ENERGY PARTITIONING AND REPRODUCTION IN PRIMIPAROUS SOWS: EFFECTS OF DIETARY ENERGY SOURCE

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ENERGY PARTITIONING AND REPRODUCTION IN PRIMIPAROUS SOWS: EFFECTS OF DIETARY ENERGY SOURCE

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Energieverdeling en reproductie van eerste-worps zeugen: effecten van energiebron in het dieet.

The hormone insulin can act as an intermediate between nutrition and reproduction in the pig and it is known that dietary energy source can influence plasma insulin concentration. The first aim of this study was to investigate effects of dietary energy source (fat: less insulin-stimulating or starch: more insulin-stimulating) on reproductive performance. Because reproductive performance is also affected by the metabolic status of lactating sows, it has also been investigated whether effects of dietary energy source on reproduction are dependent on the metabolic status of the sows. This was the second aim of the research described in this thesis.

The different energy sources did not affect milk production and milk composition, piglet body composition, and energy and protein balance of the sow, when fed at a low feeding level during lactation. However, at a high feeding level, sows fed the fat-rich diet produced milk with a higher fat percentage, resulting in piglets with an increased body fat content. This increased fat deposition into the litter resulted in a more negative energy balance than when sows were fed a starch-rich diet.

Feeding the starch-rich diet resulted in a higher plasma insulin concentration and tended to increase LH pulse frequency during lactation compared to the fat-rich diet. Feeding the starch-rich diet after weaning resulted in a lower risk that sows remain anestrous after weaning than when the fat-rich diet was fed. No effects of dietary energy source on weaning-to-estrus interval, ovulation rate, or uterine, placental, and embryonic traits were found. Furthermore, no relationships between plasma insulin concentration and reproductive traits were found. No interactions between metabolic status and dietary energy source on reproductive performance were found.

From this study, it can be concluded that insulin-stimulating diets affect LH pulsatility and return to estrus, especially in restricted fed lactating sows, but hardly affect ovarian and uterine traits.

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STELLLINGEN

1. Behalve het plasma insulinegehalte kan ook de plasma IGF-1 concentratie beïnvloed worden door de energiebron in het dieet van lacterende eerste-worps zeugen.
   (dit proefschrift)

2. Sturing van de plasma insulineconcentratie, door middel van energiebronnen in het dieet van lacterende eerste-worps zeugen, heeft nauwelijks invloed op de reproductie.
   (dit proefschrift)

3. Verhoging van de voeropname van lacterende eerste-worps zeugen leidt bij een vetrijk dieet tot een verhoogde melkvetsynthese en niet tot een verbetering van de energiebalans van de zeug.
   (dit proefschrift)

4. De verstrekking van een vetrijk dieet na het spenen aan eerste-worps zeugen met een relatief lage voeropname tijdens de lactatie, geeft een hogere kans op niet of vertraagd in bronst komen, dan wanneer een zetmeel-rijk dieet verstrekt wordt.
   (dit proefschrift)

5. In eerste-worps zeugen is voerbeperking tijdens de lactatie meer bepalend voor de reproductieresultaten na het spenen dan de metabole status van deze dieren tijdens de lactatie.

6. Op grond van de Bijbel zou het voor christenen niet acceptabel moeten zijn om op een industriële wijze veehouderij te bedrijven.
   (n.a.v. J.G. Schenderling, Mens en dier in theologisch perspectief. Dissertatie, 1999)

7. Omdat antidepressiva vrijwel altijd bijwerkingen hebben, is dubbel blind onderzoek naar de werking van deze middelen vrijwel onmogelijk.

8. Hoewel alcohol als een conserveermiddel beschouwd kan worden, heeft het een negatief effect of de houdbaarheidsduur van geheimen.

9. Wanneer de betekenis van 'zitten blijven' in de politiek een gelijke betekenis zou hebben als het begrip 'zitten blijven' op de lagere school, zou de personele bezetting van het kabinet er momenteel geheel anders uitzien.

10. Een oldtimer is als de vrouw van een ander: je mag er wel naar kijken maar niet aanraken.

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H. van den Brand
Wageningen, 30 mei 2000

Voor mijn ouders

Voorwoord

Hoever ben je met je boekje? Deze en vergelijkbare vragen zijn met name in het afgelopen jaar van verschillende kanten gesteld. Het antwoord verschilde van 'nog lang niet af' tot 'het begint erop te lijken'. Maar wanneer dit gelezen wordt, kan er gesteld worden dat het af is. En dat bijna binnen de gestelde vier jaar. Dat betekent dus direct dat je dat niet alleen gedaan kunt hebben. In mijn geval is dat dan ook zeker niet het geval. Ik wil vanaf deze plaats dan ook de personen die mij hebben geholpen in de afgelopen vier jaar bedanken, met het besef dat ik daarin nooit volledig zal zijn. In de eerste plaats zijn dat mijn directe begeleiders. Bas, in het begin als co-promoter en pas op het laatst als promotor. Ik ben bijzonder vereerd dat ik je eerste promovendus mag zijn. Je, soms wilde, ideeën waren uitermate inspirerend. En of dat bloedend hart op termijn nog hersteld kan worden moeten we maar eens bepraten. Nicoline, je tomeloze inzet deed soms vermoeden dat het jouw project was. Ook na versie vier viel er altijd nog wel wat te schaven aan de manuscripten. Ik waardeer het dan ook dat je als mijn co-promotor wilt fungeren. Johan, je betrokkenheid tijdens het project leek wel eens wat variabel, maar je eindspurt was geweldig. Mede dankzij jou weet ik nu ook een klein beetje van klimaat respiratie.

Bij de uitvoering van de experimenten was ik voor een groot deel afhankelijk van collegae. Frits, hoewel ons werkwijzen niet altijd parallel liepen, is de persoonlijk waardering niet verminderd en is het toch allemaal tot een goed einde gekomen. Dat je mijn paranimf wilt zijn, vind ik dan ook groots. Marcel en Koos, door jullie uiterst nauwgezette dataverzameling en analyses was de uitvoering van de experimenten bij jullie in goede handen. Het is dat je maar twee paranimfen mag hebben... Wouter, ook na een lange dag canuleren was je humeur (schijnbaar) nog uitermate goed; Emmy, na bloedje 6034 ging je nog gewoon door, ook al was dat om vier uur in de nacht. Allen hartelijk dank!

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Tijdens de uitgebreide experimenten gaven velen binnen de leerstoelgroep een mentale dan wel fysieke bijdrage. Ik wil dan ook alle collegae bedanken voor hun meeleven tijdens het project. Met name wil ik mijn mede AIO's van het 'Promotion Team' noemen, met wie op de AIO-zolder vele uren doorgebracht zijn: Lisette, Pieter, Dorothé, John, Gustavo en Jorine: bedankt!

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CONTENTS

GENERAL INTRODUCTION

INTRODUCTION

The number of piglets reared per sow per year is a major determinant for the profitability of pig breeders. This number of piglets depends on litter size, postnatal survival rate, and number of litters per sow per year. Especially in primiparous sows reproduction efficiency is suboptimal. This is expressed as postlactational disorders like a prolonged weaning-to-estrus interval (WEI; Vesseur et al., 1994; Koketsu and Dial, 1997), a higher percentage of anestrous sows (Vesseur et al., 1994), possibly a lower ovulation rate, and a lower embryonal survival rate. The latter two lead to a smaller subsequent litter size (Vesseur et al., 1994; Koketsu and Dial, 1997).

LH PULSATILITY AND FOLLICLE DEVELOPMENT

In the last decades, much research has been performed to unravel the physiological mechanisms involved in reproduction of sows. Two organs play a major role in the regulation of estrus and ovulation: the hypothalamus-pituitary and the ovary. The hypothalamus pulsatile secretes gonadotrophin-releasing hormone (GnRH) and acts therefore as a pulse generator for the secretion of luteinizing hormone (LH) by the pituitary.

During early lactation the pulsatile secretion of LH is low, but in general increases during lactation (Tokach et al., 1992; Koketsu et al., 1996). During lactation LH is secreted with low frequency and high amplitude. Immediately after weaning a characteristic LH pattern (high frequency, low amplitude) is shown. The LH pulse frequency during lactation is correlated with the LH pulse frequency on the day of weaning (Shaw and Foxcroft, 1985; Tokach et al., 1992; Zak et al., 1998). In animals with a depressed LH secretion during and after lactation, the WEI is prolonged (Shaw and Foxcroft, 1985; Tokach et al., 1992; Paterson and Pearce, 1994).

On the ovary level, follicle development in early lactation is suppressed, but with progressing lactation a gradual restoration of follicle growth to larger sized categories occurs (Kunavongkrit et al., 1982), although follicles do not reach the ovulatory state (Kunavongkrit et al., 1982; Rojanasthien et al., 1987). The reason for this suppressed follicle development during early lactation is not completely clear. Evidence has been presented that the lack of sufficient follicle stimulating hormone (FSH) and(or) LH secretion by the pituitary causes this suppression (for review see Kemp et al., 1998). Antral follicle development up to 4 mm is stimulated by FSH, whereas LH seems to be necessary for further growth and maturation of follicles (Driancourt et al., 1995, Brüssow et al., 1996). De Rensis et al. (1991) demonstrated that follicle development during lactation is positively correlated with plasma LH concentration. The characteristic LH pattern after weaning induces the growth of antral follicles to Graafian follicles. This follicle recruitment also depends on the size and the quality of the antral follicle pool at weaning (Kemp et al., 1998).

ENERGY AND PROTEIN BALANCE AND THEIR RELATION WITH REPRODUCTION

During lactation, a suckling related suppression of LH secretion occurs (De Rensis et al., 1993), which is mediated by endogenous opioids acting at the hypothalamic level (Armstrong et al., 1988). The suckling intensity is high in early lactation and decreases with time during lactation (Jensen and Recén, 1989; Brooks and Burke, 1998). Furthermore, the negative energy balance of sows during progressing lactation depresses LH secretion (Zak et al., 1997a, 1998; Quesnel et al., 1998). At a constant feed intake, the relative influence of the negative energy balance on LH secretion seems to increase during the lactation period, due to an increase in milk production (Quesnel and Prunier, 1995). Because a restoration of LH pulse frequency is found when lactation progresses (Tokach et al., 1992; Koketsu et al., 1996), it can be suggested that the inhibition of the LH secretion by the negative metabolic status is less pronounced than that due to suckling. However, when sows are in a severe negative energy and protein balance during lactation, restoration of the LH pulsatility can be absent or delayed. This is particularly the case in primiparous sows. These sows have not reached their mature body weight and therefore they need nutrients for body development. However, due to the limited feed intake capacity, primiparous sows mobilize body fat and protein during lactation to meet their requirements for maintenance and milk production. Because of the relatively low feed intake in these sows, LH pulsatility during and after lactation is depressed and the WEI is prolonged (Koketsu et al., 1998; Zak et al., 1998) compared to multiparous sows.

A severe negative energy and protein balance during lactation also acts on the ovary. A low lactational feed intake is associated with suppressed follicle development (Zak et al., 1997b; Quesnel et al., 1998a), impaired oocyte maturation (Zak et al., 1997b), lower ovulation rate (Zak et al., 1997a), lower plasma progesterone concentration in subsequent pregnancy (Kirkwood et al., 1987a), and higher embryonal mortality (Kirkwood et al., 1987b; Zak et al., 1997b). The delayed or absent follicle development after weaning in sows with a severe negative energy and protein balance is possibly due to the depressed LH secretion. Furthermore, other intermediates (e.g. insulin, insulin-like growth factor-I (IGF-1)) are suggested to play a role in the relationship between the metabolic status and follicle development.

It can be concluded that a negative energy and protein balance (body weight loss) during lactation are important determinants of subsequent reproductive performance of sows (Clowes et al., 1998; Zak et al., 1998). However, relationships between fat and protein loss during lactation and subsequent reproduction are hardly investigated.

THE ROLE OF INSULIN IN THE RELATIONSHIP BETWEEN NUTRITION AND REPRODUCTION

Several studies have already shown that insulin might be an intermediate between nutrition and reproduction, acting on both hypothalamus-pituitary and ovary level. For example Tokach et al. (1992), Koketsu et al. (1996), and Quesnel et al. (1998b) found correlations between plasma insulin concentration of lactating sows and LH pulse frequency during and after lactation. Furthermore, exogenous insulin injections in gilts increased the LH pulse frequency (Cox et al., 1987). The observation that LH and FSH release by cultured pituitary cells is enhanced after insulin administration (Adashi et al., 1981) also supports the potential role of insulin at the brain level.

On the ovary, insulin receptors are present (Ladenheim et al., 1984) and administration of insulin increased the differentiation of cultured granulosa cells (May and Schomberg, 1981; Poretsky and Kalin, 1987). Furthermore, exogenous insulin injections in gilts have been found to decrease the number of atretic follicles (Matamoros et al., 1990) and to increase ovulation rate (Cox et al., 1987). In primiparous sows, insulin injections after weaning also resulted in an increased number of live born piglets (Ramirez et al., 1997).

Considering the potential role of insulin in reproduction, it can be suggested that diets that enhance plasma insulin concentration can be a tool to improve reproductive performance. It can be expected that starch-rich diets stimulate the secretion of insulin, due to the high glucose content. In multiparous sows fed a starch-rich diet, Kemp et al. (1995) found a higher LH pulse frequency in early lactation as well as a higher preovulatory LH surge and progesterone concentration postweaning, compared with sows fed a fat-rich diet. Plasma insulin concentration can also be affected by feed intake (Koketsu et al., 1996, 1998; Quesnel et al., 1998b) and feed intake affects the sow's metabolic status (see above). Therefore, it should be considered whether there is an interaction between feed intake and dietary energy source on insulin secretion and reproductive traits.

In Figure 1 the possible relationships between nutrition (both feed intake and dietary energy source) and reproduction, as well as the potential role of insulin in this relationship, are summarized.

DEFINITION OF THE PROBLEM

As already mentioned, feed intake capacity of primiparous sows during lactation is limited. Lactational energy intake can be increased by increasing dietary energy density. Drochner (1989) reviewed effects of additional dietary fat and concluded that in multiparous sows the metabolizable energy intake during lactation with ad libitum feed intake increased with on

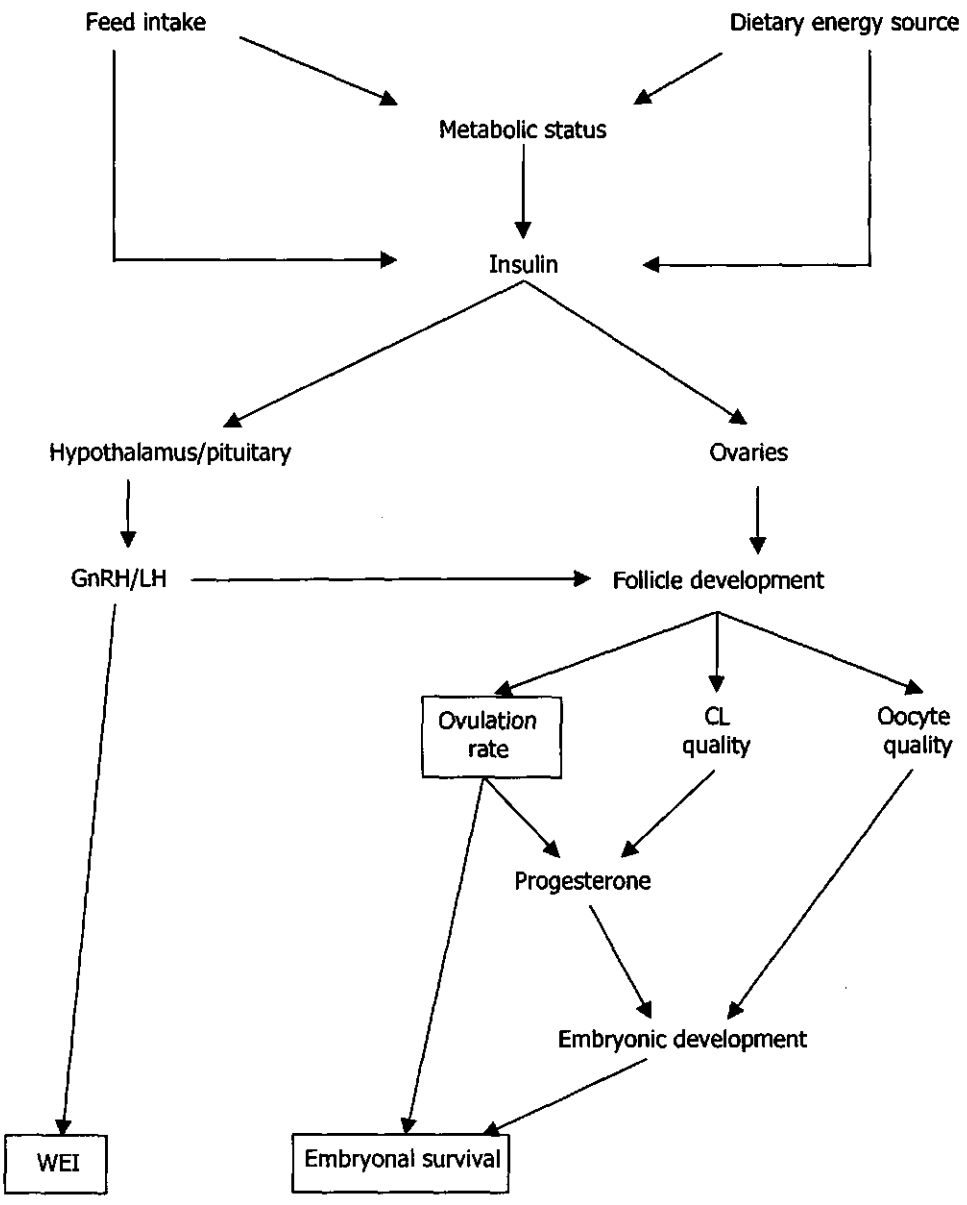

Figure 1. Potential relationships between nutrition and reproduction and the role of insulin in this mechanism. WEI = weaning-to-estrus interval, CL = corpora lutea. Characteristics in borders affect the number of piglets reared per year.

average 12% (range 3 to 32). However, this potential positive effect of fat-rich diets on energy balance is probably reduced because of the increased milk energy output with those diets (Shurson et al., 1986; Schoenherr et al., 1989). Moreover, a high dietary fat concentration can be negative for subsequent reproductive performance due to effects of a lower plasma insulin concentration. Based on above-mentioned relationships between insulin and reproduction, it can be suggested that feeding of starch-rich diets is positive for reproductive performance. Thus, the benefits of feeding fat-rich diets seem disputable, both from the diet quantity (energy balance) and diet quality (insulin stimulation) point of view.

Possible positive effects of starch-rich diets might be dependent on feed intake. It can be suggested that with a high feed intake during lactation, no effect of dietary energy source will be found on reproduction, because of the relatively mild negative energy balance. At the same time, it can be suggested that, with a low feed intake, insulin-stimulating diets can improve reproduction results, especially in sows that are in a severe negative energy balance. On the other hand, it can also be imagined that the negative energy balance overrides every positive effect of insulin-stimulating diets on reproduction. This means that the interaction between feed intake and dietary energy source on reproduction needs to be investigated.

AIM OF THE THESIS

The first objective of this thesis is to study effects of two specific dietary energy sources (fat: less insulin-stimulating or starch plus sugar: more insulin-stimulating), fed during different parts of the reproduction cycle, on reproductive traits in primiparous sows. The second objective is to study whether effects of these dietary energy sources on reproduction are dependent on the metabolic status (induced by feed intake) of primiparous sows during lactation.

OUTLINE OF THE THESIS

To investigate effects of different dietary energy sources on plasma insulin concentration and reproductive traits, diets had to be composed that differ in the potency to stimulate insulin secretion. Therefore, an experiment was conducted in which effects of different dietary energy sources on plasma insulin and glucose concentration in gilts were examined. In Chapter 1 the results of this experiment are described.

Based on the results described in Chapter 1, the fat and starch plus sugar diets were selected to be used in an experiment, which was performed to investigate effects of dietary energy source and feeding level on energy and nitrogen balance and on reproductive traits in primiparous sows. A second objective of this experiment was to investigate whether there

are relationships between nutritionally manipulated plasma insulin concentration and reproductive performance. The results of this experiment are described in Chapter 2 to 5. Effects of dietary energy source and feeding level during lactation on energy and protein balance are described in Chapter 2. Chapter 3 and 4 describe effects of dietary energy source and feeding level during lactation on reproductive traits during lactation, the periestrus period, and the subsequent pregnancy. Furthermore, relationships between plasma insulin concentration and reproduction are examined.

In the results described in Chapter 3 and 4, nutritionally manipulated plasma insulin concentrations were not related to reproductive traits. Therefore, additional analyses were performed to investigate effects of feeding level during lactation and dietary energy source on another important metabolic factor: IGF-1. Furthermore, relationships between IGF-1 concentrations and reproductive traits were calculated. Chapter 5 describes the results obtained from these analyses.

In the experiment described in Chapter 2 to 5, dietary energy sources were fed during lactation and up to d 35 of subsequent pregnancy. Therefore, it is not possible to distinguish specific effects of dietary energy source during lactation, between weaning and estrus, or during early pregnancy on reproduction. To clarify this, a subsequent experiment was conducted in which both dietary energy sources were fed between weaning and estrus or during early pregnancy. The results from this experiment are described in Chapter 6.

Finally, in the General Discussion, the results of the different experiments, are combined and discussed.

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Chapter 1

EFFECTS OF DIETARY ENERGY SOURCE ON PLASMA GLUCOSE AND INSULIN CONCENTRATION IN GILTS

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ABSTRACT

Since it is known that insulin plays a role in reproductive processes, the dietary energy source could be an effective tool to influence reproductive processes in sows. The effects of dietary energy source on plasma glucose and insulin concentration were studied. Five gilts were used in a Latin square design with three diets over three periods. Diets contained either 238 g/kg maize starch (Starch), 178 g/kg maize starch plus 60 g/kg dextrose (Sugar), or 96 g/kg tallow (Fat) as main energy source and were fed isocalorically. All other ingredients were similar for the three diets. Results showed similar preprandial glucose concentrations for all diets. Plasma glucose concentration at 24 min after feeding was higher ($P<0.05$) for the Sugar diet compared to the Fat diet. Sixty minutes after feeding the plasma glucose concentration was lower ($P<0.05$) for the Sugar diet compared to the two other diets. The postprandial insulin response was greater ($P<0.05$) in the Sugar fed gilts than in the Fat fed gilts and remained at a higher level. Postprandial insulin concentrations in Starch fed gilts were intermediate and did not differ from both other diets. The ratio between average and maximum insulin and glucose concentrations was higher in the Sugar and Starch diet compared to the Fat diet. The results show that dietary energy source can affect postprandial plasma insulin levels (both peak level after feeding and long term level) as well as the ratio between insulin and glucose.

INTRODUCTION

Several studies have shown that insulin is positively related with reproductive processes (Cox et al., 1987; Matamoros et al., 1990; Tokach et al., 1992; Ramirez et al., 1994; Booth et al., 1996). Plasma insulin levels can be altered by feeding level (Booth et al., 1996), metabolic status (Close et al., 1991), and exogenous insulin injection (Cox et al., 1987), but also by dietary energy source (Kemp et al., 1993, 1995). Objective of the present study was to investigate effects of specific dietary energy sources (dextrose, starch, or fat) on plasma glucose and insulin levels in gilts. When the dietary energy source significantly affects the plasma insulin levels, further research can be implemented to study the effects of diet composition on reproductive processes.

MATERIALS AND METHODS

The experiment was designed as a Latin square with three diets in three periods. Each period started with 7 d of adaptation to the diet. On d 8 and 10, blood samples (6 mL each) were taken. After the last day of sampling in each period, diets were changed.

Five commercial crossbred gilts (Yorkshire x Dutch Landrace) aged 7 mo were brought to the experimental farm and housed individually in pens of 9 m^2. From an age of approximately 8 mo onwards all gilts were given 20 mg of Altrenogest orally (Regumate®; Hoechst Roussel Vet. N.V., Brussels, Belgium), daily for 18 d, to synchronize the cycle. At an age of 9 mo all gilts were surgically fitted with a permanent jugular vein catheter according

to the method described previously by Soede et al. (1994). Three days after surgery (d 0) each gilt was assigned to one of three diets.

Three experimental diets were produced, which only differed in energy source (Table 1). All diets consisted of a basal diet with sufficient protein, vitamins, and minerals. To this basal diet different energy sources were added to produce isocaloric diets. The starch-rich diet (**Starch**) contained 238 g/kg maize starch. In the starch/sugar-rich diet (**Sugar**), 60 g of the maize starch from the Starch diet was replaced by dextrose. The fat-rich diet (**Fat**) contained 96 g/kg tallow as the major energy source. The gilts were fed 18.5 MJ NE of the diets daily, in two equal portions at 0800 and 1600. Water was available ad libitum. At the beginning and end of the experiment gilts were weighed and backfat thickness was measured using a method similar to Verstegen et al. (1979).

The procedure of blood sampling is described previously by Soede et al. (1994). Blood samples were taken at -60, -48, -36, -24, -12, 0, 12, 24, 36, 60, 84, 120, 156, 228, 300, and 372 min relative to the 0800 feeding. Blood samples were collected in ice-cooled polypropylene tubes containing 100 µL of EDTA-solution (144 mg/mL saline; Titriplex® III, Merck Nederland B.V., Amsterdam, The Netherlands) and centrifuged at 2,000 x *g* for 10 min at 4°C. Plasma was stored at -20°C until analyses.

The plasma insulin concentration was quantified in a single RIA (Leuvenink et al., 1997). The maximum binding for [^{125}I] insulin was 25.5%. The sensitivity was 4.2 µIU/mL at 80% binding. The intraassay CV was 8.5%. The plasma glucose concentration was quantified using a commercial kit (GOD-PAP, Boehringer, Mannheim, Germany).

Statistical methods

The analyses were performed with the GLM procedure (SAS program, Cary, NC, USA). A preliminary analysis showed no differences in plasma glucose or insulin between sampling d 8 and 10 in either of the periods for either of the sampling times. Therefore, results per sampling time are averaged per period. The preliminary analysis also showed no effect of cycle stage on plasma glucose or insulin concentration. Both basal glucose and basal insulin concentrations were calculated per sow per period as the mean value of the samples taken at 60, 48, 36, 24, 12, and 0 min before feeding. The areas under the curve (**AUC**) during the sampling period were calculated as the area corrected for basal glucose or insulin concentrations. Data for the moment of sampling relative to feeding, basal concentrations, the area under the curve, the ratio between maximum insulin and glucose (I_{MAX}/G_{MAX}) and the ratio between the area under the curve of insulin and glucose (I_{AUC}/G_{AUC}) per sow per period were analyzed using a model that accounted for the variance associated with sow, diet, and period. Data are presented as means±SEM.

Table 1. Composition of the experimental diets (as fed)

Ingredient	Starch, g	Sugar, g	Fat, g
Barley	238	238	238
Wheat middlings	50	50	50
Toasted soybeans	57	57	57
Extracted soybeans	115	115	115
Extracted sunflower seed	178	178	178
Extracted rape seed	36	36	36
Meat and bone meal	48	48	48
Alfalfa meal	2	2	2
Limestone	8.3	8.3	8.3
Monocalcium phosphate	7.1	7.1	7.1
Salt	2.4	2.4	2.4
L-Lysine HCl	1.2	1.2	1.2
DL-Methionine	1.2	1.2	1.2
Vitamin-mineral premix	17.8	17.8	17.8
Maize starch	238	178	-
Dextrose	-	60	-
Tallow	-	-	81
Total, g[a]	1,000	1,000	843
Calculated content	g/1,000 g	g/1,000 g	g/843 g
Crude protein	211.4	211.2	210.5
Crude fat	33.2	33.2	113.7
Starch	357.2	305.4	149.8
Sugar	16.1	75.5	16.1
kJ NE (for swine)[b]	8,800	8,800	8,800
Digestible lysine[c]	8.4	8.4	8.4

[a] 1,000 g of the Starch and Sugar diet and 843 g of the Fat diet are isocaloric and isonitrogenic.
[b] According to the Centraal Veevoederbureau (CVB, 1988).
[c] Fecal digestibility (CVB, 1988)

RESULTS

Weight and backfat thickness at the start of the experiment were 143±4 kg and 13.7±0.8 mm, respectively, and at the end of the experiment, 154±3 kg and 14.8±0.7 mm, respectively. On the sampling days, the diet was consumed within 1 h after feeding.

Basal plasma glucose concentrations were similar ($P>0.10$) for the three diets (69.0±2.6 vs 70.4±1.2 vs 72.4±0.9 mg/100 mL for Sugar, Starch, and Fat, respectively; Figure 1). Plasma glucose concentration after feeding showed a greater increase on the Sugar diet compared to the Fat diet. This resulted in a higher plasma glucose concentration for the Sugar diet 24 min after feeding (Sugar vs Fat: 88.7±4.2 vs 78.7±4.3 mg/100 mL; $P<0.05$). Plasma glucose concentration for the Starch diet was intermediate and did not differ significantly from the other diets (84.2±4.7 mg/100mL). At 60 min after feeding, plasma glucose concentration of the Sugar fed gilts had decreased and differed from both other groups (Sugar vs Starch vs Fat: 69.0±4.9 vs 77.2±7.1 vs 78.4±3.0 mg/100 mL; $P<0.05$).

The maximum glucose concentration was 92.8±4.4, 93.1±4.2, and 89.2±1.6 mg/100mL (P>0.10) for Sugar, Starch, and Fat, respectively. The AUC was similar (P>0.10) for the three diets (2,695±1,526 vs 2,059±1,679 vs 2,607±476 mg/6.2 h for Sugar, Starch, and Fat, respectively).

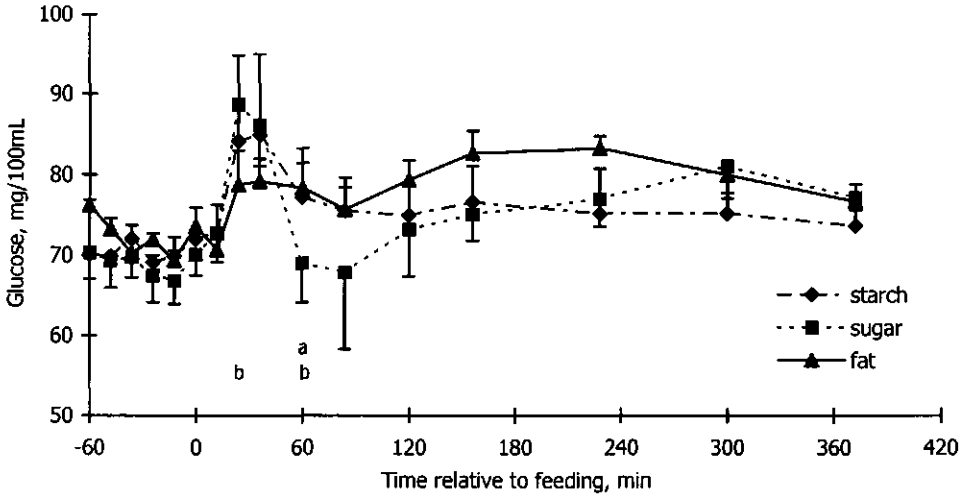

Figure 1. Plasma glucose concentrations (means±SEM) for the Starch, Sugar, and Fat groups. Means with a different character differ significantly; a = Sugar vs Starch; b = Sugar vs Fat (P<0.05).

The basal plasma insulin concentration was similar (P>0.10) for the three diets (Sugar, Starch, and Fat: 7.0±0.8, 7.1±0.6, and 7.6±0.7 μIU/mL, respectively; Figure 2). After feeding, the insulin concentration in gilts fed Starch or Sugar showed a faster increase compared to the Fat diet. This resulted in a significant (P<0.05) different plasma insulin level at 24 min after feeding (44.2±5.6 vs 39.2±10.7 vs 20.6±6.2 μIU/mL for Sugar, Starch, and Fat, respectively). At 36 min after feeding, the insulin concentration was higher (P<0.05) in the Sugar fed gilts than in gilts fed the Fat diet; the Starch group had an intermediate insulin level and did not differ from both other diets (62.0±12.2, 29.1±9.1 and 43.5±10.1 μIU/mL, respectively). Plasma insulin concentration for the Sugar diet remained at a higher level (not significant) from 120 till 372 min after feeding compared to both other diets. The maximum insulin concentrations was 65.6±5.4 and 42.2±6.4 μIU/mL (P<0.05), for Sugar and Fat, respectively. Starch was intermediate (57.7±6.3 μIU/mL) and did not differ significantly from both other groups. The AUC was greater (P<0.05) for the Sugar diet than for the Fat diet (7,078±231 vs 3,533±520 μIU/6.2 h), whereas the Starch diet was intermediate (4,915±1,039 μIU/6.2 h) and not significantly different from both other diets (P>0.10).

Analyses within diets showed no significant (P>0.10) correlation between maximum insulin and glucose. The ratio between maximum insulin and glucose concentration (I_{MAX}/G_{MAX}) was higher (P<0.05) in the Sugar and Starch diet compared to the Fat diet (70.8±5.2, 62.2±6.9, and 48.4±7.9 μIU/mg, respectively). The ratio between the insulin and glucose AUC (I_{AUC}/G_{AUC}) was 1.47±1.30, -0.71±1.60, and 2.42±0.96 μIU/mL for Sugar, Starch, and Fat, respectively (P=0.19).

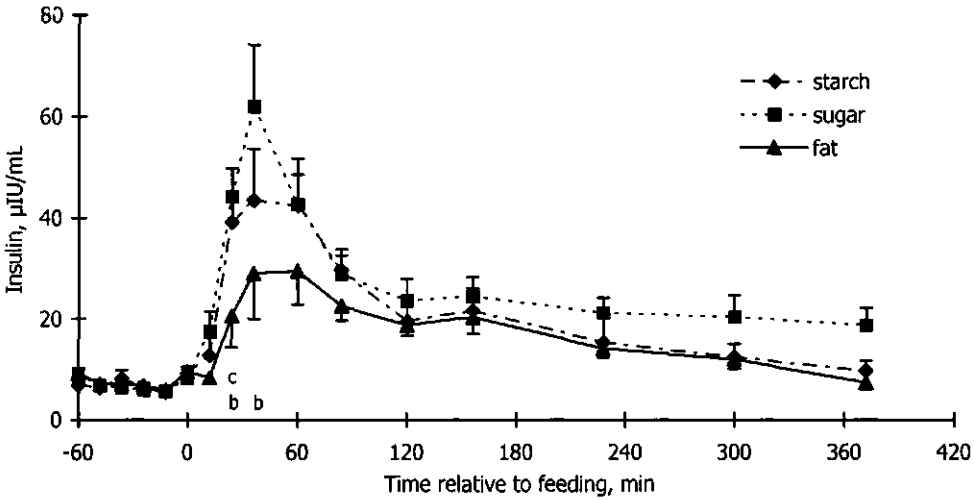

Figure 2. Plasma insulin concentrations (means±SEM) for the Starch, Sugar, and Fat groups. Means with a different character differ significantly; b = Sugar vs Fat; c = Starch vs Fat (P<0.05).

DISCUSSION

The aim of this experiment was to investigate the effects of specific dietary energy sources on the plasma glucose and insulin concentrations in gilts. A Latin square design was used for this experiment because insulin response to a diet is quite variable between animals (P<0.05).

The plasma glucose profiles differed between the three diets. The postprandial patterns of the plasma glucose concentration in this study were similar to those found by Ponter et al. (1991). A carbohydrate-rich diet (with sucrose) resulted in a higher glucose peak immediately after feeding and decreased sooner after the peak compared to a fat-rich diet. In the present study, the average glucose concentration was not different for the three diets. Newcomb et al. (1991) and Ponter et al. (1991) also found no differences in average plasma glucose concentrations in pigs fed either a carbohydrate-rich diet or a soybean-oil-rich diet. Kemp et al. (1993) found no differences in plasma glucose level in Meishan gilts fed dextrose

or soybean-oil as the major energy source. It can be concluded that, although the average glucose concentration was similar for the three energy sources, the patterns in plasma glucose concentration differed between diets.

In gilts and lactating sows, Kemp et al. (1995) found a slightly higher (not significant) postprandial insulin level in a starch-rich diet compared to a fat-rich diet. Newcomb et al. (1991) and Ponter et al. (1991) found significantly higher postprandial insulin concentrations in sows fed starch diets compared to sows fed fat diets (8.1 vs 5.0 μU/mL and 65.0 vs 31.0 mU/L per min, respectively). Ponter et al. (1991) and Kemp et al. (1995) used maize starch as the major starch source, whereas Newcomb et al. (1991) used wheat starch. As the major fat source soybean-oil was used (Newcomb et al., 1991; Kemp et al., 1995) or a combination of soybean-oil and tallow (Ponter et al., 1991).

The source of dietary starch or fat or the combination of starch and fat sources can probably explain differences in plasma insulin response between experiments. A major part of soybean-oil consists of poly-unsaturated fatty acids (C18:2 and C18:3) and tallow mostly consists of saturated and mono-unsaturated fatty acids (C18:0 and C18:1; CVB, 1989; NRC, 1994). Poly-unsaturated fatty acids were found to increase the postprandial insulin levels more than saturated fatty acids (Thomas and Williams, 1996; Thomas et al., 1997). Therefore, diets with soybean-oil probably increase insulin secretion more than diets with tallow as the major energy source, which may explain the difference in insulin response between the results of Kemp et al. (1995) and the present study. Kemp et al. (1993) found a significantly higher insulin concentration when Meishan gilts were fed with dextrose compared to soybean-oil as the major energy source. These results are in accordance with the results of the present study. In pigs, dextrose-rich diets gave a higher insulin production than starch and fat-rich diets.

The ratio between maximum concentration of plasma insulin and glucose was not significantly different for Sugar and Starch, whereas Fat was lower. Ehrensvärd et al. (1981) found a significantly ($P<0.05$) lower I_{AVG}/G_{AVG} ratio in pigs fed a fat-rich diet compared to pigs fed a fat-poor diet. Because within diets no correlation between maximum insulin and glucose was found, it can be stated that I_{MAX}/G_{MAX} is mostly affected by insulin. To maintain blood glucose homeostasis, insulin output by the pancreas will be higher in gilts fed a glucose-rich diet (Sugar and Starch) to increase glucose uptake by the target cells. Because in the calculation of the AUC is corrected for basal concentration it is possible to have negative areas for both insulin and glucose. This is the reason that the average I_{AUC}/G_{AUC} for the Starch diet is negative.

This study shows that plasma insulin levels (both postprandial peak level and long term level) as well as the ratio between insulin and glucose can significantly be affected by dietary energy source.

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Chapter 2

ENERGY BALANCE OF LACTATING PRIMIPAROUS SOWS AS AFFECTED BY FEEDING LEVEL AND DIETARY ENERGY SOURCE

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ABSTRACT

Effects of feeding level and major dietary energy source used during lactation on sow milk composition, piglet body composition, and energy balance of sows were determined. During a 21-d lactation, 48 primiparous sows were fed either a Fat-rich (134.9 g/kg fat; 196.8 g/kg starch plus sugar) or a Starch-rich (33.2 g/kg fat; 380.9 g/kg starch plus sugar) diet at either a High (44 MJ NE/d; 1050 g protein/d) or a Low (33 MJ NE/d; 790 g protein/d) feeding level. Within each feeding level, the two diets were fed to provide an isocaloric and isonitrogenous intake. At the Low feeding level, no differences in milk production, milk composition, or piglet body composition were found as a result of feeding the two dietary energy sources. However, at the High feeding level, sows fed the Fat-rich diet produced milk with higher fat (8.4 vs 6.9%) and energy (5.38 vs 4.77 kJ/g) concentrations as well as a higher piglet body fat concentration (152.1 vs 135.4 g/kg) compared with the Starch-rich diet. At the Low feeding level, the energy balance (d 6 to 20) of the sows was similar when fed either the Fat or the Starch-rich diet (-558 and -515 $kJ.kg^{-0.75}.d^{-1}$), but at the High feeding level, the energy balance was more negative in sows fed the Fat compared with the Starch-rich diet (-544 vs -372 $kJ.kg^{-0.75}.d^{-1}$). This suggests that at the High feeding level, dietary energy in the form of fat is mostly used for milk fat synthesis, resulting in fatter piglets. On the other hand, at the High feeding level, Starch as major energy source is used for growth of the piglets, as confirmed by protein deposition, and also results in a less negative energy balance for the sows. From this experiment, it can be concluded that effects of substituting maize starch for fat, in the diet of lactating sows, on milk composition, piglet body composition, and energy balance of the sows are dependent on feeding level.

INTRODUCTION

During lactation, weight loss due to fat and protein mobilization can vary considerably between sows (Mullan and Williams, 1990). Primiparous sows, in particular, are unable to consume sufficient energy and protein to meet their requirements for maintenance and milk production, resulting in a (severe) negative energy and nitrogen balance.

In order to increase energy intake during lactation, the energy density of the diet can be increased by adding fat. However, additional fat in the diet of lactating sows diet has been found to increase milk energy output by increasing the milk fat concentration (for review see Drochner, 1989). The consequences of extra milk energy output on the energy balance of lactating sows have not been well investigated. It is also not known whether the effect of dietary energy source on energy balance is dependent on feeding level during lactation.

Therefore, this study was conducted to determine the interactions between feeding level and dietary energy source on energy use by primiparous lactating sows and their piglets.

MATERIALS AND METHODS

General design

From d 3 (range 0 to 5) of lactation onwards (d 0 is farrowing), 48 (eight batches of six) first-litter Yorkshire x Dutch Landrace sows were allotted to be used in a 2 x 2 factorial experiment. Treatments were feeding level (**High**: 44 MJ NE/d; 1050 g protein/d or **Low**: 33 MJ NE/d; 790 g protein/d) and major dietary energy source (**Fat**: tallow (134.9 g/kg fat; 196.8 g/kg starch plus sugar) or **Starch**: maize starch plus dextrose (33.2 g/kg fat; 380.9 g/kg starch plus sugar)). From d 6 to 20 of lactation, energy and nitrogen balance of the sows were determined. Piglets were weaned on d 22. The experiment was conducted between autumn 1996 and spring 1997. The Institutional Animal Care and Use Committee of the Wageningen Agricultural University approved all experimental protocols.

Animals, housing, and diets

During gestation, 70 gilts were fed 2.1 kg/d of a commercial diet (CP: 135 g/kg; ileally digestible lysine: 4.1 g/kg; NE: 8.8 MJ/kg). As part of a larger experiment, these sows were surgically fitted with a permanent jugular vein catheter 8 d (range 6 to 11) before expected parturition. On d 3 (range 0 to 5) after farrowing, six sows in each batch were selected, based on patency of the catheter and body weight, paired on the basis of body weight, and allotted to one of two groups.

These two groups of three sows each were housed individually in crates (0.85 x 2.5 m) with their piglets in metabolism cages (2.5 x 1.8 m). Each group of three sows was housed in one of two identical, large, open-circuit, indirect, climatic respiration chambers (Verstegen et al., 1987). Chamber temperature was kept at 18°C and relative humidity was set at 65%. Air velocity was below 0.2 m/s. For the piglets, a wooden shelter with an electric heating lamp was used to create a microclimate. Animals were exposed to 12 h of light (0700 to 1900) and 12 h of relative darkness.

On d 3 after farrowing, litters were standardized; each sow received nine piglets. Piglets from all sows in each batch were mixed and 58 piglets were selected based on body weight. Extreme heavy and light piglets were not used. Four piglets (one of each body weight quantile) were randomly selected for analysis of body composition. Two other sows in a nearby farrowing stable nursed 2 of these piglets, together with other piglets. These extra sows were fed either the Fat or the Starch-rich diet at the same feeding level as the sows in the climatic respiration chambers. The other 54 piglets were divided into nine groups of six piglets with similar body weight. Piglets within each of these groups were randomly assigned to one of the six sows in the climatic respiration chambers.

All sows in batch 1, 3, 5, and 7 were assigned to a High feeding level (44 MJ NE/d; 1050 g protein/d), whereas sows in the other four batches got a Low feeding level (33 MJ NE/d; 790 g protein/d). Within each batch, three sows were fed the Fat-rich diet, whereas the other 3 sows got the Starch-rich diet. The three sows that were fed the same diet were housed in the same climatic respiration chamber.

Both experimental diets consisted of the same basal diet with the same amount of protein, vitamins, and minerals (Table 1). The basal diet was supplemented with either tallow (Fat: 134.9 g/kg fat; 196.8 g/kg starch plus sugar) or maize starch plus dextrose (Starch: 33.2 g/kg fat; 380.9 g/kg starch plus sugar). Diets were formulated to create a contrast in plasma insulin concentration, because insulin is associated with reproduction. Dextrose was used in the Starch diet instead of only maize starch, because dextrose increased the plasma insulin concentrations more than maize starch (Van den Brand et al., 1998). Within each feeding level, diets were fed to provide isocaloric and isonitrogenous intake, based on the calculated NE and protein content of the two diets. At the High feeding level, sows were fed 4.22 and 5.00 kg/d and at the Low feeding level 3.16 and 3.75 kg/d for the Fat and Starch-rich diets, respectively. Feeding level was linearly increased between d 1 and 8 after farrowing from 8.8 to 44 MJ NE/d and from 6.6 to 33 MJ NE/d for the High and Low feeding level, respectively. Sows were fed twice daily (0800 and 1530). No creep feed was offered to the piglets. Water was available ad libitum for sows and piglets.

On d 6 and 20, sows and piglets were weighed individually and backfat thickness of the sows was measured according to Verstegen et al. (1979). The metabolic body weight used in the calculations for the energy balance parameters was the average of the d 6 and 20 weights for both sows and piglets.

Milk composition

On d 6, 13, and 20 of lactation, milk samples (10 to 25 mL) were collected by hand from all functional nipples during three to six subsequent sucklings by removing three or four piglets. Milk was stored in polypropylene tubes at -70°C until analyses.

Dry matter content was determined gravimetically after drying 2 mL of homogenized milk in an oven at 103°C until a constant weight was reached. Quantification of the protein, fat, and lactose concentration was performed with the infrared absorption technique (Milco-Scan 605, Foss Electric, Benelux). The ash content was calculated by subtracting fat, protein, and lactose from dry matter. The energy content of the milk was calculated from the fat, protein, and lactose concentration according to Klaver et al. (1981).

Body composition of the piglets

To measure energy and nitrogen retention in the piglets, the comparative slaughter method was used. On d 6 of lactation, the four selected piglets in each batch, which were housed in the nearby stable, and on d 22 (weaning) two piglets from each litter (one of the five

heaviest; one of the four lightest, randomly) were sacrificed by embrutamid (T61, Hoechst, Brussels, Belgium). Piglets were frozen at -20°C until mincing and homogenization. Representative samples of the carcasses were analyzed per batch (d 6) or per litter (d 22).

Table 1. Composition of the experimental diets (as fed)

Ingredient	Starch, g		Fat, g	
Barley	238		238	
Wheat middlings	50		50	
Toasted soybeans	57		57	
Extracted soybeans	115		115	
Extracted sunflower seed	178		178	
Extracted rape seed	36		36	
Meat and bone meal	48		48	
Alfalfa meal	2		2	
Limestone	8.3		8.3	
Monocalcium phosphate	7.1		7.1	
Salt	2.4		2.4	
L-Lysine HCl	1.2		1.2	
DL-Methionine	1.2		1.2	
Vitamin-mineral premix[a]	17.8		17.8	
Maize starch	178		-	
Dextrose	60		-	
Tallow	-		81	
Total, g[b]	1,000		843	
Content	Calculated	Analyzed	Calculated	Analyzed
	g/1,000 g		g/843 g	
Crude protein	211.2	199.1	210.5	198.9
Crude fat	33.2	30.7	113.7	110.4
Starch	305.4	304.8	149.8	144.3
Sugar	75.5	46.2	16.1	9.9
kJ NE (for swine)[c]	8,800	--	8,800	--
Digestible lysine[d]	8.4	--	8.4	--

[a] Provided the following per kg of premix: vitamin A: 900,000 IU, vitamin D_3: 180,000 IU, vitamin E: 4,000 mg, riboflavin: 500 mg, niacin amide: 3,000 mg, d-pantothenic acid: 1,200 mg; choline chloride: 35,000 mg, vitamin B_{12}: 4 mg, vitamin K: 300 mg, vitamin C: 5,000 mg, folic acid: 100 mg, biotin: 10 mg, $CoSO_4.7H_2O$: 250 mg, $Na_2SeO_3.5H_2O$: 20 mg, KI: 50 mg, $FeSO_4.7H_2O$: 40,000 mg; $CuSO_4.5H_2O$: 8,000 mg; MnO_2: 7,000 mg, $ZnSO_4.H_2O$: 20,000 mg.

[b] 1,000 g of the Starch diet and 843 g of the Fat diet are isocaloric and isonitrogenic.

[c] According to the Centraal Veevoederbureau (CVB, 1988).

[d] Fecal digestibility (CVB, 1988).

Dry matter content was determined by drying the samples in an oven at 50°C under a vacuum of 13 kPa, using anhydrous calcium chloride as a drying agent. After 24 h, the vacuum was lowered to 1.5 kPa for another 24 h, until a constant weight was reached. Nitrogen content was analyzed in fresh samples by Kjeldahl analysis. Fat content was determined by extraction of freeze-dried samples with petroleum-ether and drying the extract at 80°C in a vacuum oven (10 kPa) to a constant weight. Ash was determined in oven-dried samples in a muffle furnace at 550°C. Glycogen was calculated by subtracting

fat, protein, and ash from dry matter. Energy content was measured in freeze-dried samples using bomb calorimetry (IKA C 7000, IKA Analysentechnik, Heitersheim, Germany).

A regression analysis showed no effect of body weight on d 6 on the body composition of the piglets. Therefore, the average body composition on d 6 was used as the initial body composition. However, on d 22, body composition was dependent on body weight. The relationship between body composition and body weight differed between the two energy sources, but was not affected by feeding level. Therefore, to estimate body composition on d 20, body composition on d 22 was corrected for body weight within each energy source. Using the corrected body composition and the body weight on d 20, the nutrient deposition in the body between d 6 and 20 could be calculated. Energy (**RE_{litter}**; MJ/d) and nitrogen (**N_{litter}**; g/d) retention of the piglets were calculated by subtracting the energy and nitrogen in the body on d 6 from that on d 20.

Energy and nitrogen balance of sows

Milk energy output (**LE**; MJ/d) was estimated with the following equation:

$$LE = ((RE_{litter}/k_g) + MEm_{litter})/0.93 \quad [1]$$

in which 0.93 represents the ME/GE ratio of the milk (CVB, 1995), whereas the maintenance energy of the litter (**MEm_{litter}**) was assumed to be 470 $kJ.BW^{-0.75}.d^{-1}$ (Campbell and Dunkin, 1983; Burlacu et al., 1985; Verstegen et al., 1985; Beyer, 1986) and k_g (efficiency of metabolizable milk energy for energy retention in the piglets) was assumed to be 0.75 (Burlacu et al., 1985; Verstegen et al., 1985, Beyer, 1986, Babinszky, 1992; Mullan et al., 1993). Milk energy output divided by the milk energy concentration resulted in the milk output per day in kg.

From d 6 onwards, energy and nitrogen balance were determined per chamber during two balance periods of 7 d each. During each balance period, feces and urine were collected quantitatively per sow and sampled for energy and nitrogen analysis. Gross energy values were determined using bomb calorimetry and nitrogen content by Kjeldahl analysis. Metabolizable energy (**ME_{tot}**; MJ/d) intake was calculated by subtracting the energy content of feces and urine from feed. To estimate metabolizable energy intake of the sow (**ME_{sow}**; MJ/d), ME_{tot} was corrected for energy in feces and urine of the piglets, which was estimated from the LE, according to the following equation:

$$ME_{sow} = ME_{tot} + 0.07 * LE \quad [2],$$

in which 0.07 accounts for the losses of energy in feces and urine of the piglets.

Within each balance period, two 48-h respiration measurement periods (d 9 and 10; d 12 and 13; d 16 and 17; d 19 and 20 of lactation) were conducted in 9-min intervals. Heat production (**HP_{tot}**; MJ/d: sows and piglets together) was determined indirectly by measuring the O_2 consumed and CO_2 and CH_4 produced, and calculated according to the formula of Brouwer (1965).

Total energy retention (**RE_{tot}**; MJ/d) of sows and piglets together was calculated by subtracting the HP_{tot} from ME_{tot}. Subtracting RE_{litter} from the RE_{tot} resulted in the energy retention of the sows (**RE_{sow}**; MJ/d). The total retention of N (**N_{tot}**; g/d) was estimated from N in feed, feces, urine, and dust as well as from aerial NH_3 and in NH_4^+ of water that condensed on the heat exchanger. To calculate the N retention of the sow (**N_{sow}**; g/d), N_{litter} was subtracted from N_{tot}. Energy retention as protein (**$RE_{p\text{-}sow}$**; MJ/d) was derived from N_{sow}, whereas energy retention as fat (**$RE_{f\text{-}sow}$**; MJ/d) was calculated by subtraction of $RE_{p\text{-}sow}$ from RE_{sow}.

Statistical analyses

Body weight and backfat loss of the sow, average milk composition, litter growth, and body composition of the piglet as well as energy and nitrogen balance of the sows were analyzed with the following model:

$$Y_{ijk} = \mu + F_i + e1_{ij} + E_k + (FxE)_{ik} + e2_{ijk},$$

where Y_{ijk} = dependent variable; μ = overall mean; F_i = feeding level (i = High, Low); $e1_{ij}$ = error term 1, which represents the random effect of $batch_j$ (j = 1 to 4) nested within feeding level; E_k = energy source (k = Fat, Starch); $(FxE)_{ik}$ = interaction between feeding level and energy source; and $e2_{ijk}$ = residual error. The effect of feeding level was tested against error term 1. The effect of energy source and the interaction between feeding level and energy source were tested against the residual error. The SAS (1990) package was used for statistical analyses.

For body weight and backfat loss of the sow, litter performance, and milk- and body composition, the sow was used as the experimental unit, whereas for energy and nitrogen balance, the chamber was used as the experimental unit. No milk samples were taken in the first batch (High feeding level); therefore, 9 experimental units remained for milk composition. Due to losses of some of the feces in one balance period, energy and nitrogen balance could not be calculated for one chamber in one batch (High Fat). Therefore, 3 experimental units remained for this treatment.

RESULTS

Milk composition

Use of the High feeding level compared with the Low feeding level resulted in a higher milk lactose concentration (5.3 vs 5.2%; SEM=0.04; P=0.05; Table 2), a lower milk protein concentration (5.2 vs 5.5%; SEM=0.04; P=0.008) and a tendency towards a lower milk ash concentration (1.2 vs 1.4%; SEM=0.05; P=0.08). Sows fed the Fat-rich diet produced milk with a higher dry matter (20.2 vs 19.0%; SEM=0.3; P=0.003), protein (5.5 vs 5.2%; SEM=0.04; P<0.001), and ash (1.4 vs 1.2%; SEM=0.1; P=0.002) concentration, and a lower

lactose concentration (5.1 vs 5.3%; SEM=0.03; P<0.001) in comparison with sows fed the Starch-rich diet

For the milk fat and energy concentration, an interaction between feeding level and dietary energy source was found. At the Low feeding level, no effect of dietary energy source was found, whereas at the High feeding level, sows fed the Fat-rich diet produced milk with a higher fat (1.5%) and energy (0.61 kJ/g) concentration than sows fed the Starch-rich diet.

The calculated daily LE and milk production were higher in sows fed the High compared with sows fed the Low feeding level (50.0 vs 42.2 MJ/d; SEM=1.2; P=0.004 and 9.8 vs 8.3 kg/d; SEM=0.3; P=0.02, respectively; Table 2). Dietary energy source did not influence LE or milk production per day.

Table 2. Milk composition and calculated milk output

Feeding level	High		Low		SEM	P-values[a]		
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source	Interaction
Number of sows	9	9	12	12				
Dry matter, %	20.3	18.5	20.1	19.5	0.4	0.18	0.003	0.12
Fat, %	8.4[a]	6.9[b]	7.6[ab]	7.8[ab]	0.3	0.77	0.04	0.02
Protein, %	5.4	5.1	5.7	5.2	0.1	0.008	<0.001	0.09
Lactose, %	5.2	5.4	5.1	5.3	0.1	0.05	<0.001	0.40
Ash, %	1.4	1.1	1.5	1.3	0.1	0.08	0.002	0.60
Energy, kJ/g	5.38[a]	4.77[b]	5.15[ab]	5.12[ab]	0.14	0.48	0.02	0.04
LE[b], MJ/d	51.2	48.8	40.8	43.8	1.7	0.004	0.86	0.14
Milk production, kg/d	9.6	9.9	8.0	8.6	0.4	0.02	0.21	0.70

[a] Statistical significance; Interaction=the feeding level x energy source interaction; Within a row, LSmeans lacking a common superscript letter differ (P<0.05).
[b] LE=milk energy output.

Growth and body composition of the piglets

Initial body weight of the piglets on d 6 was similar for all treatment groups (2.3 kg; Table 3). Average body composition of the piglets on d 6 for dry matter, ash, fat, protein, glycogen, and energy was 248.1±4.4, 28.8±0.4, 74.1±4.7, 140.2±1.5, 4.9±1.0 g/kg, and 6.30±0.19 kJ/g, respectively (mean±SE). On d 20, body weight of the piglets from sows fed the High feeding level was higher than that of piglets from sows fed the Low feeding level (5.9 vs 5.3 kg; SEM=0.2; P=0.03), due to a higher average daily gain between d 6 and 20 (258 vs 217 g/d, respectively; SEM=7; P=0.005).

Piglets of sows fed the Fat-rich diet had a higher body dry matter concentration than piglets of sows fed the Starch-rich diet (331 vs 324 g/kg; SEM=2; P=0.05). Interactions between feeding level and energy source were observed for body ash, fat, protein (all P<0.05), and energy concentration (P<0.10). At the Low feeding level, none of these

parameters differed between the piglets of sows fed the Fat or the Starch-rich diet. However, at the High feeding level, the body fat and energy concentrations in piglets of sows fed the Fat-rich diet were higher than that in piglets of sows fed the Starch-rich diet (16.7 g/kg and 0.61 kJ/g, respectively). Body ash and protein tended to be lower in piglets of sows fed the Fat-rich diet compared with those fed the Starch-rich diet (0.8 and 3.9 g/kg, respectively; $P<0.10$).

Body dry matter, protein, energy (all $P<0.05$), and ash deposition ($P<0.10$) were higher in piglets of sows fed the High feeding level than of sows fed the Low feeding level. Body ash deposition was higher and body protein deposition was lower in piglets of sows fed the Fat-rich diet compared with those fed the Starch-rich diet. Regarding the daily deposition of body fat, a tendency for an interaction between feeding level and energy source was found. Fat deposition was higher in piglets from sows fed the High Fat treatment than those fed the Low feeding level; deposition in the High Starch treatment was intermediate and not different from the other treatment groups (Table 3).

Table 3. Piglet body weight on d 6 and 20 of lactation, daily weight gain between d 6 and 20, body composition of piglets on d 22 of lactation and daily nutrient deposition per piglet between d 6 and 20

Feeding level	High		Low		SEM	P-values[a]		
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source	Inter-action
Number of sows	12	12	12	12				
BW[b] d 6, kg	2.3	2.3	2.2	2.3	0.1	0.80	0.60	0.07
BW[b] d 20, kg	5.9	5.9	5.1	5.4	0.1	0.03	0.23	0.29
Daily gain, g/d	256	261	209	224	5	0.005	0.21	0.53
Concentration								
Dry matter, g/kg	338.2	325.4	323.4	322.1	3.4	0.17	0.05	0.11
Ash, g/kg	27.1[a]	27.9[ab]	28.9[b]	28.4[b]	0.3	0.04	0.64	0.04
Fat, g/kg	152.1[a]	135.4[b]	132.8[b]	134.1[b]	3.1	0.19	0.07	0.04
Protein, g/kg	152.9	156.8	155.8	154.9	0.9	0.84	0.14	0.03
Glycogen, g/kg	6.2	5.4	5.8	4.7	0.7	0.79	0.21	0.83
Energy, kJ/g	9.69	9.08	9.00	9.01	0.12	0.14	0.07	0.06
Deposition								
Dry matter, g/d	99.7	96.5	78.0	83.5	3.7	0.003	0.75	0.24
Ash, g/d	7.7	7.0	7.0	6.2	0.2	0.08	0.005	0.85
Fat, g/d	50.1	44.6	35.6	39.2	2.5	0.008	0.69	0.08
Protein, g/d	40.9	43.5	34.8	37.2	1.2	0.02	0.05	0.94
Glycogen, g/d	1.9	1.4	1.4	0.9	0.3	0.58	0.12	0.99
Energy, kJ/d	2,969	2,793	2,245	2,439	122	0.003	0.95	0.14

[a] Statistical significance; Interaction=the feeding level x energy source interaction; Within a row, LSmeans lacking a common superscript letter differ ($P<0.05$).

[b] BW=body weight of the piglets.

Feeding level and body weight loss of sows during lactation

The calculated NE intake between d 6 and 20 of lactation was 40.5 (range 35.8 to 41.6), 39.6 (range 35.9 to 41.6), 29.9 (range 27.4 to 31.1), and 30.3 (range 26.8 to 31.2) MJ NE/d, for sows in the High Fat, High Starch, Low Fat, and Low Starch treatment group, respectively. This was respectively 97.5, 95.4, 96.1, and 97.5% of the feed offered to these sows.

Body weight loss from d 6 to 20 of lactation was higher in sows fed the Low compared with the High feeding level (12.3 vs 7.0 kg; SEM=1.0; P=0.02; Table 4), whereas sows fed the Fat-rich diet lost more weight than sows fed the Starch-rich diet (10.9 vs 8.4 kg; SEM=0.9; P=0.05). Backfat loss was not affected by treatments.

Table 4. Body weight and backfat losses of sows during lactation (d 6 to 20)

Feeding level	High		Low		SEM	P-values[a]		
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source	Inter-action
Number of sows	12	12	12	12				
BW[b] d 6, kg	158	160	156	160	2	0.81	0.22	0.66
BW[b] loss, kg	8.9	4.8	12.8	11.9	1.2	0.02	0.05	0.18
Backfat d 6, mm	15.5	16.7	15.0	15.5	0.6	0.33	0.19	0.62
Backfat loss, mm	3.2	2.6	2.8	2.8	0.3	0.89	0.28	0.23

[a] *Statistical significance; Interaction=the feeding level x energy source interaction.*
[b] BW=body weight of the sows.

Nitrogen balance of the sows

Nitrogen intake and excretion in feces and urine were higher in sows fed at the High feeding level compared with those fed at the Low feeding level (149 vs 113 g/d, SEM=2 and 95 vs 74 g/d, SEM=1, respectively; P<0.001; Table 5). The High feeding level for the sows also resulted in a higher N_{litter} than the Low feeding level (60 vs 51 g/d; SEM=2; P=0.02), whereas N_{litter} of sows fed the Starch diet was higher than that of sows fed the Fat diet (58 vs 53 g/d; SEM=0.4; P<0.001). N_{sow} was not affected by treatments.

Energy balance of the sows

Intake of GE and ME as well as HP_{tot} was higher in sows fed the High compared with the Low feeding level (Table 5). Sows fed the Starch diet had a higher ME_{sow} (1275 vs 1159 $kJ.kg^{-0.75}.d^{-1}$; SEM=27; P=0.03), HP_{tot} (1112 vs 1080 $kJ.kg^{-0.75}.d^{-1}$; SEM=8; P=0.03) and ME/GE ratio (0.81 vs 0.77; SEM=0.004; P<0.001) than sows fed the Fat diet.

An interaction between feeding level and energy source was found for the energy retention in the litter (expressed as $kJ.kg^{-0.75}{}_{sow}.d^{-1}$). This was seen as a greater increase in energy retention due to dietary fat than dietary starch as total energy increased. The calculated heat production of the sows also showed an interaction. The HP_{sow} of sows fed

the High Starch treatment was higher than that of sows in the other treatments. For both total energy and fat retention in the sow, an interaction between feeding level and energy source was observed. At the Low feeding level, no effect of energy source was observed, whereas at the High feeding level, the Fat-rich diet resulted in a more negative energy balance and fat retention than did the Starch-rich diet (172 and 159 $kJ.kg^{-0.75}_{sow}.d^{-1}$, respectively).

Table 5. Nitrogen (g/d) and energy ($kJ.BW^{-0.75}_{sow}.d^{-1}$) balance during lactation

Feeding level	High		Low		SEM	P-values[a]		
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source	Inter-action
Number of groups	3	4	4	4				
N intake[b]	147	151	112	115	4	<0.001	0.35	0.88
N excretion	97	93	75	74	3	<0.001	0.43	0.65
N_{litter}	58	63	48	54	1	0.02	<0.001	0.57
N_{sow}	-8	-5	-11	-12	2	0.12	0.54	0.29
GE intake	1691	1774	1324	1370	51	<0.001	0.27	0.73
ME intake	1218	1359	949	1045	37	<0.001	0.03	0.59
ME_{sow}	1303	1436	1016	1115	39	<0.001	0.03	0.69
HP_{tot}	1127	1166	1033	1058	11	0.04	0.03	0.52
HP_{sow}	514^{a}	615^{b}	477^{a}	502^{a}	10	<0.001	0.002	0.01
RE_{litter}	635^{a}	565^{ac}	473^{b}	503^{bc}	16	0.009	0.24	0.03
RE_{sow}	-544^{a}	-372^{b}	-558^{a}	-515^{a}	20	0.18	0.004	0.03
$RE_{p\text{-}sow}$	-28	-16	-40	-42	6	0.12	0.48	0.31
$RE_{f\text{-}sow}$	-516^{a}	-357^{b}	-519^{a}	-473^{a}	16	0.24	0.002	0.02
ME/GE	0.77	0.81	0.77	0.81	0.01	0.98	<0.001	0.50

[a] Statistical significance; Interaction=the feeding level x energy source interaction; Within a row, LSmeans lacking a common superscript letter differ ($P<0.05$); Each group consisted of 3 sows.

[b] N intake=nitrogen intake by the sow; N excretion=nitrogen excretion in feces and urine by the sow and the piglets; N_{litter}=nitrogen retention in the litter; N_{sow}=nitrogen retention in the sow; GE intake=gross energy intake by the sow; ME intake=metabolizable energy intake by the sow not corrected for fecal and urinary losses of the litter; ME_{sow}=estimated metabolizable energy intake of the sow, corrected for fecal and urinary losses of the litter; HP_{tot}=heat production of sow and litter together; HP_{sow}=estimated heat production of the sow; RE_{litter}=retained energy in the litter; RE_{sow}=retained energy in the sow; $RE_{p\text{-}sow}$=retained energy as protein in the sow; $RE_{f\text{-}sow}$=retained energy as fat in the sow; ME/GE=ratio between metabolizable and gross energy intake in the sow.

DISCUSSION

The effect of dietary nutrient supply on milk production and milk composition in the sow has been extensively described (for review see Pettigrew, 1995; Williams, 1995; Noblet et al., 1998). Williams (1995) concluded that the composition of milk is 'largely immutable' because sows mobilize their body reserves to cover the deficiencies in diets. However, several studies showed that particularly milk fat can be affected by adding fat to the diet (for review see Babinszky, 1998).

Drochner (1989) showed a linear relationship between dietary fat content and milk fat concentration. Because in the present study, the amount of dietary fat offered was higher in the Fat-rich diet, the higher milk fat concentration was expected. However, this only was found at the High feeding level. At the Low feeding level, the amount of dietary fat was also higher in the Fat-rich diet, but no difference in milk fat was found between the two diets. The energy balance of the sows also did not differ when fed either one of the two diets. It can be suggested that the surplus of dietary fat in the Fat-rich diet, when provided at the Low feeding level, was used as a energy source for maintenance and milk synthesis.

The calculated milk production was in the range found by other authors (for review see Mackenzie and Revell, 1998). The higher milk production for sows fed the High feeding level agrees with studies of Verstegen et al. (1985) and Tokach et al. (1992), but conflicts with others (Noblet and Etienne, 1986; Pluske et al., 1998). In general, it can be concluded from extensive reviews that a linear relationship between feeding level (both a higher energy and protein intake) and milk yield exists (Tokach et al., 1992; Pettigrew, 1995; Williams, 1995; Noblet et al., 1998). The effect of dietary energy source on milk output has rarely been investigated under the condition that sows are fed at a level to provide an isocaloric and isonitrogenous intake. In agreement with the present study, Lellis and Speer (1983) and Babinszky (1992) did not find differences in milk output between sows fed either a carbohydrate or a fat-rich diet, whereas Coffey et al. (1982) found a higher milk production in sows fed a fat-rich diet.

The higher milk output in sows fed at the High feeding level results in a higher nutrient deposition in the body of the piglets than when the Low feeding level was provided. This agrees with studies of Campbell and Dunkin (1983) and Noblet and Etienne (1986). In the latter study, no differences in body nutrient deposition were found between piglets of sows fed at either a high or a low feeding level, but also no difference in milk production of the sows was observed.

The difference in milk composition between the treatment groups was also observed in the piglet body composition. Using the Low feeding level, no difference in milk composition or body deposition was found between piglets of sows fed either the Fat or the Starch-rich diet. However, at the High feeding level, the Fat-rich diet resulted in a higher body fat concentration and also in a (not significant) higher energy concentration than did the Starch-rich diet. The higher milk fat concentration of sows in this treatment seems to result in more fat retained in the body of the piglets. This agrees with other studies in which the addition of fat to the maternal diet resulted in a higher body fat concentration of the piglets (Drochner, 1989). Whether the postweaning performance of piglets is influenced by the degree of body fatness at weaning needs further study.

Although piglets in the High Fat group had a not significant higher energy deposition than piglets in the High Starch group, no difference in daily gain was observed. Because 1 g of protein retention results in 5.2 g gain and 1 g of fat retention results in 1.17 g gain (Noblet and Etienne, 1987a), and protein retention was slightly higher in piglets from the High Starch treatment, the daily gain was similar for both energy sources.

The higher fat and protein deposition in the piglets of sows fed the High feeding level resulted in higher energy and nitrogen retention in the litter. The same pattern between treatment groups, as observed in the milk composition and body composition of the piglets, was found again in the energy retention in the litter.

Although the nitrogen intake of the sows at the High feeding level was higher than of sows fed the Low feeding level, no difference in nitrogen retention was found. The higher nitrogen intake by the sows fed the High feeding level was partly excreted in the feces and urine and furthermore deposited in the body of the piglets. King and Dunkin (1986b) and Noblet and Etienne (1987b) also did not observe a difference in N_{sow} during lactation between sows fed either a high or a low feeding level. However, in other studies (Verstegen et al., 1985; King and Dunkin, 1986a; Clowes et al., 1998), a positive effect of feeding level during lactation on N_{sow} was found. In the latter studies, the difference between the feeding levels was greater than in the present study.

The role of dietary energy source on the nitrogen balance of the sow has received little investigations. In agreement with the present study, Babinszky (1992) found no effect of feeding a starch or a fat-rich diet on the nitrogen balance of lactating sows. Lellis and Speer (1983) found a lower nitrogen balance in sows fed tallow during lactation than in sows fed a dextrose-rich diet. However, in the latter study, nitrogen balance in both treatment groups was strongly positive (29.0 and 23.8 g N/d for dextrose and tallow, respectively), whereas in the present study, and the study of Babinszky (1992), the nitrogen balance was negative or about zero.

The GE and ME intake of the sows as well as the HP of sows plus piglets, was higher in sows fed the High than in sows fed the Low feeding level. However, the ME intake also differed between the two energy sources, whereas the GE intake was not different. This means that the ME/GE ratio of the Fat diet is lower than that of the Starch diet, probably due to a lower digestibility (DE/GE) of the nutrients in the Fat-rich diet (Nellsen et al., 1985; Babinszky, 1992). Noblet et al. (1993) and Shi and Noblet (1993) also suggested that the addition of fat to the diet results in a lower ME/GE ratio of the total diet. This contrasts with a study of Schoenherr et al. (1989), who found a similar DE/GE and ME/GE ratio of diets with either maize starch or white grease as the major energy source.

In sows fed the Low feeding level, energy retention was similar for the two energy sources. Due to the lower ME intake of the sow and the higher milk energy output in the High Fat treatment, the energy balance of the sows was similar to the energy balance of the sows fed at the Low feeding level. Only sows fed the Starch diet at a High feeding level had a less negative energy balance. Fat, as an extra dietary energy source, did not have an added value regarding the negative energy balance of primiparous lactating sows.

From the present study, it can be suggested that dietary fat as an energy source fed at a high feeding level for lactating sows, is preferably secreted as milk fat. This results in a higher milk energy output, higher energy retention in the piglets, but also in a more negative energy balance of the sows. Starch as an energy source at a high feeding level is used for both a higher energy retention in the litter and a less negative energy balance of the sows. At a low feeding level, no effect of dietary energy source on these parameters was found.

IMPLICATIONS

The present study demonstrated that isocaloric substitution of maize starch by animal fat at a high feeding level results in a more negative energy balance for lactating sows, due to a lower ME/GE ratio of the diet and higher energy retention in the piglets. Adding fat to the diet of lactating sows does not contribute to a less negative energy balance, but resulted in fatter piglets when sows were fed at a high feeding level. Whether this has long-term effects on the carcass quality of these piglets when grown out to slaughter need to be investigated.

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Chapter 3

DIETARY ENERGY SOURCE AT TWO FEEDING LEVELS DURING LACTATION OF PRIMIPAROUS SOWS: I. EFFECTS ON GLUCOSE, INSULIN, AND LUTEINIZING HORMONE AND ON FOLLICLE DEVELOPMENT, WEANING-TO-ESTRUS INTERVAL, AND OVULATION RATE

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ABSTRACT

Our objective was to study the effects of dietary-induced insulin enhancement during and after lactation on the reproductive performance of primiparous sows. During a 21-d lactation period, 48 sows were allotted to a 2 x 2 factorial experiment. Treatments were feeding level (High or Low: 44 MJ or 33 MJ NE/d) and dietary energy source (Fat or Starch). After weaning, all sows received the same amount of feed (31 MJ NE/d from weaning to estrus and 17.5 MJ NE/d from breeding until slaughter) of the same energy source as fed during lactation. On d 7, 14, and 21 of lactation and d 22 (weaning), blood samples were taken every 12 min for 12 h and analyzed for plasma glucose, insulin, and LH. Sows were slaughtered on d 35 of the subsequent pregnancy, and ovulation rate was assessed. During lactation, postprandial plasma glucose and insulin concentrations were higher for sows fed the Starch diet than for those fed the Fat diet ($P<0.001$), whereas feeding level had no effect. Basal and mean LH concentrations were not affected by treatments. The LH pulse frequency on d 7 of lactation was greater for sows fed the Starch diet than for those fed the Fat diet (0.52 vs 0.17 pulses/12 h; $P=0.03$). The High compared with the Low feeding level resulted in a greater LH pulse frequency on d 21 of lactation (0.89 vs 0.47 pulses/12 h; $P=0.05$) and on d 22 (8.63 vs 5.77 pulses/12 h; $P=0.02$), in a higher percentage of sows that exhibited estrus within 10 d after weaning (96 vs 63%; $P=0.01$), and a tendency for a higher ovulation rate (18.0 vs 16.2; $P=0.09$). Plasma glucose and insulin concentrations were not related to any of the LH traits. The LH pulse frequency after weaning was related to the weaning-to-estrus interval (WEI) and was best explained by a linear-plateau model. In sows fed the Low feeding level, follicle size after weaning was correlated with LH pulse frequency after weaning and with the WEI, whereas in sows fed the High feeding level these correlations were not significant. Our results indicate that an improved dietary-induced insulin status during and after lactation does not overcome the inhibitory effects of lactation on subsequent reproduction at any of the feeding levels.

INTRODUCTION

Nutrition and the metabolic status of sows during lactation can affect their reproductive performance after weaning (Foxcroft, 1996; Pettigrew, 1998). The metabolic hormone insulin acts as one of the intermediates between nutrition and reproduction. In primiparous sows, insulin concentrations are correlated with LH pulsatility (Tokach et al., 1992). Exogenous insulin reduces follicle atresia in prepubertal gilts (Matamoros et al., 1991), increases ovulation rate in cyclic gilts (Cox et al., 1987), and increases farrowing rate in primiparous sows (Ramirez et al., 1997). Endogenous insulin concentrations can be affected by exogenous insulin administration (Cox et al., 1987), feeding level (Quesnel et al., 1998b) or dietary energy source (Van den Brand et al., 1998).

Dietary energy source may also affect reproductive hormones. In multiparous sows, feeding a carbohydrate-rich diet during and after lactation increased the preovulatory LH peak and progesterone concentration in comparison with feeding a fat-rich diet (Kemp et al., 1995a). In primiparous sows, effects of dietary-induced plasma insulin manipulation on reproduction have not been investigated. Whether there is an interaction between feeding level and dietary energy source in their effects on reproductive performance is also unclear.

Thus, this study was designed to investigate the effects of fat- or starch-rich diets, provided at two feeding levels during lactation, on the subsequent reproductive performance of primiparous sows.

MATERIALS AND METHODS

General design

From d 3 (range 0 to 5) of lactation onward, 48 (eight batches of six sows) first-litter Yorkshire x Dutch Landrace sows were allotted to a 2 x 2 factorial experiment. Treatments were feeding level (**High**: 44 MJ NE/d or **Low**: 33 MJ NE/d) and major dietary energy source (**Fat**: tallow or **Starch**: maize starch plus dextrose). After weaning (d 22 after farrowing), sows remained on the same diet fed during lactation, but all received the same amount of feed: 31 MJ NE/d during the weaning-to-estrus interval (**WEI**) and 17.5 MJ NE/d from breeding to slaughter on d 35 of subsequent pregnancy. The Institutional Animal Care and Use Committee of the Wageningen Agricultural University approved all experimental protocols.

Animals, diets, and housing

During gestation, 70 gilts received an increasing amount (d 0 to 60: 1.8 kg/d; d 60 to 90: 2.2 kg/d; d 90 to parturition: 2.8 kg/d) of a commercial diet (CP: 135 g/kg; ileally digestible lysine: 4.1 g/kg; crude fat: 47 g/kg; starch: 343 g/kg; sugar: 52 g/kg; NE: 8.8 MJ/kg). These gilts were surgically fitted with permanent jugular vein catheters on d 8 (range 6 to 11) before parturition, according to the method described previously by Soede et al. (1997).

On d 3 (range 0 to 5) after farrowing, 48 sows (six sows per batch) were selected, based on patency of the catheter and body weight, and allotted to one of the treatments. The six sows in each batch were paired, based on body weight, and allotted to one of two climatic respiration chambers (Verstegen et al., 1987). In these chambers, the three sows were housed individually with their piglets in metabolism cages. Each sow received nine piglets. In each batch, piglets from all sows were mixed, and 54 piglets were selected based on body weight. Extremely heavy and light piglets were not used. The selected 54 piglets were divided into nine groups of six piglets with similar body weight. Piglets within each group were randomly assigned to one of the six sows.

All six sows in each batch were assigned to one of two feeding levels (High: 44 MJ NE/d or Low: 33 MJ NE/d). Within each batch, sows in each chamber received a diet with either fat or starch as the major energy source. Both diets consisted of the same basal diet with sufficient protein, vitamins, and minerals (Table 1). To this basal diet, maize starch plus dextrose (Starch) or tallow (Fat) was added. The diets were fed to be isocaloric and isonitrogenous. Sows were fed twice daily (0800 and 1530). Water was available to sows and piglets for ad libitum consumption.

Table 1. Composition of the experimental diets (as fed)

Ingredient	Starch, g		Fat, g	
Barley	238		238	
Wheat middlings	50		50	
Toasted soybeans	57		57	
Extracted soybeans	115		115	
Extracted sunflower seed	178		178	
Extracted rape seed	36		36	
Meat and bone meal	48		48	
Alfalfa meal	2		2	
Limestone	8.3		8.3	
Monocalcium phosphate	7.1		7.1	
Salt	2.4		2.4	
L-Lysine HCl	1.2		1.2	
DL-Methionine	1.2		1.2	
Vitamin-mineral premix	17.8		17.8	
Maize starch	178		-	
Dextrose	60		-	
Tallow	-		81	
Total, g[a]	1,000		843	
Content	Calculated	Analyzed	Calculated	Analyzed
	g/1,000 g		g/843 g	
Crude protein	211.2	199.1	210.5	198.9
Crude fat	33.2	30.7	113.7	110.4
Starch	305.4	304.8	149.8	144.3
Sugar[b]	75.5	46.2	16.1	9.9
kJ NE (for swine)[c]	8,800	--	8,800	--
kJ ME (for swine)[c]	11,600	--	10,600	--
Digestible lysine[d]	8.4	--	8.4	--

[a] 1,000 g of the Starch diet and 843 g of the Fat diet are isocaloric and isonitrogenic.
[b] Difference in glucose content with or without extraction of starch in 40% alcohol.
[c] According to the Centraal Veevoederbureau (CVB, 1988).
[d] Fecal digestibility (CVB, 1988).

On the morning of weaning (d 22), sows were deprived of feed. After weaning, sows remained on the same dietary energy source as during lactation, receiving 31 MJ NE/d until the end of estrus and 17.5 MJ NE/d thereafter until slaughter.

One sow (high feeding level, fat-rich diet) did not consume any feed and was replaced on d 10 of lactation by another sow. Data for the replaced sow were not used, whereas data from the new sow were used from the moment of introduction into the experiment onwards. On d 3 of lactation and d 22, sows were weighed, and backfat was measured according to Verstegen et al. (1979). Initial body weight and backfat on d 3 were 161.9±1.4 kg and 17.7±0.3 mm, respectively (mean±SE).

Blood sampling

On d 7, 14, 21, and 22, blood samples were taken every 12 min for 12 h. Additional blood samples were taken every 4 h from 48 h after weaning until the end of standing estrus.

Blood samples were collected in ice-cooled polypropylene tubes containing 100 μL of EDTA solution (144 mg/mL saline), placed on ice, and centrifuged at 2,000 x *g* for 10 min at 4°C. Plasma was stored at -20°C until analyses. Due to lack of catheter patency, no plasma measurements were available for one sow (Low Starch) during the whole experiment and for one sow (High Starch) on d 21 and 22.

Plasma analyses

Plasma samples taken at -60, -48, -36, -24, -12, 0, 12, 24, 36, 48, 60, 84, 120, 156, 228, 300, and 372 min relative to the morning feeding on d 7, 14, and 21 of lactation were analyzed for glucose and insulin. Plasma glucose concentrations were determined spectrophotometrically in triplicate with the glucose oxidase-peroxidase anti-oxidase method using a commercial kit (GOD-PAP, Boehringer, Mannheim, Germany).

Plasma insulin concentrations were quantified in duplicate with a validated RIA (Leuvenink et al., 1997). The sensitivity was 7.3 μIU/mL at 80% of the maximal binding. The intra- and interassay CV (n=4) were 6.1 and 20.0%, respectively. Data for sows that did not consume the total amount of feed offered between two feeding times on a sampling day were not used for calculation of glucose and insulin concentrations.

All plasma samples of d 7, 14, 21, and 22 as well as 13 samples taken each 4-h around the expected LH surge were analyzed in duplicate for LH concentrations, with a homologous RIA using porcine LH-LER 778.4 (kindly donated by L.E. Reichert, Albany Medical College, NY), for iodination and standard curve, and rabbit anti-pLH (UCB A528, 1:400,000; Biogenesis Ltd, Poole, U.K.) as described previously (Dieleman and Bevers, 1987). Separation of bound and free LH was accomplished using a double-antibody solid-phase procedure (donkey anti-rabbit antibody-coated beads; SAC-Cel, IDS Ltd, Tyne & Wear, U.K.). The cross-reactivity was 2.7, 0.5, 1.1, and <0.1% for pFSH, pTSH, pLHα, and other pituitary peptides tested, respectively, according to the manufacturer. The limit of quantification for LH was 0.3 μg/L. The intra- and interassay CV (n=48) were 5.6 and 14.9%, respectively.

Follicle size, estrus, and ovulation rate

On d 2 after weaning, mean follicle size was determined with transrectal ultrasonography as described by Soede et al. (1997). From d 2 to 10 after weaning, estrus detection was performed at 8-h intervals, in the presence of a mature vasectomized boar, using the back pressure test.

Sows not expressing estrus within 10 d after weaning were assumed to be anestrous. This was confirmed using ultrasonography on d 10 after weaning. Sows that exhibited estrus were inseminated every day of standing estrus with a commercial dose of semen containing 3×10^9 sperm cells. On d 35 after the last insemination, sows were slaughtered, and their reproductive tracts were removed. The number of corpora lutea was counted on the ovaries. Data on uteri, placentas, and fetuses are published elsewhere (Van den Brand et al., 2000).

Statistical analyses

Basal glucose and basal insulin concentrations were calculated per sow per day of lactation as the mean value of the six samples taken before feeding. The area under the curve (**AUC**) from 0 to 372 min after feeding was calculated as the area above basal glucose or insulin concentrations.

Profiles of LH were analyzed by visual appraisal using conditions modified from McLeod and Craigon (1985). An elevation in plasma LH concentration was defined to be a pulse if 1) the peak level occurred within two samples of the previous nadir, 2) the increase was at least four times greater than the coefficient of variation of duplicate pairs of the assay, 3) the peak concentration was more than 0.3 ng/mL above the basal concentration (d 7, 14, 21) or more than 0.1 ng/mL above the average of the previous and subsequent nadir of the pulse (d 22), and 4) there were at least two samples between the peak and the subsequent nadir.

Data were analyzed with the GLM procedure of SAS (1990). The following model was used to analyze glucose, insulin, and LH data during lactation:

$Y_{ijklm} = \mu + F_i + e1_{ij} + E_k + (FxE)_{ik} + e2_{ijkl} + D_m + (FxD)_{im} + (ExD)_{km} + (FxExD)_{ikm} + e3_{ijklm}$,

where Y_{ijklm} = dependent variable; μ = overall mean; F_i = feeding level (i = High, Low); $e1_{ij}$ = error term 1, which represents the random effect of $batch_j$ (j = 1 to 4) nested within feeding level; E_k = energy source (k = Starch, Fat); $(FxE)_{ik}$ = interaction between feeding level and energy source; $e2_{ijkl}$ = error term 2, which represents the random effect of sow_l (l = 1 to 3) nested within batch, feeding level, and energy source; D_m = day of lactation (m = 7, 14, 21); $(FxD)_{im}$ = interaction between feeding level and day; $(ExD)_{km}$ = interaction between energy source and day; $(FxExD)_{ikm}$ = interaction between feeding level, energy source, and day; and $e3_{ijklm}$ = residual error. The effect of feeding level was tested against error term 1. Effect of energy source and the interaction between feeding level and energy source were tested against error term 2. Day effect and the interactions with day were tested against the residual error. When day was significant, variables were tested again per day with the same model, except that effect of day and its interactions were excluded from the model.

The LH traits on the day of weaning, follicle diameter, WEI, preovulatory LH peak, ovulation rate, and duration of estrus were also tested with the latter model. The percentage of sows that came into estrus within 10 d was tested with the Fisher exact test (SAS, 1990).

Relationships between basal, average, or maximum plasma glucose, insulin, and LH, follicle size after weaning, WEI, duration of estrus, and ovulation rate (only for sows with WEI<240 h) were analyzed by introduction of the variables into the GLM procedure as a covariate. When the interaction between the covariate and one of the treatments was

significant (P<0.10), regressions were calculated per treatment. When these interactions were not significant (P>0.10), simple overall correlations were performed.

To analyze the overall effects of WEI or LH classes after weaning on LH characteristics during lactation and on reproductive traits, a GLM procedure was used, with only WEI or LH class as class variable. All data are presented as LSmeans±SEM.

RESULTS

Feed intake, body weight loss, and backfat loss during lactation.

On d 7 of lactation, two High Fat, five High Starch, one Low Fat and on d 14 one sow (Low Fat) did not consume the total allotment of feed. The actual feed intake during lactation was 40.5 (range: 35.8 to 41.6), 39.6 (35.9 to 41.6), 29.9 (27.4 to 31.1), and 30.3 (26.8 to 31.2) MJ NE/d for High Fat, High Starch, Low Fat, and Low Starch, respectively. Energy intake differed (P<0.001) between feeding levels, but it was not different between the Fat- and the Starch-rich diet. Body weight loss during lactation was greater in sows fed the Low feeding level than in those fed the High feeding level (22.4 vs 14.0 kg respectively; SEM=1.2; P=0.003) but was not affected by dietary energy source (19.4 vs 17.0 kg for Fat and Starch, respectively; SEM=1.2; P=0.16). Backfat loss during lactation was not affected by treatments (3.2, 2.6, 2.8, and 2.8 mm for High Fat, High Starch, Low Fat, and Low Starch, respectively; SEM=0.3). Weaning weight of the piglets (d 22) was 6.3, 6.4, 5.5, and 5.8 kg for High Fat, High Starch, Low Fat, and Low Starch, respectively (SEM=0.1) and differed between the two feeding levels (P=0.03).

Plasma glucose and insulin during lactation

During each day of lactation, sows fed the Starch diet had a higher plasma glucose concentration (P<0.05) from 24 to 300 min post prandial (Figure 1) than sows fed the Fat diet, resulting in a higher overall mean glucose concentration (82.6 vs 73.9 mg/dL; SEM=1.3; P<0.001) and greater AUC (10.9 vs 4.2 g/6.2 h; SEM=0.6; P<0.001; Table 2). Basal glucose concentration was lower in the Starch diet than in the Fat diet (57.7 vs 64.8 mg/dL, respectively; SEM=1.3; P<0.001). Feeding level did not affect plasma glucose concentration at any sampling time.

Similar to the plasma glucose concentration, the plasma insulin concentration during all sampling days of lactation was higher from 24 to 300 min postprandial in sows fed the Starch diet than in those fed the Fat diet (Figure 2). Overall, mean insulin concentrations (18.2 vs 15.2 μIU/mL; SEM=0.5; P<0.001; Table 2) and the AUC (4.6 vs 3.0 mIU/6.2 h; SEM=0.2; P<0.001) were greater for sows fed the Starch diet than for those fed the Fat diet. Basal insulin concentration was not affected by dietary energy source (P=0.22), and none of the insulin traits were affected by feeding level.

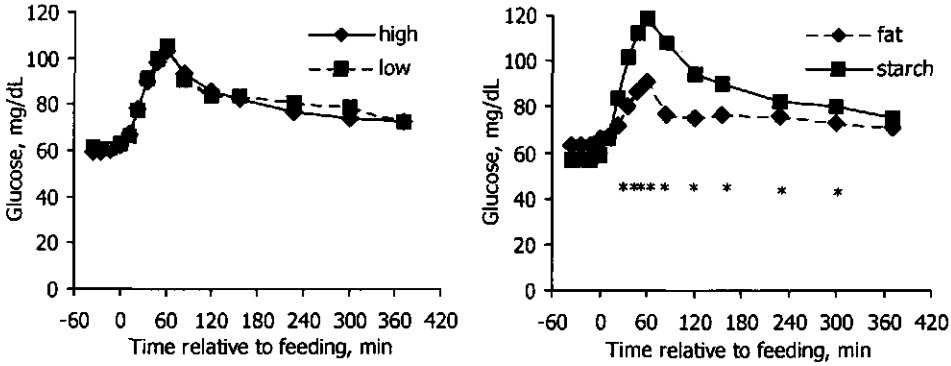

Figure 1. Average plasma glucose concentrations during lactation per feeding level (left panel) or energy source (right panel) (SEM=1.5; *=P<0.05 for Fat vs Starch).

Table 2. Average plasma glucose and insulin characteristics during lactation (d 7, 14, and 21)

Feeding level	High		Low		SEM	P-value[a]		
Energy source	Fat	Starch	Fat	Starch		Feeding Level	Energy Source	Day
Number of sows	12	11	12	11				
Glucose								
Basal, mg/dL	63.7	57.7	65.9	57.8	1.9	0.84	<0.001	<0.001
Mean, mg/dL[b]	73.0	82.5	74.7	82.7	1.9	0.80	<0.001	<0.001
AUC, g/6.2 h[ce]	4.2	10.5	4.1	11.4	0.8	0.74	<0.001	<0.001
Insulin								
Basal, μIU/mL	8.0	8.3	9.1	7.2	0.7	0.99	0.22	<0.001
Mean, μIU/mL[d]	15.3	19.1	15.1	17.2	0.8	0.39	<0.001	<0.001
AUC, mIU/6.2 h[e]	3.3	4.8	2.7	4.4	0.2	0.32	<0.001	0.12

[a] Statistical significance; the feeding level x energy source interactions were not significant.
[b] Feeding level x energy source x day of lactation interaction (P=0.03).
[c] Feeding level x day of lactation interaction (P=0.07).
[d] Feeding level x day of lactation interaction (P<0.001).
[e] AUC=area under the curve.

LH pulsatility during and after lactation

Feeding level, energy source, and day of lactation did not influence basal and mean LH concentrations (Table 3). However, the number of LH pulses on d 7 was higher in sows fed the Starch diet than in those fed the Fat diet (0.52 vs 0.17 pulses/12 h, respectively; SEM=0.11; P=0.03). On d 14, the number of LH pulses did not differ between the treatments. On d 21, the High feeding level resulted in a higher LH pulse frequency than the Low feeding level (0.89 vs 0.47 pulses/12 h, respectively; SEM=0.12; P=0.05). The effects of energy source were not significant. On the day of weaning, feeding level had a significant effect on LH pulse frequency (8.63 vs 5.77 pulses/12 h for High and Low feeding level, respectively; SEM=0.59; P=0.02). Basal and mean LH concentration and LH pulse amplitude on the day of weaning were not affected by treatments.

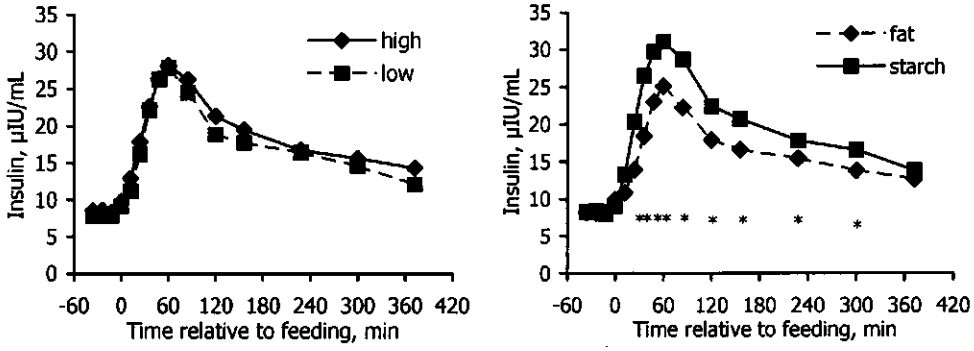

Figure 2. Average plasma insulin concentrations during lactation per feeding level (left panel) or energy source (right panel) (SEM=0.5; *=P<0.05 for Fat vs Starch).

Table 3. Plasma LH characteristics during lactation (d 7, 14, and 21) and on the day of weaning (d 22)

Feeding level	Day	High		Low		SEM	P-value[a]		
Energy source		Fat	Starch	Fat	Starch		Feeding Level	Energy Source	Day
Number of sows		12	11	12	11				
Basal, ng/mL	7	0.44	0.59	0.43	0.47				
	14	0.42	0.54	0.39	0.42	0.03	0.55	0.32	0.11
	21	0.41	0.53	0.45	0.44				
	22	0.44	0.47	0.45	0.48	0.07	0.61	0.86	--
Mean, ng/mL	7	0.45	0.62	0.43	0.50				
	14	0.45	0.58	0.40	0.44	0.03	0.47	0.24	0.13
	21	0.43	0.57	0.47	0.45				
	22	0.69	0.66	0.69	0.62	0.08	0.40	0.78	--
LH pulses/12 h	7	0.26	0.58	0.08	0.46				
	14	0.67	1.17	0.25	0.55	0.20	0.04	0.06	0.04
	21	0.67	1.06	0.58	0.37				
	22	8.33	8.92	5.25	6.29	0.79	0.02	0.31	--
Pulse amplitude ng/mL[b]	7	1.75	1.31	0.63	0.76				
	14	0.67	0.58	0.91	0.58	0.18	0.05	0.62	0.24
	21	0.65	0.84	0.78	0.89				
	22	0.27	0.45	0.35	0.28	0.07	0.46	0.54	--

[a] Statistical significance; the feeding level x energy source interactions were not significant.
[b] Feeding level x day of lactation interaction (P=0.04).

Follicle development, WEI, duration of estrus, and ovulation rate

Mean follicle diameter of all sows on d 2 after weaning was higher in sows fed the High feeding level than in those fed the Low feeding level (3.8 vs 3.0 mm, respectively; SEM=0.2; P=0.02; Table 4). Of the sows fed the Low feeding level during lactation, only 15 of 24 (63%) came into estrus within 10 d after weaning, compared with 23 of 24 (96%) sows fed the High feeding level (P=0.01). In the sows that expressed estrus within 10 d after weaning, neither WEI nor the preovulatory LH surge was affected by treatments (P>0.10).

In these sows, follicle diameter on d 2 after weaning was not affected by feeding level during lactation (P=0.12) but tended to be larger in sows fed the Starch diet than in sows fed the Fat diet (3.8 vs 3.1 mm, respectively; SEM=0.2; P=0.06).

Ovulation rate tended to be higher in sows fed the High feeding level than in those fed the Low feeding level (18.0 vs 16.2; SEM=0.6; P=0.09). Duration of estrus was longer in sows fed the Starch diet than in sows fed the Fat diet (54 vs 47 h, respectively; SEM=2; P=0.02).

Table 4. Mean postweaning reproductive traits

Feeding level	High		Low		SEM	P-value[a]	
Energy source	Fat	Starch	Fat	Starch		Feeding Level	Energy Source
All sows, n	12	12	12	12			
Follicle size d 2, mm	3.6	4.0	3.0	3.0	0.3	0.02	0.33
Sows with WEI<240 h, n	12	11	7	8	--	0.01	1.00
Follicle size d 2, mm	3.6	4.1	2.6	3.5	0.4	0.12	0.06
WEI[b], h	123	122	152	130	9	0.14	0.20
Duration of estrus, h	48	54	45	55	3	0.78	0.02
LH surge, ng/mL	4.41	4.66	4.12	4.69	0.59	0.84	0.48
Ovulation rate, n	17.9	18.2	15.5	16.9	1.2	0.09	0.50

[a] Statistical significance; the feeding level x energy source interactions were not significant.
[b] WEI=weaning-to-estrus interval.

Anestrous sows

After weaning, 10 sows remained anestrous. In these sows, LH pulse frequency after weaning was on average 5.2 (range 0 to 11 pulses/12 h), and follicle size on d 2 after weaning was on average 3.0 mm (range 1.5 to 4.0 mm).

Relationships among traits

Glucose and insulin. Glucose and insulin traits (basal, mean, or maximum) were not correlated with any of the LH traits (basal, mean, or number of pulses) during lactation and after weaning or with WEI.

LH, WEI, and follicle size. Regardless of treatment, the WEI was correlated with LH pulse frequency on d 14 (WEI (h) = 138 − 11 x number of LH pulses/12 h on d 14; r=-0.40; P=0.01) and d 21 (WEI (h) = 139 − 14 x number of LH pulses/12 h on d 21; r=-0.38; P=0.02) of lactation. The WEI was also highly correlated with the LH pulse frequency after weaning, regardless of treatments. A linear-plateau model best explained this relationship. No significant differences between treatments were observed for the slope, the break point, or the threshold. The overall relationship was as follows:

$WEI = 117(\pm 4) + (1+e^{(-16.7(\pm 3.3)*(7.3(\pm 0.5)-\text{LH pulses}))})$; ($R^2$=0.63; Figure 3).

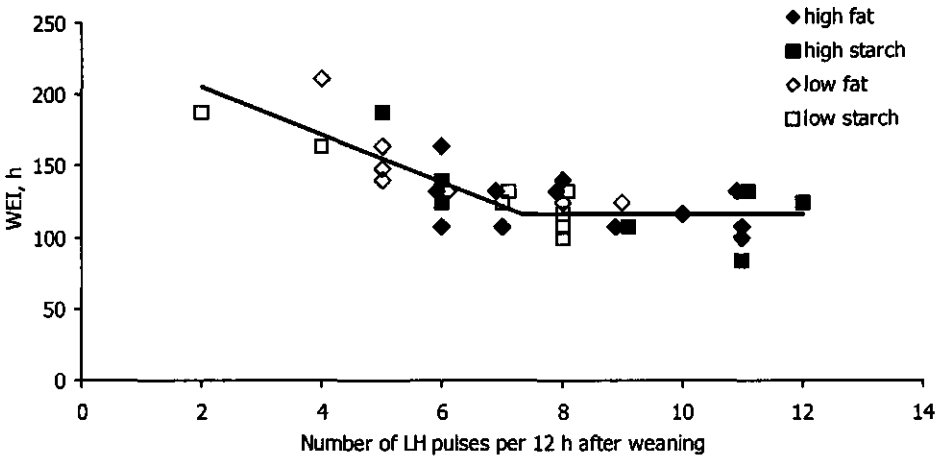

Figure 3. Overall relationship between LH pulse frequency after weaning and the weaning-to-estrus interval: WEI = $117(\pm4)+(1+e^{(-16.7(\pm3.3)*(7.3(\pm0.5)-\text{LH pulses}))})$; R^2=0.63 (WEI<240 h).

In Table 5, LH pulse frequency after weaning is divided into two classes (seven or fewer and eight or more pulses/12 h, before or after the break point, based on Figure 3), regardless of treatments. Plasma glucose and insulin traits were not different between the two classes. Basal and mean LH concentrations during lactation were higher in sows with eight or more LH pulses during 12 h after weaning. Eight or more LH pulses after weaning also was related to a larger follicle size on d 2 after weaning, a higher preovulatory LH surge, a shorter WEI, and a shorter duration of estrus, compared with sows with seven or fewer LH pulses. When the class with more than eight pulses/12 h was subdivided into a class with eight or nine pulses/12 h (n=9) and a class with 10 to 12 pulses (n=10), no significant differences were observed between these two classes for any of the traits.

Table 5. Average LH characteristics during lactation (d 7, 14, and 21) and postweaning reproductive performance as related to LH pulse frequency after weaning (WEI<240 h)

LH pulses/12 h	≤ 7	≥ 8	SEM	P-value[a]
Number of sows	18	19		
Sows fed the High feeding level, n	8	13		
LH basal, ng/mL	0.40	0.47	0.02	0.03
mean, ng/mL	0.42	0.50	0.02	0.01
number of pulses/12 h	0.47	0.72	0.11	0.11
WEI[b], h	147	115	5	<0.001
Follicle size d 2, mm	2.90	4.05	0.22	<0.001
LH surge, ng/mL	4.05	5.10	0.36	0.05
Ovulation rate, n	16.7	17.8	0.8	0.34
Duration of estrus, h	55	47	2	0.02

[a] Statistical significance.
[b] WEI=weaning-to-estrus interval.

In sows fed the High feeding level, follicle size on d 2 after weaning was not related to LH pulse frequency after weaning, whereas for sows fed the Low feeding level, a positive correlation was found (follicle size (mm) = 1.4 + 0.2 x number of LH pulses/12 h after weaning; r=0.57; P=0.005). In the sows fed the High feeding level during lactation, WEI was not related to follicle size on d 2 after weaning, whereas for sows fed the Low feeding level, a strong negative correlation was found (WEI (h) = 193 – 22 x follicle size at d 2 after weaning (mm); r=-0.66; P=0.007). In Table 6, the WEI is a priori divided into four classes, based on the number of sows per class, regardless of treatments. The LH pulse frequency during lactation and after weaning, follicle size, and ovulation rate were decreased (P<0.10) with prolonged WEI. Basal and mean LH concentration also showed a slight decrease with prolonged WEI.

Table 6. Characteristics of LH and postweaning reproductive performance as related to weaning-to-estrus interval (WEI) class

WEI, h	≤ 116	124-132	140-240	> 240	SEM	P-value
Number of sows	14	14	10	10		
Sows fed the High feeding level, n	11	8	4	1		
Basal LH, ng/mL, lactation	0.48	0.43	0.39	0.37	0.05	0.37
after weaning	0.47	0.48	0.41	0.44	0.06	0.87
Mean LH, ng/mL, lactation	0.51	0.46	0.40	0.39	0.05	0.20
after weaning	0.74	0.68	0.55	0.64	0.07	0.33
LH pulses/12 h, lactation	0.87[a]	0.62[ab]	0.23[b]	0.41[ab]	0.15	0.02
after weaning	8.91[a]	8.15[a]	5.00[b]	5.22[b]	0.73	<0.001
Follicle size d 2, mm	4.0[a]	3.5[ab]	2.7[b]	2.9[b]	0.3	0.005
LH surge, ng/mL	5.21	3.98	4.60	--	0.44	0.13
Ovulation rate, n	18.2	18.1	15.3	--	0.9	0.06
Duration of estrus, h	51	49	54	--	3	0.44

[a,b] Within a row, LSmeans lacking a common superscript letter differ (P<0.05).

DISCUSSION

The present study showed that dietary energy source significantly affected plasma glucose and insulin concentration in lactating sows. In anabolic, cyclic gilts (Van den Brand et al., 1998), and even in sows in a catabolic state the Starch-rich diet could enhance plasma insulin concentration during 4.5 h after feeding. In contrast with the results of Koketsu et al. (1996, 1998) and Quesnel et al. (1998b), feeding level did not affect plasma glucose or insulin concentration. In those studies, the low feeding level was approximately 50% of the high feeding level, whereas in the present study feeding level differed only 25% between High and Low.

On d 7 of lactation, a positive effect of the Starch diet on LH pulse frequency was observed, irrespective of feeding level, whereas on d 21 of lactation, and after weaning, the High feeding level resulted in a higher LH pulse frequency. Because the effect of energy source was absent on d 14 and 21, whereas on d 21 a positive effect on LH pulsatility at the High feeding level was observed, the effect of feeding level on LH pulse frequency seems to become stronger during lactation and to override the effect of dietary energy source. Whether a stronger contrast in diet composition should result in more pronounced effects on LH pulsatility is disputable. For example, addition of more fat to the diet can result in less acceptability (digestibility) or a lack in sufficient glucose for maintenance and milk production, resulting in excessive weight loss and a severe depression of LH secretion.

In a comparable experiment with multiparous lactating sows, Kemp et al. (1995a) found similar results in LH pulse frequency during lactation. The more negative energy balance with progressing lactation, due to an increase in milk production with a similar feed intake, could be the reason that no effect of dietary energy source on LH pulsatility at the end of lactation was found. An increased body weight loss (negative energy balance) during lactation is associated with a lower LH pulse frequency on d 21 of lactation (Kemp et al., 1995b).

In sows fed the Low feeding level, a lower LH pulse frequency after weaning was found compared with the High feeding level, which is in accordance with Koketsu et al. (1996) and Zak et al. (1997a, 1998). The more negative energy balance during (a part of) lactation, independent of energy source, seems to depress the generation of an effective LH signal by the hypothalamus-pituitary axis during and after lactation, which was also suggested by Baidoo et al. (1992) and Tokach et al. (1992).

The percentage of sows that exhibited estrus within 10 d after weaning was higher in sows fed the High feeding level than in those fed the Low feeding level, irrespective of energy source. Prunier et al. (1993) and Caroll et al. (1996) found similar results. Furthermore, in sows expressing estrus within 10 d, the WEI was not affected by treatments, probably due to the low number of observations that remained in the Low feeding level.

The lower ovulation rate in sows fed the Low feeding level during lactation agrees with a study of Zak et al. (1997a) but contrasts with others (Quesnel and Prunier, 1998; Zak et al., 1998). When all sows were considered, follicle size after weaning was higher in sows fed the High feeding level. This effect was absent when only the sows that came into estrus within 10 d were taken into account.

In sows that remained anestrous, LH pulse frequency after weaning and follicle size on d 2 after weaning was not strongly different from those in sows that exhibited estrus. This suggests that in addition to LH pulse frequency and follicle size, other factors, such as follicle heterogeneity, may be involved in estrus exhibition.

A lower LH pulse frequency after weaning is associated with a prolonged WEI (Shaw and Foxcroft, 1985). In the present study, a threshold seemed to be present in the relationship between the number of LH pulses after weaning and the WEI. To our knowledge this is the first study that indicates a linear-plateau model for the relationship between LH pulsatility after weaning and WEI.

A prolonged WEI was also associated with a slight decrease in basal and mean LH concentration and a significant decrease in LH pulse frequency during lactation. Tokach et al. (1992) found a higher mean LH concentration and LH pulse frequency on d 14, 21, and 28 of lactation in sows with a short WEI (<9 d) compared with sows with a longer WEI (>15 d). This means that, even during lactation, LH pulse frequency is related to the WEI and(or) that a higher LH pulse frequency after weaning represents a restored hypothalamus-pituitary system that can function immediately after weaning. Paterson and Pearce (1994) did not find any relationship between LH during lactation and WEI. However, in their study, a WEI of less than 14 d was assumed to be short. In the present study, sows with a WEI longer than 10 d were assumed to be anestrous.

The relationship between LH pulse frequency after weaning and follicle size on d 2 postweaning and also between follicle size and WEI was found only in sows fed the Low feeding level. This suggests that follicle development in sows fed the High feeding level was less dependent on LH pulsatility after weaning and improved compared with the Low feeding level, possibly resulting in a higher ovulation rate for sows fed the High feeding level (Zak et al., 1997a). At the Low feeding level, follicle development on d 2 after weaning seemed to be partially a result of the increased LH pulsatility after weaning. In studies of Zak et al. (1997b) and Quesnel et al. (1998a), a reduction in feed intake during (a part of) lactation resulted in an impaired follicle development. Because growth of small follicles is independent on LH (Driancourt et al., 1995), other factors, such as insulin and IGF-1 (Quesnel et al., 1998a) seem to be involved in the early follicle development. The increased insulin status of the sows fed the Starch diet may partially explain the larger follicles on d 2 postweaning of these sows compared with sows fed the Fat diet.

In contrast with Tokach et al. (1992) and Koketsu et al. (1996), but in agreement with Paterson and Pearce (1994), insulin concentration during lactation was not correlated with LH pulsatility. Also, Quesnel et al. (1998b) did not find strong correlations between insulin and LH. Due to these ambiguous results, it can be suggested that insulin is not the most important intermediate between nutrition and LH pulsatility. Other factors, such as IGF-1, possibly can be more important for regulating the effects of nutrition on reproduction.

IMPLICATIONS

Improved dietary-induced insulin status during and after lactation does not seem to overcome the inhibitory effect of lactation on subsequent reproduction, irrespective of feeding level.

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Chapter 4

DIETARY ENERGY SOURCE AT TWO FEEDING LEVELS DURING LACTATION OF PRIMIPAROUS SOWS: II. EFFECTS ON PERIESTRUS HORMONE PROFILES AND EMBRYONAL SURVIVAL

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ABSTRACT

Our objective was to study the effects of dietary energy source (Fat or Starch) on periestrus hormone profiles and embryonal survival in primiparous sows. During lactation, 48 primiparous sows were fed either a Starch-rich or a Fat-rich diet, at either a High (44 MJ NE/d) or a Low (33 MJ NE/d) feeding level. After weaning, all sows received the same amount of feed (31 MJ NE/d from weaning to estrus and 17.5 MJ NE/d from breeding to slaughter) of the same dietary energy source fed during lactation. Around estrus, blood samples were taken to analyze the preovulatory LH surge, estradiol (E_2), and progesterone (P_4) concentrations. Sows were inseminated on each day of standing estrus. On d 35 after last insemination, all 35 pregnant sows were slaughtered and their reproductive tracts were removed. The number, weight, and length of the embryos and placentas were determined as well as the weight and length of the uterus. The LH, E_2, and P_4 profiles were similar for the treatment groups, except for the E_2 levels at 16, 12, and 8 h before the LH surge, which were lower in the sows fed the Fat-rich diet at the Low feeding level. Ovulation rate tended to be higher in sows fed the High compared to the Low feeding level during lactation (18.0 vs 16.2; P=0.09), but the number of total and viable embryos as well as embryonal survival rate were not influenced by the treatments. Neither uterine length and weight nor length and weight of the embryos and placentas were affected by treatments. However, after removal of the embryo-placental units, uterine weight was greater in sows fed the High than in those fed the Low feeding level during lactation (1.8 vs 1.6 kg; P=0.03). Plasma insulin concentration during lactation was not related to any of the uterine, placental, or embryo traits. Mean progesterone concentration between 24 and 250 h after the LH surge was positively correlated with embryonal survival. Differences in progesterone concentration between sows with high and low embryonal survival were evident from 172 h after the LH surge. From the present study, it can be concluded that altering feeding level during lactation or dietary energy source from farrowing until d 35 of subsequent pregnancy did not affect embryonic development and embryonal survival.

INTRODUCTION

In addition to a range of environmental, genetic, hormonal, and biochemical factors, maternal nutrition can influence embryonic development and embryonal survival (Ashworth and Pickard, 1998). The specific nutrients (Ashworth, 1994) and plane of nutrition (Foxcroft, 1997) during different stages of the reproductive cycle can affect embryonic development and embryonal survival. In primiparous sows, a low feeding level during lactation is associated with an increased embryonal mortality (Kirkwood et al., 1990; Baidoo et al., 1992; Zak et al., 1997a), possibly due to impaired ovarian follicle development in restricted-fed sows (Zak et al., 1997b; Quesnel et al., 1998).

An intermediate between nutrition and follicle development could be the metabolic hormone insulin (see Pettigrew and Tokach, 1993 for review). Insulin is correlated with LH pulsatility (Tokach et al., 1992), and insulin (Matamoros et al., 1991) and LH (Driancourt et al., 1995) seem important for follicle development. Furthermore, Kemp et al. (1995) found a higher LH surge and higher progesterone concentrations in sows fed a carbohydrate-rich diet (more insulin stimulation) than in sows fed a fat-rich diet (less insulin stimulation). A higher

progesterone concentration is associated with an increase in embryonal survival (Ashworth, 1991; Jindal et al., 1996). Therefore, insulin could be an intermediate between nutrition and embryonic development and embryonal survival.

To investigate whether insulin-stimulating diets, fed during a longer period (lactation, weaning-to-estrus interval, and subsequent pregnancy) can affect embryonic development and embryonal survival, an experiment with primiparous sows was conducted.

MATERIALS AND METHODS

General design

From d 3 (range 0 to 5) of lactation, primiparous Yorkshire x Dutch Landrace sows (eight batches of six sows) were allotted to a 2 x 2 factorial experiment. Treatments were feeding level during lactation (**High**: 44 MJ NE/d or **Low**: 33 MJ NE/d) and major dietary energy source (**Fat** or **Starch**) fed during the entire experiment. Each batch was assigned to one of the two feeding levels alternatively, and, within all batches, sows received either the Starch or the Fat diet. The Starch and Fat diets consisted of a basal diet, to which either tallow (Fat) or maize starch plus dextrose (Starch) was added. Within each feeding level, both diets were fed to be isocaloric and isonitrogenous. After weaning on d 22 after farrowing, all sows were fed the same diet as during lactation, but all sows received the same amount of feed (31 MJ NE/d during the weaning-to-estrus interval (**WEI**) and 17.5 MJ NE/d from breeding to slaughter).

For frequent blood sampling, all sows were surgically fitted with a permanent jugular vein catheter on d 8 (range 6 to 11) before parturition as described previously (Soede et al., 1997). On d 2 after weaning, ovarian follicles were measured with ultrasonography as described by Soede et al. (1997).

Thirty-eight sows that exhibited estrus within 10 d after weaning were inseminated with a commercial dose of semen (3×10^9 sperm cells) on each day of estrus. A full description of animal management and diet compositions has been reported elsewhere (Van den Brand et al., 2000).

Blood sampling

From 48 h after weaning, blood samples were collected at 4-h intervals until 24 h after the end of estrus. Thereafter, blood samples were taken each 12 h for 9 d. Blood samples were collected in ice-cooled polypropylene tubes containing 100 µL of EDTA solution (144 mg/mL saline), placed on ice immediately after collection, and centrifuged at 2,000 x *g* for 10 min at 4°C. Plasma was stored at -20°C until analyses. Due to the lack of catheter patency in two sows (High Starch and Low Starch), no hormone data were available for these sows.

Plasma analyses

Thirteen samples taken each 4 h around the expected LH surge were analyzed with a RIA for LH concentrations, as described elsewhere (Van den Brand et al., 2000).

Concentrations of estradiol were analyzed in duplicate with a RIA, in samples taken each 8-h from 76 to 36 h before the LH surge and in samples taken each 4 h from 36 h before to 36 h after the LH surge, as described previously (Van de Wiel et al., 1981). The interassay CV (n=21) was 10.9% at 3.2 pg/mL, and the intraassay CV was 4.5% at 8.9 pg/mL.

Plasma progesterone concentrations were measured in duplicate with a RIA in samples taken from 24 to 52 h after the LH surge in 4-h intervals and from 52 to 250 h after the LH surge in 12-h intervals, as described previously by Soede et al. (1997). The intra- and interassay CV (n=19) were 7.1 and 11.6%, respectively, at 4.3 ng/mL.

Uteri, placentas, and embryos

On d 35 after the last insemination, all pregnant sows were slaughtered, and their reproductive tracts were removed. Uterine horns were separated from the mesometrium and opened at the antimesometrial side. Samples of allantoic and amniotic fluid were taken, and embryos were separated from their placentas. Each fetus was classified as viable or nonviable, which was based on the presence of strongly hemolyzed amniotic fluid and(or) resorbed fetal membranes. Embryonal survival was calculated and defined as the number of viable embryos divided by the number of corpora lutea. Individual fetal weights and crown-rump lengths were determined. After removal from the endometrium, individual placentas were weighed, and their functional length between the necrotic tips was measured. Weight of the uterine horns, after removal of the embryo-placental units, was measured. The length of the uterine horns was measured on a wet surface. One sow (High Starch) aborted on d 35 of gestation, just before slaughter. From this sow, the number, weight, and length of the embryos, embryonal survival rate, and placenta characteristics were not available. The number of corpora lutea, luteal weight, uterus weight, and progesterone concentrations were still available.

Glucose concentrations in the allantoic and amniotic fluid were determined spectrophotometrically with the glucose oxidase-peroxidase anti-oxidase method using a validated commercial kit (GOD-PAP, Boehringer, Mannheim, Germany).

Statistical analyses

Profiles of the LH surge, estradiol, and progesterone only concern sows that came into estrus within 10 d after weaning. Embryo and placental measures were averaged per sow and used in the statistical analyses.

All data were analyzed with the GLM procedure of SAS (1990) using the following model:

$$Y_{ijk} = \mu + F_i + e1_{ij} + E_k + (FxE)_{ik} + e2_{ijk},$$

where Y_{ijk} = dependent variable; μ = overall mean; F_i = feeding level (i = High, Low); $e1_{ij}$ = error term 1, which represented the random effect of $batch_j$ (j = 1 to 4) nested within feeding level; E_k = energy source (k = Fat, Starch); $(FxE)_{ik}$ = feeding level x energy source interaction; and $e2_{ijk}$ = residual error. Effect of feeding level was tested against error term 1. Effect of energy source and the feeding level x energy source interaction were tested against error term 2.

To analyze the relationships between periestrus hormone concentrations and uterine, placental, and embryonic traits, variables were introduced into the GLM procedure as a covariate and tested against error term 2. When the interaction between the covariate and one of the treatments was significant ($P<0.10$), relationships were calculated per treatment. When these interactions were not significant, simple overall correlations were performed. In the results, only significant relationships are described.

To analyze the overall effects of embryonal survival on progesterone profiles, sows were divided into two classes, regardless of treatments: above- and below-average embryonal survival of the pregnant sows on d 35 of pregnancy (69.1%). These two classes were used in a GLM procedure with only embryonal survival as class variable. All data are presented as LSmeans±SEM.

The percentage of sows that exhibited estrus within 10 d after weaning and the percentage of sows that were pregnant on d 35 after insemination were tested with Fisher's exact test (SAS, 1990).

RESULTS

Periestrus hormone profiles

Figure 1 shows the LH surge and profiles of plasma estradiol and progesterone concentrations per treatment. Plasma estradiol concentration was significantly lower at 16, 12, and 8 h before the LH surge in sows of the Low Fat treatment than in sows of the three other treatments (feeding level x energy source interaction; $P<0.05$). Maximum estradiol concentration was also lower in sows of the Low Fat treatment than in the other treatments (25.9 vs 31.9 pg/mL; SEM=1.7; $P=0.04$). Plasma LH surge and progesterone profiles were not influenced by treatments at any sampling time.

Ovary characteristics and embryonal survival

More sows fed the High feeding level during lactation came into estrus within 10 d after weaning than sows fed the Low feeding level (96 vs 63%; $P=0.01$). Follicle size on d 2 after weaning of the sows that exhibited estrus tended to be greater in sows fed the Starch diet

than in sows fed the Fat diet (3.8 vs 3.1 mm; SEM=0.2; P=0.06; Table 1). On d 35, 35 of the 38 sows were pregnant. Overall pregnancy rate (92%) was not influenced by treatments. Although ovulation rate tended to be higher in sows fed the High than in those fed the Low feeding level during lactation (18.0 vs 16.2; SEM=0.6; P=0.09), numbers of total and viable embryos on d 35 and embryonal survival were not affected by treatments (Table 1).

Table 1. Ovarian characteristics and embryonal survival

Feeding level[a]	High		Low		SEM	P-value[b]	
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source
Sows into estrus, n	12	11	7	8	--	0.01	1.00
Follicle size d 2, mm	3.6	4.1	2.6	3.5	0.4	0.12	0.06
Pregnant sows, n	11	9/10[c]	6	8	--	1.00	1.00
Ovulation rate, n	17.9	18.2	15.5	16.9	1.2	0.09	0.50
Luteal weight, g	7.1	6.4	6.4	6.2	0.3	0.22	0.18
Viable embryos, n	13.0	11.8	10.2	11.9	1.0	0.21	0.80
Embryonal survival, %	75.0	65.6	65.0	70.4	5.0	0.64	0.70

[a] During lactation.
[b] Statistical significance; no significant feeding level x energy source interactions were observed.
[c] For ovulation rate and luteal weight, n=10; for viable embryos and embryonal survival, n=9.

Uteri, placentas, and embryos

After removal of the embryo-placental units, uterine weight was higher in sows fed the High than in sows fed the Low feeding level during lactation (1.8 vs 1.6 kg; SEM=0.1; P=0.03; Table 2). Uterine length, placental weight and length, as well as embryo weight and length, were not influenced by treatments. Glucose concentration in the allantoic and amniotic fluid was not affected by treatments.

Table 2. Uterine, placental, and embryonic development

Feeding level[a]	High		Low		SEM	P-value[b]	
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source
Number of sows	11	9/10[c]	6	8			
Uterus empty weight, kg	1.9	1.8	1.7	1.5	0.9	0.03	0.25
empty length, m	4.7	4.8	4.8	4.6	0.3	0.91	0.85
Placental weight, g	57	56	51	50	5	0.13	0.78
length, cm	44	46	42	44	3	0.44	0.45
Embryonic weight, g	4.85	5.13	4.74	4.90	0.24	0.52	0.37
length, cm	4.1	4.1	4.0	4.1	0.1	0.43	0.33
Allantois glucose, mg/dL	23.5	23.8	21.0	25.5	2.9	0.94	0.42
Amnion glucose, mg/dL	7.3	6.6	9.7	9.0	0.7	0.15	0.31

[a] During lactation.
[b] Statistical significance; the feeding level x energy source interactions were not significant.
[c] For uterine weight, n=10; for the other variables, n=9.

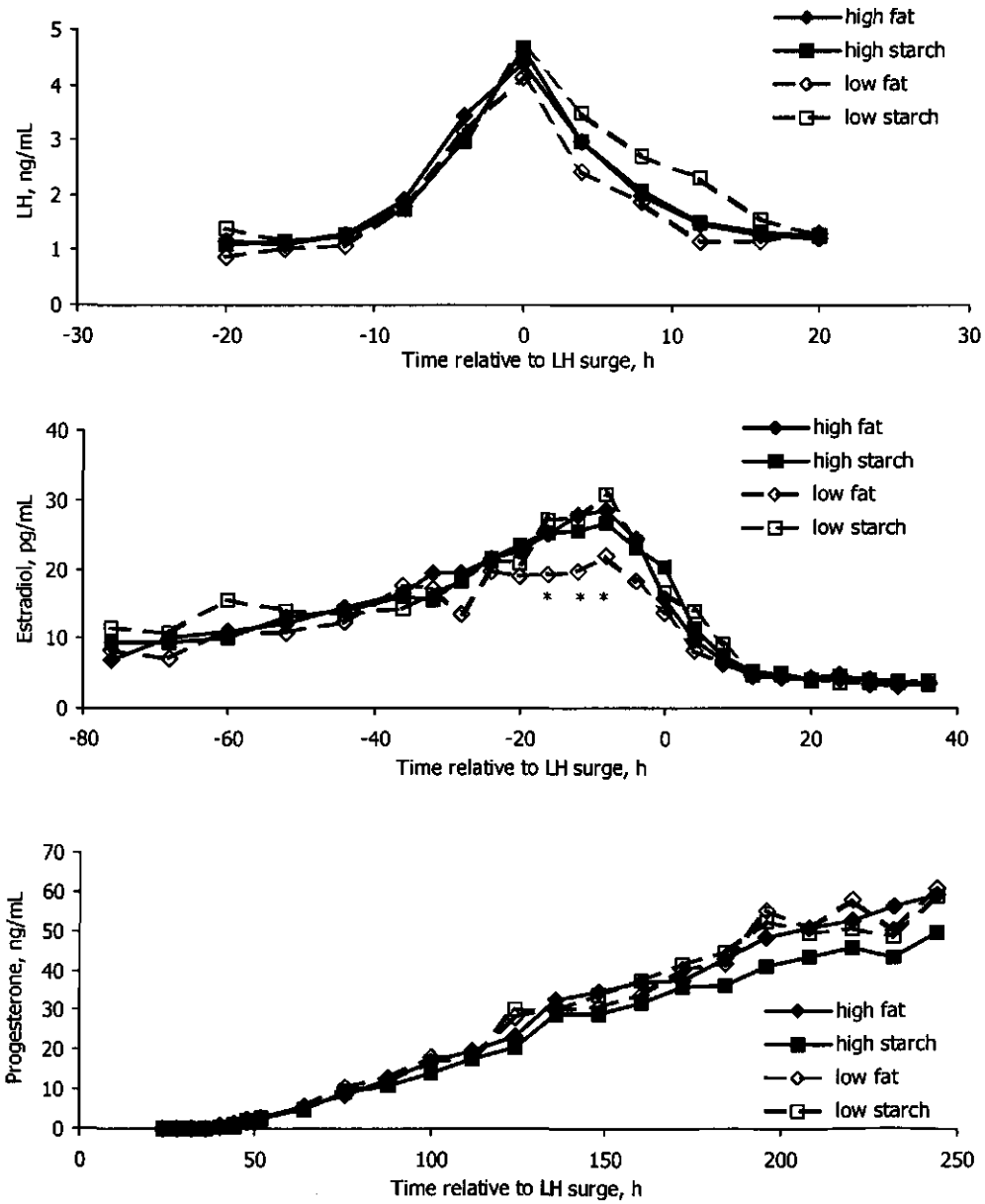

Figure 1. Periestrus LH (SEM=0.4), estradiol (SEM=1.5), and progesterone (SEM=3.2) profiles per treatment (*=P<0.05 for Low Fat vs High Fat, High Starch, and Low Starch). Number of observations for all profiles was 11, 9, 6, and 7 for High Fat, High Starch, Low Fat, and Low Starch, respectively.

Relationships between periestrus hormones and intrauterine development

Embryonic and Placental Development. In sows fed the High feeding level during lactation, the number of viable embryos (range 9 to 16) was negatively correlated with average placental weight (placental weight (g) = 58.5 - 5.2 x number of embryos; r=-0.73; P<0.001), whereas in sows fed the Low feeding level during lactation (range of 6 to 16 viable embryos), this correlation was absent. Regardless of treatment, average embryonic and placental weight were positively correlated (embryonic weight (g) = 3.90 + 0.02 x placental weight (g); r=0.38; P=0.03).

Progesterone and Embryonal Survival. The mean progesterone concentration between 24 and 250 h after the LH surge tended to be positively correlated with the number of viable embryos (viable embryos (n) = 9.39 + 0.11 x mean progesterone (ng/mL); r=0.31; P=0.09) and embryonal survival (embryonal survival (%) = 53.5 + 0.7 x mean progesterone (ng/mL); r=0.33; P=0.06), regardless of treatments (Figure 2). Differences in progesterone concentrations between sows with a higher (>69.1%) and a lower embryonal survival (<69.1%) were evident from 172 h after the LH surge (Figure 3).

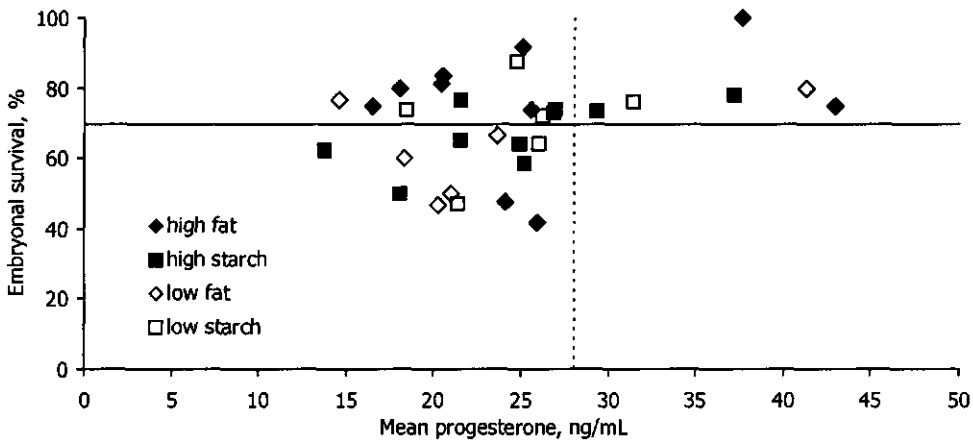

Figure 2. Relationship between mean progesterone concentration (24 to 250 h after LH surge) and embryonal survival (n=32). The horizontal line represents the average embryonal survival of all pregnant sows on d 35 (69.1%) and the vertical line is arbitrarily drawn.

Mean progesterone concentration between 24 and 250 h after the LH surge was positively correlated with glucose concentration in the amniotic fluid (amnion glucose (mg/dL) = 3.94 + 0.15 x mean progesterone (ng/mL); r=0.43; P=0.01), irrespective of treatment.

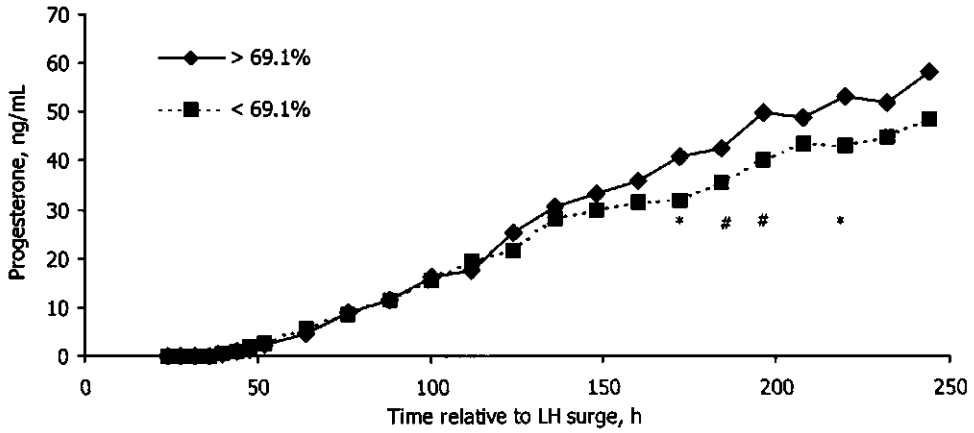

Figure 3. Plasma progesterone profiles per class of embryonal survival (<69.1%, n=13 or >69.1%, n=19; SEM=2.2; #=P<0.10, *= P<0.05).

DISCUSSION

Our objective for the present study was to influence embryonic development and embryonal survival as well as periestrus hormone profiles by nutritional manipulation of the plasma insulin concentration profiles, as previously shown by Kemp et al. (1995). During lactation, plasma insulin concentrations were higher in sows fed the Starch diet than in those fed the Fat diet, but feeding level did not affect plasma insulin concentrations (Van den Brand et al., 2000).

In contrast with Baidoo et al. (1992) and Prunier et al. (1993), plasma estradiol concentrations before the LH surge were affected by feeding level during the previous lactation. The maximum estradiol concentration was lower in sows fed the Fat-rich diet on the Low feeding level during the lactation than in sows of the other three groups. It can be speculated that the lower estradiol concentrations are due to the smaller follicle size after weaning as found in the sows of the Low Fat treatment. Kemp et al. (1995) did not observe any differences in estradiol concentration between sows fed either a starch-rich or a fat-rich diet. However, they only used a high feeding level during lactation.

In the present study, no influences of treatments on LH surge or plasma progesterone profiles were found, in contrast with the study of Kemp et al. (1995). They found a higher preovulatory LH surge and higher progesterone concentrations in sows fed a starch-rich diet than in sows fed a fat-rich diet.

In contrast with the studies of Kirkwood et al. (1987, 1990), no effect of lactational feed intake on progesterone concentration was observed. Possibly due to the relatively mild contrast in lactational feed intake in the present study (25%), no differences in progesterone concentrations were found.

Because primiparous sows seem to be more sensitive to negative energy balance during lactation than multiparous sows (Hughes, 1989), no effects of dietary energy source on LH surge and plasma progesterone concentrations were found in the present study. This might possibly explain the contrast with the study of Kemp et al. (1995) with multiparous sows.

In studies of Kirkwood et al. (1990), Baidoo et al. (1992), and Zak et al. (1997a), restricted feed intake during a part of lactation resulted in a lower embryonal survival in the subsequent pregnancy. Zak et al. (1997b) and Quesnel et al. (1998) showed that follicle development was impaired in sows that were restricted-fed during lactation. This might be the reason for the higher embryonal mortality in those sows (Zak et al., 1997a). This 'follicular imprinting' (Cosgrove and Foxcroft, 1996) might be mediated by the metabolic hormone insulin, as suggested by Quesnel et al. (1998). In the present study, no effect of feeding level during lactation on embryonic development and embryonal survival was observed, nor did feeding level influence plasma insulin concentration during lactation (Van den Brand et al., 2000) or follicle size after weaning, although ovulation rate tended to be higher in sows fed the High feeding level during lactation. In the present study, the contrast between High and Low feed intake during lactation was only 25%, whereas in the studies of Kirkwood et al. (1990), Baidoo et al. (1992), Zak et al. (1997a, b), and Quesnel et al. (1998) the difference between the high and low feeding level was approximately 50%. A restriction in feed intake during lactation of only 25% does not seem sufficient to induce differences in plasma insulin concentration and embryonal survival.

The effect of dietary energy source on embryonal survival in pigs seems to be absent. In agreement with the present study, Kemp et al. (1995) did not find an effect of feeding a starch-rich or a fat-rich diet on embryonal survival in multiparous sows, and Grandhi (1988) found no effect of fat supplementation on embryonal survival in gilts. However, in another experiment of Grandhi (1988), embryonal survival was decreased in fat-supplemented sows during early gestation, possibly due to their higher energy intake.

The greater uterus weight after removal of the embryo-placental units in sows fed the High feeding level during lactation is possibly due to the greater body weight of the sows at weaning in the High than in the Low feeding level (148 vs 140 kg; Van den Brand et al., 2000). In the present study, average placental and embryonal weight and length were not affected by treatments. In a study of Ashworth (1991) restricted fed (1.15 kg/d) cyclic gilts during two estrous cycles before insemination, had lower embryonal weight at d 30 of pregnancy than unrestricted animals (2.3 or 4.6 kg/d). The relatively mild feed restriction

during lactation in the present study did not seem to induce differences in embryonal weight at d 35 of the subsequent pregnancy. Other studies also showed no differences in embryonal (Grandhi, 1988; Perez Rigau et al., 1995) and placental weight (Perez Rigau et al., 1995) between sows fed a starch-based diet or a fat-based diet. From studies with rats (Koski et al., 1986; Kubow and Koski, 1995), it has been shown that only extreme maternal diet compositions (carbohydrate or fat free) resulted in retarded embryonal and placental development.

In agreement with the present study, Ashworth (1991), Pharazyn (1992), and Jindal et al. (1996) gave evidence that progesterone concentration is related to embryonal survival. In contrast with studies of Jindal et al. (1996, 1997) and Foxcroft (1997), no correlation was found between plasma progesterone concentration in early pregnancy (72 h after the onset of estrus) and embryonal survival. In the present study, differences in progesterone concentration between sows with more or less than average embryonal survival were evident from 172 h after the LH surge. Because, in the present study, feeding level in early pregnancy was similar for all sows, the differences in plasma progesterone concentrations are probably due to differences in progesterone production. In the studies of Jindal et al. (1996, 1997) differences in progesterone concentrations were due to differences in blood clearance rates as a result of differences in feeding level in early pregnancy. This suggests that plasma progesterone concentration is important for embryonal survival not only in very early gestation, but also in progressing pregnancy.

The positive correlation between mean progesterone concentration and glucose concentration in the amniotic fluid suggests that glucose is involved in the relationship between progesterone and embryonal survival.

From the present study, it can be concluded that feeding a Starch-rich diet resulted in a significantly higher plasma insulin concentration during lactation (Van den Brand et al., 2000) and a larger follicle size on d 2 after weaning compared with a Fat-rich diet. Although it has been demonstrated that exogenous insulin can reduce follicular atresia (Matamoros et al., 1991) and increase ovulation rate (Cox et al., 1987), in the present study no positive effect of the insulin-stimulating diet (Starch) on ovulation rate, progesterone concentration, and embryonal survival was detected.

IMPLICATIONS

Altering feeding level during lactation and dietary energy source (either Starch or Fat) fed from farrowing until early pregnancy does not seem to influence embryonic development and embryonal survival. Dietary-induced differences in plasma insulin concentration seem to play a relatively minor role in the relationship between nutrition and embryonic development and embryonal survival.

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Chapter 5

IN PRIMIPAROUS SOWS, PLASMA INSULIN-LIKE GROWTH FACTOR-I IS ASSOCIATED WITH LUTEINIZING HORMONE AND CAN BE AFFECTED BY LACTATIONAL FEED INTAKE AND DIETARY ENERGY SOURCE

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ABSTRACT

An experiment was conducted to investigate the role of feeding level and dietary energy source on plasma insulin concentration and reproductive performance of lactating primiparous sows. Results of this experiment were described previously. No relationships were found between insulin and reproductive traits. Additional analyses were performed to study effects of feeding level and dietary energy source on IGF-1 concentration and its relationships with reproductive traits. Also, effects of insulin and IGF-1 concentrations together on reproductive traits were studied. Furthermore, effects of body weight at farrowing and lactational body weight loss on IGF-1 secretion were investigated. These data are reported in this paper. Both, sows fed a high feeding level during lactation or fed a starch-rich diet had higher plasma IGF-1 concentrations during and after lactation than sows fed a low feeding level or a fat-rich diet. Plasma IGF-1 concentrations on d 21 and 22 were positively correlated or tended to be positively correlated with the total insulin secretion on d 14 and 21 of lactation ($r=0.28$ to $r=0.39$; $P=0.07$ to $P=0.01$). Plasma IGF-1 concentrations on d 21 of lactation tended to be positively related with LH pulsatility on d 22 ($P=0.10$) and the height of the preovulatory LH surge ($P=0.07$). Plasma IGF-1 concentrations on d 22 were positively related with LH pulsatility on d 22 ($P=0.03$) and the height of the preovulatory LH surge ($P=0.04$). No relationships between IGF-1 levels on either d 7, 14, 21, or 22 after farrowing or d 2 to 5 postweaning and weaning-to-estrus interval, duration of estrus, ovulation rate, follicle development, or embryonal survival were found. Plasma insulin did not have an additional effect to IGF-1 concentration for any of the reproductive traits. Sows with a low body weight at farrowing and high lactational body weight loss had the lowest plasma IGF-1 concentrations throughout and after lactation. From this study, it can be concluded that IGF-1 concentration is affected by both feeding level and dietary energy source and influences the secretion of LH. Furthermore, it can be concluded that body weight at farrowing interacts with lactational body weight loss to affect IGF-1 concentrations.

INTRODUCTION

In studies on the relationship between nutrition and reproduction, much emphasis has been given to insulin and insulin-like growth factor-I (IGF-1) as potential mediators (for review see Giudice, 1992; Pettigrew and Tokach, 1993; Spicer and Echternkamp, 1995). Most studies regarding the role of IGF-1 in reproduction are restricted to its influence on follicle development. Less emphasis has been given to relationships between systemic IGF-1 levels and the hypothalamus-pituitary axis.

An experiment was conducted to investigate effects of feeding level and dietary energy source in lactating primiparous sows on plasma insulin concentration and reproductive traits. Results of this experiment were described previously (Van den Brand et al., 2000a, b). They showed that feeding a starch-rich diet increased plasma insulin concentration compared with a fat-rich diet, whereas a reduction of 25% in feed intake did not affect plasma insulin concentration. No relationships were found between insulin and reproductive traits during and after lactation (e.g. LH pulsatility, weaning-to-estrus interval, ovulation rate, embryonal survival).

Therefore, additional analyses were performed to study effects of these diets on plasma IGF-1 levels and its relationships with reproductive traits. Several studies have already demonstrated that IGF-1 concentrations can be affected by feeding level in various species including the pig (for review see Thissen et al., 1994; Monget and Martin, 1997). Whether dietary energy source plays a role in plasma IGF-1 concentration is not clear.

The aims of this study were 1) to investigate effects of feeding level during lactation and dietary energy source on plasma IGF-1 concentration; 2) to investigate whether plasma IGF-1 concentrations are associated with reproductive traits; 3) to investigate whether insulin and IGF-1 together are related with reproduction and 4) to investigate effects of body weight at farrowing and body weight loss during lactation on IGF-1 concentrations.

MATERIALS AND METHODS

General design

During a 21-d period of lactation, 48 (eight batches of six) primiparous Yorkshire x Dutch Landrace sows were allotted to a 2 x 2 factorial experiment. Treatments were feeding level (**High**: 44 MJ NE/d; 1050 g protein/d or **Low**: 33 MJ NE/d; 790 g protein/d) and major dietary energy source (**Fat**: tallow: 134.9 g/kg fat; 196.8 g/kg starch plus sugar or **Starch**: maize starch plus dextrose: 33.2 g/kg fat; 380.9 g/kg starch plus sugar). Each sow nursed nine piglets. During lactation, sows were housed in climatic respiration chambers (Verstegen et al., 1987). After weaning (d 22) all sows received the same amount of feed (31 MJ NE/d, 740 g protein/d from weaning to estrus and 17.5 MJ NE/d, 420 g protein/d thereafter), but remained on the same dietary energy source fed during lactation. Sows that exhibited estrus after weaning were inseminated and pregnant sows were slaughtered on d 35 of subsequent pregnancy. During lactation and around estrus frequent blood samples were taken to analyze metabolic and reproductive hormones. The experiment was conducted between autumn 1996 and spring 1997. The Institutional Animal Care and Use Committee of the Wageningen Agricultural University approved all experimental protocols.

Animals and diets

On d 8 (range 6 to 11) before parturition, sows were surgically fitted with a permanent jugular vein catheter, according to the method described previously (Soede et al., 1997). On d 3 (range 0 to 5) after parturition, six sows in each batch were paired on basis of body weight and allotted to one of the treatments. All sows in batch 1, 3, 5, and 7 got the High feeding level, whereas sows in the other four batches got the Low feeding level. Within each batch, three sows were fed the Fat-rich diet and the other three sows got the Starch-rich diet. Both diets consisted of the same basal diet with sufficient protein, vitamins, and minerals. To this basal diet, either tallow (Fat) or maize starch plus dextrose (Starch) was

added. For details about the diet composition, see Van den Brand et al. (2000a). Within each feeding level, diets were fed in different rations to realize an isocalorical and isonitrogenous feed intake. Sows were fed twice daily (0800 and 1530). Water was available ad libitum for sows and piglets. No creep feed was offered to the piglets. On d 3 and 22, sows were weighed.

Blood sampling

On d 7, 14, 21, and 22 after farrowing, blood samples were taken each 12 min during 12 h. Furthermore, from 48 h after weaning, blood samples were taken at 4-h intervals until 24 h after the end of estrus. Thereafter, blood samples were taken each 12 h, for 9 d. All blood samples were collected in ice-cooled polypropylene tubes, containing 100µL of EDTA solution (144 mg/mL saline), placed on ice immediately after collection and centrifuged at 2,000 x *g* for 10 min at 4°C. Plasma was stored at -20°C until analyses.

Plasma analyses

Plasma samples taken at -60, -48, -36, -24, -12, 0, 12, 24, 36, 48, 60, 84, 120, 156, 228, 300 and 372 min relative to the morning meal on d 7, 14, and 21 of lactation were analyzed for glucose and insulin. The areas under the curve (**AUC**) were calculated from 0 to 372 min after feeding, corrected for the average concentration before feeding (-60 to 0 min) as the basal concentration. All plasma samples of d 7, 14, 21, and 22 as well as 13 samples taken each 4 h around expected LH surge were determined for LH concentrations. Plasma estradiol concentrations were analyzed in 8-h samples taken from 76 h to 36 h before the LH surge and in 4-h samples from 36 h before to 36 h after the LH surge. Mean estradiol concentration was calculated from 52 to 0 h before the LH surge. Plasma progesterone concentrations were measured in samples taken from 24 to 52 h after the LH surge in 4-h intervals and from 52 to 250 h after the LH surge in 12-h intervals. Mean progesterone concentration was calculated from 24 to 250 h after the LH surge. Details about the used detection techniques and coefficients of variation are described previously (Van den Brand et al., 2000a, b).

For d 7, 14, and 21 of lactation, d 22 (weaning), and d 2 to 5 after weaning, one sample (12.00) was analyzed in duplicate for plasma IGF-1 concentration in a single RIA as described previously (Louveau and Bonneau, 1996). The intraassay CV was 7.2% at 200 ng/mL.

Follicle size, estrus, and ovulation rate

On d 2 after weaning, mean follicle size was assessed by transrectal ultrasonography as described by Soede et al. (1997). From d 2 to 10 after weaning, estrus detection was performed at 8-h intervals (0800, 1600 and 2400, in the presence of a vasectomized boar, using the back pressure test). Sows not exhibiting estrus within 10 d after weaning were

assumed to be anestrous. Sows that expressed estrus were inseminated each day of standing estrus with a commercial dose of semen containing 3 x 10^9 sperm cells. On d 35 after the last insemination, sows were slaughtered to determine the ovulation rate and embryonal survival.

Statistical analyses

To test effects of treatments and days on IGF-1 concentration the following model was used:
$Y_{ijklm} = \mu + F_i + e1_{ij} + E_k + (FxE)_{ik} + e2_{ijkl} + D_m + (FxD)_{im} + (ExD)_{km} + (FxExD)_{ikm} + e3_{ijklm}$ [1]
where Y_{ijklm} = dependent variable; μ = overall mean; F_i = feeding level during lactation (i = High, Low); $e1_{ij}$ = error term 1, which represents the random effect of $batch_j$ (j = 1 to 4) nested within feeding level; E_k = energy source (k = Starch, Fat); $(FxE)_{ik}$ = interaction between feeding level and energy source; $e2_{ijkl}$ = error term 2, which represents the random effect of sow_l (l = 1 to 3) nested within batch, feeding level, and energy source; D_m = day after parturition (m = 7, 14, 21, 22, 24, 25, 26, 27); $(FxD)_{im}$ = interaction between feeding level and day; $(ExD)_{km}$ = interaction between energy source and day; $(FxExD)_{ikm}$ = interaction between feeding level, energy source, and day; and $e3_{ijklm}$ = residual error. The effect of feeding level was tested against error term 1. Effects of energy source and the interaction between feeding level and energy source were tested against error term 2. Day effect and the interactions with day were tested against the residual error.

Due to some missing values not all LSmeans could be estimated and therefore no comparisons between treatments and days could be performed. Therefore, effects of treatments on IGF-1 concentrations are tested again per day with the following model:

$$Y_{ijk} = \mu + F_i + e1_{ij} + E_k + (FxE)_{ik} + e_{ijk}, \quad [2]$$

where Y_{ijk} = dependent variable; μ = overall mean; F_i = feeding level (i = High, Low); $e1_{ij}$ = error term 1, which represented the random effect of $batch_j$ (j = 1 to 4) nested within feeding level; E_k = energy source (k = Fat, Starch); $(FxE)_{ik}$ = interaction between feeding level and energy source; and $e2_{ijk}$ = residual error. Effect of feeding level was tested against error term 1. Effect of energy source and the interaction between feeding level and energy source were tested against the residual error.

Overall correlation analyses were performed for IGF-1 concentrations between days, and also between IGF-1 concentrations on the different days and plasma glucose and insulin concentrations. Relationships between IGF-1 on the different days and reproductive traits were tested with model 2, except that IGF-1 concentration and its interactions with feeding level and energy source (including the triple interaction) were added to the model as covariates. Because IGF-1 concentration was influenced by treatments, overall one-way correlation analyses with IGF-1 were performed, to check whether regressions between IGF-1 and reproduction traits were consistent within and between treatments. Only for

presentation of LSmeans in Table 2, IGF-1 concentrations on d 21 or 22 were divided into 3 classes based on the number of observations, and after this, classes were introduced into model 2 as class variable.

Additional effects of insulin to IGF-1 concentrations on d 21 on reproductive traits were also tested with model 2, except that both insulin and IGF-1, and all their interactions were introduced to the model as covariates.

To analyze effects of body weight at farrowing and lactational body weight loss, also model 2 was used, except that body weight at farrowing and body weight loss, together with their interactions, were included in the model as covariates. Only for presentation of LSmeans in Figure 3, body weight on d 3 after parturition was divided into 2 classes (Light: ≤ 160 kg, n = 24 and Heavy > 160 kg, n = 24; range: 144 to 186 kg), and within each body weight class, 2 classes of body weight loss during lactation (Low: ≤ 17 kg, n = 12 and High: > 17 kg, n = 12; range 1 to 37 kg) were made.

In all analyses regarding relationships, non-significant interactions and treatments were deleted from the model. All statistical analyses were performed with the GLM-procedure of the statistical package SAS (1990).

RESULTS

Effects of day, feeding level, and dietary energy source on IGF-1

Plasma IGF-1 profiles during and after lactation for the treatments are shown in Figure 1. There was a feeding level x day interaction (P=0.02). Plasma IGF-1 concentration decreased during lactation only in sows fed the Low feeding level, whereas in sows fed the High feeding level, IGF-1 concentration remained high during the whole lactation. On the day of weaning (d 22) IGF-1 concentration decreased, and thereafter an increase in IGF-1 concentration was found in all treatment groups (Figure 1; P<0.05).

No interaction between feeding level and dietary energy source was found in IGF-1 concentration for any of the sampling days. Increasing feeding level during lactation resulted in (a tendency to) higher IGF-1 concentrations on d 21 (160 vs 102 ng/mL; SEM=17; P=0.05) and 22 (115 vs 71 ng/mL; SEM=14; P=0.07) after farrowing as well as on d 2 (198 vs 146 ng/mL; SEM=13; P=0.03), 3 (230 vs 203 ng/mL; SEM=12; P=0.10), and 4 (255 vs 221 ng/mL; SEM=12; P=0.10) postweaning. In sows fed the Starch-rich diet compared with sows fed the Fat-rich diet, IGF-1 concentrations were higher on d 7 (203 vs 166 ng/mL; SEM=10; P=0.02), 21 (154 vs 107 ng/mL; SEM=11; P=0.007), and 22 after farrowing (108 vs 77 ng/mL; SEM=10; P=0.04) and tended to be higher on d 3 postweaning (234 vs 205 ng/mL; SEM=11; P=0.08).

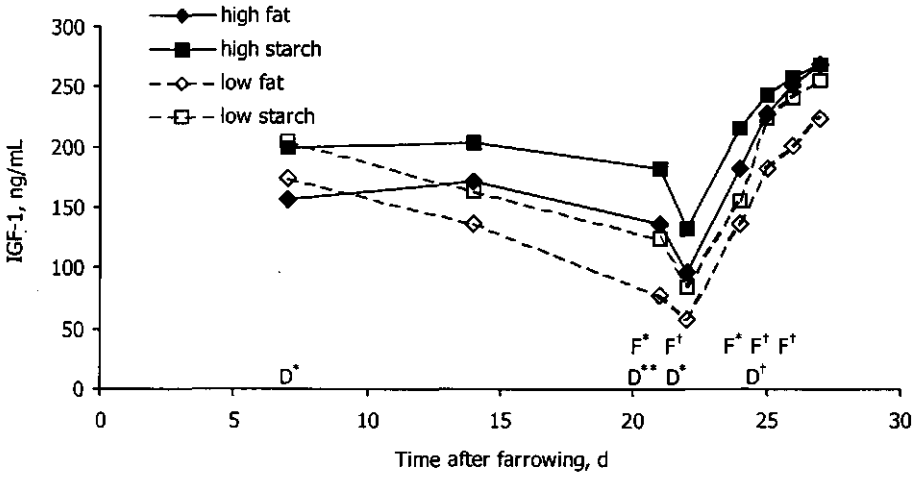

Figure 1. Plasma IGF-1 (SEM=12) profiles per treatment. F = effect of feeding level; D = effect of dietary energy source (†=P<0.10; *=P<0.05; **=P<0.01).

IGF-1 concentrations measured on the different days were positively correlated (Table 1). Plasma IGF-1 concentrations on different days were also correlated with plasma glucose and insulin AUC's on different days (Table 1).

Table 1. Coefficients of correlation between plasma IGF-1 concentration (ng/mL), glucose AUC (g/6.2 h), and insulin AUC (mIU/6.2 h) on d 7, 14, 21, and 22 (weaning) after farrowing

	IGF-1, d 7	IGF-1, d 14	IGF-1, d 21	IGF-1, d22
IGF-1, d 7	--	--	--	--
IGF-1, d 14	0.58***[a]	--	--	--
IGF-1, d 21	0.46**	0.79***	--	--
IGF-1, d 22	0.52***	0.70***	0.93***	--
Glucose AUC, d 7	0.34*	0.15	0.19	0.17
Glucose AUC, d 14	0.22	0.14	0.25	0.19
Glucose AUC, d 21	0.39**	0.25†	0.31*	0.28†
Insulin AUC, d 7	0.31†	0.20	0.23	0.20
Insulin AUC, d 14	0.40**	0.27†	0.39*	0.28†
Insulin AUC, d 21	0.35*	0.26†	0.37*	0.36*

[a] †=P<0.10; *=P<0.05; **=P<0.01; ***=P<0.001.

Relationships between IGF-1 and reproductive traits

No relationships between IGF-1 concentration on d 7 and 14 of lactation and reproductive traits were found. In Table 2, relationships between IGF-1 concentration on d 21 and 22 (weaning), with LH pulsatility, and the height of the preovulatory LH surge are shown.

Treatment corrected IGF-1 concentration on d 21 tended to be ($P<0.10$) positively related with LH pulsatility on d 22 and the height of the preovulatory LH surge. The relationships between the IGF-1 concentration on d 22 and LH pulsatility on d 22 as well as the height of the LH surge were positive ($P<0.05$). The relationships between IGF-1 and LH pulsatility were similar within all treatment groups. Figure 2 shows, as an example, the relationship between the IGF-1 concentration on d 21 of lactation and the number of LH pulses immediately after weaning (d 22). Overall, one way correlation analyses between IGF-1 concentration and LH showed comparable results, except that the regressions were somewhat stronger (Table 2). Furthermore, overall relationships (ß) remained consistent with the treatment-corrected relationships.

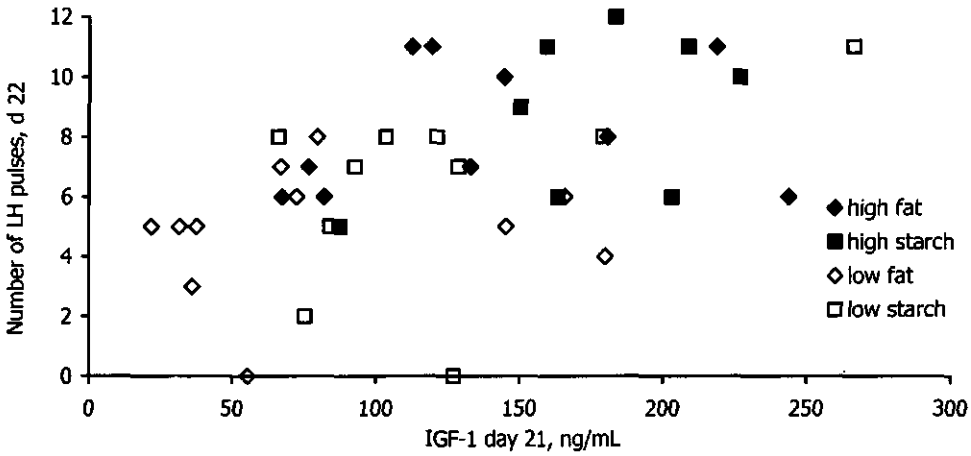

Figure 2. Relationship between IGF-1 concentration on d 21 of lactation and number of LH pulses per 12 h on the day of weaning (d 22).

After correction for treatments, no relationships were found between IGF-1 and follicle size on d 2 after weaning, weaning-to-estrus interval, duration of estrus, mean estradiol and progesterone concentration, ovulation rate, and embryonal survival (results not shown). Overall one-way analysis showed a positive relationship between IGF-1 concentration on d 21 and follicle size on d 2 after weaning ($R^2=0.11$; $ß=0.0053$ $mm.ng^{-1}.mL^{-1}$; $P=0.04$).

Additional effect of insulin to IGF-1

Addition of plasma insulin AUC to the model, together with IGF-1 on the different days, did not show significant effects of insulin above the effect of IGF-1 on LH pulsatility or other reproductive traits.

Table 2. Relationships between IGF-1 concentration on d 21 and 22 (weaning) after farrowing and LH traits.

				SEM	Treatment corrected[b]			Overall one way[b]		
					R^2	ß	P-value linear	R^2	ß	P-value linear
IGF-1 d 21, ng/mL[a]	≤ 84	85 – 162	≥ 163							
Number of observations	14	14	14							
High feeding level	3	8	10							
Fat-rich diet	11	5	5							
LH pulses d 21, n/12 h	0.54	0.46	0.95	0.20	0.34	0.0035	0.15	0.13	0.0040	0.02
LH pulses d 22, n/12 h	6.00	7.39	7.89	0.77	0.55	0.0143	0.10	0.25	0.0233	0.001
LH surge, ng/mL	3.82	4.43	5.56	0.53	0.31	0.0138	0.07	0.09	0.0081	0.09
IGF-1 (d 22, ng/mL)[a]	≤ 52	53 – 114	≥ 115							
Number of observations	14	14	14							
High feeding level	4	7	11							
Fat-rich diet	9	7	5							
LH pulses d 22, n/12 h	6.22	7.03	8.18	0.77	0.59	0.0199	0.03	0.20	0.0234	0.004
LH surge, ng/mL	3.79	4.31	5.62	0.47	0.34	0.0193	0.04	0.14	0.0121	0.03

[a] LSmeans estimated with model: Y = μ + feeding level + batch(feeding level) + energy source + feeding level x energy source + IGF-1 class + e.

[b] Treatment corrected: Model: Y = μ + feeding level + batch(feeding level) + energy source + feeding level x energy source + IGF-1 + e. Overall one way: Model: Y = μ + IGF-1 + e.

Effect of body weight and lactational body weight loss on IGF-1 concentration

After correction for treatments (feeding level and dietary energy source), a significant interaction between body weight at farrowing and lactational body weight loss was depicted for plasma IGF-1 concentration on d 14, 21, 22 (weaning), 26, and 27 after farrowing. Light sows with a high lactational body weight loss had lower plasma IGF-1 concentrations than other sows (Figure 3).

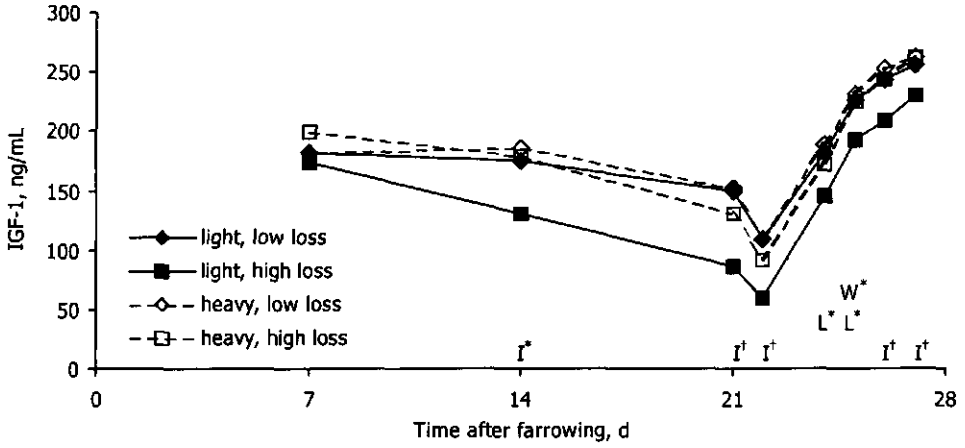

Figure 3. Effect of body weight at farrowing and lactational body weight loss (corrected for treatments) on plasma IGF-1 profiles (SEM=8). Light = body weight at farrowing ≤ 160 kg; heavy = body weight at farrowing > 160 kg; low loss = lactational body weight loss ≤ 17 kg; high loss = lactational body weight loss > 17 kg; W = effect of body weight at farrowing; L = effect of lactational body weight loss; I = interaction between body weight at farrowing and lactational body weight loss; †=P<0.10; *=P<0.05. Significance is tested with the following model: Y = μ + body weight class + body weight loss class + interaction between body weight and body weight loss classes + e, with the values corrected for treatments.

DISCUSSION

Higher plasma IGF-1 concentrations in sows fed the High feeding level during lactation are in agreement with previous results (Quesnel et al., 1998; Zak et al., 1998; Messias de Bragança and Prunier, 1999). Even a restricted feed intake during one week of lactation resulted in a decrease of IGF-1 concentration (Zak et al., 1997), suggesting a rapid effect of feed intake on IGF-1 concentration. The role of dietary energy source on IGF-1 concentration has hardly been investigated in the pig. In dairy cattle, no differences in IGF-1 and insulin concentrations were found between cows receiving one of three levels of dietary fat (Beam and Butler, 1997). Our data show that giving sows a starch-enriched diet has a positive

effect on both plasma IGF-1 and insulin (Van den Brand et al., 2000a) concentration. Moreover, a positive correlation between plasma IGF-1 and insulin concentration is observed, in agreement with data obtained by Quesnel et al. (unpublished results) in restricted fed lactating sows and cyclic gilts. This positive relationship between insulin and IGF-1 agrees well with the finding that insulin stimulates in vitro production of IGF-1 by rat liver cells (Daughaday et al., 1976; Johnson et al., 1989). When feed intake is high, insulin levels are high (Koketsu et al., 1998; Quesnel et al., 1998), and are probably not limiting for IGF-1 production. Contrarily, when feed intake is low, plasma insulin concentration is low, and probably not high enough to mediate maximum production of IGF-1 by the liver.

The interaction between body weight at farrowing and lactational body weight loss demonstrates that the combination of both factors determines plasma IGF-1 concentration throughout lactation and even after weaning. It seems that increasing body weight at farrowing can prevent the negative influence of excessive weight loss during lactation on plasma IGF-1 concentration. Therefore, rearing strategy and feeding management during pregnancy and lactation could be important determinants for subsequent IGF-1 production. A positive relationship between body weight and IGF-1 concentration was also found in prepubertal gilts (Booth et al., 1994).

Our data show that IGF-1 concentration does not vary during lactation in primiparous sows receiving the high feeding level, but decreases during lactation in sows at the low feeding level. This is in agreement with previous experiments with well-fed multiparous sows (Schams et al., 1994) and underfed primiparous sows (Kusina et al., 1999). The present study is, to our knowledge, the first one that carefully describes the postweaning plasma IGF-1 pattern: Schams et al. (1994) only measured on d 3 postweaning, Caroll et al. (1996) on d 1 and 4 after weaning, and Messias de Bragança and Prunier (1999) on d 1 and 8 after weaning.

It is also the first time that a decrease in IGF-1 is described on the day of weaning. This decrease is probably due to the fact that sows were deprived of feed on that specific day. During the following days, IGF-I concentrations increased, especially in sows which were restricted fed during lactation. As a consequence, the effect of the lactational feed intake on IGF-I was reduced and, on d 5 postweaning, the difference between lactational feeding levels was obliterated. This is in good agreement with data from Caroll et al (1996) and Messias de Bragança and Prunier (1999) showing that the IGF-I concentration of restricted fed sows during lactation restore within a few days postweaning to comparable levels as those observed in sows fed ad libitum during lactation.

The positive relationship of IGF-1 measured just before and after weaning with LH pulsatility determined on the day of weaning, and the height of the preovulatory LH surge suggests that IGF-1 not only acts at the ovarian level (see for review Giudice, 1992; Spicer and Echternkamp, 1995), but also at the hypothalamic-pituitary level. This is supported by the results of Whitley et al. (1995). They found, in vitro, an increased LH secretion by porcine anterior pituitary cells when IGF-1 was added to the medium. Pettigrew and Tokach (1993) also found a positive correlation between IGF-1 concentration and LH secretion in lactating sows. However, such relationship between IGF-1 and LH pulse frequency just before and after weaning was not observed by Quesnel et al. (1998).

The feed deprivation on the day of weaning resulted in a depressed plasma IGF-1 concentration. It should be noticed that this occurred at the time when LH pulse frequency increased and around the time when preovulatory follicles were probably recruited. Therefore, it should be questioned whether this deprivation of feed on the day of weaning may influence the subsequent reproductive performance, especially in sows that were light at weaning.

Plasma insulin concentration did not have significant relationships with reproductive traits (Van den Brand et al., 2000a, b). Together with IGF-1, insulin did not have an additional effect on reproductive traits. This suggests that, in the present experiment, IGF-1 rather than plasma insulin may have mediated the effect of the feeding regimen on the reproductive axis. A reason for this phenomenon can possibly be found in the high variation in insulin concentration during the day (pre- and postprandial), whereas IGF-1 concentration is more constant.

IMPLICATIONS

From the present study, it can be concluded that IGF-1 just before and after weaning is related with LH pulsatility of primiparous sows. A high feeding level during lactation and a starch-rich diet enhanced IGF-1 concentrations. A high body weight at farrowing may compensate for a detrimental effect of severe lactational body weight loss regarding IGF-1 concentrations around weaning. This all implicates that increasing body reserves at farrowing and giving a starch-rich diet during and after lactation could be tools to improve IGF-1 production and reproductive performance of primiparous sows.

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Chapter 6

EFFECTS OF POSTWEANING DIETARY ENERGY SOURCE ON REPRODUCTIVE TRAITS IN PRIMIPAROUS SOWS

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ABSTRACT

An experiment was conducted to study effects of major dietary energy source fed from weaning to ovulation or from ovulation to d 35 of pregnancy on reproductive traits in primiparous sows. Dietary energy sources were used to manipulate the plasma insulin concentration. One-hundred-thirteen sows were assigned to a 2 x 2 factorial experiment. From weaning to ovulation sows were fed at 2 times maintenance either a diet with tallow (Fat) or maize starch plus dextrose (Starch) as major energy source. From the first meal after ovulation onwards, sows within each treatment were alternately assigned to either the Fat or the Starch diet and were fed at 1.25 times maintenance. Estrus detection was performed 3 times a day from d 2 to 9 postweaning and sows were inseminated each day of standing estrus. On d 35 of pregnancy, sows were slaughtered and their reproductive tracts were removed. Plasma insulin concentration was higher is sows fed the Starch-rich diet compared with sows fed the Fat-rich diet both before (1.30 vs 0.97 ng/mL; P=0.08) and after ovulation (1.14 vs 0.58 ng/mL; P<0.001). Plasma glucose and IGF-1 concentration, both on d 4 after weaning and d 32 of pregnancy, did not differ between dietary energy sources. The percentage of sows exhibiting estrus within 9 d after weaning was 52 and 67%, for the Fat and Starch diet before ovulation, respectively (P=0.11), whereas the weaning-to-estrus interval was 134 vs 123 h, respectively (P=0.12). Survival analysis showed that sows fed the Fat-rich diet had a 1.6 times higher risk to remain anestrous until d 9 postweaning than sows fed the Starch-rich diet (P=0.04). No clear effect of dietary energy source, either before or after ovulation, on uterine, placental, and embryonic development on d 35 of pregnancy was found. From this experiment, it can be concluded that postweaning dietary energy source affected timing and occurrence of estrus postweaning, but hardly affected uterine, placental, and embryonic development.

INTRODUCTION

Both insulin and IGF-1 have been proposed to be intermediates between nutrition and reproduction in the pig. Cox (1997) reviewed effects of insulin on follicle development, ovulation rate, weaning-to-estrus interval (**WEI**), and farrowing rate. However, these effects are inconsistent because some studies showed a positive effect of insulin on reproduction, whereas in other studies no effect or even a negative effect was found. Investigations on effects of IGF-1 have mostly been restricted to follicle development, although some associations have been shown between plasma IGF-1 concentration and LH secretion (Pettigrew and Tokach, 1993; Whitley et al., 1995). This suggests that plasma IGF-1 can act at the hypothalamus-pituitary level. Effects of insulin mentioned above are all based on correlation analysis or found after exogenous insulin injections. Both insulin (Ponter et al., 1991; Van den Brand et al., 2000a) and IGF-1 concentrations (Chapter 5) can also be affected by dietary energy source. It was also shown that dietary energy source can affect LH pulsatility, but did not influence the WEI, ovulation rate, or embryonal survival (Van den Brand et al., 2000a, b). However, in the latter studies dietary energy sources were fed from farrowing until d 35 of subsequent pregnancy. It is therefore not clear in which phase (lactation, WEI, pregnancy) dietary energy source is really important for reproduction.

Effects found during pregnancy may be a result of changes during the WEI or even the lactation (Kemp, 1998). Therefore, this study was performed to distinguish effects of dietary energy sources fed between weaning and ovulation or during early pregnancy on reproduction.

MATERIALS AND METHODS

General design

One-hundred-thirteen primiparous sows, in eight batches, were assigned to a 2 x 2 factorial experiment. After weaning, sows were assigned to a diet with as major dietary energy source either tallow (**Fat**, n=56) or maize starch plus dextrose (**Starch**, n=57). From the first feeding after ovulation onwards, sows within each treatment were alternately assigned to either the Fat or Starch diet. Sows were inseminated each day of standing estrus and slaughtered on d 35 of pregnancy. The experiment was conducted during summer 1999. The institutional Animal Care and Use Committee of the Wageningen University approved all experimental protocols.

Animals and diets

On d 2.6 (range 0 to 7) after farrowing, primiparous Yorkshire x Dutch Landrace sows were weighed and backfat thickness was measured according to the method described by Verstegen et al. (1979). During lactation sows were fed with liquid feeding (calculated nutrient intake: 790 g CP/d, 38 g ileally digestible lysine/d, 1,836 g starch plus sugar/d, 267 g fat/d, 48 MJ NE/d). Within 2 d postpartum, piglets were cross-fostered between sows. After a lactation period of 23.6 (SD=3.3) d, sows weaned 10.1 (SD=1.3) piglets. On the morning of weaning, sows were deprived of feed and brought from the commercial farm to the experimental farm. Immediately after arrival, sows were weighed and backfat thickness was measured. Based on body weight at weaning, lactational body weight loss, and backfat thickness at weaning, sows were paired and assigned to one of two experimental diets. Both diets consisted of the same basal diet, with sufficient protein, vitamins, and minerals (Table 1). To this basal diet either tallow (Fat) or maize starch plus dextrose (Starch) was added. Diets were fed in different amounts to provide an isocaloric and isonitrogenous intake. From the first meal after observed ovulation onwards, sows within each treatment were alternately assigned to either the Fat or the Starch diet. All sows were fed at 2 times maintenance (MEm=440 $kJ.kg^{-0.75}.d^{-1}$; CVB, 1994) from weaning to ovulation and at 1.25 times maintenance thereafter.

Sows were fed twice daily (0900 and 1700). Water was available ad libitum. During the whole experiment, feed refusals were collected once a day and analyzed for dry matter content.

Table 1. Composition of the experimental diets (as fed)

Ingredient	Starch, g		Fat, g	
Barley	238		238	
Wheat middlings	50		50	
Toasted soybeans	57		57	
Extracted soybeans	115		115	
Extracted sunflower seed	178		178	
Extracted rape seed	36		36	
Meat and bone meal	48		48	
Alfalfa meal	2		2	
Limestone	8.3		8.3	
Monocalcium phosphate	7.1		7.1	
Salt	2.4		2.4	
L-Lysine HCl	1.2		1.2	
DL-Methionine	1.2		1.2	
Vitamin-mineral premix[a]	17.8		17.8	
Maize starch	178		-	
Dextrose	60		-	
Tallow	-		81	
Total, g[b]	1,000		843	
Content	Calculated	Analyzed	Calculated	Analyzed
	g/1,000 g		g/843 g	
Crude protein	211.2	201.3	210.5	199.8
Crude fat	33.2	36.4	113.7	116.2
Starch	305.4	286.3	149.8	140.5
Sugar	75.5	69.1	16.1	21.4
kJ NE (for swine)[c]	8,800	--	8,800	--
kJ ME (for swine)[c]	11,600	--	10,600	--
Digestible lysine[d]	8.4	--	8.4	--

[a] Provided the following per kg of premix: vitamin A: 900,000 IU, vitamin D_3: 180,000 IU, vitamin E: 4,000 mg, riboflavin: 500 mg, niacin amide: 3,000 mg, d-pantothenic acid: 1,200 mg; choline chloride: 35,000 mg, vitamin B_{12}: 4 mg, vitamin K: 300 mg, vitamin C: 5,000 mg, folic acid: 100 mg, biotin: 10 mg, $CoSO_4.7H_2O$: 250 mg, $Na_2SeO_3.5H_2O$: 20 mg, KI: 50 mg, $FeSO_4.7H_2O$: 40,000 mg; $CuSO_4.5H_2O$: 8,000 mg; MnO_2: 7,000 mg, $ZnSO_4.H_2O$: 20,000 mg.

[b] 1,000 g of the Starch diet and 843 g of the Fat diet are isocaloric and isonitrogenic.

[c] According to the Centraal Veevoederbureau (CVB, 1988).

[d] Fecal digestibility (CVB, 1988).

Estrus detection and time of ovulation

From d 3 to 9 after weaning, estrus detection was performed 3 times a day (0800, 1600, and 2400) in the presence of a mature boar, using the back pressure test. Sows not expressing estrus within 9 d after weaning were checked for corpora lutea by ultrasonography. When only small follicles and no corpora lutea were found sows were anestrous and removed from the experiment. Sows that ovulated without showing estrus (n=3) were also removed from the experiment. Sows that exhibited estrus were inseminated each day of standing estrus with a commercial dose of semen containing 3×10^9 sperm cells. During estrus, time of ovulation was assessed by transcutaneous ultrasonography at 8-h intervals.

Ovaries, uteri, placentas, and embryos

On d 35 after the last insemination, pregnant sows (confirmed by ultrasonography on d 24 to 28 after the last insemination) were slaughtered and their reproductive tracts were removed. The corpora lutea were dissected from the ovaries and total luteal weight was determined. Both uterine horns were separated from the mesometrium and opened at the anti-mesometrial side. Embryos were separated from their placentas and classified as viable or not viable (characterized as strongly haemolyzed amniotic fluid and(or) resorbed fetal membranes). Weight and crown-rump length of the embryos were measured. Embryonal survival was calculated as the number of viable embryos divided by the number of corpora lutea. After removal from the endometrium, individual placentas were weighed and the functional length (between the necrotic tips) was measured. After removal of the embryo-placental units, weight and length of the uterine horns were determined.

Blood sampling

On d 4 after weaning one blood sample (10 mL) was taken by vena puncture in all sows, at 1 h after the morning meal, because in a previous experiment (Van den Brand et al., 2000a) the maximum insulin concentration was reached at 1 h after feeding. On d 32 (range 30 to 34) of pregnancy, again one blood sample (10 mL) was taken from all pregnant sows at 1 h after the morning meal. Blood samples were collected in ice-cooled polypropylene tubes containing 100 µL of EDTA solution (144 mg/mL saline), placed on ice immediately after collection and centrifuged at 2,000 x *g* for 10 min at 4°C. Plasma was stored at –20°C until analyses.

Plasma analyses

Blood samples from sows that consumed the total amount of feed offered within 1 h after feeding (d 4 postweaning: n=35 for Fat; n=22 for Starch; d 32 of pregnancy: n=35 for Fat; n=27 for Starch) were analyzed for glucose, insulin, and IGF-1 concentrations.

Concentrations of glucose were determined spectrophotometrically in triplicate by the glucose oxidase-peroxidase anti-oxidase method using a commercial kit (GOD-PAP, Boehringer, Mannheim, Germany).

Plasma insulin concentrations were determined in duplicate with a RIA using the procedure reported for ovine follicle stimulating hormone (Erkens et al., 1992) with minor modifications. Porcine insulin (27.8 USP units/mg; Sigma, St. Louis, USA, No. I5523), used for the preparation of tracer and standards (0.005 to 5.12 ng per tube), was dissolved in one volume of 0.01 M $NaHCO_3$ followed by four volumes of 0.5 M Na_2HPO_4, 0.02% (w/v) NaN_3, pH 7.6, to a stock concentration of 120 µg/mL. Columns of Sephadex G215-coarse (30 x 0.9 cm) and Sephadex G50-fine (90 x 1.6 cm) were used for the purification of iodinated insulin. Sample volume was 200 µL. Guinea-pig anti-porcine insulin serum (Sigma, No. I8510) was used at a final dilution of 1:260,000. Antibody bound and free hormone were separated by

means of one mL 1 to 8 diluted anti-guinea-pig solid phase suspension (IDS, Boldon, England, No. AA-SAC3). Detection limit was 0.035 ng/mL. Plasma dilution curves were parallel to the standard curve. Mean recovery of 0.32, 0.64, 1.28 and 2.56 ng of insulin standard added to 200 µL of two plasma samples was 104, 99, 98, and 96%, respectively. Inter- (n=7) and intraassay (n=24) CV of a control sample with an insulin concentration of 1.31 ng/mL were 4.8 and 6.5%, respectively.

Plasma IGF-1 concentrations were measured in duplicate by a validated RIA (J.H.F. Erkens, unpublished results), using rabbit anti-hIGF-1 serum AFP4892898, obtained through NHPP, NIDDK, and Dr. A.F. Parlow. The inter- and intraassay CV were 6.8 and 3.8%, respectively.

Statistical analyses

Statistical analyses were performed with the GLM-procedure of the statistical package SAS (1990). Preliminary statistical analyses showed no interactions (P>0.25) between treatments (diet before, diet after), for any of the dependent traits. Therefore, all statistical models were reduced to the main effects (diet before, diet after, and batch).

To test effects of dietary energy source before ovulation on the WEI, duration of estrus, interval from weaning-to-ovulation (**IWO**), and ovulation rate, as well as plasma glucose, insulin, and IGF-1 concentration on d 4 postweaning, the following model was used:

$$Y_{ij} = \mu + \text{diet before}_i + \text{batch}_j + e_{ij}, \quad [1]$$

where Y_{ij} = dependent variable; μ = overall mean; diet before_i = effect of dietary energy source before ovulation (i = Fat, Starch); Batch_j = effect of batch (k = 1 to 8); e_{ij} = residual error.

For uterine, placental, and embryonic traits, as well as total luteal weight, plasma glucose, insulin, and IGF-1 concentrations on d 32 of pregnancy, the following model was used:

$$Y_{ijk} = \mu + \text{diet before}_i + \text{diet after}_j + \text{batch}_k + e_{ijk}, \quad [2]$$

where Y_{ijk} = dependent variable; μ = overall mean; diet before_i = effect of dietary energy source before ovulation (i = Fat, Starch); diet after_j = effect of dietary energy source after ovulation (j = Fat, Starch); Batch_k = effect of batch (k = 1 to 8); e_{ijk} = residual error.

To calculate relationships between traits, a covariate and its interactions with treatments were introduced into model 1 or 2. Thereafter, non-significant interactions and treatments were deleted from the model.

To calculate the risk that sows not exhibit estrus within 9 d postweaning, Cox proportional hazard regression (survival analysis) was performed (STATA Corp, 1997). This analysis combines the occurrence of estrus within 9 d postweaning with the timing of estrus when sows came into estrus. The proportion of sows exhibiting estrus within 9 d after weaning and the percentage of pregnant sows was compared with Fisher's exact test (SAS, 1990).

RESULTS

Body weight, backfat thickness, and feed intake

Sows farrowed at an age of 342 (SD=18) d. Average body weight and backfat thickness of the sows after farrowing were 170 (SD=14) kg and 15.8 (SD=2.9) mm, respectively. Lactational body weight loss and backfat loss were 22 (SD=10) kg and 2.4 (SD=1.5) mm, respectively. This was 13.0 (SD=5.9) % and 15.0 (SD=8.7) % of body weight and backfat at farrowing, respectively.

Sows that exhibited estrus within 9 d after weaning, realized a feed intake before ovulation of 1.75 and 1.58 (SEM=0.07; P=0.09) times maintenance, for Fat and Starch, respectively. Realized feed intake of pregnant sows after ovulation was 1.25 times maintenance for all sows.

WEI, IWO, and duration of estrus

Sixty-seven sows expressed estrus within 9 d postweaning. Three sows (all Fat diet) ovulated, without expressing estrus. The percentage of sows exhibiting estrus within 9 d after weaning was 52 (n=29) and 67 % (n=38) for Fat and Starch, respectively (P=0.11). Average WEI was 134 and 123 h (P=0.12; Table 2) for sows fed the Fat and Starch diet, respectively. Cox proportional hazard regression showed that sows fed the Fat diet had a 1.6 higher risk to remain anestrous until d 9 postweaning than sows fed the Starch-rich diet (P=0.04; Figure 1). No significant effect of dietary energy source before ovulation on duration of estrus, IWO, or ovulation rate was found (Table 2).

Table 2. Effects of dietary energy source before ovulation on estrus and ovulation

	Before ovulation		SEM	P-value
Energy source	Fat	Starch		
Number of sows at start	56	57		
Number of sows in estrus	29	38		0.11
WEI, h	134	123	5	0.12
Duration of estrus, h	55	55	2	0.75
IWO[b], h	167	160	4	0.15
Ovulation rate, n	19.5	19.7	0.8	0.86

[a] WEI=weaning-to-estrus interval.
[b] IWO=interval-weaning-to-ovulation.

Overall, sows not showing estrus within 9 d postweaning had a lower backfat thickness at farrowing (14.9 vs 16.4 mm; SEM=0.4; P=0.008) and at weaning (12.6 vs 14.0 mm; SEM=0.4; P=0.008) than sows that expressed estrus within 9 d postweaning. No difference in body weight at farrowing or lactational body weight loss was found between both categories of sows.

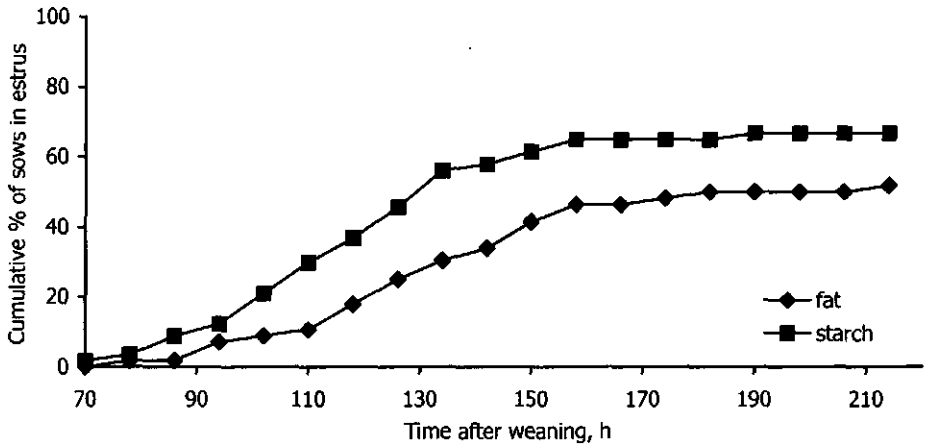

Figure 1. Cumulative percentage of sows showing estrus before d 9 postweaning per dietary energy source before ovulation.

Ovulation rate, fetuses, uteri, and placentas

Five sows returned to estrus after insemination. All these 5 sows were fed the Fat diet before ovulation and 4 of these sows were fed the Starch diet after ovulation. Percentage of weaned sows that were pregnant on d 35 after last insemination was 43 and 67% for sows that received the Fat and Starch diet before ovulation, respectively (P=0.02).

Ovulation rate did not differ between sows fed the two dietary energy sources before ovulation. Hardly any effect of dietary energy source, either before or after ovulation, on uterine, placental, or embryonic traits was found (Table 3). Total luteal weight and implantation area tended to be greater in sows fed the Fat-rich diet after ovulation compared to sows fed the Starch-rich diet. After correction for the number of viable embryos, the tendency in the latter effect remained (258 vs 230 cm^2; SEM=12; P=0.08)

Table 3. Effects of dietary energy source before and after ovulation on uterine, placental, and embryonic traits

	Before ovulation		After ovulation		SEM	P-value[a]	
Energy source	Fat	Starch	Fat	Starch		Before	After
Number of sows	24	38	35	27			
Viable embryos, n	12.0	11.9	11.5	12.5	0.7	0.86	0.29
Embryonal survival, %	62	61	60	63	3	0.93	0.37
Luteal weight, g	6.8	6.5	6.9	6.4	0.2	0.29	0.09
Empty uterine weight, kg	1.7	1.8	1.8	1.8	0.1	0.59	0.85
Empty uterine length, m	4.6	4.6	4.6	4.6	0.2	0.79	0.82
Embryonal weight, g	4.9	5.0	4.9	5.0	0.1	0.61	0.39
Embryonal length, cm	4.1	4.1	4.1	4.1	0.03	0.51	0.57
Placental weight, g	55	58	58	54	2	0.27	0.14
Placental length, cm	39	40	40	38	1	0.43	0.25
Implantation area, cm^2	251	238	259	229	12	0.43	0.06

[a] Statistical significance. the interaction before x after was not significant.

Glucose, insulin, and IGF-1

No effect of dietary energy source was found on plasma glucose concentration (d 4 postweaning: 103.1 mg/100 mL (range 79.6 to 130.4); d 32 of pregnancy: 100.5 mg/100 mL (range 54.8 to 153.7)). Also no effect on IGF-1 concentration was found (d 4 postweaning: 120 ng/mL (range 50 to 214); d 32 of pregnancy: 74 ng/mL (range 45 to 112)). Plasma insulin concentration on d 4 postweaning tended to be higher in sows fed the Starch diet compared to sows fed the Fat diet before ovulation (0.97 vs 1.30 ng/mL; SEM=0.13; P=0.08), and on d 32 of pregnancy this difference was significant (0.58 vs 1.14 ng/ml; SEM=0.10; P<0.001, for Fat and Starch after ovulation, respectively).

Relationships between body weight or backfat and reproductive traits

A higher lactational body weight loss resulted in a prolonged WEI (ß=0.73 h/kg; R^2=0.14; P=0.04) and also a higher backfat loss was associated with an extended WEI (ß=4.7 h/mm; R^2=0.14; P=0.04).

Hardly any relationships between body weight (loss) or backfat thickness (loss) and uterine, placental, or embryonic traits were found. Only a positive association was found between luteal weight and body weight at weaning (ß=0.03 g/kg; R^2=0.17; P=<0.001) and between luteal weight and backfat thickness at weaning (ß=0.14 g/mm; R^2=0.11; P=0.01).

Relationships between glucose, insulin, or IGF-1 and reproductive traits

Plasma IGF-1 concentration on d 32 of pregnancy was negatively related with average placental weight (ß=-0.25 $g.ng^{-1}.mL^{-1}$; R^2=0.18; P=0.002) and average placental length (ß=-0.12 $cm.ng^{-1}.mL^{-1}$; R^2=0.27; P=0.04). These relationships remained after correction for the number of embryos. Plasma glucose and insulin levels, either at d 4 postweaning or d 32 of pregnancy, were not associated with any of the reproductive traits. Overall, plasma glucose concentration was higher in sows showing estrus within 9 d postweaning compared to anestrous sows (98.9 vs 106.6 mg/100 mL; SEM=2.0; P=0.009).

DISCUSSION

The metabolic hormone insulin and the growth factor IGF-1 are associated with several reproductive traits (Cox, 1997). It was suggested that insulin has a direct effect on the ovaries; it increases ovulation rate (Cox et al., 1987) by decreasing the number of atretic follicles (Matamoros et al., 1990). Also an indirect effect of insulin on reproduction, via the hypothalamus-pituitary, is suggested by results of Tokach et al. (1992), Koketsu et al. (1996) and Quesnel et al. (1998). They found a positive correlation between plasma insulin concentration and LH secretion. Described effects of IGF-1 on reproduction are mostly restricted to direct effects on follicle development (Cox, 1997), although some evidence has been given that IGF-1 can act at the hypothalamus-pituitary level. Pettigrew and Tokach

(1993) found a positive correlation between plasma IGF-1 concentration and LH pulse frequency in lactating sows and Whitley et al. (1995) found a positive effect of IGF-1 administration to cultured porcine pituitary cells on LH secretion.

Plasma insulin concentration (Ponter et al., 1991; Van den Brand et al., 2000a) and IGF-1 concentration (Chapter 5) can be enhanced by feeding starch-rich diets during lactation. Also in the present study this positive effect of the Starch-rich diet on plasma insulin level both before and after ovulation was demonstrated, although a positive effect of the starch diet on IGF-1 concentration was lacking. In another study (Chapter 5), it was also shown that IGF-1 concentration hardly differ between the two dietary energy sources when fed postweaning. When insulin is an effector of reproduction, a positive effect of starch-rich diets on reproduction could be expected.

In a previous experiment (Van den Brand et al., 2000a, b), fat and starch-rich diets were fed to primiparous sows from farrowing to d 35 of subsequent pregnancy. In the present experiment diets were fed between weaning and ovulation or during the early pregnancy, to separate effects of diets during the different periods of the reproductive cycle (lactation, IWO, early pregnancy).

In the present experiment 15% more sows came into estrus within 9 d postweaning and an 11 h shorter WEI was found in sows fed the Starch diet compared with sows fed the Fat diet. The risk that sows did not show estrus within 9 d postweaning was higher in sows fed the Fat-rich diet than in sows fed the Starch-rich diet. These effects of postweaning dietary energy source on the occurrence and timing of onset of estrus are somewhat unexpected. It is suggested that LH pulsatility directly after weaning is an important determinant of the WEI, which is positively related with the LH pulse frequency during lactation (Shaw and Foxcroft, 1985; Zak et al., 1998). In the present experiment all sows received the same diet during lactation. This suggests that the effect of LH pulse frequency during lactation is not the only factor affecting subsequent WEI.

It can be suggested that when the LH pulsatility after weaning is high and also a good follicle pool is available, postweaning nutrition will not affect the WEI. When the LH pulse frequency after weaning and(or) the follicle pool is suboptimal, it can be imagined that nutrition can play a role in the stimulation of postweaning LH secretion and therefore in follicle recruitment and return to estrus. In the present study the percentage of sows showing estrus within 9 d postweaning was low, which suggests that LH pulsatility postweaning was not optimal. Because the Starch-rich diet enhanced the plasma insulin concentration and insulin is positively associated with LH pulse frequency (Tokach et al., 1992; Koketsu et al., 1996; Quesnel et al., 1998) a positive effect of the Starch-rich diet on WEI can be expected. This can be the reason that in postweaning flushed sows a higher percentage of sows showed estrus (Fahmy and Dufour, 1976; Carroll et al., 1996).

The relatively low percentage of sows exhibiting estrus within 9 d postweaning is probably caused by 1) the relative low feed intake, probably due to the switch from liquid feed during lactation to solid feed after weaning and(or) 2) the relatively high lactational body weight loss of the sows. Sows lost on average 13.0% of their body weight during lactation. Vesseur et al. (1994) showed that in primiparous sows with more than 12.5% of weight loss during lactation 43.4% of the sows had not shown estrus before d 15 postweaning. This is comparable with the 41% of sows not expressing estrus before d 9 postweaning in the present study. Whittemore (1996) reviewed effects of lactational feed intake on percentage of anestrous sows postweaning and concluded that a high lactational body weight loss, due to a low feed intake, results in a higher percentage of anestrous sows and an extended WEI. This is in agreement with the results of the present study.

In the present study, feed intake before ovulation tended to be lower in sows fed the Starch-rich diet than in sows fed the Fat-rich diet, probably due to the higher percentage of sows showing estrus (and largely being off feed in that period). When feed intake before ovulation would have been similar between the two diets, possibly larger differences in WEI between dietary energy sources were found.

Although plasma insulin levels were higher in sows fed the Starch-rich diet, no increase in ovulation rate was found. For an increase in ovulation rate it can be suggested that the enhancement of insulin by feeding starch-rich diets in the present study is not large enough. Cox et al. (1987) gave exogenous insulin injections to gilts and found an increased ovulation rate. It seems that a higher concentration of insulin is necessary to stimulate ovulation rate than physiologically can be reached by dietary factors.

Effects of dietary energy source on uterine, placental, and embryonic development are hardly investigated. Grandhi (1988), Perez Rigau et al. (1995) and Van den Brand et al. (2000b) found no effect of feeding either a fat-rich of a starch-rich diet during early pregnancy on development of uteri, placentas, or embryos. The tendency to a higher luteal weight and greater implantation area in sows fed the Fat-rich diet is hard to explain. It seems that the insulin-stimulating diet did not have a strong effect on development of uteri, placentas, or embryos in primiparous sows.

Hardly any relationship between insulin or IGF-1 concentration and uterine, placental, and embryonic traits were found. This is in agreement with results found by Van den Brand et al. (2000b). The relative strong relationship between IGF-1 concentration and placental size remained consistent after correction for the number of viable embryos. Whether this relationship has a physiological background is not clear.

IMPLICATIONS

From the present experiment it can be concluded that feeding a starch-rich diet from weaning to ovulation compared to a fat-rich diet, enhances plasma insulin concentration, and has a positive effect on the occurrence and timing of estrus within 9 d postweaning. Dietary energy source from weaning to ovulation or in early pregnancy seems to have hardly any effect on uterine, placental, or embryonic traits.

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GENERAL DISCUSSION

INTRODUCTION

In the last 50 years large changes have occurred in pig husbandry. In the past, sows were mostly housed outdoor, whereas nowadays most sows are housed in climate controlled stables. Furthermore, the number of sows per farm has increased considerably. In 1950 the average number of sows in The Netherlands was about 10 (Dommerhold, 1951) on mixed farms, whereas in 1998 this number had increased to 220, (SIVA, 1999), mostly in specialized farms. Besides the number of sows per farm, the productivity per sow increased in that period. The number of weaned piglets per sow per year was about 19 in 1950 (Dommerhold, 1951), and increased to 22 in 1998 (SIVA, 1999), especially due to the higher number of litters per year (2.0 vs 2.3). Furthermore, milk production increased considerably in that period (from approximately 7 to 10 kg/d; Mackenzie and Revell, 1998), resulting in a higher litter growth rate. Coinciding with this increased production, body fatness of sows has considerably decreased over the last 5 decades, and lactational feed intake did not increase.

This increased production together with smaller body fat reserves requires an optimal nutrient intake during the several stages of the reproductive cycle. Especially during lactation, when nutrient demands for milk production are very high, an optimal nutrient intake is required. When the offered amount of nutrients do not cover the requirements, sows will use their body reserves to keep milk production at an adequate level.

Consequently, nutritional requirements of highly prolific sows nowadays differ from that of sows 50 years ago. In the fifties, the diet of lactating sows could consist of fodder beets, sugar beets, and potatoes, together with 'good pasture land' (Dommerhold, 1951). Nowadays more insight in the physiology of digestion and metabolism, as well as in the metabolic demands of sows (for e.g. milk production) has resulted in an optimized diet composition. Minerals and vitamins are added to the diet and the protein content and quality in the diet is optimized by addition of synthetic amino acids.

Despite these optimized diets, lactational body weight loss of sows is still considerable, especially in primiparous sows (Mullan and Williams, 1990; Vesseur et al., 1994). Because these sows have not yet reached their mature body weight, nutrients are necessary for growth. Furthermore, in these sows the gastro-intestinal tract limits the consumption of large amounts of feed. Body weight losses during lactation can affect subsequent reproduction characteristics, such as the weaning-to-estrus interval (WEI; Vesseur et al., 1994), ovulation rate (Zak et al., 1997a) or embryonal survival (Kirkwood et al., 1990; Baidoo et al., 1992; Zak et al., 1997a).

Therefore, nutrition of sows, especially during lactation, is an important determinant for optimal reproductive performance of primiparous sows. In the past, research on the impact

of nutrition on reproduction has mainly been focused on feed intake (both energy and protein), whereas hardly any attention has been given to dietary energy source. The reason that dietary energy source can play a role in reproduction of sows, is related to its effect on plasma insulin concentration (Newcomb et al., 1991; Ponter et al., 1991). Insulin is thought to affect several reproductive traits as summarized by e.g. Pettigrew and Tokach (1993) and Cox (1997). Therefore, insulin-stimulating diets might improve reproductive performance of sows. Because the metabolic status of sows also affects reproductive performance, it should be investigated whether effects of nutritionally manipulated plasma insulin concentration on reproduction in sows interacts with the energy and(or) protein balance.

This thesis attempts to give more detailed insight into effects of dietary energy source on reproductive performance of primiparous sows. Furthermore, it gives more insight into the interaction between dietary energy source and metabolic status on reproductive performance of primiparous sows. In this thesis the use of dietary energy sources is restricted to enzymatically digestible maize starch and sugar (more insulin-stimulating) and tallow (less insulin-stimulating). Metabolic status was manipulated by changing lactational feed intake (near ad libitum or 25% less than near ad libitum).

EFFECTS OF DIETARY ENERGY SOURCE AND FEEDING LEVEL ON ENERGY AND PROTEIN PARTITIONING DURING LACTATION

When nutrient intake during lactation is limited, sows will use their body fat and body protein reserves to maintain their milk production. Consequently, most sows are in a negative energy balance and probably also in a negative protein balance during lactation. On the other hand, piglets during lactation are in a positive energy and protein balance, which is highly desired. Therefore, effects of dietary energy source or feed intake during lactation on energy partitioning need to be discussed for sows and piglets, separately.

Milk production and composition

The results found in the present study, regarding milk production (Chapter 2), are generally in agreement with other studies. It can be concluded that even a mild restriction of feed intake (25% in the current study) can decrease milk production. Dietary energy source seems to have only a minor effect on milk production, in terms of quantity. This has been found earlier when diets are fed to provide an isocaloric and isonitrogenous feed intake (Lellis and Speer, 1983; Babinszky, 1992). In studies in which fat was supplemented to the diet or in which ad libitum feed intake was applied during lactation (and thus energy intake was increased), sometimes a higher milk production was found in sows fed a fat-rich diet (Shurson et al., 1986), although others found no difference in milk production (Schoenherr et al., 1989; Tilton et al., 1999).

Regarding effects of dietary energy source and feed intake on milk composition, in the current study an interaction was found for milk fat concentration. In sows fed the fat-rich diet at the high feeding level, dietary fat seems to be secreted into the milk, whereas in sows fed the starch-rich diet at the high feeding level, less dietary fat was available for secretion into the milk. In sows fed at the low feeding level, mobilization of body fat is higher and fatty acids from body fat are partly secreted into the milk, regardless of dietary energy source. Consequently, milk fatty acid composition reflects the fatty acid composition of the diet (when dietary feed and fat intake is relatively high) or of the body (when sows are in a severe negative energy balance; Boyd and Kensinger, 1998).

In general, it can be concluded that feeding of fat-rich diets (isocaloric or supplemental) to lactating sows results in an increase in milk fat concentration. Based on literature, Drochner (1989) calculated a strong linear relationship between dietary fat content and milk fat concentration. However, the absolute fat content in milk of fat fed sows differs strongly between studies (Chapter 2: 7.6 to 8.4%; Tilton et al., 1999: 9.6%; Babinszky, 1992: 8.0 to 10.5%; Shurson et al., 1986: 11.2%; Boyd et al., 1982: 14.9%). This is dependent on several factors such as absolute fat concentration in the diet, fatty acid composition of the dietary fat, absolute feed intake, milk quantity, technique of milking, and bred of the sows.

On the other hand, milk protein and lactose concentrations seem to be less dependent on dietary energy source and feed intake of sows (Den Hartog et al., 1987; Pluske et al., 1998; King et al., 1999), although Van Kempen et al. (1985) and Noblet and Etienne (1986) earlier found a higher milk protein concentration in restricted fed sows.

Due to the lower milk production (g/d) and higher milk fat concentration (Armstrong et al., 1986; Noblet and Etienne, 1986; Pluske et al., 1998) in sows with a low feed intake during lactation, the milk fat production (g/d) is in general similar between sows with a low or a high feed intake (Van Kempen et al., 1985; Noblet and Etienne, 1986). This was also confirmed in the present study for sows fed the starch-rich diet, but not for sows fed the fat-rich diet. In sows fed the fat-rich diet, the extra ingested dietary fat at the high feeding level compared with the low feeding level seems to have a stimulating effect on the output of milk fat. This is summarized for the present study (Chapter 2) in Table 1. It can be concluded that extra dietary fat intake of approximately 120 g/d resulted in an extra milk fat output of approximately 200 g/d.

Table 1. Calculated daily fat contents available from feed or body and daily milk fat output

Feeding level	High		Low	
Energy source	Fat	Starch	Fat	Starch
Dietary fat intake, g/d	452	146	334	112
Mobilization of body fat, g/d	568	401	561	522
Fat in milk, g/d	806	683	608	671

In conclusion, dietary energy source had no effect on milk quantity, whereas a high feeding level did increase milk quantity. However, in terms of fat and energy output in the milk a clear interaction was found. At the low feeding level fat output was similar for both dietary energy sources. At the high feeding level fat output in the milk was increased in sows fed the fat-rich diet compared with those fed the starch-rich diet.

Piglet growth and body fatness

Litter growth rate of sows fed the high feeding level during lactation was higher compared with sows fed the low feeding level (Chapter 2), being probably due to the difference in milk production. This is confirmed by the calculated efficiency with which piglets convert milk to body gain of 4.2 (g/g); being similar for all treatment groups. The calculated value is in the range found by other authors. Babinszky (1992) reported efficiency ratios between 4.0 and 4.5 and no difference between piglets of sows fed either a starch or a fat-rich diet. Pluske et al. (1998) observed no difference in the efficiency ratio of milk to gain between piglets of restricted fed, ad libitum fed, or superalimented lactating sows (3.8 to 4.2 g milk per g gain), and Beyer (1986) found no difference in efficiency between first, second, and fourth parity sows (4.0 to 4.3). Beyer and Jentsch (1994) found a decrease in efficiency ratio of milk to gain between the first and fourth week of lactation (3.5 to 5.0 g milk/g gain). This suggests that neither feed intake nor dietary energy source nor parity, but stage of lactation affects the efficiency of utilization of milk for gain by the piglets. That stage of lactation influences the efficiency of utilization of milk for growth can be explained by the increasing fraction of total milk intake required for maintenance. Because milk production is influenced by feed intake and not by dietary energy source, lactational feeding level seems to be a more important tool to affect litter growth than dietary energy source.

Whether higher milk fat concentrations are beneficial for piglets or not is disputable. It can be suggested that high milk fat concentrations can lead to digestive disorders (diarrhea) in young piglets. In the present study (Chapter 2) no visual differences in feces of the piglets were observed, but the milk fat concentration of sows fed the fat-rich diet was not very high (7.6 to 8.4%). It can be proposed that extremely high milk fat concentrations can result in fat diarrhea during lactation. On the other hand, based on literature, it can be suggested that an increased milk fat content is beneficial for young piglets, due to the higher energy concentration, because the glycogen stores in the body of newborn piglets are depleted at approximately 48 h after birth (Elliot and Lodge, 1977). The higher fat concentration in milk of sows fed a fat-rich diet during lactation can result in a higher survival rate of especially small piglets. Several studies have shown a (slight) improved piglet survival rate during lactation when fat-rich diets were offered to sows during late gestation and(or) lactation (Drochner, 1989; Schoenherr et al., 1989; Pettigrew and Moser, 1991; Shurson and Irvin, 1992; Azain, 1993). Seerley (1984) has stated that the largest improvement of piglet survival

after parturition is found when fat-rich diets are fed during late gestation, and less when these diets were fed during lactation. The suggested optimal fat level in the sow's diet for piglet survival is between 7.5 and 15.0% (Seerley, 1984).

Because milk fat is highly digestible (Pluske and Dong, 1998; King et al., 1999) it could be expected that the interaction between dietary energy source and feeding level in milk fat concentration also was found in body fat concentration and deposition of the piglets. This higher body fat concentration might be a potential risk for the health of the piglets. After weaning, the change from milk to solid feed has consequences for the enzyme capacity of the digestive tract and the morphology and function of the gut. It can be imagined that for fatter piglets this can result in a drop in feed intake after weaning, because of their larger body reserves (Stahly et al., 1980). On the other hand, it can be suggested that fatter piglets have more body reserves and that they therefore will better adapt to postweaning stresses, such as solid feed instead of milk, and therefore have less postweaning problems.

Effects of body fatness at weaning on slaughter quality at market weight are hardly investigated. Friend (1974) found that an increase in body fat content of piglets at weaning persisted to market weight, whereas Stahly et al. (1980) found no effect of body fatness at weaning on carcass fatness at market weight. Because lean meat percentage is an important factor for the profitability of the pig farm, attention to body fatness of piglets at weaning should be given.

It can be concluded that lactational feed intake of sows but not isocalorically fed dietary energy sources seems to affect litter growth rate. Feeding of fat-rich diets increased milk and piglet body fat concentration when fed at a high feeding level and might increase preweaning survival rate. Whether higher body fatness of piglets at weaning, due to feeding of fat-rich diets to sows, is beneficial for the piglet is disputable.

Energy and protein balance of the sows

In the present study, within feeding levels, different amounts of feed were offered to the sows to provide an isocaloric and isonitrogenous feed intake between dietary energy sources, based on the calculated NE content. In Chapter 2, it was demonstrated that at the high feeding level the total retained energy in the litter and sow together was 91 and 193 $kJ.kg^{-0.75}_{sow}.d^{-1}$ for the fat and starch diet, respectively. At the low feeding level these values were −85 and −12 $kJ.kg^{-0.75}_{sow}.d^{-1}$, respectively.

It can be concluded that the NE of the sows was not similar for the starch and fat diet, within feeding levels. This difference in energy balance is partly due to the 4% lower ME/GE ratio of the fat-rich diet. Fat supplementation can result in a lower digestibility of the complete diet as suggested by Noblet et al. (1993) and Shi and Noblet (1993) and found by Babinszky (1992).

More specifically, it can be proposed that the use of tallow (generally mono-unsaturated and saturated fatty acids) as fat source in the fat-rich diet depressed the digestibility of the fat content. From long chain (mono-un)saturated fatty acids it is known that the digestibility is relatively low in young piglets (Cera et al., 1988, 1989) and also in growing-finishing pigs (Stahly, 1984). In growing-finishing pigs, a high ratio between unsaturated and saturated fatty acids (>2.0) is important for a high fat digestibility (Stahly, 1984; Powles et al., 1993, 1995). Data on digestibility of fatty acids by lactating sows are lacking. The fat-rich diet in our study had an unsaturated/saturated fatty acids ratio of approximately 1.3, and it can be expected that the digestibility of the fat content in the fat-rich diet is lower than of the (low) fat content in the starch-rich diet. The somewhat lower heat production in sows fed the fat-rich diet does not compensate the negative effects of the lower ME/GE ratio on retained energy.

In general, a higher feed intake of sows during lactation results in a less negative energy balance (Verstegen et al., 1985; Noblet and Etienne, 1987). However, as demonstrated in the present study, this depends of the used dietary energy source. An additional energy supply of 25% in the form of fat, together with an additional protein supply of 25%, resulted in a 25% higher milk energy output and therefore in a similar negative energy balance as in sows that were fed at a low feeding level during lactation. When the 25% additional energy was given as starch, together with 25% extra protein, milk energy output increased only 11% and was furthermore used to reduce the depth of the negative energy balance.

Because the protein and fat balance, as described in Chapter 2, only concerned the period from d 6 to 20 of lactation, total lactational body protein and fat losses were not measured. This was also not possible because the protein and fat balance was measured as an average of three sows per climatic respiration chamber. To calculate the relative body fat and protein losses during lactation, the absolute amount at the start of lactation should be known. In several studies, formulas are composed to calculate these amounts based on body weight and backfat thickness (P2) (King et al., 1986; Whittemore and Yang, 1989). CVB (1994) also composed such formulas for Dutch sows, based on results of Everts and Dekker (1995). These formulas were:

$$\text{Body fat (kg)} = -11.58 + 0.1027 * \text{BW (kg)} + 1.904 * \text{backfat (mm)}$$

$$\text{Body protein (kg)} = 1.90 + 0.1711 * \text{BW (kg)} - 0.3113 * \text{backfat (mm)}$$

Based on these formulas the body fat and protein contents at farrowing and weaning were calculated for the present experiment (Chapter 2). The results of these calculations are summarized in Table 2.

Table 2. Body fat and protein contents at farrowing and at weaning (LSmeans)

Feeding level	High		Low		SEM	P-value[a]	
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source
Farrowing							
Body weight, kg	161.6	161.6	161.0	163.3	2.7	0.90	0.66
Backfat thickness, mm	17.6	18.7	17.3	17.3	0.6	0.19	0.42
Body fat, kg	38.6	40.6	37.9	38.1	1.3	0.28	0.39
Body protein, kg	24.1	23.7	24.1	24.5	0.5	0.62	0.94
Weaning							
Body weight, kg	146.0	149.1	137.8	141.8	2.3	0.20	0.14
Backfat thickness, mm	12.3	14.2	12.2	12.7	0.6	0.28	0.05
Body fat, kg	26.8	30.8	25.7	27.1	1.3	0.23	0.05
Body protein, kg	23.1	23.0	21.7	22.2	0.3	0.21	0.52
Lactational weight loss, kg	15.6	12.5	23.2	21.6	1.6	0.003	0.16
Lactational fat losses, %	30.8	24.1	32.3	29.3	1.8	0.33	0.01
Lactational protein losses, %	4.0	2.9	9.7	9.2	1.1	0.002	0.47

[a] Statistical significance; the feeding level x energy source interactions were not significant.

The relative body fat losses during lactation were lower in sows fed the starch-rich diet compared with those fed the fat-rich diet, whereas relative protein losses were higher in sows fed the low feeding level compared with those fed the high feeding level. For both traits, no interaction between feeding level and dietary energy source was found (P>0.32). These relative body fat and protein losses during the whole lactation agree with the results calculated in Chapter 2 for the period between d 6 and 20 of lactation. These results suggest that the extra protein intake in sows fed the fat-rich diet at the high feeding level is partly secreted into the milk, but mainly used for reduction of the negative protein balance, in contrast with effects of the extra fat intake, which is largely secreted into the milk. In sows fed the starch-rich diet at the high feeding level, both extra energy and protein intake are partly used for milk production and furthermore for reduction of the negative energy and protein balance.

In the present study (Chapter 2), effects of energy sources were compared between feeding levels and consequently not only energy intake is increased at the high feeding level, but also the protein intake. It can be discussed whether other results would have been obtained when only energy intake was increased and the protein intake was similar for the both levels of energy intake. It can be imagined that no difference in protein balance between feeding levels was found in that situation, but that energy balance would not be strongly different from the present study.

A question is why sows at the low feeding level used so much body protein. Possibly the protein content in the diet was not sufficient to maintain the milk production at an adequate level. At the low feeding level, sows received 790 g fecal digestible CP per day. Assuming a

requirement for maintenance of 0.45 g $N.kg^{-0.75}d^{-1}$ (Everts and Dekker, 1994; 127 g CP/d for a sow of 160 kg), 663 g CP remains for milk production. Milk production at the low feeding level was approximately 8.5 kg per day with a protein content of 5.4%. Efficiency of fecal digestible CP for the utilization of milk CP is about 0.70 (Burlacu et al., 1985; CVB, 1995; King et al., 1995), resulting in a requirement for milk production of 655 g CP. In this situation, the daily offered dietary protein should be sufficient for this milk production. However, efficiency of the utilization of dietary protein for milk protein is variable between studies, probably dependent on the amino acid composition. For example, Beyer (1986) found an efficiency of 0.61 between fecal digestible nitrogen and milk nitrogen. When in the calculations above, an efficiency lower than 0.70 is used, a deficiency of dietary CP arises. In that case the sows must have used body protein to produce sufficient milk for the piglets.

Another possible explanation for the high body protein loss at the low feeding level is that the dietary energy available for maintenance and milk production was too low (as can be seen by the high body fat losses), and that a part of the dietary protein is used as energy source. It can also be suggested that the glucose supply for milk lactose production was too low and that therefore glucogenic amino acids are used to produce milk lactose. In sows fed the fat-rich diet at the low feeding level, glucose supply from starch plus dextrose was 585 g/d. Assuming that the ME/GE ratio of maize starch and dextrose is approximately 100%, available glucose for lactose production was maximal 585 g/d. The glucose requirement for maintenance is 2.21 mg glucose per minute per kg BW (Linzell et al., 1969), resulting in a glucose requirement for maintenance for a sow of 160 kg of 510 g/d. For production of milk with 4.5% lactase, Boyd and Kensinger (1998) calculated a glucose requirement of 14.1 g/dL. Average milk production at the low feeding level was 8.5 kg/d (with 5.2% lactose), resulting in a daily glucose requirement for milk production of 1200 g. It can be concluded that the glucose demand for maintenance and milk production largely exceeded the glucose supply from feed. Therefore, sows will use body protein and possibly body fat for lactose production.

Effects of ad libitum feed intake during lactation

In the present study, sows were restricted fed during lactation. However, in practice, sows are mostly fed ad libitum during lactation. Therefore, the question arises how dietary energy source will affect milk production, milk composition, body composition of the piglets as well as energy and protein balance of the sows, when sows would have been fed ad libitum.

Drochner (1989) concluded from a literature study that the average metabolizable energy intake of ad libitum fed sows was 12% (range 3 to 32) higher in sows fed a fat-rich diet than in sows fed a starch-rich diet. The extra consumed energy in sows fed a fat-rich diet is largely in the form of fat. Based on results of the present study (Chapter 2), it can be suggested that this extra fat have a milk fat stimulating effect, resulting in an increased milk

fat output. It can also be suggested that, because of the higher energy intake, the milk production will increase a little, as already shown. This all will result in piglets with a higher body fat content and possibly a slight increase in daily weight gain. The expectation is that, due to the higher milk fat secretion, the energy balance of the fat fed sow will not be considerably improved. In ad libitum fed sows with a starch-rich diet, possibly the energy balance of the sows will be less negative, because the extra amount of starch will be used both for milk production and reduction of the negative energy balance. When, with ad libitum feeding, also the protein intake will increase, it can be suggested that the protein balance can reach a value near or equal to zero.

The target of the present study was to compose diets that differ in plasma insulin stimulation and to investigate effects of these diets on reproduction in primiparous sows. Furthermore, it would be investigated whether these effects were dependent on the metabolic status (energy and protein balance) of sows. It is generally assumed that energy and(or) protein balances of sows during lactation largely impacts postweaning reproductive performance.

Therefore, it can be suggested that, based on the results discussed above, sows fed the low feeding level will have impaired reproduction results. It can also be expected that sows fed the fat-rich diet at the high feeding level would have lower reproductive performance, because of the higher fat losses, compared to sows fed the starch-rich diet.

EFFECTS OF TREATMENTS ON PLASMA INSULIN CONCENTRATION

Dietary energy source

In all experiments performed in this study, plasma insulin concentration was higher in sows fed a starch-rich diet compared to sows fed a fat-rich diet. This means that in gilts (Chapter 1) and lactating sows (Chapter 3) as well as in sows postweaning (Chapter 6) an effect of dietary energy source on plasma insulin concentration was found. From these results it can be concluded that the effect of dietary energy source on plasma insulin concentration is not dependent on the physiological and metabolic status of the sow, although average plasma insulin concentration decreased with time during lactation (Chapter 3).

In the present study (Chapter 1 and 3), dietary energy source only affected postprandial plasma insulin concentration. The basal (preprandial) concentration was not affected and also from 4.5 h postprandial onwards no significant effect of dietary energy source was found on plasma insulin concentration. This can suggest that the used diets were not able to induce a sustained higher plasma insulin concentration during the day.

Feeding level during lactation

In the present study no effect of feeding level during lactation on plasma insulin concentration was found at any sampling moment. Moreover, no effect of feeding level on

basal insulin concentration was found. As already mentioned in Chapter 3, a larger contrast in feed intake (about 50%), can result in a difference in average plasma insulin concentration (Koketsu et al., 1996a, 1998; Quesnel et al., 1998b). In practice, primiparous sows are mostly fed ad libitum during lactation and therefore it is not to be expected that plasma insulin concentration will be low due to a low feed intake.

It can be concluded that differences in plasma insulin concentration probably can be achieved by imposing a larger difference in feed intake. Because the high feeding level is in general ad libitum or near ad libitum, effects should be expected by further decreasing the low feed intake.

EFFECTS OF DIETARY ENERGY SOURCE AND FEEDING LEVEL DURING LACTATION ON REPRODUCTION

A target of the present study was to investigate whether plasma insulin concentration could be enhanced by manipulation of the diet, as a tool to improve reproductive performance. It was shown that feeding a starch-rich diet could increase plasma insulin level. Based on these results and information from literature on the proposed role of insulin in reproduction (Pettigrew and Tokach, 1993; Cox, 1997) it could be expected that reproductive performance in sows fed a starch-rich diet would be improved. Whether this occurred will be discussed in this paragraph, as well as effects of feeding level during lactation on reproductive traits.

Dietary energy source

LH pulsatility during lactation tended to be higher in sows fed the starch-rich diet (Chapter 3). However, when calculated per day of lactation, a significant difference in number of LH pulses between the two dietary energy sources was only found on d 7 of lactation. On d 14 no effect of either feeding level or dietary energy source was shown, and on d 21 only an effect of feeding level and not of dietary energy source was found. This suggests that the stimulating effect of a starch-rich diet on LH pulsatility is demonstrated especially in early lactation, when milk production is not yet maximal (Mackenzie and Revell, 1998) and the effect of the negative energy balance on LH pulsatility is still relatively mild. In progressing lactation the effect of the negative energy balance increases and seems to override the effect of dietary energy source on LH pulse frequency. Comparable results were found by Kemp et al. (1995) in multiparous sows.

The risk that sows remained anestrous after weaning did not differ between the fat and starch-rich diet (Cox proportional hazard regression; P=0.49). In sows fed the high feeding level during lactation no effect of dietary energy source on return to estrus was found (Chapter 3). However, at the low feeding level, a 22 h (not significant) shorter WEI was found in sows fed the starch-rich diet compared with those fed the fat-rich diet (Figure 1).

Probably due to the low number of observations no statistically significant interaction between dietary energy source and feeding level during lactation on WEI was found (P=0.25). It can be suggested that dietary energy source can reduce the negative effect of low lactational feed intake on return to estrus. When lactational feed intake is relatively high, dietary energy source did not affect return to estrus.

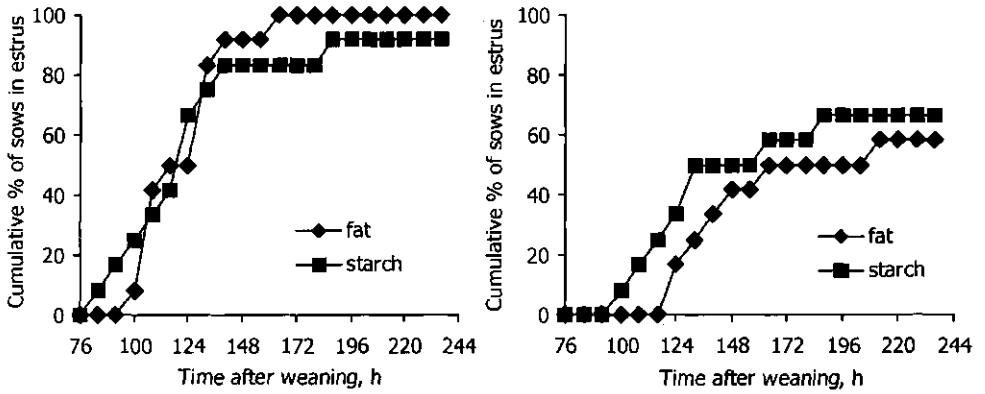

Figure 1. Cumulative percentage of sows showing estrus before d 10 postweaning per dietary energy source for the high (left panel) and low (right panel) feeding level during lactation (n=12 per treatment).

The suggestion that dietary energy source can reduce the negative effect of low lactational feed intake on return to estrus is confirmed by the experiment described in Chapter 6. In sows fed the fat-rich diet only after weaning, the risk was 1.6 times higher to remain anestrous until d 9 postweaning than in sows fed the starch-rich diet (P=0.04).

The difference between the two studies was that in the first experiment (Chapter 3) dietary energy source differed from farrowing until next pregnancy, whereas in the latter experiment (Chapter 6) dietary energy sources differed only between weaning and ovulation. This means that nutrition after weaning still can influence the WEI, even though the WEI is associated with the LH pulse frequency immediately after weaning. This LH pulsatility after weaning is associated with LH pulse frequency during lactation (Shaw and Foxcroft, 1985; Tokach et al., 1992). It can be suggested that in sows with a high LH pulse frequency after weaning and a well-developed follicle pool, no effect of dietary energy source fed after weaning on the WEI will occur. However, in sows with a relatively severe negative energy balance during lactation, LH pulse frequency postweaning is lower and size of the follicles is smaller (Zak et al., 1997b; Quesnel et al., 1998a).

Therefore, it can be suggested that nutrition postweaning can still affect the WEI by stimulation of LH pulsatility and(or) follicle development. Because the starch-rich diet increased LH pulse frequency during lactation, it can be suggested that starch-rich diets can shorten the WEI of sows with a severe negative energy balance during lactation. This suggestion is also supported by the fact that follicle size on d 2 postweaning was increased in sows fed the starch-rich diet (Chapter 3 and 4). Effects of dietary energy sources on follicle development are hardly described in literature, especially in pigs.

The results described in Chapter 4 and 6, furthermore showed that the used dietary energy sources hardly affected periestrus hormone profiles, ovulation rate, and embryonal survival rate as well as uterine, embryonic, and placental development. Thus, it can be suggested that insulin-stimulating diets positively affect reproductive performance on hypothalamus-pituitary level, including the return to estrus, especially in sows fed at a low feeding level during lactation, but hardly affect reproductive traits at uterus level.

Feeding level during lactation

The number of LH pulses per 12 h during lactation was higher in sows fed the high feeding level than those fed the low feeding level. This difference was most pronounced in late lactation and immediately postweaning (Chapter 3). Additional analyses showed that sows fed the low feeding level also had a 1.7 times larger risk (Cox proportional hazard regression; P=0.10; Figure 1) to remain anestrous until 240 h postweaning than sows fed the high feeding level during lactation. This delayed return to estrus in restricted fed sows during lactation is in agreement with results found by Kirkwood et al. (1987), Baidoo et al. (1992), and Koketsu et al. (1996b).

When all sows, including the anestrous sows, were taken into account, the low feeding level resulted in a delayed follicle development (Chapter 3), which is in agreement with Zak et al. (1997b) and Quesnel et al. (1998a). This is possibly due to the lower LH secretion in sows fed at a low feeding level, because LH is necessary for follicle development beyond 4 mm (Driancourt et al., 1995; Brüssow et al., 1996). Whether an impaired follicle development, due to a low feed intake during lactation, results in a lower ovulation rate is unclear. In most studies regarding effects of lactational feed intake, no difference in ovulation rate was found. Only Zak et al. (1997a) found a dramatically lower ovulation rate in sows that were restricted fed during one week of lactation and in the present study a tendency was found for a lower ovulation rate in the sows the low feeding level during lactation (16.2 vs 18.0; P=0.09).

In literature from the seventies and eighties, a low feed intake during lactation often resulted in a dramatic increase in the WEI and the percentage of sows that remain anestrous after weaning. Nowadays, the WEI only differs one to two days between sows with a high or

low lactational feed intake. It can be suggested that breeding programs have resulted in a short WEI in modern hybrid sows, independent of feed intake during lactation. It can be suggested that this short period is not long enough to restore lactational body weight losses and that therefore follicle development is impaired, resulting in a lower ovulation rate and a lower embryonal survival. However, other recent studies regarding effects of lactational feed intake did not find any effect on ovulation rate (Quesnel and Prunier, 1998; Zak et al., 1998). Therefore, more research is necessary to unravel the physiological mechanisms involved in the relationship between lactational feed intake and ovulation rate.

Effects of lactational feed intake on periestrus hormone profiles are not extensively investigated. In general, hardly any effect of lactational feed intake on periestrus hormone profiles is described in literature. More effects of lactational feed intake are found in embryonal survival. Several studies demonstrated that a low lactational feed intake may result in increased embryonal mortality (Kirkwood et al., 1990; Baidoo et al., 1992; Zak et al., 1997a). Grandhi (1992) found a lower embryonal survival rate (73.3%) in sows that lost more than 14 kg of body weight during lactation than in sows that lost less than 14 kg of body weight in that period (82.9%). In the present study no effect of lactational feed intake was found on embryonal survival in subsequent pregnancy (70.4 vs 67.9 for the high and low feeding level, respectively). This is possibly due to the relatively small contrast in feed intake and the low number of observations. Because embryonal mortality is highly variable, a large number of sows is needed to demonstrate statistically significant differences.

Effects of lactational feed intake on uterine, embryonic, and placental development are not extensively described in literature. In general, no effects of lactational feed intake on these traits are found, in agreement with the present study.

Based on the results obtained from the present study, it can be suggested that a relatively mild restriction of lactational feed intake already affects LH pulsatility and return to estrus. Based on literature, it can be suggested that a more severe restriction of lactational feed intake can lead to impaired follicle development and embryonal survival, which is not strongly supported by the present study. Effects of lactational feed intake on periestrus hormone profiles and development of uteri, embryos, and placentas seem to be marginal.

RELATIONSHIPS BETWEEN INSULIN AND REPRODUCTIVE TRAITS

In the present study no significant relationships between plasma insulin concentrations and reproductive traits during and after lactation were found, in contrast with several other studies as summarized by e.g. Pettigrew and Tokach (1993) and Cox (1997).

It can be discussed why no relationships between plasma insulin concentration and reproductive traits were found in the present study. Firstly, it might be that insulin is not

involved in reproductive performance of sows and that therefore no relationships were found. However, this contrast with many findings described in literature, about effects of insulin on reproductive traits and is therefore hard to believe. Secondly, it can be suggested that higher plasma insulin levels than physiologically can be reached by diet manipulation are needed to induce effects in reproductive performance. In studies in which effects of insulin on ovulation rate (Cox et al., 1987), follicle atresia (Matamoros et al., 1990), farrowing rate (Ramirez et al., 1997), or WEI (Cox, 1997) were found, exogenous insulin injections were given to sows at different times with different frequencies. Thirdly, it can be suggested that dietary manipulated plasma insulin concentration may affect reproductive performance, but only when a sustained high level is present. In the present study, plasma insulin concentration was increased two times a day for about 4.5 h after feeding. In studies of Tokach et al. (1992) and Koketsu et al. (1996a) who fed sows 24 times a day with hourly intervals, resulting in a sustained high plasma insulin concentration, a positive correlation between plasma insulin concentration and LH pulse frequency was found. It may be therefore that not the postprandial insulin peak level is important for reproduction, but that a long term increased insulin concentration is needed to affect LH secretion, and possibly other reproductive traits.

EFFECTS OF DIETARY ENERGY SOURCE ON PLASMA IGF-1 CONCENTRATION AND ITS RELATIONSHIPS WITH REPRODUCTIVE TRAITS

Because no relationships between plasma insulin concentration and reproductive traits were found, additional analyses were performed to analyze plasma IGF-1 concentration. It was shown that IGF-1 concentration was increased in sows fed the high feeding level during lactation and also in sows fed the starch-rich diet (Chapter 5). After weaning, all sows returned to the same IGF-1 level, regardless of feed intake during lactation and dietary energy source. Comparable results were found in a subsequent experiment (Chapter 6) in which also no effect of dietary energy source postweaning on IGF-1 concentration was found. It seems that dietary energy source or feed intake does not affect IGF-1 concentration when sows are in an anabolic status. In ad libitum fed gilts, Gaughan et al. (1996) found no effect on IGF-1 level between animals fed a fat-rich diet and animals fed a fat-poor diet. In sows in a catabolic status, plasma insulin concentration is correlated with IGF-1 concentration (Chapter 5; H. Quesnel et al., unpublished results). It can be suggested that when feed intake is high, insulin concentration is high (Koketsu et al., 1998; Quesnel et al., 1998b), and probably not limiting for IGF-1 production. Contrarily, when feed intake is low, plasma insulin concentration is low, and probably not high enough to mediate maximum production of IGF-1 by the liver. In that situation an insulin-stimulating diet (starch) can increase the IGF-1 concentration.

In the present study only significant relationships between IGF-1 and LH pulse frequency at the end of lactation and just after weaning were found. Also a positive relationship between IGF-1 concentration and the height of the preovulatory LH surge was found. More evidence that IGF-1 is involved in the hypothalamus-pituitary system is given by Whitley et al. (1995). They found increased LH secretion of in vitro incubated porcine anterior pituitary cells when IGF-1 was added to the medium.

Nevertheless, no relationship between IGF-1 and follicle size on d 2 postweaning was found in the present study. This is somewhat unexpected because several studies have demonstrated that IGF-1 is involved in follicle development (for reviews see Spicer and Echternkamp (1995), Cox (1997), and Monget and Martin (1997)). A possible reason that IGF-1 concentration in the present study was not related with follicle size can be found in the fact that follicle size was determined by ultrasound at only one moment and therefore detailed information about the quality of the follicle development (e.g. atresia) is lacking.

It can be concluded that in the present study plasma IGF-1 concentration rather than plasma insulin concentration was associated with reproductive traits. This is possibly due to the more sustained higher IGF-1 concentration during the day (Schams et al., 1994; Kraetzl et al, 1998), compared to the more variable plasma insulin concentration.

RELATIONSHIPS BETWEEN ENERGY AND PROTEIN BALANCE AND REPRODUCTION

The second objective of the present study was to investigate whether effects of dietary energy source on reproductive performance are dependent on the metabolic status of the sows. Differences in metabolic status were created by changing feed intake during lactation. In literature, most research regarding effects of lactational body weight loss and reproduction is performed by creating large contrasts in feed intake. The low feed intake is often 50% below ad libitum feed intake or near maintenance level. Because in that situation it can be expected that the negative effects of low feed intake override all effects of dietary energy source, in the present study is chosen for a relative mild contrast in lactational feed intake (25%). Based on the results obtained from the present study, it can be suggested that not dietary energy source, but lactational feed intake has the largest impact on reproductive performance of primiparous sows. Therefore, based on the measured energy balance during lactation (Chapter 2) per respiration chamber, individual energy balances of the sows were calculated. These calculated individual energy balances were not related with reproductive performance. Therefore, for the experiment described in Chapter 2 to 5, additional relationships were calculated between body fat and protein and reproductive performance, based on the formulas of the CVB (1994). These calculated amounts of body fat (range 18 to 41 kg) and protein (range 21 to 28 kg) at farrowing or the amounts of

lactational body fat (range 6 to 17 kg) and protein (range –1 to 6 kg) losses during lactation were also not related with any reproductive trait. In the subsequent experiment (Chapter 6), also no relationships between protein or fat (losses) and reproductive traits were found. In this experiment body fat at farrowing ranged from 21 to 51 kg and body protein from 22 to 32 kg. At weaning these ranges were for body fat: 17 to 48 kg and for body protein: 17 to 30 kg. During lactation sows lost on average 19% (range –8 to 50) body fat and 11% (range –4 to 25) body protein.

Based on these results, it can be suggested that primiparous sows can anticipate on a relatively wide range of body fat and protein loss during lactation without affecting reproductive performance. As demonstrated, sows lost on average 30% (range 14 to 49) of the body fat and approximately 6% (range -5 to 20) of body protein during lactation and no relationship with reproduction was found (Chapter 2 to 5). Apparently, sows have the possibility to suffer relatively large body fat and protein losses, before this affects reproductive performance. It seems that restoration mechanisms of primiparous sows after weaning are well developed.

CONCLUDING REMARKS

Resuming the results obtained from the present study, it can be concluded that effects of dietary energy source on reproductive traits are limited. Uterine, embryonic, and placental traits were never affected by dietary energy source, fed either during lactation, the weaning-to-estrus interval, or early pregnancy (Chapter 3, 4, and 6). Effects of 25% reduction in lactational feed intake had more impact on reproductive performance of primiparous sows than dietary energy source. Only in sows with relatively low lactational feed intake, the fat-rich diet increased the risk that sows remained anoestrous after weaning (Chapter 3 and 6).

A more endocrinological and physiological approach demonstrated a negative effect of the fat-rich diet on LH pulsatility during lactation. This seems to be dependent on the metabolic status of the lactating animal. Especially in a less catabolic situation (early lactation), LH pulsatility seemed to be depressed in sows fed a fat-rich diet compared to those fed a starch-rich diet. In a more catabolic status (in later lactation), the severe negative energy balance overrides effects of dietary energy source on LH pulsatility. Although not measured, it can be suggested that fat-rich diets after weaning (in an anabolic status) negatively affect LH pulsatility and therefore follicle growth and moment of ovulation. This can result in a delayed return to estrus, as found in Chapter 3 and 6. In Chapter 3 (in which diets were fed during and after lactation) this was found only for sows fed at the low feeding level. In Chapter 6 (in which lactational body weight loss was comparable with that of sows at the low feeding level in Chapter 3 and experimental diets were fed only after weaning) the

negative effect of fat-rich diets on the return to estrus was significant. This may be trough the less insulin-stimulating effect of fat-rich diets.

As shown in Chapter 3, the relationship between LH pulsatility on the day of weaning and the WEI has a linear-plateau form. This suggests that only in sows in which LH pulse frequency after weaning is below a certain threshold (7 pulses per 12 h in this study) the WEI is affected by the LH release. Highly catabolic sows during lactation have an increased chance to fall into that category. In these sows, stimulation of LH release by dietary or other factors (e.g. boar stimulation) may be beneficial to stimulate follicle growth and ovulation.

Because a more severe negative energy balance seems to override the potential effects of dietary energy source, prevention of high lactational body weight losses is recommended. As shown in Chapter 2, fat-rich diets did not reduce lactational body weight loss, due to the milk fat output stimulating effect of these diets. Furthermore, fat-rich diets fed during lactation resulted in a smaller stimulation of insulin and IGF-1 secretion than starch-rich diets did (Chapter 1, 3, 5, and 6). Both insulin and IGF-1 are assumed to be important in hypothalamus-pituitary stimulation of LH and follicle growth and development. That IGF-1 is related with LH pulsatility is confirmed in this study (Chapter 5).

Based on these results, it can be concluded that feeding of fat-rich diets to primiparous sows, seem to depress hypothalamus-pituitary action, resulting in a delayed return to estrus. In Chapter 3 and 4 these effects were limited, probably due to the low number of observations; in Chapter 6 with more observations these effects were more clear. Further research on a larger scale is necessary to substantiate effects found in the present study. Furthermore, effects of maternal dietary energy source on litter performance during lactation and after weaning should be investigated.

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Introduction

As a result of extensive changes in pig husbandry in the last 50 years, nutritional requirements of especially lactating sows nowadays differ strongly from those of sows in the past. Although diets are optimized to meet the requirements, sows still loose body reserves during lactation. Especially in primiparous sows, losses of body reserves during lactation are severe. These sows have not reached their mature body weight and therefore need nutrients for body development. However, due to a limited feed intake capacity, lactating primiparous sows mobilize body fat and protein to meet their requirements for maintenance and milk production.

In general, these losses of body reserves result in impaired reproductive performance after weaning. The number of sows that remain anestrous after weaning is considerable and in sows that show estrus, weaning-to-estrus interval (WEI) is prolonged, ovulation rate seems decreased and embryonal mortality is increased.

Therefore, nutrition is an important factor for optimal reproductive performance, especially in primiparous sows. An intermediate between nutrition and reproduction is the hormone insulin. Insulin is associated with the pulse frequency of luteinizing hormone (LH), WEI, ovulation rate, and farrowing rate. Feeding level, exogenous insulin injections, and diet composition can affect plasma insulin concentration. Effects of dietary energy source on plasma insulin concentration and its relationships with reproductive performance are hardly investigated.

This study was conducted in primiparous sows to investigate: 1) effects of two specific dietary energy sources (fat: less insulin-stimulating vs starch: more insulin- stimulating) fed during different parts of the reproduction cycle, on reproductive traits, and 2) whether effects of these dietary energy sources on reproduction are dependent on the metabolic status during lactation (induced by feeding level).

Dietary energy sources and plasma insulin concentration (Experiment 1)

To investigate effects of dietary manipulated plasma insulin concentration on reproductive performance, firstly diets had to be composed that differ in insulin stimulation. Therefore, an experiment was conducted in cyclic gilts in which three diets, differing in major dietary energy source, were investigated in their ability to stimulate plasma insulin secretion (Chapter 1). The studied major dietary energy sources were tallow, maize starch, and maize starch plus dextrose. The diet with tallow gave only a slight postprandial increase in plasma insulin level. The maize starch diet resulted in a higher postprandial insulin concentration, but two hours after feeding the plasma insulin concentrations were not different between the diet with tallow and with maize starch. The diet with maize starch plus dextrose resulted in the highest postprandial insulin levels and remained at a higher level during approximately 4.5 h after feeding. Preprandial insulin concentrations did not differ between diets.

Design Experiment 2

Because the diet with tallow (fat) and the diet with maize starch plus dextrose (starch) gave the largest contrast in plasma insulin concentration, these two diets were used in a large experiment with lactating primiparous sows. Sows received either the fat- or starch-rich diet from farrowing up to d 35 of the subsequent pregnancy. During lactation, sows were fed either a high (44 MJ NE/d; 1050 g CP/d) or a low (33 MJ NE/d; 790 g CP/d) feeding level. This was done to study, in addition to the main effects, the interactions between dietary energy source and feeding level on energy partitioning and reproduction. Within each feeding level, diets were fed to be isocaloric and isonitrogenous. After weaning, all sows remained at the same experimental diet, but all received the same amount of energy and protein (from weaning to estrus: 31 MJ NE/d; 740 g CP/d; from breeding to slaughter: 17.5 MJ NE/d; 420 g CP/d).

During lactation, energy and nitrogen balance were determined and blood samples were collected to analyze insulin and LH profiles. After weaning (day 22 after farrowing), additional blood samples were taken to analyze periovulatory profiles of estradiol, LH, and progesterone. Sows were inseminated each day of standing estrus and slaughtered on d 35 of pregnancy. Results obtained from this experiment are described in Chapter 2 to 5.

Dietary energy source and energy partitioning (Experiment 2)

Effects of dietary energy source and feeding level on milk production, milk composition, piglet body composition, and energy partitioning of lactating primiparous sows are described in Chapter 2. At the low feeding level no differences between the two dietary energy sources were observed for milk composition, body composition of the piglets, or energy and nitrogen balance of the sow. At the high feeding level, however, the fat-rich diet resulted in milk with a higher fat concentration and in piglets with a higher body fat concentration compared with the starch-rich diet. This resulted in an interaction between dietary energy source and feeding level for energy balance of the sows. The energy balance of sows fed the low feeding level and of sows fed the fat-rich diet at the high feeding level were all similar, but the energy balance of sows fed the starch-rich diet at the high feeding level was less negative. These results suggest that extra fat in the diet enhances milk fat output, whereas extra starch is used for both milk production and prevention of severe body reserve losses of the sow.

Dietary energy source, feeding level, and reproductive traits (Experiment 2)

Whether the treatments affected plasma insulin profiles and reproductive traits during and after lactation is described in Chapter 3 and 4. Plasma insulin concentration was higher in sows fed the starch-rich diet than in sows fed the fat-rich diet during lactation. LH pulse frequency during lactation tended to be lower in sows fed the fat-rich diet compared to those fed the starch-rich diet. At the high feeding level, no effect of dietary energy source on WEI

was found. However, at the low feeding level, the fat-diet resulted in a 22 h longer WEI compared with the starch-rich diet. Dietary energy source did not affect other reproductive traits.

Feeding level did not affect plasma insulin profiles during lactation. Sows fed the high feeding level during lactation had a higher LH pulse frequency during and after lactation, a lower risk to remain anestrous after weaning, and a higher ovulation rate compared with sows fed the low feeding level. Periovulatory profiles of estradiol, LH, and progesterone hardly differed between treatments. No differences between treatments were observed for the number of embryos, uterine-, and placental development.

Plasma insulin concentrations during lactation were not related with the determined reproductive traits. Furthermore, no relationships were found between energy- or nitrogen balance and reproductive characteristics.

Based on the results obtained from experiment 2, it can be concluded that dietary energy source during lactation affects plasma insulin concentration but has minor effects on reproductive performance of primiparous sows. A reduction of 25% in lactational feed intake seems to have more impact on reproductive traits.

Overall analyses, regardless of treatments, showed that the relationship between the number of LH pulses on the day of weaning and the WEI was best explained by a linear-plateau model. An increase from two to seven LH pulses per 12 h resulted in a linear decrease in WEI, whereas more than 7 pulses did not shorten the WEI further. Furthermore, it was demonstrated that the mean plasma progesterone concentration in early pregnancy was positively related with the percentage of embryonal survival, especially in progressing pregnancy (from 170 h after the LH surge onwards).

Dietary energy source and reproductive performance (Experiment 3).

In the experiment described above (Chapter 2 to 4), sows were fed either the fat- or starch-rich diet from parturition until d 35 of subsequent pregnancy. It is therefore, impossible to distinguish effects of dietary energy source fed during the lactation period, the WEI, or the early pregnancy, on reproduction. Effects found during pregnancy may be a result of changes during WEI or even lactation. Therefore, another experiment was conducted in which primiparous sows were fed either the fat or starch-rich diet during the weaning-to-ovulation interval or during early pregnancy (until d 35). The results obtained from this experiment are described in Chapter 6. Sows fed the fat-rich diet before ovulation had a higher risk to maintain anestrous after weaning than sows fed the starch-rich diet. No effect of dietary energy source fed either before ovulation or during early pregnancy was found on uterine, placental, and embryonic traits.

IGF-1 and reproductive performance (Experiment 2 and 3)

Because plasma insulin concentration did not show relationships with reproductive traits (Chapter 3 and 4), additional analyses were performed to determine plasma IGF-1 (insulin-like growth factor-I) concentration during and after lactation, and its relationships with reproductive characteristics. In literature, IGF-1, together with insulin, is often posited as an intermediate between nutrition and reproduction in the pig. Results of these analyses are described in Chapter 5. Plasma IGF-1 concentration was higher in sows fed the high feeding level during lactation and also in sows fed the starch-rich diet. Furthermore, IGF-1 concentrations on d 21 of lactation and on d 22 (weaning) were positively related with the LH pulse frequency on d 22 and the height of the preovulatory LH surge. Finally, IGF-1 concentration in sows with a low body weight at farrowing and severe lactational body weight loss was decreased compared to heavier sows at farrowing or sows with less lactational body weight loss.

Conclusions and implications

The major question to be answered in the present study was whether dietary energy source affects plasma insulin concentrations and reproductive performance of primiparous sows. Based on the results obtained from the three experiments, it can be concluded that fat-rich diets fed during lactation depress the secretion of insulin compared to starch-rich diets. The LH secretion by the pituitary during lactation tended to be decreased in sows fed the fat-rich diet, possibly explaining the finding that the return to estrus was delayed in these sows. However, this lower LH pulsatility and delayed return to estrus were not related to plasma insulin concentration. Dietary energy source does not seem to affect reproductive traits on the uterus level.

The second question to be answered was whether effects of dietary energy source on reproductive performance are dependent on the metabolic status of sows during lactation. In the present study, no interaction between dietary energy source and metabolic status on reproductive traits was found, even though the energy balance of the lactating sows was affected by dietary energy source.

Based on these results, the use of fat-rich diets for primiparous sows, and probably also for multiparous sows, needs to be critically evaluated. Based on the metabolic and reproductive point of view, starch-rich diets seem to be more beneficial for sows than fat-rich diets. Effects of fat-rich diets on litter performance after weaning need to be investigated further.

SAMENVATTING

Introductie

De varkenshouderij heeft in de afgelopen 5 decennia grote veranderingen ondergaan. Hierdoor verschillen de huidige nutritionele behoeften, van met name lacterende zeugen, aanzienlijk met die van zeugen in het verleden. Ondanks dat diëten zijn geoptimaliseerd om zoveel mogelijk aan de behoeften te voldoen, verliezen zeugen lichaamsreserves gedurende de lactatie. Dit geldt met name voor eersteworps zeugen. Deze zeugen hebben nog niet hun volwassen gewicht bereikt en hebben daarom nog nutriënten nodig voor groei. Omdat hun voeropnamecapaciteit beperkt is, mobiliseren lacterende eersteworps zeugen lichaamsreserves om aan de behoefte voor onderhoud en melkproductie te voldoen.

Over het algemeen resulteren grote verliezen van lichaamsreserves tijdens de lactatie in verminderde reproductieresultaten na het spenen. Het aandeel zeugen dat niet in oestrus komt is aanzienlijk en wanneer zeugen in oestrus komen is het interval tussen spenen en bronst (ISB) verlengd, lijkt de ovulatiegraad verlaagd te zijn en is de embryonale sterfte verhoogd.

De voeding is daarom een belangrijke factor voor optimale reproductieresultaten van met name eersteworps zeugen. Een potentiële intermediair tussen voeding en reproductie is het hormoon insuline. Er zijn bijvoorbeeld relaties gevonden tussen het insulinegehalte en de afgifte van luteiniserend hormoon (LH), het ISB, de ovulatiegraad en het afbigpercentage. Het plasma insulineniveau kan beïnvloed worden door de voeropname, exogene insuline injecties en de dieetsamenstelling. Het is bekend dat ook de energiebron in het dieet kan leiden tot verschillen in de plasma insulineconcentratie. Effecten hiervan op de reproductie van zeugen zijn echter nauwelijks onderzocht.

Deze studie met eersteworps zeugen was opgezet om te onderzoeken: 1) wat de effecten zijn van specifieke energiebronnen in het voer (vet: minder insuline stimulerend of zetmeel: meer insuline stimulerend) op de reproductieresultaten, wanneer deze gevoerd werden tijdens verschillende fasen van de reproductiecyclus, en 2) of de effecten van energiebronnen in het voer op de reproductie afhankelijk zijn van de metabole status van de zeugen tijdens de lactatie. De metabole status werd beïnvloed door verandering van de voeropname.

Energiebronnen in het dieet en de plasma insulineconcentratie (experiment 1)

Om te onderzoeken wat het effect is van de, met behulp van voeding gemanipuleerde, plasma insulineconcentratie op de reproductieresultaten, moesten eerst diëten worden samengesteld die verschilden in insulinestimulatie. Daarom is een experiment gedaan met cyclische gelten om het effect van de energiebron in het dieet op het plasma insulinegehalte te bestuderen. De bestudeerde energiebronnen waren: rundvet, maïszetmeel en maïszetmeel plus dextrose. Het dieet met rundvet resulteerde in een kleine verhoging van het plasma insulinegehalte na het voeren. Het dieet met maïszetmeel gaf een hogere

insulineconcentratie na voeren, maar twee uur na het voeren was geen verschil meer zichtbaar tussen het dieet met rundvet en met maïszetmeel. Het dieet met maïszetmeel plus dextrose als energiebronnen resulteerde in de hoogste plasma insulinepiek na het voeren en het insulinegehalte bleef op een hoger niveau gedurende ongeveer 4.5 uur na het voeren. Plasma insulineconcentraties voor het voeren verschilden niet tussen de diëten.

Proefopzet experiment 2

In het eerste experiment gaven de diëten met rundvet (vet) en met maïszetmeel plus dextrose (zetmeel) het grootste contrast in plasma insulineconcentratie (zowel piek als langere termijn). Daarom zijn deze twee diëten gebruikt in een groot experiment met lacterende eersteworps zeugen. Zeugen kregen vanaf werpen tot dag 35 van de volgende dracht het vetrijke (134.9 g/kg vet; 196.8 g/kg zetmeel plus suiker) of het zetmeelrijke (33.2 g/kg vet; 380.9 g/kg zetmeel plus suiker) dieet verstrekt. Tijdens de lactatie kregen de zeugen een hoog (44 MJ NE/d; 1050 g ruw eiwit/d) of een laag (33 MJ NE/d; 790 g ruw eiwit/d) voerniveau. Het voerniveau werd geïntroduceerd om naast het effect van energiebron in het dieet ook de interactie tussen energiebron in het voer en voerniveau op energieverdeling en reproductie te bestuderen. Binnen elk voerniveau werden de diëten zodanig verstrekt dat de energie- en eiwitopname gelijk was. Na spenen kregen alle zeugen hetzelfde dieet als tijdens de lactatie, maar het voerniveau was voor alle dieren gelijk (van spenen tot bronst: 31 MJ NE/d; 740 g ruw eiwit/d; van inseminatie tot slachten: 17.5 MJ NE/d; 420 g ruw eiwit/d).

Tijdens de lactatie werden de energie- en eiwitbalans van de zeugen bepaald en werden bloedmonsters genomen om insuline en LH in het bloedplasma te analyseren. Na het spenen, op dag 22 na het werpen, werden additionele bloedmonsters genomen voor de analyse van oestradiol-, LH- en progesteronprofielen. De zeugen werden iedere dag van de bronst geïnsemineerd en geslacht op dag 35 van de dracht. Uteri, placentae en embryo's werden gewogen en de kwaliteit ervan werd bepaald.

Energiebron in het dieet en de energieverdeling (experiment 2)

De effecten van de energiebron in het dieet en het voerniveau op de melkproductie, melksamenstelling, lichaamssamenstelling van de biggen en energieverdeling van de lacterende eersteworps zeugen staan beschreven in hoofdstuk 2. Bij het lage voerniveau werden geen verschillen tussen de beide diëten gevonden wat betreft melkproductie, melksamenstelling, lichaamssamenstelling van de biggen en energie- en eiwitbalans van de zeugen. Bij het hoge voerniveau resulteerde het vetrijke dieet in melk en biggen met een hoger vetgehalte in vergelijking met het zetmeelrijke dieet. Er was daardoor een interactie tussen de energiebron in het dieet en het voerniveau voor wat betreft de energiebalans van de zeugen. De energiebalansen van de zeugen op het lage voerniveau en van de zeugen gevoerd met het vetrijke dieet op het hoge voerniveau waren gelijk, terwijl de energiebalans

van de zeugen gevoerd met het zetmeelrijke dieet op het hoge voerniveau minder negatief was. Deze resultaten suggereren dat extra vet in het dieet de productie van melkvet verhoogd, terwijl extra zetmeel gebruikt wordt voor zowel melkproductie als de beperking van grote verliezen aan lichaamsreserves van de zeug.

Energiebron in het dieet, voerniveau en reproductie parameters (experiment 2)

Of de energiebron in het dieet en het voerniveau effect hadden op de plasma insulineprofielen en op de reproductieparameters tijdens en na de lactatie is beschreven in hoofdstuk 3 en 4. De plasma insulineconcentratie tijdens de lactatie was hoger in zeugen die gevoerd werden met het zetmeelrijke dieet dan in zeugen die gevoerd werden met het vetrijke dieet. De pulsfrequentie van LH tijdens de lactatie tendeerde naar een lager niveau bij zeugen die gevoerd werden met het vetrijke dieet in vergelijking met zeugen die gevoerd werden met het zetmeelrijke dieet. Bij het hoge voerniveau werden geen verschillen in ISB gevonden tussen de diëten, maar bij het lage voerniveau resulteerde het voeren van het vetrijke dieet in een 22 uur langere ISB dan het voeren van het zetmeelrijke dieet. Andere reproductie parameters werden niet beïnvloed door de energiebron in het dieet.

Het voerniveau tijdens de lactatie had geen invloed op de plasma insulineconcentratie. Zeugen die gevoerd werden op het hoge voerniveau tijdens de lactatie hadden een hogere pulsfrequentie van LH tijdens en na de lactatie, een grotere kans om in bronst te komen na het spenen en een hogere ovulatiegraad vergeleken met zeugen die op een laag niveau gevoerd werden tijdens de lactatie. Plasma gehalten van oestradiol, LH en progesteron rondom de bronst verschilden nauwelijks tussen zeugen in de verschillende behandelingen. Ook waren er geen verschillen in het aantal embryo's en de ontwikkeling van de uterus en placenta tussen de behandelingen.

Insulineconcentraties in het plasma waren niet gerelateerd met reproductieparameters en ook werden er geen relaties gevonden tussen de energie- en eiwitbalans van de zeugen en reproductieparameters.

Uit de bovenstaande resultaten kan geconcludeerd worden dat de energiebron in het dieet wel het plasma insulinegehalte beïnvloedt, maar slechts marginale effecten heeft op de reproductie van de zeugen. Een reductie van 25% in voerniveau tijdens de lactatie had een grotere impact op de reproductie van eersteworps zeugen.

Verdere analyses, onafhankelijk van de behandelingen, lieten een relatie zien tussen het aantal LH pulsen op de dag van spenen en het ISB. Deze relatie werd het beste verklaard met een lineair-plateau model. Een toename van twee tot zeven LH pulsen per 12 uur resulteerde in een lineaire afname van het ISB, terwijl meer dan zeven pulsen per 12 uur geen verdere verkorting van het ISB opleverde. Verder bleek dat de gemiddelde progesteronconcentratie in de vroege dracht positief was gerelateerd met het percentage embryonale overleving.

Energiebron in het dieet en reproductie (experiment 3)

In het boven beschreven experiment werden zeugen gevoerd met het vetrijke of zetmeelrijke dieet vanaf werpen tot en met dag 35 van de volgende dracht. Daarom is het onmogelijk om de effecten van de energiebron in het dieet tijdens de lactatie, tijdens het ISB en tijdens de vroege dracht op de reproductie te onderscheiden. De effecten die gevonden werden tijdens de dracht kunnen een gevolg zijn van veranderingen tijdens het ISB of zelfs tijdens de lactatie. Daarom is een derde experiment uitgevoerd waarin eersteworps zeugen werden gevoerd met het vetrijke of zetmeelrijke dieet gedurende het interval tussen spenen en ovulatie of tijdens de vroege dracht (tot dag 35). De resultaten van dit experiment staan beschreven in hoofdstuk 6. Zeugen die het vetrijke dieet verstrekt kregen voor de ovulatie hadden een grotere kans om niet in bronst te komen dan zeugen die het zetmeelrijke dieet kregen. De energiebron in het dieet had geen effect op uterine, placentale of embryonale parameters.

IGF-1 and reproductie (experiment 2 en 3)

Omdat de insulineconcentratie in het plasma niet gerelateerd was met reproductieparameters (hoofdstuk 3 en 4) zijn ook de plasma IGF-1 (insulin-like growth factor-I) concentraties tijdens en na de lactatie bepaald, om relaties tussen de IGF-1-concentratie en reproductieparameters te bestuderen. Dit is gedaan omdat in de literatuur IGF-1 samen met insuline vaak genoemd worden als potentiële intermediairen tussen voeding en reproductie. De resultaten van deze analyses zijn weergegeven in hoofdstuk 5. De plasma IGF-1-concentratie was hoger in zeugen die gevoerd werden op een hoog voerniveau tijdens de lactatie of die gevoerd werden met het zetmeelrijke dieet. De IGF-1-concentratie op dag 21 van de lactatie en op dag 22 (spenen) waren positief gerelateerd met de pulsfrequentie van LH op de dag van spenen en de hoogte van de pre-ovulatoire LH piek. Tenslotte was de IGF-1-concentratie lager in zeugen met een laag gewicht bij werpen die veel gewicht verloren tijdens de lactatie. Zeugen die zwaarder waren direct na het werpen of die minder gewicht verloren tijdens de lactatie hadden een hogere plasma IGF-1-concentratie.

Conclusies en implicaties

De belangrijkste vraag van deze studie was of de energiebron in het dieet de plasma insulineconcentratie en de reproductie van eerste-worps zeugen beïnvloedt. Op basis van de resultaten van de drie experimenten kan geconcludeerd worden dat het vetrijke dieet resulteerde in een lagere plasma insulineconcentratie vergeleken met het zetmeelrijke dieet. De LH-afgifte door de hypofyse was ook verlaagd in zeugen gevoerd met het vetrijke dieet en dat verklaarde waarschijnlijk het later in bronst komen van deze zeugen na het spenen. Deze lagere pulsfrequentie van LH en het vertraagde in bronst komen waren echter niet

gerelateerd met de plasma insulineconcentratie. Uterine, placentale en embryonale parameters lijken niet beïnvloed te worden door de energiebron in het dieet.

De tweede vraag van deze studie was of de effecten van energiebron in het dieet op de reproductie afhankelijk waren van de metabole status van de zeugen tijdens de lactatie. In deze studie werden geen interacties gevonden tussen de metabole status en reproductieparameters, ondanks dat de energiebalans van de zeugen beïnvloed was door de energiebron in het dieet.

Gebaseerd op deze resultaten moet het gebruik van vetrijke rantsoenen door eerste-worps zeugen en waarschijnlijk ook door meerdere worps zeugen kritisch geëvalueerd worden. Gezien de effecten op de metabole status en de reproductieresultaten lijken vetrijke rantsoenen, in vergelijking met zetmeelrijke rantsoenen, nadelig te zijn voor eerste-worps zeugen. De effecten van vetrijke voeders op de ontwikkeling van de biggen na het spenen dienen verder onderzocht te worden.

CURRICULUM VITAE

Hendrik van den Brand werd op 7 oktober 1969 geboren te Kootwijkerbroek (gemeente Barneveld). In 1988 behaalde hij het V.W.O. diploma aan het Van Lodenstein college te Amersfoort. In datzelfde jaar werd begonnen met de studie Intensieve Veehouderij aan de Christelijke Agrarische Hogeschool te Dronten. Deze studie werd in januari 1992 afgesloten, waarna in februari 1992 werd aangevangen met de studie Zoötechniek aan de Landbouwuniversiteit te Wageningen. In juni 1994 studeerde hij hier cum laude af, met als oriëntaties Veevoeding en Veehouderij. Na zijn afstuderen was hij gedurende 6 maanden werkzaam als technisch-commercieel medewerker bij een handel in tweedehands goederen. In 1995 werd een functie gevonden als onderzoeker/proefstalbegeleider bij een producent van voeders voor vleeskalveren. In april 1996 werd hij aangesteld als Onderzoeker in Opleiding (OIO) bij de vakgroep Veehouderij van de Landbouwuniversiteit te Wageningen en verrichtte hij het in dit proefschrift beschreven onderzoek. Voor zijn onderzoek kreeg hij in 1998 de 'Young Scientist Award' van de European Association of Animal Production, sectie Physiology. Sinds 1 mei 2000 is hij als onderzoeker/relatiebeheerder pluimvee werkzaam bij Stichting Instituut voor de Veevoeding 'De Schothorst' te Lelystad.

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