P < 0.001$, $R^2 = 0.983$, respectively), indicating that protein and fat growth accelerated after d 69 of gestation. Fetal protein and fat accretions were 0.25 and 0.06 g/d ($P < 0.001$) before d 69 of gestation, and increased to 4.63 and 1.09 g/d ($P < 0.001$) after d 69 of gestation. Protein needs for tissue protein gains increased 19-fold after d 69 of gestation. Results of this study indicate that the growth of the fetus and fetal tissues occurs at different rates during gestation and support the practice of a two-phase feeding strategy (before and after approximately d 70 of gestation) for pregnant gilts.

Key Words: Fat, Fetus, Gestation, Growth, Pigs, Protein

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Introduction

Porcine fetal growth accelerates during the second half of pregnancy (Knight et al., 1977; Wu et al., 1999; Pond and Mersmann, 2001). Several factors, including genetics, nutrition, and gestational stage, are the major determinants of growth rates in fetal pigs (Anthony et al., 1995; Allen, 2001; Fall et al., 2003). Ullrey et al. (1965) demonstrated that the growth rates of some porcine fetal tissues varied with gestational stages. However, compositional changes in fetal tissues during gestation have not been characterized. The availability of such data is crucial for estimation of nutrient needs for fetal tissue growth at a specific gestational stage.

Nutrient needs for fetal tissue growth affect overall maternal nutrition (NRC, 1998). Notably, maternal dietary nutrients are primarily directed toward support of fetal tissue growth (Trottier and Johnston, 2001). When maternal nutrient intake is insufficient, especially for pregnant gilts, their growth, longevity, and reproduction efficiency will be reduced. Thus, adequate feeding of pregnant gilts is important not only for fetal growth and development but also for sow reproductive and lactational performance (Schoknecht, 1997; Kim and Easter, 2003). Thus, nutrient needs of pregnant gilts should be based on dynamic compositional changes in individual fetal tissues during gestation, so as to establish an effective feeding strategy for pregnant gilts. The objective of this study was to determine rates of nutrient deposition in fetal tissues and to estimate nutrient requirements for fetal pig growth.

Materials and Methods

Animals and Experimental Design

An animal care and use protocol was approved by the Animal Care and Use Committee of Texas Tech

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²Correspondence: Box 42141, 123 Animal Science Bldg. (phone: 806-742-2532; fax: 806-742-2335; e-mail: sungwoo.kim@ttu.edu).

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Table 1. Composition of the gestation diet

Ingredient	%, as-fed basis
Corn grain, yellow	72.45
Soybean meal, de-hulled	11.00
Molasses cane	5.00
Potassium chloride ^a	0.25
Salt	0.35
Vitamin-mineral premix ^b	1.50
Oil, vegetable	0.50
Dicalcium phosphate	2.20
Limestone	0.50
Alfalfa meal	5.00
Calculated composition	
DM, %	89.20
ME, Mcal/kg	3.10
CP, %	12.20
Lysine, %	0.56
Cystine + methionine, %	0.44
Tryptophan, %	0.13
Threonine, %	0.45
Ca, %	0.94
Available P, %	0.47
Total P, %	0.69

^aDYNA K POT CHL, IMC Global, Lake Forest, IL.

^bVitamin-mineral premix provided the following per kilogram of complete diet: 23.3 mg of Mn as manganous oxide; 37.5 mg of Fe as iron sulfate; 51.9 mg of Zn as zinc oxide; 4.7 mg of Cu as copper oxide; 0.36 mg of I as ethylenediamine dihydroiodide; 0.11 mg of Se as sodium selenite; 3,777.8 IU of vitamin A as vitamin A acetate; 412.5 IU of vitamin D₃; 31 IU of vitamin E; 1.4 IU of vitamin K as menadione sodium bisulfate; 27.5 µg of vitamin B₁₂; 6.9 mg of riboflavin; 22 mg of D-pantothenic acid as calcium pantothenate; 27.5 mg of niacin; and 828.8 mg of choline as choline chloride.

University. Thirty-three gilts (158.2 ± 3.8 kg, Camborough-22, Pig Improvement Co., Franklin, KY), which produced a total of 320 fetuses, were used in this study. Gilts were housed in individual standard gestation crates at the Texas Tech University Swine Research Farm in New Deal. All gilts were checked for heat once daily in the morning and bred with unfrozen semen via artificial insemination twice during an estrous cycle (18 to 24 h apart). Pregnant gilts were provided, and consumed, 2 kg/d (as-fed basis) of gestation diet once daily (at 0900) (Table 1), which met NRC nutrient requirements (1998). Soybean meal was used as a major protein source, and corn was used as a major energy source in the diet, providing 89.2% DM, 12.2% CP, 0.56% lysine, 3.1 Mcal/kg ME, and 0.94% Ca (as-fed basis; Table 1). All gilts had free access to water throughout the entire study. At the beginning of the study, six gilts were assigned randomly to be slaughtered at d 0, 45, 60, 75, 90, 102, or 110 of gestation (Table 2). Final numbers of gilts in each slaughter group varied between three to six (totaling 33 gilts) due to pregnancy failure in some gilts (Table 2).

Slaughter and Sample Collection

Gilts were transported to the Texas Tech University Meat Laboratory in Lubbock at 1700 before slaughter, where they were withheld from feed. Gilts were weighed

Table 2. The number of gilts allotted per day of gestation and the number of fetuses collected

Variable	Day of gestation						
	0	45	60	75	90	102	110
No. of gilts	6	6	4	5	3	5	4
No. of fetuses	—	79	54	50	33	65	39
No. of fetuses/gilt	—	13.2	13.5	10.0	11.0	13.0	9.8
SE	—	1.8	1.9	1.7	0.6	1.2	1.3

and then slaughtered in the morning (0800), in compliance with standard university practices. Reproductive tracts were collected during the slaughter process. Weights of the entire reproductive tracts were measured. The uterus was placed on a table, allowing for both horns to be separated for measurement of the horn length. Each horn was separated into long (**L**) or short (**S**) sides. Fetuses were separated from the uterine horn by cutting the placenta at the base of the amniotic sac and then again at the base of the umbilicus. Individual fetuses were weighed, and then a medial incision was made to expose internal organs. The heart, liver, lung, gastrointestinal tract (**GIT**), kidneys, and spleen were collected via blunt dissection. Spleens were collected from the fetuses after d 75 of gestation to ensure proper organ separation. Partial placental collections were made for chemical analyses because the whole placenta could not be collected due to rupture during carcass processing. The weights of all fetal carcasses and fetal tissues were recorded. Following gestation d 45, fetal brains were collected and weighed.

Sample Processing

Following tissue collection, individual samples were stored at -20°C for further analysis. Fetal samples from the L side were thawed at a 4°C for 2 to 6 h. Samples from the same gilt were pooled by tissue. The pooled carcass and pooled individual tissues were then reweighed. Samples were then placed in a freeze dryer (TD44-0 Dura-Top freeze dryer, FTS Systems, Chatswood, Australia) until fully dried (approximately 7 to 14 d). The dried samples were then weighed and ground with a commercial blender (Waring Products, New Hartford, CT) to produce a homogenous mixture.

Chemical Analyses

Dry matter content was determined by the desiccation of the tissue at 105°C for 4 h in a forced air oven (Procedure No. 950.46; AOAC, 1995). Crude protein content (N × 6.25) was determined using the combustion method (LECO FP 2000, Leco Corp., St. Joseph, MI; Procedure No. 968.06; AOAC, 1995). Crude fat was determined from dried tissue using the Soxhlet extraction method, with petroleum ether as the binary extracting solution (Novakofski et al., 1989). Ash was measured by the combustion of dried tissue at 500°C for 8 h (Proce-

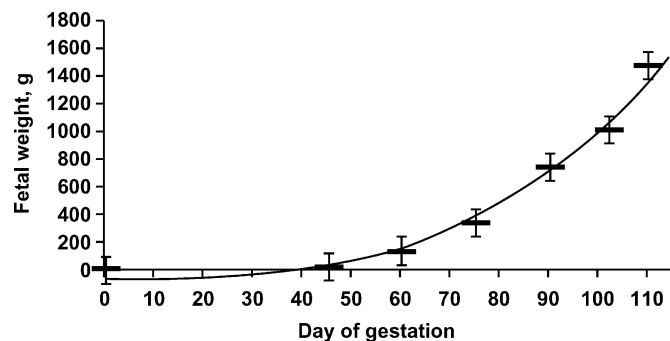


Figure 1. Fetal weight increased cubically ($P < 0.001$) as day of gestation progressed ($y = 0.00108 x^3 - 62.922$, $R^2 = 0.943$, where y = fetal weight (g) and x = day of gestation).

ture No. 923.03; AOAC, 1995). Chemical analysis was not performed for all fetal tissues at d 45, 60, and 75 of gestation due to limited sample size.

Statistical Analyses

Data were analyzed as a completely randomized design. Analyses were performed using the GLM procedure of the SAS (SAS Inst., Inc., Cary, NC). Gilt was the experimental unit. The model included day of gestation as the main effect to separate the means among treatments. Least squares means, the LSD procedure, and pooled standard errors were used to evaluate the differences among means. Data were also analyzed using PROC REG of SAS to describe the quantitative (linear, quadratic, or cubic) changes of weight of each tissue as day of gestation progressed. The NLREG software (Sherrod, 1992) was used to obtain the breakpoint from the multi-phasic regression for the protein content in the fetus. Homogeneity of the data was tested using Bartlett's test for homogeneity of variance, as described by SAS.

Results

Fetus and Fetal Carcass

Weights of the fetus increased cubically ($P < 0.001$, $R^2 = 0.941$) as gestation progressed (Figure 1). Fetal BW was the greatest ($P < 0.05$) on d 110 of gestation, and the smallest ($P < 0.05$) on d 45 and 60 of gestation (Table 3). Weight of fetal carcasses increased cubically ($P < 0.001$, $R^2 = 0.942$) as gestation progressed. Fetal carcass weight was the greatest ($P < 0.05$) on d 110 of gestation and the smallest ($P < 0.05$) on d 45 and 60 of gestation (Table 3). Dry matter content of the fetal carcass was greater ($P < 0.05$) on d 102 than on d 75 of gestation (Table 3) with no correlation ($P = 0.244$) for day of gestation. Crude protein content in the fetal carcass was greatest ($P < 0.05$) on d 45 and 60 and the smallest ($P < 0.05$) on d 110 of gestation, with no correlation ($P = 0.441$) for day of gestation.

Fetal Tissues

Weights of fetal GIT, liver, heart, lung, kidney, and brain increased cubically ($P < 0.001$, $R^2 = 0.910$, 0.882 , 0.938 , 0.917 , 0.927 , and 0.990 , respectively) as gestation progressed. There were no changes in GIT DM ($P = 0.470$), CP ($P = 0.218$), and crude fat ($P = 0.376$) compositions during gestation. Ash content in GIT was greater ($P < 0.05$) on d 90, 102, and 110 than on d 60 and d 75 of gestation (Table 3). Crude protein content in liver was greater ($P < 0.05$) on d 45, 60, 75 than on d 110 of gestation. Ash content in heart was greater ($P < 0.05$) on d 60 than on d 102 and 110 of gestation. Crude protein content in lung was greater ($P < 0.05$) on d 45 than on d 102 and 110 of gestation. Ash content in kidney was the greatest ($P < 0.05$) on d 60 and the smallest ($P < 0.05$) on d 110 of gestation. Crude protein content in brain was the greatest ($P < 0.05$) on d 60 of gestation (Table 3). Unless indicated otherwise, no correlations ($P > 0.05$) with day was detected. The liver:fetal BW ratio decreased quadratically ($P < 0.001$, $R^2 = 0.841$), whereas GIT to fetal body weight ratio increased quadratically ($P < 0.001$, $R^2 = 0.958$) (Table 4).

Total Amounts of Protein and Fat in Fetus

Total amounts of protein content in the fetus increased quadratically ($P < 0.001$, $R^2 = 0.906$) as gestation progressed. When the data were analyzed to obtain a multiphasic regression with two linear equations by NLREG software, a breakpoint (where two linear curves cross) occurred on d 69 of gestation ($P < 0.001$). The R^2 and P -value of the model were 0.988 and < 0.001 , respectively (Figure 2). Fetal protein gain was 0.25 g/d ($P < 0.001$) before d 69 of gestation, and increased to 4.63 g/d ($P < 0.001$) after d 69 g of gestation. Similarly, total amounts of fat in the fetus increased quadratically ($P < 0.001$, $R^2 = 0.904$) as gestation progressed. When the data were analyzed to obtain a multiphasic regression with two linear equations by NLREG software, a breakpoint occurred on d 69 of gestation ($P < 0.001$, $R^2 = 0.983$). Fetal fat gain was 0.06 g/d ($P < 0.001$) before d 69 of gestation and increased to 1.09 g/d ($P < 0.001$) after d 69 g of gestation.

Discussion

Results from this study demonstrate that the composition of individual fetal tissues undergoes dynamic changes during gestation. Additionally, protein and fat accretions in the fetus accelerate after d 69 of gestation. Collectively, these findings indicate increased maternal protein and fat needs by pregnant gilts to support fetal tissue growth, especially after d 69 of gestation.

Weight of fetuses increased cubically as gestation progressed, indicating that fetal weight gain accelerated during late gestation. Fetal weights of this study were similar to, and greater than, those reported previously (Wise et al., 1997; Wu et al., 1999; Leenhouders

Table 3. Weight and chemical composition of the fetus and fetal tissues on different days of gestation

Variable	Day of gestation						SEM ^a
	45	60	75	90	102	110	
No. of gilts	6	4	5	3	5	4	—
No. of fetuses	79	54	50	33	65	39	—
Fetal wt, g ^b	21.33 ^c	136.63 ^{cd}	334.96 ^d	740.79 ^e	1,005.20 ^f	1,473.20 ^g	99.01
Fetal carcass							
Weight, g ^b	17.27 ^c	114.49 ^{cd}	288.35 ^d	631.15 ^e	864.92 ^f	1258.8 ^g	84.81
DM, %	22.50 ^{cd}	25.15 ^{cd}	20.20 ^c	29.23 ^{cd}	31.32 ^d	25.52 ^{cd}	0.13
Ash, % ^h	17.07 ^c	21.49 ^d	24.07 ^d	17.83 ^c	17.03 ^c	17.16 ^c	0.83
CP, % ^h	63.94 ^c	60.41 ^c	57.44 ^d	59.09 ^d	57.93 ^d	51.08 ^e	1.03
Crude fat, % ^h	15.97 ^c	15.13 ^c	11.67 ^d	14.40 ^{cd}	14.01 ^{cd}	12.44 ^d	1.33
Fetal gastrointestinal tract							
Weight, g ^b	0.52 ^c	4.08 ^{cd}	13.19 ^d	38.19 ^e	55.39 ^f	90.63 ^g	6.01
DM, %	—	20.48	16.10	21.91	17.97	23.20	0.14
Ash, % ^h	—	9.26 ^c	8.62 ^c	8.31 ^d	8.49 ^d	8.28 ^d	0.14
CP, % ^h	—	72.10	70.89	71.00	71.15	72.79	0.39
Crude fat, % ^h	—	15.33	15.44	15.23	14.61	13.11	1.49
Fetal liver							
Weight, g ^b	2.19 ^c	8.93 ^{cd}	14.47 ^d	27.84 ^e	29.51 ^e	44.06 ^f	2.95
DM, %	23.52	26.44	20.89	31.72	25.03	29.42	0.13
Ash, % ^h	8.33	7.61	6.75	6.23	8.42	8.28	0.42
CP, % ^h	75.83 ^c	78.94 ^c	78.95 ^c	72.21 ^{cd}	67.58 ^{cd}	58.38 ^d	1.89
Crude fat, % ^h	—	—	—	19.46 ^c	16.55 ^c	24.80 ^d	1.48
Fetal heart							
Weight, g ^b	0.28 ^c	1.06 ^{cd}	2.31 ^d	6.46 ^e	8.88 ^f	12.08 ^g	0.84
DM, %	—	21.49 ^{cd}	16.40 ^c	23.01 ^{cd}	19.56 ^{cd}	25.75 ^d	0.13
Ash, % ^h	—	7.56 ^c	6.61 ^{cd}	6.76 ^{cd}	6.33 ^d	6.31 ^d	0.14
CP, % ^h	—	77.37 ^{cd}	71.10 ^c	76.82 ^{cd}	77.87 ^d	76.89 ^{cd}	0.89
Fetal lung							
Weight, g ^b	0.51 ^c	5.37 ^{cd}	11.25 ^d	25.23 ^e	33.24 ^f	49.68 ^g	3.35
DM, %	25.43	20.13	24.02	19.89	18.04	26.59	0.18
Ash, % ^h	8.43 ^d	8.52 ^c	7.66 ^{cd}	6.78 ^d	7.11 ^d	7.28 ^{cd}	0.22
CP, % ^h	75.01 ^c	65.10 ^d	62.73 ^d	69.38 ^e	69.55 ^e	70.38 ^e	0.91
Fetal kidney							
Weight, g ^b	0.57 ^c	2.71 ^d	5.04 ^d	10.83 ^e	11.75 ^e	15.74 ^f	1.09
DM, %	—	21.25	19.23	23.13	17.89	24.97	0.14
Ash, % ^h	—	9.11 ^c	7.25 ^{de}	7.40 ^d	7.13 ^{de}	6.59 ^e	0.20
CP, % ^h	—	71.92 ^c	73.28 ^{cd}	74.82 ^d	74.24 ^{cd}	72.98 ^{cd}	0.38
Fetal brain							
Weight, g ^b	—	3.13 ^c	3.57 ^c	9.88 ^{cd}	17.45 ^d	25.46 ^e	2.15
DM, %	—	18.12	26.35	19.08	18.85	17.95	0.24
Ash, % ^h	—	11.82 ^c	10.96 ^c	9.46 ^{cd}	7.28 ^d	8.30 ^{cd}	0.46
CP, % ^h	—	63.23 ^c	58.59 ^d	58.90 ^d	59.11 ^d	58.44 ^d	0.46
Crude fat, % ^h	—	—	31.34	30.49	30.48	32.22	2.40
Placenta							
DM, %	14.98 ^c	19.99 ^{cd}	19.35 ^{cd}	26.40 ^d	15.44 ^c	19.32 ^{cd}	0.14
Ash, % ^h	12.37 ^c	11.02 ^c	8.94 ^d	9.52 ^d	10.01 ^d	9.56 ^d	0.29
CP, % ^h	69.96 ^c	74.29 ^d	74.80 ^d	74.29 ^d	73.33 ^d	72.41 ^{cd}	0.91

^aPooled standard error of the mean.

^bWithin a row, weight increased cubically as gestation progressed ($P < 0.001$).

^{c,d,e,f,g}Within a row, means without a common superscript letter differ ($P < 0.05$).

^hDM basis.

et al., 2002) during early and late gestation, respectively. Fetal weights on d 100 to 114 of gestation from this study were approximately 28 to 30% greater than those reported by Wise et al. (1997), Wu et al. (1999), and Leenhouders et al. (2002), but up to 50% greater than those reported more than 27 yr ago (Ullrey et al., 1965; Knight et al., 1977). These results indicate the dramatic improvement in fetal growth during the last 25 to 40 yr. This is because sows have been selected for

high lean gain and high prolific performance (Burrin, 2001; Pond and Mersmann, 2001). It is reasonable to conclude that fetal growth is enhanced as the sow is genetically improved or modified.

In this study, a fetus accreted 0.25 g/d of protein until d 69, but accreted 4.63 g/d after d 69 of gestation. If the average number of fetuses in a pregnant gilt is 12, then the amounts of protein accreted in fetal tissues of each dam would be 3.0 and 55.6 g/d for before and after

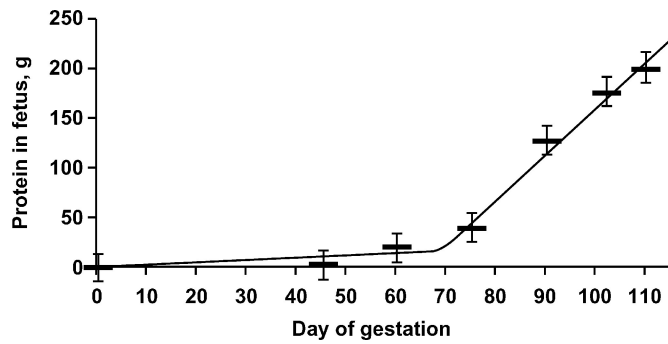


Figure 2. Breakpoint of the fetal protein content (g) occurred at d 68.5 of gestation ($R^2 = 0.988$, $P < 0.001$), showing that fetal protein accretion mainly occurred after d 68.5 of gestation; the regression equation before d 68.5 was: $0.249 \times (x - 68.5) + 17.078$. After d 68.5 the equation was: $4.629 \times (x - 68.5) + 17.078$, where x is day of gestation.

d 69 of gestation, respectively. Pregnant gilts consumed a constant amount of 244 g/d of CP or 11.2 g/d of lysine during the entire gestation period in this study. Using the coefficients for true ileal digestibility for pregnant sows (Stein et al., 2001), the amounts of true ileal digestible (TID) protein and TID lysine from the gestation diet were calculated to be 221.4 and 10.3 g/d, respectively. Use of dietary protein to support fetal protein accretion dramatically increased after d 69 of gestation, thereby limiting the amount of dietary protein available for maternal use. The amount of TID lysine needed for the maternal maintenance can be estimated on the basis of 36 mg/kg of $BW^{0.75}$ (NRC, 1998) to be 1.6 g/d when BW is 158.2 kg (initial BW of pregnant gilts in this study). This value is equivalent to 34.4 g/d TID protein (TID lysine is 4.65% of TID protein in the gestation diet of this study). Additional amounts of protein are needed to support mammary gland growth, especially for pregnant gilts. Protein accretion in mammary tissue would be close to 11 g/d, based on the assumption that pregnant gilts have 14 mammary glands (Kim et al., 1999) and a major portion of the mammary protein gain occurs after d 70 of gestation (Kensinger et al., 1982; Sorensen et al., 2002). Then, considering the amounts of protein for maternal maintenance, fetal tissue accretion, and mammary tissue accretion, TID protein available for maternal growth would be approxi-

mately 184 and 120 g/d before and after d 69 of gestation, respectively. Thus pregnant gilts have 35% less protein available for maternal growth after d 69 than before d 69 of gestation.

Maternal growth continues during gestation, especially for pregnant gilts or young sows. Supporting their protein gain is of nutritional and physiological importance because insufficient maternal protein gain during gestation results in low BW after lactation and delays return to estrus (Johnston et al., 1989; Dourmad, 1991). In this study, fat accretion in the fetus increased after d 69 of gestation, indicating that the fetal pig requires more fat and energy from maternal sources. However, increasing the provision of dietary fat or energy to pregnant gilts may not be an ideal means for increasing sow's productivity because excessive maternal fat gain during gestation decreases voluntary feed intake during lactation (Baker et al., 1969; Weldon et al., 1994; Revell et al., 1998) and decreases sow longevity (Dourmad et al., 1994). The data on fetal protein accretion allow for accurate estimation of protein requirement for pregnant gilts, and provides a compelling experimental basis for phase feeding (before and after approximately d 70 of gestation) with different dietary protein levels; however, the effect of this strategy on reproductive and lactation performance of gilts requires further investigation.

The GIT:fetal weight ratio increased as gestation progressed, indicating that the growth of GIT accelerated during late gestation. It has recently been recognized that, during late gestation, the placental transfer of arginine from the gilt to fetal pigs is insufficient to support fetal requirements for arginine, the most abundant N carrier in the body protein (Wu et al., 1999). This necessitates endogenous synthesis of citrulline and arginine from glutamine/glutamate and proline in the fetus, which occurs exclusively in the small intestine (Wu et al., 2004). Thus, a marked increase in the fetal gut mass plays a key role in supporting the most rapid growth of the fetus during late gestation. Another important function of the small intestine is to provide arginine (an essential AA) for the neonate (Wu and Knabe, 1995) because the milk of most mammals (including the pig) is remarkably deficient in arginine (Wu and Knabe, 1994; Davis et al., 1994). Therefore, the rapid growth of the fetal gut during late gestation is

Table 4. Liver or gastrointestinal tract (GIT) to fetal weight ratio on different days of gestation

Variable	Day of gestation						SEM ^a
	45	60	75	90	102	110	
Ratio of liver weight to fetal BW, % ^b	10.70	6.30	4.24	3.74	2.94	2.96	0.68
Ratio of GIT weight to fetal BW, % ^c	2.47	2.98	3.95	5.14	5.51	6.16	0.29

^aPooled standard error of the mean.

^bWithin a row, ratio decreased quadratically as gestation progressed ($P < 0.001$).

^cWithin a row, ratio increased quadratically as gestation progressed ($P < 0.001$).

crucial for arginine homeostasis and growth of sow-reared piglets (Wu et al., 2004).

The liver:fetal weight ratio decreased as gestation progressed indicating the growth of liver occurred mainly during early gestation. Dyce et al. (1996) and Bazer et al. (2001) also found that fetal liver growth occurs rapidly in early stages of gestation and slows as fetal growth progresses. One explanation for this rapid liver growth is the marked increase in erythropoietic activity within the liver during early gestation (Dyce et al., 1996; Reece, 1997). During prenatal growth, the formation of erythrocytes occurs in the liver, spleen, and bone marrow, whereas during postnatal growth, erythrocyte formation takes place almost exclusively in the bone marrow (Reece, 1997).

Fetal malnutrition results in low birth weight, decreased muscle fiber number, and decreased postnatal growth performance (Dwyer et al., 1994). Mahan and Vallet (1997) suggested that the gestating sow may have a period of increased need for certain nutrients (e.g., minerals and vitamins), but the exact time was not identified. Wu et al. (1998) have shown that fetal growth restriction results in part from maternal dietary protein deficiency. Thus, establishing an effective strategy for feeding pregnant gilts on the basis of accurate nutrient needs for both fetal and maternal growth will enhance sow productivity and improve the efficiency of swine production. Considering that nutrient needs for fetal growth dramatically increase after d 69 of gestation, dietary requirements of pregnant gilts before and after d 69 of gestation may differ substantially. Our results of different rates of fetal protein accretion during gestation support the practice of a two-phase feeding strategy (before and after approximately d 70 of gestation) for pregnant gilts.

Implications

Protein accretion in fetal pigs accelerates after d 69 of gestation. Specifically, fetal protein accretion was 3.0 and 55.6 g/d before and after d 69 of gestation, respectively, in pregnant gilts. In view of different protein requirements for fetal tissue gain before and after d 70 of gestation, the current practice of providing a constant amount of dietary protein to pregnant gilts would limit its availability for maternal gain after d 69 of gestation, thereby potentially compromising both reproductive and lactation performance. Our findings support the practice of increasing provision of dietary protein to pregnant gilts after approximately d 70 of gestation to maximize fetal growth and sow productivity.

Literature Cited

- Allen, L. H. 2001. Biological mechanisms that might underlie iron's effects on fetal growth and preterm birth. *J. Nutr.* 131:581S–589S.
- Anthony, R. V., S. L. Pratt, R. Liang, and M. D. Holland. 1995. Placental-fetal hormonal interactions: Impact on fetal growth. *J. Anim. Sci.* 73:1861–1871.
- AOAC. 1995. *Official Methods of Analysis*. 16th ed. P.A. Cunniff, ed. AOAC Int., Gaithersburg, MD.
- Baker, D. H., D. E. Becker, H. W. Norton, C. E. Sasse, A. H. Jensen, and B. G. Harmon. 1969. Reproductive performance and progeny development in swine as influenced by feed intake during pregnancy. *J. Nutr.* 97:489–495.
- Bazer, F. W., J. J. Ford, and R. S. Kensinger. 2001. Reproductive physiology. Pages 150–224 in *Biology of the Domestic Pig*. W. G. Pond and H.J. Mersmann, ed. Cornell Univ., Ithaca, NY.
- Burrin, D. G. 2001. Nutrient requirements and metabolism. Pages 309–389 in *Biology of the Domestic Pig*. W. G. Pond and H. J. Mersmann, ed. Cornell Univ., Ithaca, NY.
- Davis, T. A., H. V. Nguyen, R. Garcia-Bravo, M. L. Fiorotto, E. M. Jackson, D. S. Lewis, D. R. Lee, and P. J. Reeds. 1994. Amino acid composition of human milk is not unique. *J. Nutr.* 124:1126–1132.
- Dourmad, J. Y. 1991. Effect of feeding level in the gilt during pregnancy on voluntary feed intake during lactation and changes in body composition during gestation and lactation. *Livest. Prod. Sci.* 27:309–319.
- Dourmad, J. Y., M. Etienne, A. Prunier, and J. Noblet. 1994. The effect of energy and protein intake of sows on their longevity: A review. *Livest. Prod. Sci.* 40:87–97.
- Dyce, K. M., W. O. Sack, and C. J. G. Wesing. 1996. Pages 146–147 in *Textbook of Veterinary Anatomy*. 2nd ed. W. B. Saunders Co., Philadelphia, PA.
- Dwyer, C. M., N. C. Stickland, and J. M. Fletcher. 1994. The influence of maternal nutrition on muscle fiber number development in the porcine fetus and on subsequent postnatal growth. *J. Anim. Sci.* 72:911–917.
- Fall, C. H. D., C. S. Yajnik, S. Rao, A. A. Davies, N. Brown, and H. J. W. Farrant. 2003. Micronutrients and fetal growth. *J. Nutr.* 133:1747S–1756S.
- Johnston, L. J., R. L. Fogwell, W. C. Weldon, N. K. Ames, D. E. Ullrey, and E. R. Miller. 1989. Relationship between body fat and postweaning interval to estrus in primiparous sows. *J. Anim. Sci.* 67:943–950.
- Kensinger, R. S., R. J. Collier, F. W. Bazer, C. A. Ducsay, and H. N. Becker. 1982. Nucleic acid, metabolic and histological changes in gilt mammary tissue during pregnancy and lactogenesis. *J. Anim. Sci.* 54:1297–1307.
- Kim, S. W., and R. A. Easter. 2003. Amino acid utilization for reproduction in sows. Pages 203–222 in *Amino Acids in Animal Nutrition*. 2nd ed. J. P. F. D Mello, ed. CAB International, Wallingford, U.K.
- Kim, S. W., W. L. Hurley, I. K. Han, H. H. Stein, and R. A. Easter. 1999. Effect of nutrient intake on mammary gland growth in lactating sows. *J. Anim. Sci.* 77:3304–3315.
- Knight, J. W., F. W. Bazer, W. W. Thatcher, and D. E. Franke. 1977. Conceptus development in intact and unilaterally hysterectomized-ovariectomized gilts: Interrelations among hormonal status, placental development, fetal fluids and fetal growth. *J. Anim. Sci.* 44:620–636.
- Leenhouders, J. I., E. F. Knol, P. N. de Groot, H. Vos, and T. van der Lende. 2002. Fetal development in the pig in relation to genetic merit for piglet survival. *J. Anim. Sci.* 80:1759–1770.
- Mahan, D. C., and J. L. Vallet. 1997. Vitamin and mineral transfer during fetal development and the early postnatal period in pigs. *J. Anim. Sci.* 75:2731–2738.
- Novakofski, J., S. Park, P. J. Bechetel, and F. K. McKeith. 1989. Composition of cooked pork chops: Effect of removing subcutaneous fat before cooking. *J. Food. Sci.* 54:15–17.
- NRC. 1998. *Nutrient Requirements of Swine*. 10th rev. ed. Natl. Acad. Press, Washington, DC.
- Pond, W. G., and H. J. Mersmann. 2001. General characteristics. Pages 1–40 in *Biology of the Domestic Pig*. W. G. Pond and H. J. Mersmann, ed. Cornell Univ., Ithaca, NY.

- Reece, W. O. 1997. Pages 270–271 in *Physiology of Domestic Animals*. Williams and Wilkins, Baltimore, MD.
- Revell, D. K., I. H. Williams, B. P. Mullan, J. L. Ranford, and R. J. Smits. 1998. Body composition at farrowing and nutrition during lactation affect the performance of primiparous sows: I. Voluntary feed intake, weight loss, and plasma metabolites. *J. Anim. Sci.* 76:1729–1737.
- Schoknecht, P. A. 1997. Swine nutrition: Nutrient usage during pregnancy and early postnatal growth, an introduction. *J. Anim. Sci.* 75:2705–2707.
- Sherrod, P. H. 1992. NLREG. Nonlinear Regression Analysis Program. Nashville, TN.
- Sorensen, M. T., K. Sejrsen, and S. Purup. 2002. Mammary gland development in gilts. *Livest. Prod. Sci.* 75:143–148.
- Stein, H. H., S. W. Kim, T. T. Nielsen, and R. A. Easter. 2001. Comparative standardized ileal protein and amino acid digestibilities by growing pigs and sows. *J. Anim. Sci.* 79:2113–2122.
- Trottier, N. L., and L. J. Johnston. 2001. Feeding gilts during development and sows during gestation and lactation. Pages 725–769 in *Swine Nutrition*. A. J. Austin and L. L. Southern, ed. CRC Press, Washington, DC.
- Ullrey, D. E., J. L. Sprague, D. E. Becker, and E. R. Miller. 1965. Growth of the swine fetus. *J. Anim. Sci.* 24:711–717.
- Weldon, W. C., A. J. Lewis, G. F. Louis, J. L. Kovar, M. A. Giesemann, and P. S. Miller. 1994. Postpartum hypophagia in primiparous sows: I. Effects of gestation feeding level on feed intake, feeding behavior, and plasma metabolite concentrations during lactation. *J. Anim. Sci.* 72:387–394.
- Wise, T., A. J. Roberts, and R. K. Christenson. 1997. Relationship of light and heavy fetuses to uterine position, placental weight, gestational age, and fetal cholesterol concentrations. *J. Anim. Sci.* 75:2197–2207.
- Wu, G., L. A. Jaeger, F. W. Bazer, and J. M. Rhoads. 2004. Arginine deficiency in preterm infants: Biochemical mechanisms and nutritional implications. *J. Nutr. Biochem.* (In press)
- Wu, G., and D. A. Knabe. 1994. Free and protein-bound amino acids in sow's colostrums and milk. *J. Nutr.* 124:415–424.
- Wu, G., and D. A. Knabe. 1995. Arginine synthesis in enterocytes of neonatal pigs. *Am. J. Physiol.* 269:R621–R629.
- Wu, G., T. L. Ott, D. A. Knabe, and F. W. Bazer. 1999. Amino acid composition of the fetal pig. *J. Nutr.* 129:1031–1038.
- Wu, G., W. C. Pond, T. Ott, and F. W. Bazer. 1998. Maternal dietary protein deficiency decreases amino acid concentrations in fetal plasma and allantoic fluid of pigs. *J. Nutr.* 128:894–902.

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