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Original article

Fat supplementation to the gestation diet of older sows and its effect on maternal and fetal fat metabolism*

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Summary — Sows that had had 3 previous litters were fed either a diet with no added fat (low fat) which was rich in linoleic acid (56.7% 18:2n–6), or a high fat diet containing lard, high in total saturates (28.9%) and oleic acid (37.8% 18:1n–9) during gestation. Backfat build-up in the sows on the high fat diet was accelerated compared to the low fat group. On day 110 of gestation, fetuses were removed. The fat content of the diet had no significant effect on sow weight gain during gestation, and the number or body weight of fetuses. Activities of sow liver and adipose and fetal liver malic enzyme, glucose-6-phosphate dehydrogenase (G-6-P) and acetyl-CoA-carboxylase (ACoABx) were measured. Only fetal liver ACoABx and sow adipose G-6-P were significantly affected by the sow's diet.

fetus / gestation / lipogenesis

Résumé — Supplémentation en lipides du régime de gestation et effet sur le métabolisme lipidique de la truie âgée. *Des truies ont reçu, pendant leur quatrième gestation, soit un régime sans lipides ajoutés (Low Fat) qui était riche en acide linoléique (56.7% 18:2n–6), soit un régime riche en lipides (High Fat), contenant du lard et ayant un taux élevé en acides gras saturés totaux (28,9%) et en acide oléique (37,8% 18:1n–9). Le dépôt de lard dorsal chez les truies consommant le régime «High Fat» a été accéléré par rapport au groupe «Low Fat».*

Les fœtus ont été prélevés au 110e j de gestation. La teneur en lipides du régime n'a pas eu d'effet significatif sur le gain de poids des truies pendant la gestation, ni sur le nombre ou le poids des fœtus.

Diverses activités enzymatiques ont été mesurées dans le foie ou le tissu adipeux des truies et dans le foie des fœtus : enzyme malique, glucose-6-phosphate déhydrogénase (G-6-P) et acétyl-CoA-carboxylase (ACoABx). Seules les activités de ACoABx du foie fœtal et de G-6-P du tissu adipeux de la truie étaient modifiées par la nature du régime.

fœtus / gestation / lipogenese

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INTRODUCTION

The sow, during a normal pregnancy, supplies the developing fetus with most of the nutrients needed for maintenance and growth (Battaglia and Meschia, 1978). It would appear that for the pig, unlike other species (Rosso, 1981), fetal requirements take priority, and that even severe feed restriction during gestation has little effect on litter size or birth weight (Elliot and Lodge, 1978; Ezekwe, 1981). Similarly, growth, body and internal organ composition and several metabolic parameters of the fetal pig do not appear to be influenced by short term changes in the maternal diet (Campion *et al,* 1984; Farnworth and Kramer, 1988, 1989). This is possible since a sow usually has a large pool of stored nutrients (particularly energy) that it shares with the fetus, and because of metabolic and compositional changes that are ongoing in the sow during gestation (Lodge, 1972; McNamara *et al,* 1985).

In the pig, increased parity number often results in smaller litter size, lowered birth weight, and increased numbers of stillbirths (Simensen and Karlberg, 1980; English *et al,* 1982). With each subsequent litter, the sow's nutrient pool may be decreasing in size, especially if large litters are carried through gestation, the sow is a high milk producer, or if the time between weaning and rebreeding is short.

In general, little data is available on the metabolism of the developing fetus and the factors that affect it. Although it is known that the organs and carcass of the fetal pig have a low fat content (Gortner, 1945; Becker *et al,* 1979; Farnworth and Kramer, 1988, 1989), it is still not clear how much contribution the fetus makes to its own fat stores through lipogenesis, and whether the maternal diet influences fat synthesis that may be occurring in the fetus. The purpose of this study was to determine whether changes occur in the lipid metabolism of older sows receiving different fat intakes, and whether feeding a low fat diet during gestation to older sows affects lipogenesis in fetal pig liver.

MATERIALS AND METHODS

Yorkshire sows from the Animal Research Centre SPF herd that had 3 previous litters were used for the experiment. Five sows were fed a low fat diet, and 5 a high fat diet beginning 7 d after being bred for this study. The low fat diet contained 45% corn, 35% barley, 9% soybean meal (48% crude protein), 5% bran, 1.5% limestone, 1.5% dicalcium phosphate, 1.5% lignosol, 0.5% iodized salt, 0.5% vitamin premix, and 0.5% mineral premix. The high fat diet contained 50 kg of an oil-fat blend (4 parts tallow, 1 part canola oil) per tonne of low fat diet mix. The pelleted diets were fed at a rate of 2.0 kg/d until d 110 of gestation.

Table I shows the fatty acid composition (on a relative basis) of the 2 diets fed. Because of the nature of the diets and the fat added, the level of linoleic acid (18:2n–6) of the high fat was approximately half that of the low fat diet, and the concentration of long chain fatty acids (carbon chain greater than 20) was low in both diets. Total lipid analysis of the diets indicated that the low fat diet contained 3.0% fat and the high fat diet contained 7.8% total fat.

Throughout gestation, sows were weighed and backfat measurements were taken using a Renco Lean-meater (Renco Corp, Minneapolis, MN). Backfat measurements were taken at 2 marked locations on the mid-back, on both sides of the midline. At 110 d of gestation, the sows were killed by stunning, and exsanguination. Backfat samples were dissected at the location of the backfat measurements. A total of 8 samples per sow were obtained (2 locations, 2 sides of the midline, 2 depths). Adipose samples were divided for fatty acid analysis and enzymatic analysis. The sow's uterus was removed, and individual fetuses were removed and weighed. The heaviest, lightest and average weight fetuses were identified, and samples taken for analysis. Sow liver, backfat and fetal livers were assayed for malic enzyme: ME (EC 1.1.1.40), glucose-6-phosphate dehydrogenase:G-6-P (EC

Table I. Diet fatty acid composition[1] and fatty acid consumption by sows.

Fatty acid	*Diet*		*Consumption*[3]	
	Low fat[2]	*High fat*[2]	*Low fat*	*High fat*
	Relative%		(g/day)	
C < 16	0.3	1.2	0.2	1.8
16:0	14.0	18.3	7.9	26.8
18.0	2.0	9.4	1.1	13.8
18:1n–9	21.6	37.8	12.1	55.4
18:2n–6	56.7	26.4	32.0	38.7
18:3n–3	3.3	2.3	1.9	3.4
C > 20	1.7	2.0	0.9	2.9
n–6/n–3	17.2	11.5		

[1] Major fatty acids only. [2] Average of 2 grab samples/diet. [3] Assuming 2 kg/d consumption; total fat extracted from diet samples = triglyceride; approximately 6% of triglyceride weight is glycerol.

1.1.1.49) and acetyl-CoA carboxylase:ACoABx (EC 6.4.1.2) using methods and conditions described elsewhere (Gandemer *et al,* 1979). Tissue protein content was determined using the Lowry method. The fatty acid composition of the diet, sow backfat and plasma were analyzed, using instrumentation and procedures described previously (Kramer *et al,* 1985). Data were analyzed using analysis of variance techniques (Statistical System Institute Inc 1985).

RESULTS

The feed consumption data, together with the diet lipid composition data, were used to calculate the consumptions of individual fatty acids (table I). The sows on the high fat diet ate (approximately) 3 times as much 16:0, 10 times as much 18:0 and 5 times as much 18:1n–9 as sows eating the low fat diet.

Data from the various sampling sites of the adipose tissue have been combined for clarity. The fatty acid compositions of sow plasma and adipose tissue are given in table II.

The plasma concentrations of total saturates and total monounsaturates showed no significant diet differences (data not presented), but the sows on the high fat diet had significantly increased levels of plasma 18:0. 18:2n–6 was the fatty acid found in the highest concentrations in sow's plasma. The level of plasma 18:2n–6 was significantly affected by diet, although the total n–6 fatty acids (18:2 n–6 and long chain derivatives) were not. The high fat sows had significantly elevated ($P < 0.05$) levels of total n–3 fatty acids (18:3n–3 and long chain derivatives) compared to the low fat sows. However, the levels of n–3 fatty acids found in the plasma of all sows was low (approximately 1/10 of the concentration of n–6 fatty acids).

Although there were differences in the patterns and amounts of dietary fatty acids consumed by the 2 groups of sows, the backfat fatty acid levels were very similar (for example 18:2n–6 levels). Only adipose 18:3n–3 was found to be significantly different between the 2 groups (high fat > low fat; $P < 0.05$). For both groups of sows, there were only low levels of fatty acids with chain length of 20 carbons or greater in the adipose. Long chain derivatives of 18:2n–6 and 18:3n–3 were very low; 20:1 was the most abundant long chain fatty acid (approximately 1.5% of total fatty acids). Site of adipose sampling rarely influenced fatty acid composition, but the interior backfat had significantly ($P < 0.05$) higher levels of 16:0, 18:0 and 18:1n–9, compared to the exterior (closest to the skin).

There were slight (non-significant) differences in body weight between the 2 groups of sows at the start of the experiment (table III). These differences may have contributed to the low fat sows gaining less weight over the course of the ex-

Table II. Sow plasma and adipose fatty acid composition[1].

	High fat		*Low fat*	
	Plasma	*Adipose*	*Plasma*	*Adipose*
Saturates				
16:0	14.8 ± 1.2	21.0 ± 1.4	15.6 ± 1.2	20.6 ± 1.4
18:0	14.0 ± 0.5*	11.0 ± 1.7	12.0 ± 1.0*	11.0 ± 1.7
20:0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.0
Monounsaturates				
16:1n–7	1.6 ± 0.2	2.5 ± 0.3	1.5 ± 0.1	2.5 ± 0.3
18:1n–9	21.9 ± 1.4	43.1 ± 2.4	22.2 ± 2.6	42.7 ± 2.0
18:1n–7	2.1 ± 0.1	2.9 ± 0.2	2.0 ± 0.3	2.9 ± 0.1
20:1n–9	0.4 ± 0.1	1.5 ± 0.1	0.4 ± 0.1	1.7 ± 0.2
n–6				
18:2n–6	28.2 ± 2.2*	13.5 ± 1.4*	32.0 ± 2.5*	14.0 ± 1.2*
20:3n–6	0.4 ± 0.1	0.3 ± 0.0	0.5 ± 0.3	0.3 ± 0.0
20:4n–6	8.2 ± 1.4	0.2 ± 0.0	7.5 ± 1.5	0.2 ± 0.0
22:4n–6	0.3 ± 0.1	tr[2]	0.6 ± 0.1	tr
22:5n–6	tr	tr	0.1 ± 0.1	tr
Total n–6	37.5 ± 2.3	15.0 ± 1.5	41.3 ± 2.0	15.6 ± 0.8
n–3				
18:3n–3	0.8 ± 0.1	0.8 ± 0.1*	1.0 ± 0.3	0.7 ± 0.1*
20:5n–3	0.3 ± 0.1	–[3]	0.2 ± 0.0	–
22:5n–3	1.3 ± 0.2	–	1.1 ± 0.2	tr
22:6n–3	0.5 ± 0.1	–	0.3 ± 0.1	tr
Total n–3	2.8 ± 0.3*	0.8 ± 0.1	2.6 ± 0.2	0.7±0.1
n–6/n–3	13.4	18.8	15.9	22.3

[1] Includes only major fatty acids. [2] Trace. [3] Below level of detection. * Significant diet effect, $P < 0.05$.

periment, but the rate was the same for both groups (fig 1). The low fat sows also had fewer numbers of fetuses at 110 d of gestation, the total weight of the litter carried by each sow was reduced, and the average weight of each fetus was lower. However, none of these parameters differed significantly from those for the high fat sows.

The lower weight gain in the sows receiving the low fat diet was also reflected in the reduced rate of fat accretion as measured by the fat probe. As seen in figure 1, the low fat sows lost backfat in the first 5 weeks of gestation, but tended to recover as gestation progressed. In contrast, the sows receiving the high fat diet had a steady increase in backfat thickness (taking 1 week past breeding as the starting point). In spite of the fact that the low fat sows lost backfat in the first weeks of gestation, their rate of body weight gain paralleled that of the high fat group.

Table IV contains the results of the lipogenic enzyme assays on the sow and fetal tissue. The sow liver activities of ME, G-6-P, and ACoABx were low and were not affected by diet. The fetal liver ME values were lower than the sow ME values, but the G-6-P levels were higher. Neither fetal liver ME or G-6-P activities were affected by the maternal diet. The liver ACoABx ac-

Table III. Sow and fetus data.

	Diet		
	Low fat	*High fat*	*Diet effect*
Sows			
Number	5	5	
Avg weight at start of exp (kg)	189.0 ± 21.0 [1]	212.8 ± 18.0	NS[2]
Avg weight gain at slaughter (kg)	42.8 ± 7.4	54.8 ± 4.1	NS
Fetuses			
Avg No per sow	12.2 ± 1.5	13.6 ± 2.3	NS
Avg total weight of all fetuses per sow (kg)	11.4 ± 0.7	13.7 ± 2.6	NS
Avg fetal weight (kg)	0.95 ± 0.21 (61)[3]	1.01 ± 0.23 (68)[2]	NS

[1] Mean ± standard deviation. [2] Analysis of variance test; *NS* : not significantly different $P > 0.05$. [3] Total number of fetuses sampled.

tivity of fetuses of sows receiving the high fat diet was comparable to those of the sows, but fetuses of sows receiving the low fat diet showed significantly increased activity. Results of lipogenic enzyme activity in sow backfat were obtained from 8 samples per sow (2 locations – shoulder, mid back; 2 sides of the midline – left, right; 2 depths – interior, exterior). The data in table III were combined because of the lack of significant differences ($P < 0.05$) between sampling sites of the backfat. The sole exception was for ME which was found to be significantly different depending on the depth of the sample (93.7 for interior and 116 nmol.min^{-1}.mg^{-1} protein for the exterior samples). Sow backfat ME and ACoABx activities were not affected by the diet, but the G-6-P values in the sows on the low fat diet were increased significantly compared to the high fat sow activities. No backfat samples were obtained from the fetal carcasses because of the inability to clearly differentiate between fat and muscle layers.

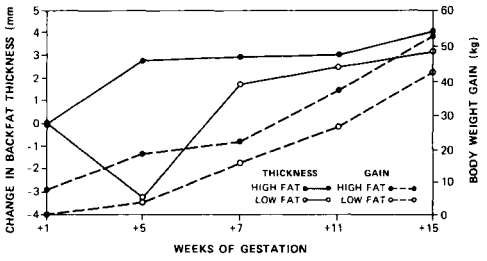

Fig 1. Changes in backfat thickness and body weights in sows fed the low and high fat diets, over the course of gestation.

DISCUSSION

In young swine, the fat content of the diet has been shown to influence the rate of lipogenic enzymes found in liver and adipose tissue in both pre- and post-weaned pigs (Allee *et al*, 1971; Wolfe *et al*, 1977). However, the rate of lipogenesis expressed on a per mg protein basis declines with age, even though carcass fat build-up continues (Anderson and Kauffman, 1973). The low rates of lipogenesis reported here

Table IV. Sow and fetal lipogenic enzyme activity[1].

	Sow			*Fetus*		
	High fat	*Low fat*	*Effect of diet*	*High fat*	*Low fat*	*Effect of diet*
			(nmol•min^{-1}•mg^{-1} protein)			
Liver[2]						
Organ wgt (g)	2710 ± 194	2596 ± 54	NS	24.1 ± 9.60	23.7 ± 7.88	NS
ME	7.1 ± 2.2	10.3 ± 0.51	NS	2.5 ± 1.9	1.5 ± 1.1	NS
G-6-P	20.4 ± 3.7	20.3 ± 4.4	NS	57.0 ± 12.0	53.0 ± 12.0	NS
ACoABx	6.1 ± 3.4	6.2 ± 3.4	NS	6.1 ± 3.0	9.7 ± 4.8	*
Protein content (mg/g tissue)	77.8 ± 10.7	73.9 ± 7.6	NS	46.0 ± 7.5	46.1 ± 6.6	NS
Backfat[3]						
ME	94.5 ± 42.3	116 ± 73.6	NS			
G-6-P	27.5 ± 29.4	54.9 ± 59.7	*			
ACoABx	0.66 ± 0.43	0.53 ± 0.43	NS			
Protein content (mg/g tissue)	1.12 ± 0.17	1.21 ± 0.35	NS			

[1] ME, malic enzyme; G-6-P, glucose-6-phosphate dehydrogenase; ACoABx, acetyl-CoA-carboxylase. [2] Liver samples from 5 sow/diet; livers from 3 fetuses (heaviest, lightest and average weight)/sow. [3] Backfat samples from 5 sows/diet, from 2 locations right and left of the midline, at 2 depths.

in sows that had had 3 previous gestations/lactations are consistent with this. However, even in spite of these low rates of lipogenesis, sow adipose ME activity increased and G-6-P activity significantly increased in response to a low fat diet.

Kasser *et al* (1981), in their study of sow and fetal fat metabolism, reported low maternal rates of fatty acid synthesis, and a lack of effect of fasting on maternal or fetal hepatic fatty acid synthesis. Only when the sows were made diabetic did they find consistent effects on fetal metabolism and body composition. This contrasts with data reported for rats where both maternal and fetal liver fatty acid syntheses were lowered by maternal fasting (Fain and Scow, 1966). Other aspects of fetal development in the pig, such as fetal skeletal muscle development, composition and fat utilization, have similarly been shown to be insensitive to changes in the maternal diet (Campion *et al,* 1984).

Kasser *et al* (1981) also reported that the sow adipose lipogenic activity was generally higher than hepatic activities, although the rates of *in vivo* fatty acid synthesis were similar. They found that the rate of some lipogenic enzymes was higher in fetal liver than in the maternal liver. Our data for glucose-6-phosphate dehydrogenase is in agreement with this.

Based on their results, Kasser *et al* (1981) concluded that the adipose tissue was the main site of lipogenesis in the fetal pig. However calculations of fatty acid synthesis using values for fetal liver weight, liver protein content, average fetal weight (tables II and III) and fetal carcass fat content (Farnworth and Kramer, 1988), to-

gether with lipogenic enzyme or fatty acid synthesis rates, would indicate that it is more likely that the liver is the main site of lipogenesis in the fetal pig. If this is so, then it is noteworthy that, in this study, fetal ACoABx was significiantly affected by maternal diet.

The mature pig has a good covering of backfat, the main constituent of which is triglyceride (Mersmann *et al,* 1973). However, as has been reported before and confirmed here, the rate of fat accretion during gestation by the sow can be influenced by diet (Salmon-Legagneur, 1965; Pond and Mersmann, 1988). The fatty acid make-up of the adipose tissue is the result of contributions from the diet together with *in vivo* lipogenesis. In young pigs, as in other species, changes in the diet can influence adipose fatty acid patterns (Koch *et al,* 1968; Castell and Falk, 1980; Field and Clandinin, 1984). Here, with older sows, dietary intervention for up to 103 d was not long enough to greatly alter the fatty acid pattern of swine adipose. This is consistent with the estimation of a half life of over 300 d for fatty acids of adipose tissue in older swine (Anderson *et al,* 1972) and the fact that at the start of the experiment, the sows had approximately 20 mm of back fat.

The sows used in this study had received adequate diets up to the time of the start of this study, and so their body reserves of nutrients were not low. In addition, the increase in adipose thickness during gestation of the low fat sows indicated that these sows were not in energy deficit during the course of the experiment. In spite of this, some differences were found in the number and size of fetuses carried by the low fat sows, and changes in lipogenic enzyme activity were observed.

Attempts to change the metabolism of the developing swine fetus, and thereby alter its body composition in anticipation of birth appears to be difficult. Desnoyers *et al* (1985) did decrease body weight, carcass triglyceride and the number of adipocytes in newborn piglets by feeding gilts a low energy (3,000 kcal DE/d) diet during gestation. However, there normally appears to be enough opportunities to buffer the fetal system against any effects of changes in the sow's diet. Added to this is the possibility that the fetus may have the ability to control its own metabolism, a hypothesis proposed before (Hentges *et al,* 1987). Changes in fetal metabolism may only be possible by direct intervention. This would limit the potential for enhancing fetal growth and development.

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