Dietary fat and reproduction in the post partum sow

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Lactating sows are not able to ingest sufficient energy to produce the large amount of milk they are presently capable of. Therefore, sows use a considerable amount of body reserves to maintain their milk production. Body weight loss is negatively associated with subsequent reproductive performance. Addition of fat to the diet is often used to increase energy intake during lactation. This review examines the effects of adding fat to the diet on subsequent reproductive performance. Fat may affect reproduction in three different ways; first, by increasing milk fat output. Higher milk fat output limits or even nullifies the effect of a higher energy intake on body weight loss in ad libitum fed sows. It has even been demonstrated that sows fed an isocaloric fat-rich diet lost more body reserves than sows fed a carbohydrate-rich diet. Second, fat-rich diets increase blood metabolite levels (non esterified fatty acids, ß-hydroxybutyrate, urea), which might negatively impact reproductive performance. Third, fat-rich diets depress secretion of insulin and IGF-1, which directly or indirectly affects LH, oestradiol and progesterone secretion and follicle development. We concluded that adding fat to the diet of lactating sows disrupts the balance between C2 and C3 compounds, which is necessary to run the Krebs cycle in an efficient way, and may negatively affect the sows' subsequent reproductive performance. Therefore, increasing energy intake during lactation might be accomplished better by adjusting other management procedures to support feed intake, such as housing temperature, water intake, and prevention of overfeeding in early lactation.

Introduction

Modern sows produce large litters and must produce sufficient milk to nurse all the piglets. Milk production greater than 10 kg/day is common nowadays (Toner *et al.*, 1996; King *et al.*, 1996; Auldist *et al.*, 1998, 2000; Renaudeau and Noblet, 2001; McNamara and Pettigrew, 2002; Ramanau *et al.*, 2004). Because feed intake capacity is limited, especially in primiparous sows, body reserves are used to maintain milk production (Van der Peet-Schwering *et al.*, 1998). Sows, which lost severe amounts of body reserves had depressed reproductive performance, expressed as prolonged weaning to oestrus interval (WOI), and reduced subsequent litter size (Vesseur *et al.*, 1994; Koketsu and Dial, 1997). Low feed intake during lactation was associated with suppressed follicle development (Zak *et al.*, 1997a; Quesnel *et al.*, 1998a; Van

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den Brand *et al.*, 2000a), impaired oocyte maturation (Zak *et al.*, 1997b), low ovulation rate (Zak *et al.*, 1997a; Van den Brand *et al.*, 2000a), lower plasma progesterone concentrations in the subsequent pregnancy (Kirkwood *et al.*, 1987a), and higher embryonic mortality (Kirkwood *et al.*, 1987b; Zak *et al.*, 1997b). Thus, it is important to maximize energy intake during lactation. Effects of lactational feed intake on reproduction were extensively reviewed by Einarsson and Rojkittikhun (1993), Dourmad *et al.* (1994), Kemp (1998), Williams (1998) and Prunier and Quesnel (2000). In many studies, energy intake was increased by supplementing fat in the diet. However, it is disputable whether or not increasing the fat content of the diet has a positive effect on lactational body weight loss and subsequent reproductive performance. This review examines the effects of adding fat to the diet on subsequent reproductive performance at three levels: 1) lactational energy metabolism and body weight loss; 2) blood metabolite levels and 3) metabolic and reproductive hormones and subsequent reproductive performance.

Effects of additional fat in the diet on energy metabolism and body weight loss

Pettigrew and Moser (1991) summarized the effects of adding fat to the diet of lactating sows and concluded that metabolizable energy (ME) intake increased when sows were fed ad libitum (Table 1). The average ME intake increased by 5.19 MJ/day, but lactational body weight change was equivocal. Energy intake increased in all 19 studies reviewed, but body weight loss increased in four of them. On average, adding fat resulted in only 1.5 kg less lactational body weight loss compared to controls. Schoenherr *et al.* (1989) confirmed these results, and found that, especially at high ambient temperatures, energy intake increased by adding fat to the diet. At 32°C, ME intake increased by 8.8 MJ/day by adding fat to the diet, whereas at 20°C this difference was only 2.5 ME/day. However, at both temperatures, body weight loss was similar for the control and fat-added groups, suggesting that additional energy in the form of fat was used for purposes other than sparing body weight. The interaction between dietary energy source and environmental temperature is probably due to the higher efficiency of fat-rich diets, and thus, lower heat production (Babinszky, 1992; Van den Brand *et al.*, 2000b). Drochner (1989) summarized 17 experiments in which 4 to 20% fat was added to the diet of lactating sows. Fat concentration in both colostrum and milk increased linearly with increasing dietary fat content; each percentage increase in dietary fat resulted in 0.5% increase in milk fat content. Assuming that milk production was 10 kg/day and feed intake was 5 kg/day, then all additional fat from the diet was likely secreted into the milk.

Table 1. Effect of adding fat to diets of ad libitum fed lactating sows (Pettigrew and Moser, 1991).

	# of comparisons*		Response (MJ/d)	Total # of sows
	Positive	Negative		
ME intake (MJ/d)				
Added fat during lactation	19	0	5.19±0.75	834
≥ 10% added fat	9	0	6.48±1.67	317
< 10% added fat	10	0	4.39±0.67	517
Lactational weight change (kg)	11	4	1.5±0.7	697
ME intake increase				
≥ 4.2 MJ/day	5	2	2.2±1.1	239
< 4.2 MJ/day	7	3	1.3±0.9	584

* Number of studies which found a positive or negative effect of fat addition on ME intake or lactational body weight change compared to a control group.

The higher body weight loss in fat fed sows was confirmed in studies in which sows were fed isocaloric diets, which differed in fat content. Babinszky (1992) compared a corn starch diet (3.7% fat) with an animal fat diet (12.5% fat). Milk energy output was higher (51.0 vs 44.8 MJ/day) and body fat loss was greater in sows fed the fat-rich diet than for sows fed the corn starch diet (506 vs 381 g/day), resulting in a more severe negative energy balance for this group of sows (-20.8 vs -14.7 MJ/day). Van den Brand *et al.* (2000b) demonstrated that this effect depended on the level of energy intake (Table 2). At a low level of energy intake, there were no differences in milk fat content or body fat loss for sows fed a starch (3.1% fat) or fat-rich (11.0% fat) diet, but at a high level of energy intake, fat content in the milk and body fat loss were greater in sows fed a fat-rich diet than in sows fed a starch-rich diet. The greater body fat loss in sows fed the fat-rich diet was probably due to the lack of sufficient blood glucose in these sows, which was also reflected in a somewhat lower milk lactose concentration. Therefore, glycerol from body reserves was used for gluconeogenesis, resulting in mobilization of body reserves. In addition, Lauridsen and Danielsen (2004) demonstrated that lactational body weight loss depends on the fat source used. Six treatment diets were prepared by adding 8% of one of 6 different fat sources to the control diet. Although not significant, body weight loss during a 28-day lactation period ranged from 2.7 (fish oil) to 11.0 (sunflower oil) kg, with 6.7 kg body weight loss for the control group. However, milk fat output (kg/day) was significantly higher in some fat supplemented diets compared to the control group. Thus, in most studies (Averette *et al.*, 1999; Tilton *et al.*, 1999a; Jones *et al.*, 2002; Lauridsen and Danielsen, 2004), addition of fat to sow diets resulted in higher milk fat output, whereas effects on lactational body weight loss were negligible or absent.

Table 2. Effect of lactational energy intake and type of diet on milk production and energy balance of primiparous sows (Van den Brand *et al.*, 2000b).

Energy intake (MJ NE/d)	High: 44		Low: 33	
Diet type	Fat	Starch	Fat	Starch
Milk production (kg/d)	9.6^{a}	9.9^{a}	8.0^{b}	8.6^{b}
Milk fat (%)	8.4^{a}	6.9^{b}	7.6^{ab}	7.8^{ab}
Protein gain (g/d)	-50	-31	-69	-75
Fat gain (g/d)	-568^{a}	-401^{b}	-511^{a}	-521^{a}

^{a,b} Values within a row lacking a common superscript differ ($P<0.05$).

Glucose and fat intermediary metabolism pathways

Based on results mentioned above, we suggest that the indirect effects of fat-rich diets on reproduction via lowering the mobilization of body reserves are limited. On the other hand, fat-rich diets probably alter intermediary metabolism, and thereby, affect reproductive performance. During lactation, sows lose body reserves, which mainly consist of fat. Fat consists of C2-compounds (two carbon atom fragments), which are precursors for production of acetyl-CoA. Acetyl-CoA, together with oxaloacetate from C3 compounds (three carbon atom fragments), in a ratio of 1:1, is necessary to run the Krebs cycle. At the same time, sows are producing milk, the amount of which is largely determined by the availability of lactose (Boyd *et al.*, 1995). Because glucose (C3) is the main precursor of lactose, lactation results in decreased availability of C3 compounds. The state of negative energy balance is characterized by elevated blood non-esterified fatty acids (NEFAs). In the liver, NEFAs are normally oxidized or esterified into triglycerides. Triglycerides are stored in the liver or exported as part of a very low-density lipoprotein (VLDL) for metabolism by extra-hepatic tissue, such as the mammary gland, which secretes them as milk fat. Oxidation of NEFAs may be complete, via acetyl-CoA or incomplete resulting in production of ketone bodies, e.g. ß-hydroxybutyrate (BHBA). This pathway has been investigated less in sows than in cows. In the case of negative energy balance in lactating sows, the amount of C2 compounds is out of balance with the amount of C3 compounds. This is because of the abundant availability of C2 compounds from body reserves and the limited availability of C3 compounds due to a drain from the C3 pool for lactose production in milk. This restricts complete oxidation of fatty acids, which results in increased production of ketone bodies such as BHBA. When fat was supplemented in the diet, the amount of C2 precursors increased further, resulting in an even greater disruption in the balance between C2 and C3 compounds (Figure 1a and 1b), and probably an increase in blood BHBA levels.

Effect of starch or fat diets on metabolites during lactation

In the last several decades much attention has been given to the nutritional signals affecting the hypothalamus, pituitary and/or the reproductive organs. Potential signals between nutrition and reproduction can be divided into hormones (insulin, leptin, growth hormone, thyroxine, triiodothyronine, glucocorticoids), growth factors (IGF-1, IGF-II) and metabolites (glucose, NEFA, BHBA, urea). Several authors have reviewed these intermediates and their relationships with reproduction (Booth, 1990; Einarsson and Rojkittikhun, 1993; Cosgrove and Foxcroft, 1996; Prunier and Quesnel, 2000; Barb *et al.*, 2001b). These relationships are briefly discussed in this review, but most attention is given to the effect of dietary energy source on the metabolites, NEFA, BHBA and urea.

NEFAs

Low feed intake and severe body weight loss during lactation are associated with increased levels of blood NEFAs. Effects were found in early (Kraetzl *et al.*, 1998), mid (Messias de Bragança and Prunier, 1999) and late lactation (Prunier *et al.*, 1993; Quesnel *et al.*, 1998b). Weldon *et al.* (1994) found higher blood NEFA levels in lactating sows fed at a high level during gestation compared to sows fed at a normal level, which was probably due to low feed intake for the sows fed at a high level. These results were confirmed by Revell *et al.* (1998), who found higher blood levels of NEFA in fat postpartum sows compared to lean postpartum sows, which was probably due to the considerably lower feed intake of the fat sows during lactation. Hultén *et al.* (2002) divided sows into high and low catabolism groups based on average blood NEFA concentrations. Sows in the high catabolism group (relatively high blood NEFA concentration) lost considerably more weight during lactation than the low catabolism group. These studies demonstrated that high plasma NEFA concentrations reflect the metabolic state of lactating sows (Hultén *et al.*, 2002). This is supported by results of Valros *et al.* (2003), who found relatively strong correlations between sow body weight loss and pre- and post-feeding plasma NEFA concentrations ($r = 0.61$ and $r = 0.75$, respectively).

Evidence for relationships between plasma NEFA concentration and reproduction in the pig is scarce, and in most cases, weak. Although not significant, Tokach *et al.* (1992) and Paterson and Pearce (1994) reported that plasma NEFA concentrations were higher during late lactation in sows with a prolonged WOI (> 15 days), compared to sows with a relatively short WOI (< 9 days). Mejia-Guadarrama *et al.* (2002) found a non-significant negative correlation between preprandial plasma NEFA concentration and the WOI. This is probably due to the weak negative correlation between plasma NEFA concentration and number of plasma LH pulses in late lactation (Tokach *et al.*, 1992) or the day after weaning (Quesnel *et al.*, 1998b). The latter study also demonstrated a negative correlation between plasma NEFA concentration on the day before weaning and the diameter of the 10 largest follicles on the day of weaning. Relationships between plasma NEFA concentration on the day of weaning or two days after weaning and follicle development were weak (Quesnel *et al.*, 1998b). No correlations between preprandial plasma NEFA concentration and ovulation rate or number of viable embryos at day 30 of gestation were found by Mejia-Guadarrama *et al.* (2002). The question remains; is there a direct effect of NEFAs on reproduction or does the relationship between NEFA and reproduction only reflect the more severe catabolic state of the lactating sow, thereby indirectly affecting reproduction.

Studies on the effect of dietary energy source on plasma NEFA concentration largely produced comparable results. Plasma NEFA concentration was higher after feeding a fat-rich diet than after feeding a carbohydrate-rich diet in prepubertal gilts (Formigoni *et al.*, 1996), in sows during gestation (Coffey *et al.*, 1987; Newcomb *et al.*, 1991) and in lactating sows (Coffey *et al.*, 1987; Kveragas *et al.*, 1988; Tilton *et al.*, 1999b; Jones *et al.*, 2002). Based on these studies, we concluded that carbohydrate-rich diets reduced the increase in plasma NEFA concentration during lactation, probably by reducing the amount of fat available from the feed, but also by reducing the amount of mobilized body fat.

If there is a direct negative effect of NEFAs on reproductive performance, fat-rich diets should also have a detrimental effect on reproductive performance of sows. The higher amount of NEFAs in the blood originates from dietary fat or from body reserve losses, as explained in Figure 1b. It is likely that the sow can not distinguish NEFAs originating from feed and NEFAs originating from body reserves. When fat-rich diets increase plasma NEFA concentration, it is likely that reproductive performance will be suppressed.

BHBA

In addition to NEFAs, BHBA is a metabolic indicator of energy balance in pigs. As summarized in Fig. 1, BHBA is especially produced when the complete oxidation pathway through acetyl-CoA fails to process all triglycerides, because of a lack of sufficient oxaloacetate. Barb *et al.* (1997) found an increase in plasma NEFA and BHBA concentrations in prepubertal and mature gilts after acute feed deprivation. This is supported by the findings of Revell *et al.* (1998) who found greater blood BHBA levels in sows during lactation compared to gestation.

Dietary energy source clearly affects blood BHBA levels. Fat-rich diets increased blood BHBA levels in piglets (Lin *et al.*, 1995), in sows during gestation (Newcomb *et al.*, 1991) and in lactating sows (Jones *et al.*, 2002) compared to control or carbohydrate-rich diets. Reduction of BHBA levels by carbohydrate-rich diets is supported by the fact that insulin reduced ketone body production (both BHBA and acetoacetate) in vitro in pig hepatocytes (Fernández-Fígares *et al.*, 2004). Whether or not there is a relationship between BHBA levels in the blood and reproduction in pigs is largely unknown. Tokach *et al.* (1993) found no relationship between blood BHBA level and WOI or plasma LH pulse frequency during lactation.

Urea

Urea is a product of protein break-down. Blood urea concentration increases slightly during lactation (Nelssen *et al.*, 1985; Baidoo *et al.*, 1992; Hultén *et al.*, 2002; Valros *et al.*, 2003); probably due to the more severe catabolic state of the sow in late lactation. Mobilized body reserves not only consist of fat, but also of protein, which needs to be oxidized (Van der Peet-Schwering *et al.*, 1998), and thereby, results in higher blood urea levels. Prunier *et al.* (1993) found an increase in blood urea levels only in primiparous sows fed at a low level during lactation (2.5 kg/day), but a

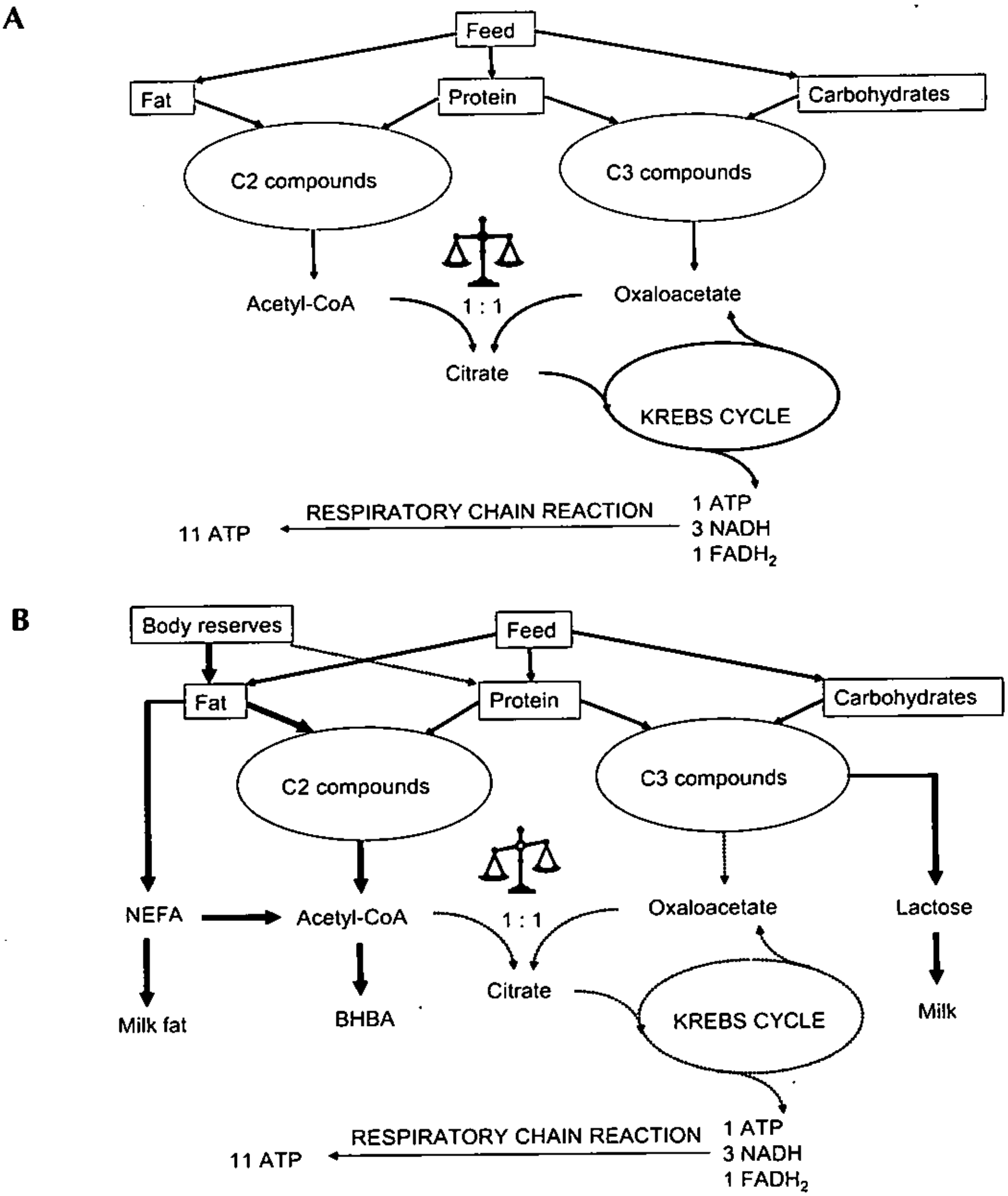

Fig. 1 Carbohydrate and lipid metabolism in a non-lactating sow (a) and a lactating sow in a negative energy balance (b). Weight of the arrows represents the amount of the several nutrients. C2 and C3 compounds = fragments containing 2 and 3 C-atoms, respectively; ATP = Adenosine Triphosphate; NADH = Nicotinamide Adenine Dinucleotide; FADH2 = Flavin Adenine Dinucleotide

slight decrease with progressing lactation when sows were fed at a high level (5.5 kg/day). In the latter study, high feed intake in the lactating sow resulted in lower plasma urea concentration compared to low feed intake. This was supported by Hultén *et al.* (1993) who found higher plasma urea levels during lactation in sows that were fat prepartum (18.8 mm backfat) compared to sows that were lean prepartum (12.9 mm backfat); probably due to a lower lactational feed intake for the fat sows. However, Rojkittikhun *et al.* (1993b) did not find higher plasma urea levels in sows in a more severe catabolic state. Sows that lost more than 25 kg of body weight during lactation had plasma urea levels comparable to sows which lost less than 25 kg of body weight. On the other hand, Sterning *et al.* (1997) found a significant positive correlation between relative body weight loss during lactation and plasma urea concentration in late lactation, whereas Valros et *al.* (2003) found a significant negative correlation between sow body weight loss in early lactation and urea concentration. These ambiguous results can possibly be explained by the protein content of the feeds used.

Studies of the effects of dietary energy source on plasma urea levels in sows are limited. Newcomb *et al.* (1991) found no effect of dietary energy source (starch, soybean oil, medium chain triglycerides) on plasma urea levels in late gestation, but Nelssen *et al.* (1985) and Jones *et al.* (2002) found higher plasma urea concentrations in lactating sows fed a fat-rich diet compared to a carbohydrate-rich diet. Ponter *et al.* (1994) also found higher plasma urea levels in piglets fed a fat-rich diet compared to a carbohydrate-rich diet, suggesting that protein breakdown is higher in animals on a fat-rich diet. Based on these results, the question becomes; what is the reason for higher blood urea concentration in sows fed a fat-rich diet? In general, blood urea concentration was positively related to a more severe catabolic state. Furthermore, pigs fed a fat-rich diet had a limitation in their dietary supply of glucose (C3) and consequently tried to generate glucose via gluconeogenesis. Gluconeogenic amino acids and glycerol are precursors of glucose (Jones *et al.*, 2002). Oxidation of protein to supply the glucogenic amino acids required for glucose synthesis results in a higher concentration of the by-product, urea, in the blood.

Effects of high blood urea concentration on reproduction of sows have rarely been described. Tokach *et al.* (1992) found a very weak negative correlation between blood urea concentrations and plasma LH pulse frequency in late lactation. In dairy cattle, relationships between urea and reproduction are clearer than in sows (for review see Butler, 1998).

Effects of dietary energy source on metabolic hormones and growth factors

In addition to metabolites, metabolic hormones and growth factors are influenced by nutrition and act as intermediaries between nutrition and reproduction. This section focuses on the role of insulin and IGF-I in the relationship between nutrition and reproductive function. Attention is given only to insulin and IGF-I because these are affected by dietary energy source.

Insulin

Several studies showed that insulin might be an intermediary between nutrition and reproduction; acting at both the hypothalamus-pituitary and ovarian level. For example, Tokach *et al.* (1992), Koketsu *et al.* (1996) and Quesnel *et al.* (1998b) found correlations between plasma insulin concentration and plasma LH pulse frequency during and after lactation in sows. Furthermore, exogenous insulin increased plasma LH pulse frequency in gilts (Cox *et al.*, 1987). The observation that LH and FSH release by cultured rat pituitary cells were enhanced after insulin administration (Adashi *et al.*, 1981) also supports a role for insulin at the pituitary. Insulin receptors are present in the ovary (Ladenheim *et al.*, 1984) and administration of insulin increased differentiation of cultured granulosa cells (May and Schomberg, 1981; Poretsky and Kalin, 1987). Finally, exogenous insulin in gilts decreased the number of atretic follicles (Matamoros *et al.*, 1990) and increased the ovulation rate (Cox *et al.*, 1987).

The effect of dietary energy source on plasma insulin concentration is very clear. Carbohydrate-rich diets increased plasma insulin concentration more than fat-rich diets, in both non-lactating and lactating pigs (Newcomb *et al.*, 1991; Ponter *et al.*, 1991; Kemp *et al.*, 1995; Van den Brand *et al.*, 1998, 2000a; Jones *et al.*, 2002). The pattern of insulin secretion was largely influenced by the type of carbohydrate or fat. Van den Brand *et al.* (1998) demonstrated a considerably higher plasma insulin peak level after feeding dextrose combined with maize starch than after feeding maize starch alone. Furthermore, plasma insulin level remained higher during 4.5 h after feeding the dextrose rich diet. Insulin response may be affected by the fatty acid composition of fat-rich diets. In cattle, poly-unsaturated fatty acids increased postprandial insulin levels more than saturated fatty acids (Thomas and Williams, 1996; Thomas *et al.*, 1997). Comparable results should be expected in lactating sows, but controlled experiments on the effect of different fat sources on blood insulin concentrations, to our knowledge, have not been conducted in sows. It is clear that carbohydrate-rich diets increase post-prandial blood insulin level more than fat-rich diets. The amount of increase depends on the carbohydrate source and possibly on the fat source in the diet. We suggest that diets, which enhance plasma insulin concentration, may be a tool to improve reproductive performance.

IGF-I

Blood IGF-I concentrations in lactating sows depend on feed intake. High feed intake during lactation resulted in a higher blood IGF-I level (Quesnel *et al.*, 1998b; Zak *et al.*, 1998; Messias de Bargança and Prunier, 1999; Van den Brand *et al.*, 2001a). Restricted feed intake during one week of lactation decreased blood IGF-I concentration (Zak *et al.*, 1997a), suggesting a rapid effect of feed intake on blood IGF-I concentration. In prepubertal and mature gilts, acute feed deprivation markedly decreased blood IGF-I concentration (Barb *et al.*, 1997; 2001a). Blood IGF-I concentration was related to blood insulin (Van den Brand *et al.*, 2001a), leptin and GH concentrations (Barb *et al.*, 2001a,b), suggesting that IGF-I is an important intermediary among nutrition, metabolism and reproduction. Potential relationships between IGF-I and pituitary hormones related to reproduction were described by Barb *et al.* (2001b). Additionally, Van den Brand *et al.* (2001a) found positive relationships between IGF-I concentration on the day before weaning or the day of weaning and plasma LH pulse frequency on the day of weaning and the preovulatory LH surge.

The role of dietary energy source on IGF-I secretion has rarely been investigated in the pig. Van den Brand *et al.* (2001a) found higher plasma IGF-I concentrations at the end of lactation and the day of weaning after feeding a carbohydrate-rich diet than after feeding a fat-rich diet. However, after weaning, blood IGF-I concentration increased to similar levels, regardless of dietary energy source and lactational feed intake. This agrees with data from Caroll *et al.* (1996), Messias de Bragança and Prunier (1999) and Van den Brand *et al.* (2001b). They showed that blood IGF-I levels were lower in feed restricted sows during lactation, than in sows fed ad libitum. However, feed restricted sows restored their blood IGF-I concentration within a few days post-weaning to levels comparable to those in sows fed ad libitum during lactation. It seems that dietary energy source does not affect IGF-I concentration when sows are in an anabolic status. Gaughan *et al.* (1996) found no differences in IGF-I levels among gilts fed a fat-rich diet or a fat-poor diet ad libitum. Plasma insulin concentration was correlated with IGF-I concentration in sows in a catabolic status (Van den Brand *et al.*, 2001a), and it appears in this situation, that insulin facilitated IGF-I production by the liver (Daughaday *et al.*, 1976; Johnson *et al.*, 1989; Butler *et al.*, 2003).

Effects of dietary energy source on reproductive performance

LH, oestradiol, and progesterone secretion

The number of studies regarding the effects of dietary energy source on reproductive hormones in sows is limited. Van den Brand *et al.* (2000a) used two levels of feed intake, and within each feeding level, fed a fat-rich or a carbohydrate-rich diet to lactating primiparous sows. Plasma LH pulse frequency during lactation was higher in sows given the higher level of feed than in sows given the lower level of feed (P = 0.04). In addition, sows fed the carbohydrate-rich diet tended to have a higher plasma LH pulse frequency than sows fed the fat-rich diet (Fig. 2; P = 0.06). There was no effect of lactational dietary energy source on plasma LH pulse frequency on the day of weaning (6.79 vs 7.61 per 12 h, for the fat and starch-rich diet, respectively, P = 0.31). In the same sows, there was no effect of dietary energy source on post-weaning oestradiol and progesterone profiles as well as on the preovulatory LH surge (Van den Brand *et al.*, 2000c). However, in multiparous sows, Kemp *et al.* (1995) found higher plasma oestradiol concentrations, a higher preovulatory LH surge and higher plasma progesterone concentrations when feeding a starch-rich diet compared to a fat-rich diet. This suggests that, in sows in a less severe negative energy balance, starch-rich diets stimulated reproductive endocrinology both at the pituitary and ovary. When sows were in a more severe negative energy balance, the effects of dietary energy source on reproductive endocrinology seemed to be limited.

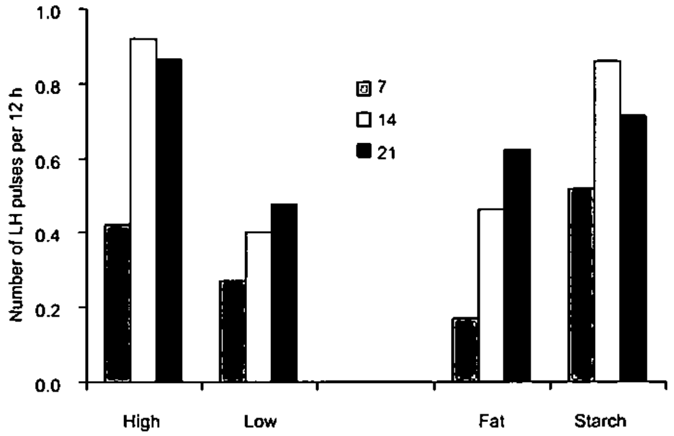

Fig. 2 Effect of feeding a fat or starch-rich diet at two feeding levels on LH pulse frequency during day 7, 14 and 21 of lactation. Overall SEM = 0.20. Feed intake: P = 0.04; Dietary energy source: P = 0.06 (Van den Brand *et al.*, 2000a).

Follicle development, WOI and ovulation rate

Ziêcik *et al.* (2002) found no effect of dietary energy source (starch, glucose or fat) on number and size of healthy and atretic follicles in gilts. Van den Brand *et al.* (2000a) found no differences in follicle size on day 2 after weaning when feeding a fat or carbohydrate-rich diet during and after lactation. However, when only sows that came into oestrus after weaning were taken into account, follicle size tended to be higher in sows fed the carbohydrate-rich diet (3.2 vs 3.8 mm; P = 0.06). The percentage of sows, which came into oestrus within 10 days after weaning, was similar for both dietary energy sources. In another experiment, in which the carbohydrate-rich or fat-rich diets were fed only after weaning, more primiparous sows in the carbohydrate-rich group entered postpartum oestrus earlier than those in the fat-rich group (Van den Brand *et al.*, 2001b; P = 0.04). Sows in this experiment lost 13% of their body weight, suggesting that, in sows that are predisposed to a prolonged WOI, carbohydrate-rich diets help to overcome this problem. In most cases, the WOI was not affected by dietary energy source fed during lactation (Rodriguez-Marquez and Cuaron, 1990; Johnston et *al.*, 1994; Van den Brand et *al.*, 2000a; Jones et *al.*, 2002), although Van den Brand et *al.* (2000a) showed that the WOI was 22 h shorter in sows fed a starch-rich diet at a low feeding level during lactation than in sows fed the fat-rich diet (130 vs 152 h, respectively; not significant).

Ovulation rate was greater in gilts fed a molasses rich diet compared to a control diet or a soy oil rich diet (14.5 vs 12.1 vs 11.9, respectively; Rodriguez-Marquez and Cuaron, 1990) and Cox et *al.* (1987) found that exogenous insulin increased the ovulation rate in gilts. However, this could not be confirmed in other studies using exogenous insulin (Rojkittikhun et *al.*, 1993a; Quesnel and Prunier, 1998). Van den Brand et *al.* (2000a) also found no effect of dietary energy source during lactation on subsequent ovulation rate in primiparous sows (17.0 vs 17.7 for the starch and fat-rich diet, respectively; $P = 0.50$). Based on these results, we conclude that carbohydrate-rich diets may have positive effects on reproduction traits, however, these effects are not very pronounced.

Conclusion

Increasing energy intake by addition of fat to the diet of lactating sows has limited or even negative effects on the reproductive performance of sows. Three pathways reacted negatively when feeding fat-rich diets. First, increasing dietary fat increased milk fat output, but also stimulated body fat loss. Second, fat-rich diets increased blood metabolite levels, which are possibly negatively related to reproductive performance. Third, fat-rich diets depressed secretion of insulin and IGF-1, which are directly or indirectly positively related with the concentration of reproductive hormones. Thus, we suggest looking to other ways to increase energy intake or to decrease body weight loss during lactation. Management factors to support feed intake, such as housing temperature, water intake and prevention of overfeeding in early lactation have more beneficial effects on reproductive performance than feeding fat-rich diets.

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