

Dietary Fat during Pregnancy and Lactation Increases Milk Fat and Insulin-Like Growth Factor I Concentrations and Improves Neonatal Growth Rates in Swine^{1,2}

Lori A. Averette, Jack Odle,³ Marcia H. Monaco* and Sharon M. Donovan*

Department of Animal Science and North Carolina Institute of Nutrition, North Carolina State University, Raleigh, NC 27603 and *Department of Food Science and Human Nutrition and Division of Nutritional Sciences, University of Illinois, Urbana, IL 61801

ABSTRACT Primiparous ($n = 24$) and multiparous ($n = 24$) sows were used to examine the effects of supplemental dietary fat and induction of parturition (d 112) on colostrum and milk composition and suckling piglet growth. Sows were assigned to one of eight treatments on d 90 of gestation that included variables such as parity (1 vs. ≥ 3), dietary fat (0 vs. 10%), and farrowing (natural vs. induction via lulalyse on d 112). Piglets suckling fat-supplemented dams grew up to 25% faster than control pigs nursing unsupplemented sows (250 vs. 200 g/d; $P < 0.01$). Improved growth was correlated with elevated milk fat and insulin-like growth factor (IGF) concentrations associated with fat supplementation. Dietary fat elevated milk fat concentration at 48 and 72 h postfarrowing by 21.6 and 22.6%, respectively ($P < 0.05$). Compared with nonfat-fed controls, multiparous sows fed 10% fat showed a more consistent rise in milk fat concentration, with 26% and 41% elevations for induced or naturally farrowing sows, respectively, vs. a 19% reduction or a 1% elevation in induced or naturally farrowing gilts ($P < 0.01$). The concentration of milk IGF-I tended to be lower in gilts than in multiparous sows ($P < 0.2$, 95.7 vs. 117.4 $\mu\text{g/L}$), and levels were particularly low in milk from induced gilts receiving no additional dietary fat (44.7 $\mu\text{g/L}$). However, fat supplementation elevated IGF-I to levels (110.6 $\mu\text{g/L}$) exceeding those measured in unsupplemented, naturally farrowing control sows and gilts (95.8 $\mu\text{g/L}$). In conclusion, supplemental dietary fat elevates milk fat in multiparous sows more than primiparous gilts regardless of farrowing treatment (induced vs. natural farrowing) and improves piglet growth throughout lactation irrespective of parity or farrowing treatment. The potential of supplemental dietary fat to reverse the reductions in milk IGF-I observed in first-parity females and in dams induced to farrow merits further investigation. *J. Nutr.* 129: 2123–2129, 1999.

KEY WORDS: • dietary fat • insulin-like growth factor • milk composition • swine • lactation

Fifty percent of preweaning mortality in the U.S. swine herd occurs during the first 3 d after birth (USDA 1997). With the additional knowledge that piglets are born with as little as 2% of body weight as fat (Curtis et al. 1966, Friend 1974, Seerley et al. 1974) and that reserves of stored glycogen also are limited (Boyd et al. 1978), the importance of rapid and adequate colostrum intake by the newborn pig is clear (Noblet et al. 1997). In addition, the widespread adoption of segregated early-weaning strategies to reduce disease transfer from mother to offspring involves the weaning of piglets as early as 10–14 d of age. The success of this management technique is dependent on rapid piglet growth during the brief suckling period. But what can be done to enhance early postnatal growth?

Increasing the fat content in colostrum may increase the

energy supply to newborn piglets, thereby improving survival (Pettigrew 1981) and perhaps growth rate. The fatty acid profile and amount of milk fat can be manipulated by the source of dietary fat provided to the dam both in late gestation and throughout lactation (Jackson et al. 1995, Seerley et al. 1974). Further enhancement of neonatal tissue development may occur when piglets consume colostrum high in growth factors such as insulin-like growth factor (IGF)⁴-I and -II due to their mitogenic potential (Burrin et al. 1997, Houle et al. 1997, Odle et al. 1996). Because milk composition is linked to mammary development (Kensinger et al. 1986), primiparous sows may secrete milk lower in energy and/or growth factor content. In addition, milk from dams induced to farrow early may contain less milk fat because considerable lipid secretion does not occur until parturition is imminent (Jackson et al. 1995, Kensinger et al. 1986). We hypothesized that supplemental dietary fat would correct the putative reduction in milk fat and/or growth factor content associated with induced far-

¹ Presented in part at Experimental Biology 97, April 1997, New Orleans, LA [Averette, L.A. & Odle, J. (1997) Effects of dietary fat on milk composition and litter performance of induced and naturally-farrowing swine. *FASEB J.* 11: A415 (abs.)].

² Supported in part by the Fats and Proteins Research Foundation, and by the North Carolina Agricultural Research Service.

³ To whom correspondence should be addressed.

⁴ Abbreviations used: CP, crude protein; IGF, insulin-like growth factor; ME, metabolizable energy; PGF_{2 α} , prostaglandin F_{2 α} .

TABLE 1
Composition of diets¹

Item	Diet			
	0% Fat Gestation	10% Fat Gestation	0% Fat Lactation	10% Fat Lactation
	<i>g/100 g</i>			
Ingredient				
Corn	82.9	70.6	77.9	65.7
Soybean meal (48%)	13.9	16.3	19.0	21.1
Fat (choice white grease)	—	10.0	—	10.0
Dicalcium phosphate	1.1	1.3	1.0	1.2
Limestone	1.1	1.1	1.2	1.1
Vitamin/Trace mineral premix ²	0.3	0.4	0.3	0.4
Salt	0.5	0.5	0.5	0.5
Analyzed				
Ether extract, %	3.02	13.16	2.64	12.39
Calculated				
Crude protein, %	14.0	14.0	16.0	16.0
Lysine, %	0.64	0.69	0.79	0.82
ME, kJ/kg	13,828	15,652	13,836	15,631
Phosphorus, %	0.6	0.6	0.6	0.6
Calcium, %	0.75	0.75	0.75	0.75

¹ As-fed basis.

² Each kilogram of mix contained the following: Mn, 19.48 g; Zn, 42.68 g; Fe, 32.17 g; Cu, 7.77 g; I, 11.57 mg; Se, 10.28 mg; retinyl acetate, 757 mg; cholecalciferol, 12.6 mg; vitamin E, 10,056.6 mg; menadione, 226.3 mg; thiamine, 251.4 mg; riboflavin, 1760 mg; niacin, 8800 mg; pantothenic acid, 6537 mg; pyridoxine, 440 mg; choline, 91703 mg; folic acid, 330 mg; biotin, 23.57 mg; and vitamin B-12, 8.8 mg.

rowing, especially in primiparous dams. Thus our objectives were to examine interactions among dietary fat (0 vs. 10%), parity (gilts vs. parity ≥ 3) and farrowing (natural vs. induced) treatments, and their effects on milk composition as well as sow and litter performance.

MATERIALS AND METHODS

Gilts ($n = 24$) and sows ($n = 24$; parity ≥ 3) (Pig Improvement Co., lines 231/233) were selected from the swine farm of the Lake-Wheeler Field Laboratory (North Carolina State University, Raleigh, NC) and randomly assigned to one of four treatment groups according to a $2 \times 2 \times 2$ factorial design. Treatments included diet (0 vs. 10% choice white grease), parity and farrowing (natural vs. induced on d 112) variables. The dietary treatments were initiated on d 90 of gestation and were continued throughout the 21-d lactation period. From d 90 of gestation until farrowing, dams received 2 kg daily of their respective gestation diets (Table 1). The NRC (1988) recommends that gestation diets contain 12% crude protein (CP), 0.43% lysine and 13431 kJ (3210 kcal) metabolizable energy (ME)/kg. For gestation, diets were formulated to contain 17% more CP and 55% more lysine than NRC (1988) recommendations. Energy content of the gestation and lactation diets in our study were similar. The control diet provided 13.828 MJ (3305 kcal) ME/kg and the fat-supplemented diet provided 15.652 MJ (3741 kcal) ME/kg, exceeding the NRC requirement by either 3 or 16.5%, respectively. On d 109, dams were moved into crates in the farrowing house. After farrowing, lactation diets were consumed by dams ad libitum (Table 1). Lactation diets exceeded NRC (1988) recommendations for CP (13%) and lysine (0.60%) by 18.8 and 34.2%, respectively. Dams had free access to water.

The gilts and sows were allowed to farrow naturally or were induced to farrow by an intramuscular injection of 15 mg prostaglan-

din $F_{2\alpha}$ (PGF_{2 α} , Upjohn, Kalamazoo, MI) on d 112. Induced sows farrowed within 24–36 h of injection. Average gestation length for induced pigs was 114 d, whereas gestation length for naturally farrowing pigs averaged 116 d.

Mammary secretions were collected from the right first thoracic gland beginning at the birth of the first pig (0 h) and subsequently at 3, 6, 9, 12, 24, 48, 72 and 168 h postpartum. Pigs were denied access to the right first thoracic gland for the first four sampling times. Samples were collected by hand stripping of the gland for 0 through 6 h, when there was free flow of colostrum. For subsequent sampling times, 0.5 mL of oxytocin (20,000 USP units/L, Anpro Pharmaceutical, Arcadia, CA) was administered intramuscularly to facilitate milk letdown. Samples were stored at -20°C until they were analyzed for total protein (Lowry et al. 1951; BSA standard), lactose (Teles et al. 1978), fat (Babcock method; AOAC 1984), and IGF-I and -II (Donovan et al. 1994). The protein and lactose colorimetric assays were run in triplicate (average CV $\leq 4\%$), and standard curves were linear ($r^2 \geq 0.995$). Babcock fat analyses were performed in duplicate, using 8% bottles. Milk IGF-I and -II concentrations were measured by specific RIA as previously described (Donovan et al. 1994). Before assay, IGF binding proteins were extracted by acid gel filtration chromatography (Donovan et al. 1994). Dilution factors used in the IGF-I assay were as follows: for 0-, 6- and 12-h samples, 1:40 to 1:60; for the 24-h samples, 1:30; and for the 48-h samples, 1:5. Interassay and intra-assay coefficients of variation for the IGF-I assay were 2 and 7%, respectively. Dilution factors used in the IGF-II assay were as follows: for 0-, 6- and 12-h samples, 1:30 to 1:40; for the 24-h samples, 1:15; and for the 48-h samples, 1:10. Interassay and intra-assay coefficients of variation for the IGF-II assay were 8 and 6%, respectively.

Dam weights were recorded on d 90, d 109, at farrowing and at weaning. Dam feed intake was recorded daily during lactation. Piglets born alive, stillborns and mummies were recorded on d 1 of lactation. Piglets were weighed at birth, d 7 and 14 and at weaning (mean, 21 d). Dams were required to nurse 7–12 piglets to remain in the study. When females farrowed > 12 piglets, extra piglets (beyond 12) were randomly selected and removed within 48 h postfarrowing. If a dam with < 7 piglets farrowed within 24 h of a dam receiving the same treatment who had > 12 pigs, 1–2 piglets were cross-fostered so that the dam did not have to be removed from the experiment. No cross-fostering was applied to any litter after 48 h when the number of piglets on each sow was recorded to determine survival (%) from 48 h to d 21.

Statistical analysis. Performance data were analyzed using the GLM procedure of the Statistical Analysis System (SAS 1985) appropriate for a $2 \times 2 \times 2$ factorial, randomized complete block design. Milk composition data were modeled according to a split-plot in time (Steel and Torrie 1980) appropriate for a factorial experiment. The whole-plot error (error A) was used to evaluate the significance of the main-plot effects (fat, parity and induction variables), and the residual error term was used to test the significance of the time effect and the interactions between main-plot and time effects. Effects with $P \leq 0.1$ are considered meaningful, and $P \leq 0.05$ is significant.

RESULTS

Sow and litter performance. Overall, performance data (Table 2) were similar, in general, to values reported by others (Coffey et al. 1994, Seerley et al. 1981, Shurson et al. 1986, Tilton et al. 1999). Feed consumption during lactation was not affected by parity or dietary fat and averaged 4.54 kg/d for all eight treatments. Lactation feed intake tended to be higher (13%) in dams allowed to farrow naturally compared with dams given PGF_{2 α} on d 112 (4.82 vs. 4.27 kg/d; $P < 0.07$). To our knowledge, feed intake has not been reported for induced dams compared with that of naturally farrowing dams. Increased respiration rate and increased nervousness were signs observed in dams receiving an infusion of PGF_{2 α} (Diehl et al. 1974); these behaviors also are associated with sick animals who tend to reduce their feed intake (O'Grady et al. 1985).

TABLE 2

Effects of dietary fat and induction of parturition on farrowing and lactation parameters of sows and gilts¹

Response criteria	Sows (n = 24)				Gilts (n = 24)				SEM
	Induced		Natural		Induced		Natural		
	0% Fat	10% Fat	0% Fat	10% Fat	0% Fat	10% Fat	0% Fat	10% Fat	
Dam lactation feed intake, kg/d	4.42	4.19	4.85	4.49	4.36	4.00	4.78	4.96	0.43
Dam body weight change, kg									
d 90–109 ²	9.69	0.00	2.87	1.73	10.60	12.55	10.63	9.85	4.74
d 109 to farrowing	-22.10	-9.77	-8.48	-5.23	-13.60	-16.70	-15.08	-15.52	2.91
Farrowing to weaning	-0.98	-7.15	-7.72	-4.16	2.43	-3.93	-0.88	-7.43	4.06
Piglets born alive, ² n	14.43	11.67	11.50	10.33	9.50	9.67	10.00	9.83	1.08
Stillborn piglets, ³ n	1.57	2.83	0.17	0.83	—	0.5	0.17	0.5	0.46
Mummified piglets, ⁴ n	0.14	1.33	0.33	0.17	—	0.17	0.17	—	0.25
Piglets at 48 h, n	12.00	10.50	10.83	9.83	9.50	9.50	9.67	10.00	0.75
Piglets weaned, ⁵ n	10.29	8.00	9.00	8.67	9.17	8.67	9.00	8.67	0.70
Survival, ⁶ %	85.97	78.70	83.89	88.66	96.48	91.03	92.82	88.43	4.74
Piglet weight gain, ⁷ kg/d	0.22	0.28	0.25	0.31	0.18	0.20	0.31	0.28	0.03

¹ Sows (\geq parity 3) and gilts (parity 1) were allowed to farrow naturally or induced to farrow via prostaglandin injection on d 112 of gestation and were fed diets containing 0 or 10% supplemental fat.

² Parity effect ($P < 0.01$).

³ Parity effect ($P < 0.01$); fat effect ($P < 0.04$); induction effect ($P < 0.02$); parity \times induction ($P < 0.01$).

⁴ Parity effect ($P < 0.03$).

⁵ Fat effect ($P < 0.05$).

⁶ Calculated from number of piglets at 48 h. Parity effect ($P < 0.01$).

⁷ Averaged over 3 wk of lactation. Parity effect ($P < 0.01$); fat effect ($P < 0.01$); induction effect ($P < 0.01$).

Primiparous dams gained more (10.9 ± 1.5 kg) than multiparous dams (3.6 ± 1.4 kg) during gestation (d 90–109; $P \leq 0.01$). However, treatment effects on weight loss at parturition and during lactation were not detected ($P > 0.10$).

Supplemental fat and induction of farrowing did not affect the number of piglets born alive (Table 2); however, gilts farrowed 9.75 ± 0.5 live piglets, which was 19% less than ($P < 0.01$) the number born to multiparous sows (11.98 ± 0.5). The number of stillborn pigs was correspondingly affected by parity, with 0.29 ± 0.23 stillborns per litter for gilts and 1.35 ± 0.23 for sows ($P < 0.01$). Diet also affected stillbirths with 0.48 ± 0.23 for dams consuming the nonfat control diet compared with 1.17 ± 0.23 for dams consuming the diet with 10% supplemental fat ($P < 0.04$). Induction of farrowing with prostaglandin resulted in a $>$ twofold elevation in stillbirths, with 0.42 for naturally farrowing dams compared with 1.23 for dams induced to farrow on d 112 ($P < 0.02$). An 82% reduction in the number of mummies was observed in gilts compared with multiparous sows (0.08 vs. 0.49 mummies/litter; $P < 0.03$), but no effects of diet or farrowing induction were observed.

Piglet average daily gains over each week of lactation (data not shown) and over the entire lactation interval (Table 2) were increased by up to 25% when dams were fed supplemental dietary fat ($P < 0.01$). Total litter weaning weight was elevated by 14% in dams fed 10% dietary fat ($P < 0.06$, data not shown), despite a reduced number of pigs weaned compared with the nonfat control group ($P < 0.05$). Piglets nursing multiparous sows gained 9% faster than those nursing first-parity gilts ($P < 0.01$). Similarly, pigs suckling dams that farrowed naturally grew 30% faster than pigs nursing dams that were induced to farrow ($P < 0.01$). Survival from 48 h to weaning was 20.6% higher in gilts than in sows (94.7 ± 3.7 vs. 78.5 ± 3.6 ; $P < 0.01$). Heavier breeding weights and higher parity have been associated with increased piglet mortality (Newton and Mahan 1993).

Milk composition. Milk fat concentrations were relatively low and constant ($\sim 6\%$) during the first 9 h postfarrowing and then increased significantly at 12 h and thereafter (time main effect, $P < 0.01$), peaking at 48–72 h particularly in the fat-supplemented dams (Fig. 1A; fat \times time, $P < 0.01$). Indeed, milk fat concentration was 22% higher at 2–3 d postfarrowing in dams fed supplemental fat. Furthermore, the effect of supplemental fat was influenced by parity and by induction of farrowing (fat \times parity \times induction, $P < 0.01$; Fig. 1B). When supplemental fat was fed to multiparous sows, regardless of prostaglandin treatment, a more consistent positive response was observed in milk fat concentration compared with first-parity gilts. That is, milk fat concentration of sows was elevated by supplemental fat regardless of whether they were induced or farrowed naturally, whereas dietary fat had no effect on naturally farrowing gilts and tended to reduce milk fat percentage in induced gilts.

Milk protein concentration declined 80% over wk 1 postfarrowing ($P < 0.01$, data not shown). There were no differences in milk protein due to dietary fat, parity or induction of farrowing ($P > 0.10$). Conversely, milk lactose increased 90% from 0 to 168 h ($P < 0.01$) and also was unaffected by treatment (data not shown).

Milk IGF-I and IGF-II concentrations decreased by 93 and 76%, respectively, over the first 48 h postfarrowing (Table 3, $P < 0.01$). At all sampling times, concentrations of IGF-I were numerically higher in colostrum of fat-fed dams than in unsupplemented controls, but differences were greater over the first 12 h (fat \times time interaction, $P < 0.1$). In general, concentrations of IGF-I were lowest in milk from induced dams receiving no supplemental fat and highest in naturally farrowing dams fed supplemental fat, with other treatments intermediate (Fig. 2A; fat \times induction \times time, $P < 0.05$). Overall, milk IGF-I concentration in gilts was numerically lower than in sows (95.7 ± 11.8 vs. 117.4 ± 13.9 $\mu\text{g/L}$, $P < 0.2$), but was particularly low (44.7 $\mu\text{g/L}$) in induced gilts

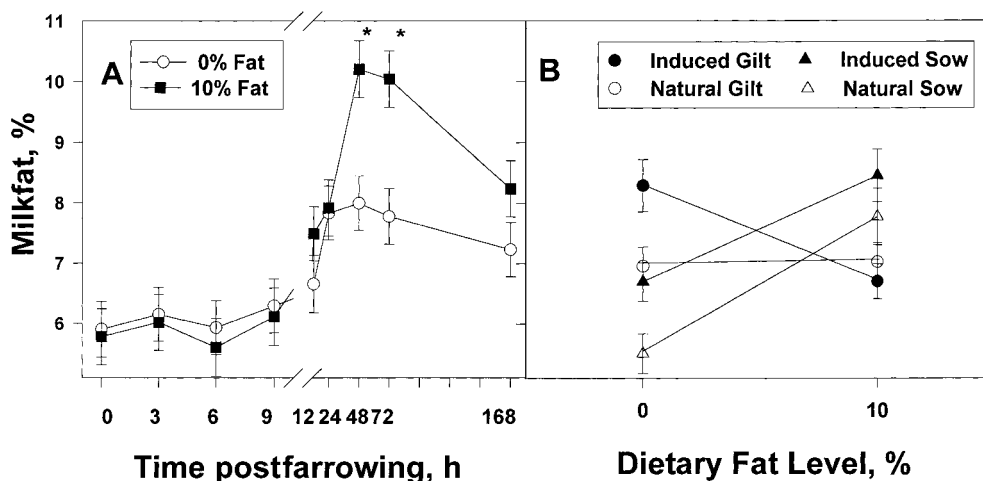


FIGURE 1 Effects of feeding 10% supplemental dietary fat to first parity gilts and multiparous sows during pregnancy and lactation on milk fat concentrations. *Panel A:* Effects of feeding 10% supplemental fat on milk fat concentrations during wk 1 postfarrowing. Error bars represent \pm SEM; $n = 24$ observations per mean. Open symbols represent values from dams fed no supplemental fat; closed symbols represent data from fat-supplemented dams. Time effect ($P < 0.01$); dietary fat \times time interaction ($P < 0.01$). *Values differ from corresponding nonfat-fed controls at 48 and 72 h ($P < 0.05$). *Panel B:* Effects of feeding 10% supplemental dietary fat and induction of farrowing (via injection of prostaglandin on d 112 of gestation) on milk fat concentration from first-parity gilts and multiparous sows. "Natural" refers to control dams allowed to farrow naturally without induction. Milk fat concentrations represent the mean of nine samples taken during wk 1 postfarrowing. Fat \times induction \times parity interaction ($P < 0.01$). Error bars represent \pm SEM (per whole-plot error A).

fed no supplemental fat (Fig. 2B). Fat supplementation of induced gilts elevated IGF-I to concentrations exceeding the unsupplemented, naturally farrowing sows and gilts (Fig. 2B; fat \times parity \times induction, $P < 0.1$). However, average IGF-I concentrations reached the highest levels in naturally farrowing, fat-supplemented sows and gilts.

DISCUSSION

The findings from this research have obvious ramifications for production agriculture but perhaps also to human nutrition

TABLE 3

Effects of dietary fat on swine milk insulin-like growth factor (IGF)-I and IGF-II concentrations over the first 48 h postfarrowing¹

Time, h	IGF-I ^{2,3,4,5}		IGF-II ^{2,6}	
	0% Fat	10% Fat	0% Fat	10% Fat
	$\mu\text{g/L}^7$			
0	167.49	227.63	99.85	83.70
6	113.52	193.76	80.73	78.73
12	88.17	153.28	71.85	61.25
24	32.07	61.26	33.48	26.08
48	6.20	22.33	22.28	21.13

¹ Sows (\geq parity 3) and gilts (parity 1) were allowed to farrow naturally or induced to farrow via prostaglandin injection on d 112 of gestation and were fed diets containing 0 or 10% supplemental fat. Tabulated values are averaged over parity and farrowing (induced vs. natural) treatments. Milk samples were collected at the times indicated, with time 0 marked by the birth of the first piglet.

² Time main effect ($P < 0.01$).

³ Fat \times time ($P < 0.10$).

⁴ Fat \times induction \times time ($P < 0.05$, cf. Fig. 2A).

⁵ Fat \times parity \times induction ($P < 0.10$, cf. Fig. 2B).

⁶ Fat \times parity \times induction \times time ($P < 0.10$; data not shown).

⁷ Pooled SEM = 14.3 and 5.7 for IGF-I and IGF-II, respectively.

insofar as pigs may serve as model species for lactational biology. The data clearly show an effect of dietary fat during gestation and lactation on milk composition, with subsequent effects on growth and development of the suckling neonate. Although this concept is not new, to our knowledge, this study is the first to show an effect of maternal nutrition (fat intake) on milk IGF-I concentration with a corresponding increase in milk fat and in growth of the neonate.

Effects on milk nutrients. The importance of feed (energy) intake in reproducing females, especially during late gestation and lactation, and its direct effect on fetal and neonatal growth and development is unequivocal. If diets do not adequately provide for the maintenance and production needs of modern high lean genotype sows, then energy provided to the litter is reduced and performance suffers (Pettigrew et al. 1993). Indeed, because piglet endogenous energy stores are limited at birth, sufficient milk energy intake during the first 72 h after birth is imperative to ensure survival. Inadequate supply of exogenous nutrients weakens the piglet, making it more susceptible to death from other factors such as crushing, disease and hypothermia (USDA 1997). Therefore, increasing the energy content of colostrum could improve neonatal survival and growth. We showed previously (Jackson et al. 1995) that dietary fat could abrogate reductions in milk fat concentration of sows induced to farrow prematurely (d 110–115). This study was designed to expand on these findings by comparing effects in first-parity gilts to multiparous sows.

Considering the potential impact on mammary development of gilts, Weldon et al. (1991) studied the effects of increased dietary energy during 75–90 d of gestation on mammary development and found that the mammary parenchymal weight and DNA content were significantly lower in gilts fed the excess energy. They concluded that the increase in energy was detrimental to secretory tissue development. Thus, the timing of dietary fat supplementation to the dams is an important consideration. Histology studies by Kensinger et al. (1982 and 1986) indicate that the growth of the mammary tissue is complete by d 90, and the differentiation of alveolar epithelial cells begins subsequently. This marks the beginning

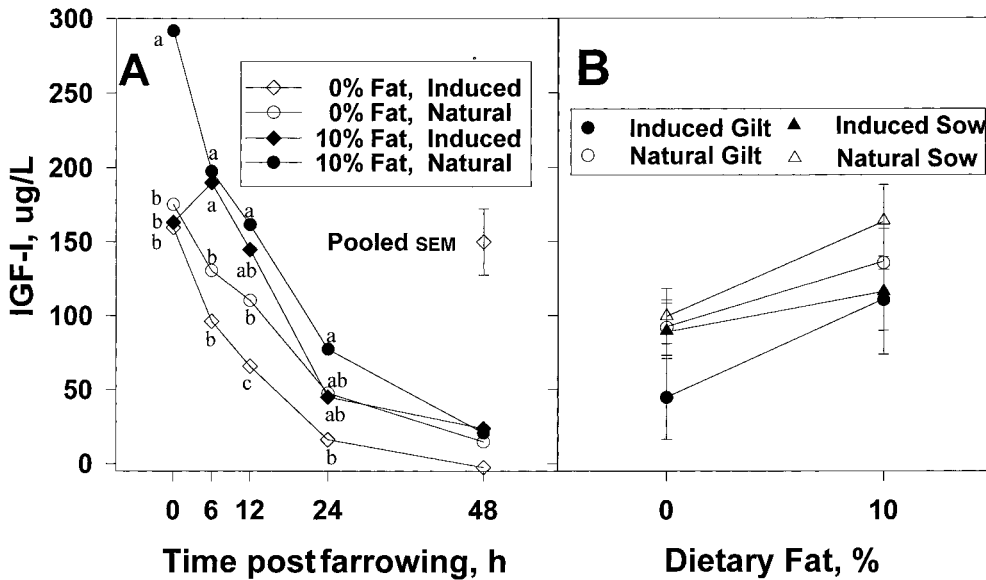


FIGURE 2. Effects of feeding 10% supplemental dietary fat and induction of farrowing (via injection of prostaglandin on d 112 of gestation) on concentrations of insulin-like growth factor I in colostrum from first-parity gilts and multiparous sows. "Natural" refers to control dams allowed to farrow naturally without induction. *Panel A:* Time effect ($P < 0.01$); fat \times induction \times time interaction ($P < 0.05$). ^{a,b,c}Values within the same sampling time with different superscripts differ ($P < 0.05$). *Panel B:* Values represent the mean of five samples taken over the first 48 h postfarrowing. Fat \times induction \times parity interaction tendency ($P < 0.10$). Error bars represent \pm SEM (per whole-plot error A).

of lactogenesis, and no further negative effects of supplemental dietary energy have been found after this time. Furthermore, d 90 marks the point at which small lipid droplets are visible in the basal portion of the differentiating epithelial cell (Kensinger et al. 1986). Therefore, if increased energy is added to the diet in lipid form, it may be most beneficial to begin feeding supplementation after d 90 of gestation. Because epithelial cell differentiation does not appear to be complete until d 4 of lactation (Kensinger et al. 1986), we hypothesized that premature parturition (especially in gilts) may have a detrimental effect on the fat content of secretions expressed during the second stage of lactogenesis. However, this was not observed. Among the control dams not supplemented with dietary fat, induction of farrowing increased milk fat concentration compared with naturally farrowing dams, without regard to parity. In contrast, the milk fat content of sows could be increased further by dietary fat supplementation, but gilts failed to respond.

Although many others have shown that dietary fat supplementation increases sow's milk fat (Boyd et al. 1978, Jackson et al. 1995, Pettigrew 1981, Seerley et al. 1974, Stahly et al. 1981), the reason that first-parity gilts failed to respond remains unclear; it may be due to the variability in mammary development and body energy reserves of gilts compared with multiparous sows. De novo fatty acid synthesis by the gilt mammary gland may not be as well developed; when metabolic signals such as insulin/glucagon are influenced by the ratio of energy supplied by dietary fat and carbohydrate, then a reduction in milk fat may occur. As a proportion of body fat at farrowing, fat loss during lactation in parity 1 and 2 sows was greater ($P < 0.04$) than fat loss in older (parity ≥ 3) sows (Clowes et al. 1994). Alternatively, because an energy dependency exists for milk production (Tokach et al. 1992), the amount of energy consumed can change the amino acid demand for milk synthesis. The lysine to energy ratio of the diets used in this study were not constant, and increased protein may benefit the gilt because the growth rate of lean tissue is high in young dams (Whittemore and Yang 1989).

The milk protein and lactose concentrations (data not shown) followed the pattern (decreasing and increasing, respectively) previously reported (Jackson et al. 1995). Additionally, no treatment differences were noted in either study. Research by Shurson et al. (1986) also failed to detect differ-

ences in milk protein when 10% dietary fat was fed to sows. If there are no changes in protein or lactose levels and the milk fat concentration increases (as observed), the percentage of energy per gram of milk provided by the protein or lactose will decrease. This should not alter the volume of colostrum or milk consumed by the piglet because they do not appear to regulate intake according to the energy density of the milk (Le Dividich et al. 1997). Because piglet milk intake was not affected by milk fat concentration, a 31.5% increase in ME was measured (LeDividich et al. 1997). Because low birth weight is associated with increased mortality, provision of extra energy by an increase in colostrum and milk fat levels when sow diets are supplemented with fat may have a positive influence on survival (Cieslak et al. 1983). Other benefits produced include the increase in preweaning gain. A 25% increase in average daily gain in piglets suckling sows fed fat and an overall 14% increase in litter gain in fat-supplemented dams were observed in this study. Supplemental fat has been shown to increase the volume of milk produced by the sow as much as 33.6% (Coffey et al. 1982). However, this may be of less relative importance because Atwood and Hartmann (1992) noted a higher correlation between piglet weight and the amount of ingested fat than the volume of milk intake.

In summary, induction of premature parturition did not result in milk fat depression as reported previously (Jackson et al. 1995), nor were first-parity gilts more susceptible to such putative effects as originally hypothesized. Multiparous sows, whether induced or naturally farrowing, responded well to dietary fat supplementation with increased milk fat concentration.

Effects on milk IGF-I. IGF-I and -II play several roles during pregnancy and lactation in the sow. They are intricately involved in mammary gland function in the sow as well as having some bioactivity in the neonatal gastrointestinal tract. IGF-I may mediate the actions of growth hormone in the mammary gland. Growth hormone likely supports synthesis of milk rich in energy by playing a role in the synthesis of milk fat (Flint 1995). If increased dietary fatty acids are available, these hormones could be involved in directing the fatty acids to milk fat synthesis in the mammary gland. The IGF-I levels at each time point were greater in dams fed fat compared with those receiving no additional dietary fat (Table 3, Fig. 2). Other roles played by IGF in the mammary tissue of sows

include possible stimulation of mitogenesis and galactopoiesis (Shamay et al. 1988).

If circulating levels of IGF-I are elevated in the sow, this would likely lead to elevated levels in the colostrum and milk because serum appears to be the main source of milk IGF-I (Donovan et al. 1994). The mammary gland has very low levels of IGF-I mRNA and would not be the primary source of IGF-I in the milk (Tavakkol et al. 1988). This is likely the case for milk IGF-II as well. The ratio of IGF-I and -II levels measured in our study was not consistent with that in the previous experiment by Donovan et al. (1994). Breed can influence IGF-I and -II concentrations within a species (Baumrucker and Blum, 1993). If serum IGF concentrations vary with genotype, and the ratio of serum IGF-I and IGF-II was different in the pigs used in this study, the milk IGF-I and -II levels may have reflected this difference. Furthermore, dietary fat was not increased in those studies, and it may have influenced the serum IGF-I and -II concentrations. Unfortunately, blood samples were not collected from the dams in this experiment.

The effects of these growth factors on piglet intestinal and whole-body growth have been studied by several researchers (Baumrucker and Blum 1993, Burrin et al. 1992 and 1996, Donovan and Odle 1994, Donovan et al. 1996). The growth factor peptides in colostrum appear to pass unharmed (in part) through the stomach as a result of lower secretion of gastric acid and then bind to their receptors in the small intestine without breakdown by enzymes because of the immaturity of the neonatal gut (Lebenthal et al. 1983). Once IGF-I and -II reach the intestine, they may elicit a response in the intestinal epithelium (Burrin et al. 1996, Donovan et al. 1996). Indeed, supplementation of formula with IGF-I has been shown to increase small intestinal mass and villous height as well as lactase and sucrase activity (Burrin et al. 1996, Houle et al. 1997). If IGF-I and -II exert immunological effects on the gut (Baumrucker and Blum 1993) or speed intestinal repair after infection (Odle et al. 1996), it might prove beneficial to increase the levels of these growth factors in sow colostrum and milk via prophylactic or transgenic approaches.

In conclusion, supplemental dietary fat in sow diets can elevate milk fat concentration, especially 2–3 d postpartum, regardless of parity or parturition treatment. The increase in milk fat when dietary fat was added was more consistent in multiparous sows than in gilts. An increase in milk fat will increase the energy available to the piglet and has the potential to affect postnatal survival and growth. Indeed, piglet growth rate was improved by 25% over a 3-wk lactation period. Induction of farrowing did attenuate IGF-I concentrations in milk; however, this depression was abrogated with supplemental dietary fat. This may be of importance because the IGF may stimulate digestive enzyme activity in the neonatal intestinal epithelium and thus lead to improved nutrient assimilation. Collectively, working through elevated milk fat and/or IGF-I and -II, supplemental dietary fat appears to accelerate the growth of suckling piglets without regard to the parity of the dam (gilt vs. sow) or farrowing status (induced vs. naturally farrowing).

LITERATURE CITED

- Association of Official Analytical Chemists (1984) Official Methods of Analysis, 14th ed. AOAC, Washington, DC.
- Atwood, C. S. & Hartmann, P. E. (1992) Collection of fore and hind milk from the sow and the changes in milk composition during suckling. *J. Dairy Res.* 59: 287–298.
- Baumrucker, C. R. & Blum, J. R. (1993) Secretion of insulin-like growth factors in milk and their effect on the neonate. *Livest. Prod. Sci.* 35: 49–72.
- Boyd, R. D., Moser, B. D., Peo, E. R., Jr. & Cunningham, P. J. (1978) Effect of energy source prior to parturition and during lactation on piglet survival and growth and on milk lipids. *J. Anim. Sci.* 47: 883–892.
- Burrin, D. G., Davis, T. A., Ebner, S., Schoknecht, P. A., Fiorotto, M. L. & Reeds, P. J. (1997) Colostrum enhances the nutritional stimulation of vital organ protein synthesis in neonatal pigs. *J. Nutr.* 127: 1284–1289.
- Burrin, D. G., Shulman, R. J., Reeds, P. J., Davis, T. A. & Gravitt, K. R. (1992) Porcine colostrum and milk stimulate visceral organ and skeletal muscle protein synthesis in neonatal piglets. *J. Nutr.* 122: 1205–1213.
- Burrin, D. G., Wester, T. J., Davis, T. A., Amick, S. & Heath, J. P. (1996) Orally administered IGF-I increases intestinal mucosal growth in formula-fed neonatal pigs. *Am. J. Physiol.* 270: R1085–R1091.
- Cieslak, D. G., Leibbrandt, V. D. & Benevenga, N. J. (1983) Effect of a high fat supplement in late gestation and lactation on piglet survival and performance. *J. Anim. Sci.* 57: 954–959.
- Clowes, E. J., Aherne, F. X. & Foxcroft, G. R. (1994) Effect of delayed breeding on the endocrinology and fecundity of sows. *J. Anim. Sci.* 72: 283–291.
- Coffey, M. T., Diggs, B. G., Handlin, D. L., Knabe, D. A., Maxwell, C. V., Jr., Noland, P. R., Prince, T. J. & Cromwell, G. L. (1994) Effects of dietary energy during gestation and lactation on reproductive performance of sows: a cooperative study. *J. Anim. Sci.* 72: 4–9.
- Coffey, M. T., Seerley, R. E. & Mabry, J. W. (1982) The effect of source of supplemental dietary energy on sow milk yield, milk composition and litter performance. *J. Anim. Sci.* 55: 1388–1394.
- Curtis, S. E., Heidenreich, C. J. & Foley, C. W. (1966) Carbohydrate assimilation and utilization by newborn pigs. *J. Anim. Sci.* 25: 655–662.
- Diehl, J. R., Godke, R. A., Killian, D. B. & Day, B. N. (1974) Induction of parturition in swine with prostaglandin $F_{2\alpha}$. *J. Anim. Sci.* 38: 1229–1234.
- Donovan, S. M., Houle, V. M., Monaco, M. H., Schroeder, E. A., Park, Y. & Odle, J. (1996) The neonatal piglet as a model to study insulin like growth factor mediated intestinal growth and function. In: *Advances in Swine in Biomedical Research* (Tumbleson, M. E. & Schook, C.L.B. eds.), pp. 733–743. Plenum Press, New York, NY.
- Donovan, S. M., McNeil, L. K., Jimenez-Flores, R. & Odle, J. (1994) Insulin-like growth factors and insulin-like growth factor binding proteins in porcine serum and milk throughout lactation. *Pediatr. Res.* 36: 159–168.
- Donovan, S. M. & Odle, J. (1994) Growth factors in milk as mediators of infant development. *Annu. Rev. Nutr.* 14: 147–167.
- Flint, D. J. (1995) Hormonal regulation of uptake and metabolism of milk precursors in normal lactating mammary gland. *J. Anim. Sci.* 73: (suppl. 2.): 61–71.
- Friend, D. W. (1974) Effect on the performance of pigs from birth to market weight of adding fat to the lactation diet of their dams. *J. Anim. Sci.* 39: 1073–1081.
- Houle, V. M., Schroeder, E. A., Odle, J. & Donovan, S. M. (1997) Small intestinal disaccharidase activity and ileal villus height are increased in piglets consuming formula containing recombinant human insulin-like growth factor-I. *Pediatr. Res.* 42: 78–86.
- Jackson, J. R., Hurley, W. L., Easter, R. A., Jensen, A. H. & Odle, J. (1995) Effects of induced or delayed parturition and supplemental dietary fat on colostrum and milk composition in sows. *J. Anim. Sci.* 73: 1906–1913.
- Kensinger, R. S., Collier, R. J. & Bazer, F. W. (1986) Ultrastructural changes in porcine mammary tissue during lactogenesis. *J. Anat.* 145: 49–59.
- Kensinger, R. S., Collier, R. J., Bazer, F. W., Ducsay, C. A. & Becker, H. N. (1982) Nucleic acid, metabolic and histological changes in gilt mammary tissue during pregnancy and lactogenesis. *J. Anim. Sci.* 54: 1297–1308.
- Lebenthal, E., Lee, P. C. & Heitlinger, L. A. (1983) Impact of development of the gastrointestinal tract on infant feeding. *J. Pediatr.* 102: 1–9.
- LeDividich, J., Herpin, P., Paul, E. & Strullu, F. (1997) Effect of fat content of colostrum on voluntary colostrum intake and fat utilization in newborn pigs. *J. Anim. Sci.* 75: 707–713.
- Lowry, O. H., Rosebrough, N. J., Farr, A. L. & Randall, R. J. (1951) Protein measurement with the Folin phenol reagent. *J. Biol. Chem.* 193: 265–275.
- Newton, E. A. & Mahan, D. C. (1993) Effect of initial breeding weight and management system using a high-producing sow genotype on resulting reproductive performance over three parities. *J. Anim. Sci.* 71: 1177–1186.
- Noblet, J., Dourmad, J. Y., Etienne, M. & LeDividich, J. (1997) Energy metabolism in pregnant sows and newborn pigs. *J. Anim. Sci.* 75: 2708–2714.
- NRC. (1988) *Nutrient Requirements of Swine*. (9th Ed.) National Academy Press, Washington, D.C.
- Odle, J., Zijlstra, R. T. & Donovan, S. M. (1996) Intestinal effects of milkborne growth factors in neonates of agricultural importance. *J. Anim. Sci.* 74: 2509–2522.
- O'Grady, J. F., Lynch, P. B. & Kearney, P. A. (1985) Voluntary feed intake by lactating sows. *Livest. Prod. Sci.* 12: 355–365.
- Pettigrew, J. E. (1981) Supplemental dietary fat for periparturient sows: a review. *J. Anim. Sci.* 53: 107–117.
- Pettigrew, J. E., McNamara, J. P., Tokach, M. D., King, R. H. & Crooker, B. A. (1993) Metabolic connections between nutrient intake and lactational performance in the sow. *Livest. Prod. Sci.* 35: 137–152.
- SAS Institute Inc. (1985) *SAS User's Guide: Statistics*, 5th ed. SAS Institute, Cary, NC.
- Seerley, R. W., Pace, T. A., Foley, C. W. & Scarth, R. D. (1974) Effect of energy intake prior to parturition on milk lipids and survival rate, thermostability and carcass composition of piglets. *J. Anim. Sci.* 38: 64–69.
- Seerley, R. W., Snyder, R. A. & McCampbell, H. C. (1981) The influence of sow

- dietary lipids and choline on piglet survival, milk and carcass composition. *J. Anim. Sci.* 52: 542–550.
- Shamay, A., Cohen, N., Niwa, M. & Gertler, A. (1988) Effects of insulin-like growth factor I on deoxyribonucleic acid synthesis and galactopoiesis in bovine undifferentiated and lactating mammary tissue. *Endocrinology* 123: 804–809.
- Shurson, G. C., Hogberg, M. G., DeFeaver, N., Radecki, S. V. & Miller, E. R. (1986) Effects of adding fat to the sow lactation diet on lactation and rebreeding performance. *J. Anim. Sci.* 62: 672–680.
- Stahly, T. S., Thompson, C. M. & Cromwell, G. L. (1981) Effect of sow milk composition on the rate, efficiency and composition of gain in neonatal pigs. *J. Anim. Sci.* 53 (suppl. 1): 264 (abs.).
- Steel, R.G.D. & Torrie, J. H. (1980) *Principles and Procedures of Statistics: A Biometrical Approach*, 2nd ed. McGraw-Hill, New York, NY.
- Tavakkol, A., Simmen, F. A. & Simmen, R.C.M. (1988) Porcine insulin-like growth factor-I (pIGF-I): complementary deoxyribonucleic acid cloning and uterine expression of messenger ribonucleic acid encoding evolutionarily conserved IGF-I peptides. *Mol. Endocrinol.* 2: 674–681.
- Teles, F. F., Young, C. K. & Stull, J. W. (1978) A method for rapid determination of lactose. *J. Dairy Sci.* 61: 506–508.
- Tilton, S. L., Miller, P. S., Lewis, A. J., Reese, D. E. & Ermer, P. M. (1999) Addition of fat to the diets of lactating sows: I. Effects on milk production and composition and carcass composition of the litter at weaning. *J. Anim. Sci.* 77: 2491–2500.
- Tokach, M. D., Pettigrew, J. E., Crooker, B. A., Dial, G. D. & Sower, A. F. (1992) Quantitative influence of lysine and energy intake on yield of milk components in the primiparous sow. *J. Anim. Sci.* 70: 1864–1872.
- U.S. Department of Agriculture (1997) *National Animal Health Monitoring System, Animal and Plant Health Inspection Service, Veterinary Services. Part III: Changes in the U.S. Pork Industry 1990–1995*. Washington, D.C.
- Weldon, W. C., Thulin, A. J., MacDougald, O. A., Johnston, L. J., Miller, E. R. & Tucker, H. A. (1991) Effects of increased dietary energy and protein during late gestation on mammary development in gilts. *J. Anim. Sci.* 69: 194–200.
- Whittemore, C. T. & Yang, H. (1989) Physical and chemical composition of the body of breeding sows with differing body subcutaneous fat depth at parturition, differing nutrition during lactation and differing litter size. *Anim. Prod.* 48: 203–212.