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Original article

In primiparous sows, plasma insulin-like growth factor-I can be affected by lactational feed intake and dietary energy source and is associated with luteinizing hormone

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Abstract — During a 21-day lactation period, 48 primiparous sows were fed a fat- or a starch-rich diet (131 g fat and 183 g starch + sugar·kg^{-1} vs. 31 g fat and 351 g starch + sugar·kg^{-1}) at a high or a low level of feeding (44 vs. 33 MJ net energy per day) according to a factorial design. Blood samples were collected at days 7, 14, 21, 22 (weaning), 24, 25, 26, and 27 post-partum (p.p.). IGF-I levels were higher with the starch-rich than with the fat-rich diet at days 7, 21, 22, and 24 p.p. Plasma IGF-I concentrations on day 22 p.p. were positively related with LH pulse frequency on day 22 p.p. and the height of the pre-ovulatory LH surge. Sows with low body weight at farrowing and high lactational body weight loss had lower plasma IGF-I concentrations than others, before and after weaning. These results indicate that IGF-I concentrations are affected by both feeding level and dietary energy source and are related to the secretion of LH. Furthermore, body weight at farrowing interacts with lactational body weight loss to affect IGF-I concentrations.

IGF-I / sow / lactation / LH / energy

Résumé — Chez les truies primipares, l'IGF-I plasmatique peut être influencé par le niveau alimentaire de lactation et la source d'énergie, et est associé à la sécrétion de LH. Pendant 21 jours de lactation, 48 truies primipares reçoivent un aliment enrichi en graisse ou en amidon (131 g graisse et 183 g amidon + sucre·kg^{-1} versus 31 g graisse et 351 g amidon + sucre·kg^{-1}) sous deux niveaux énergétiques (44 versus 33 MJ énergie nette par jour) selon un schéma factoriel. Des prises de sang ont

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lieu à 7, 14, 21, 22 (sevrage), 24, 25, 26, et 27 jours post-partum (p.p.). Les concentrations plasmatiques d'IGF-I mesurées de 21 à 26 jours p.p. augmentent avec le niveau d'énergie ingérée. Par ailleurs, elles sont plus élevées chez les truies recevant le régime enrichi en amidon aux jours 7, 21, 22 et 24 p.p. Les concentrations d'IGF-I mesurées à 22 jours p.p. sont corrélées positivement avec la pulsatilité de LH au jour 22 et avec l'amplitude du pic préovulatoire de LH. Les truies les plus légères à la mise bas et qui ont perdu le plus de poids en lactation ont des concentrations d' IGF-I plus faibles que les autres. Ces résultats montrent que les concentrations plasmatiques d'IGF-I sont influencées par la source d'énergie et par le niveau énergétique et qu'elles sont liées à la sécrétion de LH. De plus, le poids vif à la mise bas et la perte de poids en lactation interagissent pour moduler les concentrations d'IGF-I.

IGF-I / truie / lactation / LH / énergie

1. INTRODUCTION

In studies on the relationship between nutrition and reproduction, much emphasis has been given to insulin and insulin-like growth factor-I (IGF-I) as potential mediators (for reviews see [5, 12, 17]). Most studies regarding the role of IGF-I in reproduction are restricted to its influence on follicular development. Less emphasis has been given to relationships between systemic IGF-I levels and the hypothalamic-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 [19, 20]. 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 pulse frequency, weaning-to-oestrus interval, ovulation rate, embryonic survival).

Therefore, additional analyses were performed to study effects of these diets on plasma IGF-I levels and its relationships with reproductive traits. Several studies have already demonstrated that IGF-I concentrations can be affected by feeding level in various species including the pig (see [11, 18]). Whether dietary energy source plays a role in plasma IGF-I concentration is not clear.

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

2. MATERIALS AND METHODS

2.1. General design

During a 21-day period of lactation, 4 (8 batches of 6) primiparous Yorkshire × Dutch Landrace sows were allotted to a 2×2 factorial experiment. Treatments were feeding level (High: 44 MJ NE per day; 1050 g protein per day or Low: 33 MJ NE per day; 790 g protein per day) and major dietary energy source (Fat: 131 g·kg^{-1} fat; 183 g·kg^{-1} starch plus sugar or Starch: 31 g·kg^{-1} fat; 351 g·kg^{-1} starch plus sugar). Each sow nursed 9 piglets. During lactation, sows were housed in climatic respiration chambers [21]. After weaning (day 22) all sows received the same amount of feed (31 MJ NE per day, 740 g protein per day

from weaning to oestrus and 17.5 MJ NE per day, 420 g protein per day thereafter), but they remained on the same dietary energy source as fed during lactation. Sows that exhibited oestrus after weaning were inseminated and pregnant sows were slaughtered on day 35 of subsequent pregnancy. During lactation and around oestrus, frequent blood samples were taken to analyse metabolic and reproductive hormones. The experiment was conducted between autumn 1996 and spring 1997.

2.2. Animals and diets

On day 8 (range 6 to 11) before parturition, sows were surgically fitted with a permanent jugular vein catheter, according to the method described previously [16]. On day 3 (range 0 to 5) after parturition, 6 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 4 batches got the Low feeding level. Within each batch, 3 sows were fed the Fat-rich diet and the other 3 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 (Tab. I). Within each feeding level, diets were fed in different amounts to realise an isocaloric and isonitrogenous feed intake. Sows were fed twice daily (0800 and 1530 h). Water was available ad libitum for sows and piglets. No creep feed was offered to the piglets. On days 3 and 22, sows were weighed and backfat thickness was measured.

2.3. Blood sampling

On days 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 oestrus. Thereafter, blood samples were taken each 12-h, for 9 days. All blood samples were collected in ice-cooled polypropylene tubes, containing 100 µL of EDTA solution (144 mg·mL^{-1} saline), placed on ice immediately after collection and centrifuged at $2\,000 \times g$ for 10 min at 4 °C. Plasma was stored at –20 °C until analyses. Due to lack of catheter patency, not for all sows all blood samples were available.

2.4. 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 days 7, 14, and 21 of lactation were analysed 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 basic concentration. All plasma samples of days 7, 14, 21, and 22 as well as 13 samples taken each 4 h around expected LH surge were determined for LH concentrations. Plasma oestradiol concentrations were analysed 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 oestradiol 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 [19, 20]. Due to a very high LH pulse frequency on the day of weaning, no number of LH pulses could be counted for 3 sows.

For days 7, 14, and 21 of lactation, day 22 (weaning) and days 2 to 5 after weaning, one plasma sample (12.00 h) was analysed in duplicate for plasma IGF-I concentration in

Table I. 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]	1000		843	
Content	Calculated	Analysed	Calculated	Analysed
	g/1000 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]	8800	–	8800	–
kJ ME (for swine)[c]	11600	–	10600	–
Digestible lysine[d]	8.4	–	8.4	–

[a] 1000 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).

a single RIA as described previously [9]. The intra-assay CV was 7.2% at 200 ng·mL^{-1}. Only one plasma sample per day was analysed for IGF-I level, because of the relatively low variation in IGF-I level throughout the day [15].

2.5. Follicle size, oestrus and ovulation rate

On day 2 after weaning, mean follicle size was assessed by transrectal ultrasonography as described by Soede et al. [16]. From days 2 to 10 after weaning, oestrus detection was performed at 8-h intervals (0800, 1600 and 2400 h, in the presence of a vasectomized boar, using the back pressure test). Sows not exhibiting oestrus within 10 days after weaning were assumed to be in anoestrus. Sows that expressed oestrus were inseminated every day of standing oestrus with a commercial dose of semen containing 3×10^9 sperm cells. On day 35 after the last insemination, sows were

slaughtered to determine the ovulation rate and embryonic survival.

2.6. Statistical analyses

To test effects of treatments and days on IGF-I concentration the following model was used:

$$Y_{ijklm} = \mu + F_i + e1_{ij} + E_k + (F \times E)_{ik} + e2_{ijkl} + D_m + (F \times D)_{im} + (E \times D)_{km} + (F \times E \times D)_{ikm} + e3_{ijklm} \quad (1)$$

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); $(F \times E)_{ik}$ = 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); $(F \times D)_{im}$ = interaction between feeding level and day; $(E \times D)_{km}$ = interaction between energy source and day; $(F \times E \times D)_{ikm}$ = interaction between feeding level, energy source, and day; $e3_{ijklm}$ = 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.

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-I concentrations are tested again per day with the following model:

$$Y_{ijk} = \mu + F_i + e1_{ij} + E_k + (F \times E)_{ik} + e_{ijk} \quad (2)$$

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); $(F \times E)_{ik}$ = interaction between feeding level and energy source; $e2_{ijk}$ = 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. To test weaning-to-oestrus interval, ovulation rate, embryonic survival and body characteristics, also model 2 was used.

Overall correlation analyses were performed for IGF-I concentrations between days, and also between IGF-I concentrations on the different days and plasma glucose and insulin concentrations. Relationships between IGF-I on the different days and reproductive traits were tested with model 2, except that IGF-I concentration and its interactions with feeding level and energy source (including the triple interaction) were added to the model as covariates. To check whether regressions between IGF-I and reproduction traits were consistent within and between treatments, because IGF-I concentration was influenced by treatments, overall one-way correlation analyses with IGF-I were performed. Only for presentation of LSmeans in Table IV, IGF-I concentrations on days 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-I concentrations on day 21 on reproductive traits were also tested with model 2, except that both insulin and IGF-I, and all their interactions were introduced to the model as covariates.

To analyse 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 day 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 (Low: ≤ 17 kg, n = 12 and High: > 17 kg, n = 12; range 1 to 37 kg) of body weight loss during lactation 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 [14]. For analysing the number of sows in oestrus and the number of pregnant sows, Fisher exact test of SAS [14] was used.

3. RESULTS

3.1. Average reproductive and body characteristics

In Table II average reproductive and body characteristics per treatment group are summarised. The number of sows in oestrus within 10 days after weaning was higher at the High feeding level (P < 0.01). Weaning-to-oestrus interval was not affected by treatments. Ovulation rate tended to be higher in sows fed the High feeding level during lactation (18.0 vs. 16.2; SEM = 0.6; P = 0.09), whereas embryonic survival was not affected by treatments.

Body weight at farrowing and weaning was not significantly affected by the treatments. Backfat thickness at weaning was higher for sows fed the Starch-rich diet compared to sows fed the Fat-rich diet (13.5 vs. 12.3 mm, SEM = 0.3; P = 0.05).

3.2. Effect of day, feeding level and dietary energy source on IGF-I

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

Table II. Average reproductive and body characteristics per treatment group.

Feeding level[a]	High		Low		SEM	P-value[b]	
Energy source	Fat	Starch	Fat	Starch		Feeding level	Energy source
All sows, n	12	12	12	12	–	–	–
Body weight at farrowing, kg	161.6	161.6	161.0	163.3	2.7	0.90	0.66
Backfat thickness at farrowing, mm	17.6	18.7	17.3	17.3	0.6	0.19	0.42
Body weight at weaning, kg	146.0	149.1	137.8	141.8	2.3	0.20	0.14
Backfat thickness at weaning, mm	12.3	14.2	12.2	12.7	0.6	0.28	0.05
Sows in oestrus, n	12	11	7	8	–	0.01	1.00
Weaning-to-oestrus interval, h	123	122	152	130	9	0.14	0.20
Pregnant sows,	11	10	6	8	–	1.00	1.00
Ovulation rate, n	17.9	18.2	15.5	16.9	1.2	0.09	0.50
Embryo 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 × energy source interactions were observed.

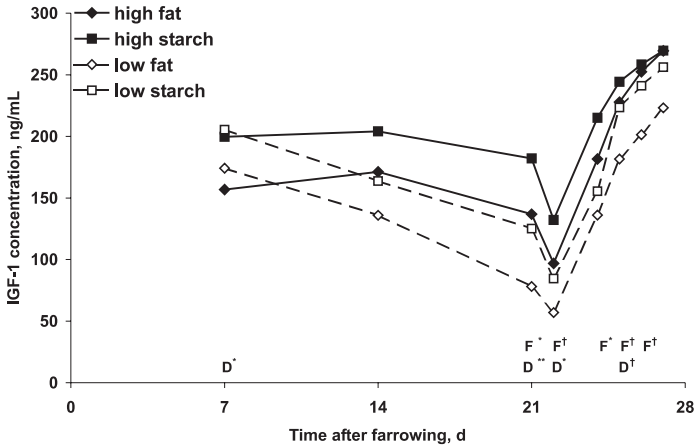

Figure 1. Plasma IGF-I (SEM = 12) profile per treatment. High = High feeding level during lactation; Low = Low feeding level during lactation; Fat = Fat-rich diet; Starch = Starch-rich diet; F = Effect of feeding level during lactation; D = Effect of dietary energy source; † $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

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

IGF-I concentrations measured on the different days were positively correlated (Tab. III). Plasma IGF-I concentrations on different days were also correlated with plasma glucose and insulin concentrations on different days (Tab. III).

3.3. Relationships between IGF-I and reproductive traits

No relationships between IGF-I concentration on days 7 and 14 of lactation and reproductive traits were found. In Table IV, relationships between IGF-I concentration on days 21 and 22 (day of weaning) with LH pulsatility and the pre-ovulatory LH surge are shown. Treatment corrected IGF-I concentration on day 21 tended to be ($P < 0.10$) positively related with LH pulsatility on day 22 (weaning) and the height of the pre-ovulatory LH surge. The relationships between IGF-I on day 22 and LH pulsatility on day 22 as well as the LH surge were positive ($P < 0.05$). The relationships between IGF-I and LH pulsatility were similar within all treatment groups. Figure 2 shows, as an example, the relationship between the IGF-I concentration on day 21 of lactation and the number of LH pulses immediately after weaning. Overall,

Table III. Coefficients of correlation between plasma IGF-I concentration (ng·mL^{-1}), glucose area under the curve (AUC; g/6.2 h), and insulin AUC (mIU/6.2 h) on days 7, 14, 21, and 22 (weaning) after farrowing.

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

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

one-way correlation analyses between IGF-I concentration and LH showed comparable results, except that the regressions were somewhat stronger (Tab. IV). Furthermore, overall relationship (β) remained consistent with the treatment-corrected relationships.

After correction for treatments, no relationships were found between IGF-I and follicle size on day 2 after weaning, weaning-to-oestrus interval, duration of oestrus, mean oestradiol concentration, mean progesterone concentration, ovulation rate, and embryonic survival (results not shown). Overall one-way analysis showed a positive relationship between IGF-I concentration on day 21 and follicle size on day 2 after weaning, although this relationship was weak ($R^2 = 0.11$; β = 0.0053; $P = 0.04$).

3.4. Additional effect of insulin to IGF-I

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

3.5. Effect of body weight and lactational body weight loss on IGF-I

After correction for treatments (feeding level and dietary energy source), an interaction between body weight at farrowing and lactational body weight loss was depicted for plasma IGF-I concentration on days 14 ($P = 0.02$), 21($P = 0.07$), 22 ($P = 0.08$), 26 ($P = 0.09$), and 27 ($P = 0.08$) after farrowing. Light sows with a high lactational body weight loss had lower plasma IGF-I concentrations than other sows (Fig. 3). Body condition at farrowing was not related to the IGF-1 concentration around weaning.

4. DISCUSSION

Higher plasma IGF-I concentrations in sows fed the High feeding level during lactation are in agreement with previous results [10, 13, 24]. Even a restricted feed intake during one week of lactation resulted in a decrease of IGF-I concentration [23], suggesting a rapid effect of feed intake on IGF-I concentration. The role of dietary

Table IV. Relationships between IGF-I concentration on days 21 and 22 (weaning) after farrowing and LH traits.

				SEM	Treatment corrected[b]			Overall one way[b]		
					R^2	β	*P*-value linear	R^2	β	*P*-value linear
IGF-I day 21, ng·mL^{-1}[a]	≤ 84	85–162	≥ 163							
Total number of sows, *n*	14	14	14							
Sows at the High feeding level	3	8	10							
Sows at the Fat-rich diet	11	5	5							
LH pulses day 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 day 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^{-1}	3.82	4.43	5.56	0.53	0.31	0.0138	0.07	0.09	0.0081	0.09
IGF-I d 22, ng·mL^{-1}[a]	≤ 52	53–114	≥ 115							
Total number of sows, *n*	14	14	14							
Sows at the High feeding level	4	7	11							
Sows at the Fat-rich diet	9	7	5							
LH pulses day 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^{-1}	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 × energy source + IGF-I class + e.
[b] Treatment corrected: Model: Y = μ + feeding level + batch (feeding level) + energy source + feeding level × energy source + IGF-I + e.
Overall one way: Model: Y = μ + IGF-I + e.

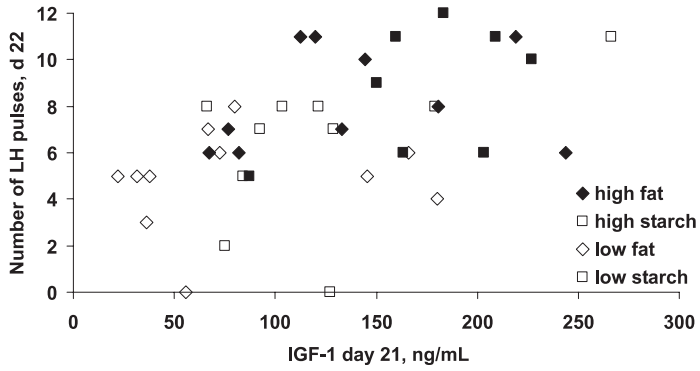

Figure 2. Relationship between IGF-I concentration on day 21 of lactation and number of LH pulses per 12 h on the day of weaning (day 22). From 3 sows the number of LH pulses was to high to count them accurately. Their IGF-1 concentrations on day 21 of lactation were 175, 197 and 253 ng·mL^{-1}.

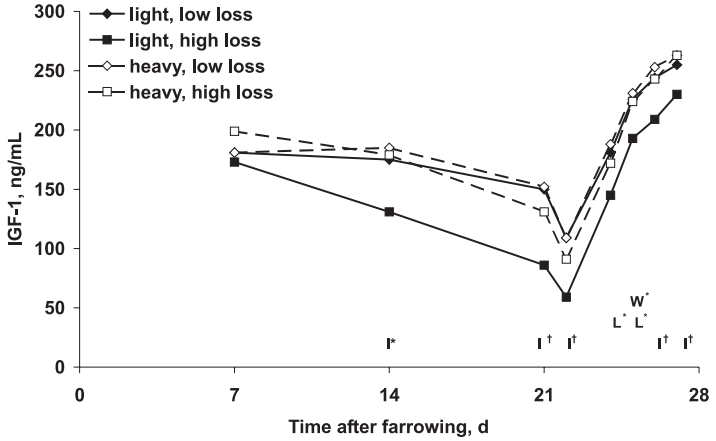

Figure 3. Effect of body weight at farrowing and lactational body weight loss (corrected for treatments) on plasma IGF profile (SEM = 8). Light = Body weight at farrowing ≤ 160 kg; Heavy = Body weight at farrowing > 160 kg; Low = Lactational body weight loss ≤ 17 kg; High = Lactational body weight loss > 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.

energy source on IGF-I concentration has hardly been investigated in the pig. In dairy cattle, no differences in IGF-I and insulin concentrations were found between cows receiving one of three levels of dietary fat [1]. Our data show that giving sows a starch-enriched diet has a positive effect on both plasma IGF-I and insulin [19] concentration. Moreover, a positive correlation between plasma IGF-I and insulin concentration is observed, in agreement with data obtained by Quesnel et al. (unpublished results) in restricted fed lactating sows and restricted fed cyclic gilts. This positive relationship between insulin and IGF-I agrees well with the finding that insulin stimulates in vitro production of IGF-I by rat liver cells [4, 6]. In cyclic gilts fed at 2.4 times

maintenance this positive relationship between insulin and IGF-1 was not found (Quesnel et al., unpublished results). It seems that the relationship between insulin and IGF-1 only exist when feed intake is relatively low. When feed intake is high, insulin levels are high [7, 13], and are probably not limiting for IGF-I production. Contrarily, when feed intake is low, plasma insulin concentration is low, and probably not high enough to mediate maximum production of IGF-I 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-I 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-I concentration. Therefore, rearing strategy and feeding management during pregnancy and lactation could be important determinants for subsequent IGF-I production. A positive relationship between body weight and IGF-I concentration was also found in prepubertal gilts [2]. In the current study sows were in a normal condition at farrowing and body weight loss and backfat thickness loss during lactation was not excessive. Even with this relatively mild contrast in lactational body weight loss and backfat thickness loss, differences in IGF-1 concentration were observed. Therefore, it seems that feed management to reduce body weight and backfat thickness loss, are tools to affect IGF-1 concentration and consequently reproductive performance.

Our data show that IGF-I 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 during lactation. This is in agreement with previous experiments with well-fed multiparous sows [15] and underfed primiparous sows [8]. The present study is, to our knowledge, the first one that carefully describes the post-weaning plasma IGF-I pattern: Schams et al. [15] only measured on day 3 post-weaning, Caroll et al. [3] on days 1 and 4 after weaning, and Messias de Bragança and Prunier [10] on days 1 and 8 after weaning.

It is also the first time that a decrease in IGF-I 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 that were restricted fed during lactation. As a consequence, the effect of the lactational feed intake on IGF-I was reduced and, at day 5 post-weaning, the difference between lactational feeding levels was obliterated. This is in good agreement with data from Caroll et al. [3] and Messias de Bragança and Prunier [10] showing that the IGF-I concentration of restricted fed sows during lactation restore within a few days post-weaning to comparable levels as those observed in sows fed ad libitum during lactation.

The positive relationship of IGF-I measured just before and after weaning with LH pulsatility determined on the day of weaning, and the pre-ovulatory LH surge suggests that IGF-I not only acts at the ovarian level (see for review [5, 17]), but also at the hypothalamic-pituitary level. This is supported by the results of Whitley et al. [22]. They found, in vitro, an increased LH secretion by porcine anterior pituitary cells when IGF-I was added to the medium. Pettigrew and Tokach [12] also found a positive correlation between IGF-I concentration and LH secretion in lactating sows. However, such relationship between IGF-I and LH pulse frequency just before and after weaning was not observed by Quesnel et al. [13]. Remarkable is the relatively large variation in IGF-1 concentration within the treatment groups; for example the Low Starch group varied in IGF-1 concentration on day 21 of lactation from 66 to 267 $ng \cdot mL^{-1}$ and a LH pulse frequency on the day of weaning from 0 to 11.

The feed deprivation on the day of weaning resulted in a depressed plasma IGF-I concentration. It should be noticed that this occurred at the time when LH pulse frequency increased and around the time when pre-ovulatory 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 [19]. Together with IGF-I, insulin did not have an additional effect on reproductive traits. This suggests that, in the present experiment, IGF-I 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-I concentration is more constant.

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

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