

Effect of dietary fat on serum parameters, and productive and reproductive performance of multiparous sows

Efecto de los lípidos de la dieta sobre parámetros séricos y desempeño productivo y reproductivo en cerdas multíparas

Rivas, F. G.;¹ Gonzalez, M. A.;² Matiller, V.;³ Williams, S. I.⁴

¹ Vetifarma S.A., La Plata, Buenos Aires, Argentina.

² Estación Experimental Agropecuaria INTA Las Breñas, Chaco, Argentina.

³ Instituto de Ciencias Veterinarias del Litoral (ICiVet-Litoral), UNL, CONICET, Esperanza, Santa Fe, Argentina.

⁴ Facultad de Ciencias Veterinarias, Universidad Nacional de la Plata, La Plata, Buenos Aires, Argentina.

Recibido 21/07/2023 – Aceptado 29/12/2023

Summary: The objective of the study was to evaluate the effect of fat inclusion on the productive and reproductive parameters of sows and their litters as well as the serum concentrations of insulin, glucose, luteinizing hormone (LH) and non-esterified fatty acids (NEFAs). Thirty multiparous sows were divided into three groups (n=10) and randomly assigned to treatments T0, T1 and T2, corresponding to gestation and lactation diets with 0%, 3.5%, and 7% of fat inclusion, respectively. Blood samples were obtained from the jugular vein the day of weaning and on days 3, 5, and 7 after. The variables recorded were the sow average daily feed intake (ADFI), average daily energy intake (ADEI), body weight loss, litter size, survival rate, and litter average daily gain (ADG), litter weight at birth and weaning and the wean-to-estrus interval (WEI). Analyses were performed using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). Fat inclusion improved the ADFI and ADEI of sows, and the piglet ADG. The WEI was reduced by 0.7 days in those sows supplemented with fat compared to the control group. Glucose, LH and insulin levels were not altered between treatments. However, NEFAs levels were higher in those sows consuming diets with no fat added.

Keywords: lipids, diets, blood parameters, sow nutrition

Resumen: Se evaluó el efecto de la inclusión de grasa sobre parámetros productivos y reproductivos de cerdas, sus camadas y en niveles séricos de insulina, glucosa, hormona luteinizante (LH) y ácidos grasos no esterificados (NEFAs). Treinta cerdas multíparas fueron divididas en tres grupos (n=10) y asignadas aleatoriamente a los tratamientos T0, T1 y T2 correspondientes a dietas de gestación y lactancia con 0, 3.5 y 7% de grasa respectivamente. Se tomaron muestras de sangre de la vena yugular el día del destete y en los días 3, 5 y 7 posteriores. Se registró la ingesta media diaria de alimento (ADFI) y energía (ADEI) de las cerdas, pérdida de peso corporal, tasa de supervivencia y ganancia media diaria de la camada (ADG), peso de la camada al nacimiento y al destete, y el intervalo destete-celo (WEI). Se empleó el procedimiento MIXED de SAS (SAS Inst. Inc., Cary, NC) para el análisis estadístico. La inclusión de grasa mejoró la ADFI, ADEI y la ADG. El WEI en las cerdas suplementadas con grasa disminuyó 0.7 días en comparación con el grupo control. No hubo diferencias en los niveles de glucosa, LH e insulina entre tratamientos, pero los niveles de NEFAs fueron superiores en las cerdas del T0.

Palabras claves: lípidos, dietas, parámetros sanguíneos, nutrición de cerdas

Introduction

Over the last few decades, genetic selection and improvements in management, health, and nutrition have led to significant increases in sow productivity (Tokach *et al.*, 2019). Higher productivity has caused sows to

mobilize more body reserves to meet increased energy requirements during gestation and lactation (Walsh *et al.*, 2012). In tropical and subtropical countries, sows are frequently exposed to ambient temperatures higher than the upper critical temperature, which is in the range of 21–22°C (de Bragança & Prunier, 1999). Under these conditions, sows reduce their feed intake in order to decrease heat production from the digestion and metabolism (Liu *et al.*, 2022). This is associated with a reduction of milk production (Black *et al.*, 1993) and, hence, of piglet growth along with a decline of the subsequent reproductive performance of the sow (Einarsson *et al.*, 2008; Hansen, 2009).

Adding fat to sow diets during late gestation and lactation is a potential approach to ensure that sows consume sufficient energy mainly in high temperature conditions due to its high energy density and low caloric increase associated with its digestion and absorption compared to other commonly used energy sources (Rosero *et al.*, 2012). Many studies have evaluated the effects of fat supplementation on reproductive performance of sows and growth performance of piglets (Pettigrew & Moser, 1991; Tummaruk *et al.*, 2014). However, the results from these studies are inconsistent, due to diverse factors such as nutritional supplementation, number of parity, farm management and environmental temperatures (Wang *et al.*, 2022).

It has been suggested that fat-rich diets may alter intermediary metabolism, and thereby, affect reproductive performance through nutritional signals affecting the hypothalamus, pituitary, and/or the reproductive organs. Potential signals linking nutrition and reproduction can be divided into hormones (for example, insulin and LH), growth factors and metabolites such as glucose and NEFAs (van den Brand & Kemp, 2006).

Low feed intake and severe body weight loss during lactation are associated with increased levels of blood NEFAs, and although several studies have demonstrated that high plasma NEFA concentrations could reflect the metabolic state of lactating sows (Hultén *et al.*, 2002) the relationship between NEFA and reproduction remains unclear. The effects of glucose at the pituitary level are limited and the results of studies are contradictory, probably because its effects are confused with those of insulin (Barb *et al.*, 1991; Koketsu *et al.*, 1996). Several studies have shown that insulin might be an intermediary between nutrition and reproduction, acting at both the hypothalamus-pituitary and ovarian levels. Studies have found correlations between plasma insulin concentration and plasma LH pulse frequency during and after lactation in sows. The effect of dietary energy source on plasma insulin concentration is very clear (van der Brand *et al.*, 2000); carbohydrate-rich diets increased plasma insulin concentration more than fat-rich diets, in both non-lactating and lactating pigs (Jones *et al.*, 2002). Comparable results should be expected in lactating sows, but experiments on the effect of fat on blood insulin concentrations in the lactating phase are limited.

Therefore, the objective of this study was to determine the effect of fat inclusion during late gestation and lactation on reproductive and productive indicators of sows and their offspring, along with serum concentrations of glucose, insulin, LH and NEFAs.

Materials and methods

The procedures described herein were approved by the Ethics and Safety Advisory Committee (CAES) of the Faculty of Veterinary Sciences at the National University of the Litoral (File FCV-0898035-17 - Internal Protocol 404-18).

Animal handling, facilities and diets

Thirty sows (Landrace x Yorkshire) with similar weight (205 ± 1.05 kg), health status and parity (2) were selected from the facilities of the National Agricultural Technology Institute at Las Breñas, Chaco, Argentina, and placed in a 300-sows commercial farm located in Concepción del Bermejo, Chaco, Arg. from January 2019 to June 2020.

From mating to day 110 of gestation, the sows were housed in individual gestation crates (2.20 x 0.65m; concrete slatted floor) and then moved to the farrowing pens (2.40 x 1.80m; thermoplastic slatted floor, infrared light and heating mat), where they remained until the day of weaning (21 days of lactation). The temperature inside the facilities was manually regulated using curtains and a dripping system. Ambient temperature (°C) and relative humidity (%) were recorded daily using 2 data loggers (Temlog 20H model) strategically located in the gestation and farrowing facilities. The recording frequency was every 1 hour for the entire duration of the experiment.

Three groups were formed with an equal number of individuals (n=10) and then randomly assigned to one of the following treatments: T0 (gestation and lactation diets without inclusion of fat), T1 (gestation and lactation diets with inclusion of 3.5% fat) and T2 (gestation and lactation diets with inclusion of 7% fat). All diets were formulated to meet or exceed NRC (2012) recommendations. The composition of the experimental diets as well as the fat used (commercial fat derived from vegetable oils) are detailed in Tables 1 and 2, respectively.

Table 1. Composition of experimental diets.

Treatments Diets	T0		T1		T2	
	Gest.	Lact.	Gest.	Lact.	Gest.	Lact.
Ingredients						
Expeller soybean (%)	22.50	38.50	22.80	39.30	23.20	39.80
Corn (%)	54.50	58.50	42.70	54.20	38.80	50.20
Wheat bran (%)	20.00	-	28.00	-	28.00	-
Gestation Premix (%)	3.00	-	3.00	-	3.00	-
Lactation Premix (%)	-	3.00	-	3.00	-	3.00
Fat (%)	-	-	3.50	3.50	7.00	7.00
Chemical composition						
Dry matter (%)	90.13	91.68	90.47	92.12	90.88	92.83
Crude protein (%)	17.11	20.50	17.02	20.50	16.86	20.50
Metabolizable energy (Kcal./Kg.MS)	3.194	3.447	3.202	3.505	3.260	3.503
Lysine (%)	0.85	1.30	0.85	1.31	0.85	1.32
Dig. Lysine (%)	0.70	1.09	0.70	1.10	0.70	1.12
Dig. Methionine (%)	0.24	0.23	0.22	0.27	0.27	0.28
Dig. Tryptophan (%)	0.17	0.17	0.17	0.23	0.23	0.24
Dig. Threonine (%)	0.44	0.43	0.42	0.61	0.61	0.62
Dig. Arginine (%)	1.01	1.05	1.04	1.33	1.34	1.35
Crude fiber (%)	3.91	2.79	4.34	2.71	4.25	2.65
Calcium (%)	0.99	0.87	1.00	0.87	1.00	0.86
Phosphorus (%)	0.60	0.65	0.65	0.64	0.64	0.66
Ash (%)	5.42	5.50	5.68	5.51	5.66	5.53

Table 2. Chemical composition of fat used

Composition	
Water (%)	3.5
Gross fat (%)	84.0
Ash (%)	12.6
Calcium (%)	9.0
Fatty acids	
Myristic acid (C14:0) (%)	0.2
Palmitic acid (C16:0) (%)	11.4
Stearic acid (C18:0) (%)	4.6
Oleic acid (C18:1) (%)	23.5
Linoleic acid (C18:2) (%)	52.0
Energy values	
Gross energy (Mcal./Kg. MS)	7.7
Metabolizable energy (Mcal./Kg. MS)	5.8
Coefficient of digestibility	0.8

The T₀ gestation diet was offered from the day of mating until day 90 of gestation to all sows and then assigned to each group their corresponding gestation diets (T₀, T₁ or T₂) until day of farrowing. From that day until next mating, sows consumed lactation diets corresponding with their assigned treatment. This mechanism was repeated at each subsequent cycle in order to ensure that the sows always received the same treatment (diets). The experimental period covered from the 2nd to 4th parity of all sows. Cross-fostering was done the first day of lactation after 24 h to allow for colostrum intake from their own mothers and assure the minimum difference between litters (± 1 piglet).

During gestation and up to the day of farrowing sows consumed 2.5 kg/sow/ twice a day (0800 and 1800 h). During lactation, food access was *ad libitum*. All the sows and their litters had free access to water. Feed was offered in a ground fine for the sows and in a micro-pelleted form for the piglets from the day 10 of life. Routine laboratory analysis (chemical composition, and particle size) of the feed and ingredients were carried out once a month at a commercial laboratory. Mycotoxins analyses were carried out every three months.

The variables recorded were the sow average daily feed intake (ADFI; only during the lactation due to the restriction on the feed intake in gestation and estimated from the difference between feed offered and feed refused by sows), average daily energy intake (ADEI), body weight loss (calculated by the difference between the weight at weaning and the weight at farrowing), litter size (after cross fostering), survival rate (from birth to weaning), litter average daily gain (ADG), litter weight at birth and litter weight at weaning.

In order to calculate the wean-to-estrus interval (WEI, monitored daily three times per day, by using boar stimuli) the beginning of the estrus period was characterized as the midpoint between the time of the first observed positive response to back pressure (immobilization reflex) and the previous period of estrus detection.

Blood Samples and Assays

On the day of weaning and on days 3, 5 and 7 post-weaning, 5ml blood samples were collected from sows by jugular venipuncture using a 18G x 2 (50/12) hypodermic needle. All samples were taken -15 and 60 min relative to the first morning meal. Blood samples were collected in ice-cooled polypropylene tubes, placed on ice immediately after collection, and centrifuged at $2,000 \times g$ for 10 min. Serum samples were stored at -20°C until analysis in a commercial laboratory (Mega Laboratory S.A., Rafaela, Santa Fe, Arg.)

Serum samples taken at -15 and 60 min relative to the morning feeding on day of weaning and on days 3, 5 and 7 post-weaning were analyzed for glucose (enzymatic hexokinase UV) and insulin (electrochemiluminescence). For non-esterified fatty acids and luteinizing hormone concentrations, serum samples taken 60 min relative to the morning feed on day of weaning and days 3, 5 and 7 post-weaning were analyzed using an enzymatic method and electrochemiluminescence method, respectively.

Statistical analyses

The experiment was designed as a completely randomized design with repeated measures in time. All data were statistically analyzed using the PROC MIXED procedure (SAS Inst. Inc., Cary, NC). Data are reported as least squares means and are considered significant if $p < 0.05$. The treatments (diets) were the main effect and the individual sow and its litter were considered as the experimental unit. Statistical model included dietary fat levels, parity and all their interactions. Ambient temperature was considered as a covariate. An autoregressive covariance structure (AR1) was applied with parity as the repeated effect in order to avoid serial correlation.

Results

Sow and litter performance

Based on the results obtained from the evaluated parameters (Table 3), body weight at farrowing and at weaning were similar in the control sows and in those whose rations were added with fat ($p > 0.05$), but the average intake daily feed ($p < 0.05$) and average daily energy intake ($p < 0.05$) were significantly greater than the control group ($p < 0.05$), as was the weaning-to-estrus interval ($p < 0.05$). Litter size and birth weight were similar between treatments ($p > 0.05$), but the average daily gain of litters of sows fed diets with added fat was greater ($p < 0.05$). When comparing the weight of the litters at weaning, it was higher in litters whose rations were added with 7% fat ($p < 0.05$). No significant differences were found in litter size at weaning or in the survival rate between treatments (Table 3).

Table 3. Effects of the treatments on sow and litter performance.

Item	Treatments			SEM ^a	p-value
	To	T1	T2		
BW ^b at farrowing, (kg)	252.80	253.50	252.00	2.24	0.547
BW at weaning (kg)	225.60	226.90	224.20	2.56	0.478
BW change (kg)	-27.20	-26.60	-27.80	0.42	0.195
ADFI ^c (kg)	4.30 ^a	6.00 ^b	6.90 ^c	0.95	0.041
ADEI ^d (Mcal/d)	14.82 ^a	21.03 ^b	24.17 ^c	0.50	0.032
Litter size	14.80	14.60	14.80	1.16	0.638
Litter weight at birth	1.18	1.21	1.20	0.12	0.732
WEI ^e (days)	5.80 ^a	5.77 ^a	5.10 ^b	0.16	0.025
Litter					
Litter size at weaning	12.30	12.50	12.70	0.10	0.070
Litter weight at weaning	4.96 ^a	5.20 ^a	5.82 ^b	0.28	0.041
Survival rate (%)	83.10	85.60	85.80	1.02	0.112
ADC ^f (kg/d)	0.18 ^a	0.19 ^a	0.22 ^b	0.06	0.037
^a SEM=standard error of the mean; ^b Body weight; ^c Average daily feed intake; ^d Average daily energy intake; ^e Wean-to-estrus interval; ^f Average daily gain; Means with different superscripts differ at p < 0.05.					

Hormones and plasma metabolites

Fat inclusion in sow's diets had no effect on serum levels of insulin and glucose (Table 4; p > 0.05). However, serum NEFA levels were significantly lower (p < 0.05) when dietary fat was added (Figure 1). No differences were detected (p > 0.05) on serum levels of luteinizing hormone among treatments (Figure 2).

Table 4. Effects of the treatments on serum levels of insulin and glucosa.

Item	Treatments			SEM ^e	p-value
	To	T1	T2		
Insulin (uU/ml)					
pre-prandial (-15min) ^f	0.96 ^a	0.89 ^a	1.04 ^a	0.22	0.321
post-prandial (+60min) ^g	1.15 ^b	1.02 ^b	1.20 ^b	0.15	0.078
Glucose (g/l)					
pre-prandial (-15min)	0.45 ^c	0.34 ^c	0.40 ^c	0.09	0.094
post-prandial (+60min)	0.50 ^d	0.39 ^d	0.41 ^d	0.08	0.100
^e SEM= standard error of the mean; ^{f,g} Relatives to the first morning meal; In the same row, means with different superscripts differ at p < 0.05.					

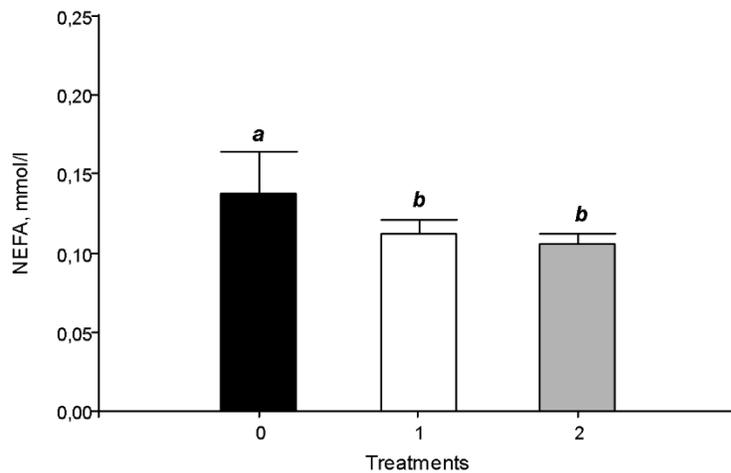


Figure 1. Effects of the treatments on serum non-esterified fatty acids levels. Bars with different letters (a;b) differ at $p < 0.05$.

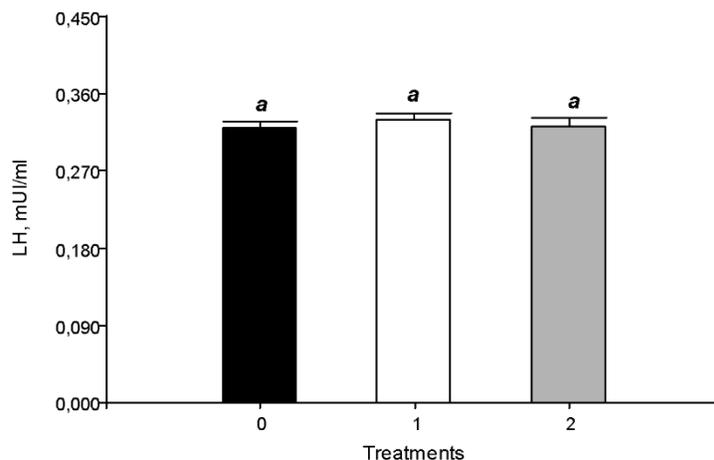


Figure 2. Effects of the treatments on serum luteinizing hormone levels. Bars with same letters do not differ at $p < 0.05$.

Discussion

Fat is used commonly as a supplemental ingredient in swine diets. From a nutritional perspective, fat is a highly concentrated source of energy, providing essential fatty acids to the animal organism, and has a lower heat increment associated with digestion and metabolism than carbohydrates, fiber, or protein (Rosero *et al.*, 2012). Consequently, studies have shown a higher animal performance when fat was added to diets, especially under heat stress conditions (Cho & Kim, 2012; Li *et al.*, 2019; Pettigrew, 1981). In this study, average ambient temperature was 26.5°C, which is higher than the upper critical temperature for sows (21-22°C) and the maximum temperature recorded was 43.2°C which is a very common situation in the swine production systems from the subtropical region of Argentina.

When we took into consideration only studies performed under termoneutral condition so fat inclusion did not alter or even decreased ADFI and ADEI (Neal *et al.*, 1999; Quiniou *et al.*, 2008; Shurson *et al.*, 1986), but in this study fat inclusion increased significantly the ADFI and the ADEI. This may be due to the fact that under tropical conditions dietary fat addition increases ADFI and consequently the ADEI (Christon *et al.*, 1999; Rosero *et al.*, 2012; Schoenherr *et al.*, 1989). Mean ambient temperature during the experiment was 26.5°C (max: 43.2°C; min: -3.8°C) and a HR of 66.5%.

This difference on the response of the fat supplementation according to the ambient temperature could be related with metabolism of satiety hormones released by the gastrointestinal tract. In the pig, those hormones

are mainly cholecystokinin, glucagon like peptide-1, peptide tyrosine tyrosine and ghrelin (Steinert *et al.*, 2013). A high-fat meal can effectively induce secretion of these satiety hormones compared to high-starch diets (Seimon *et al.*, 2009).

Another factor involved could be the molecular structure of fatty acids. Carbon chain length and saturation of fatty acids impacts the effect of dietary fat on appetite and releasing of satiety hormones (Kaviani & Cooper, 2017). Fatty acids with longer carbon chain lengths had stronger effects on stimulation of appetite compared to shorter chain lengths of carbons. Hormones involved in regulation of feed intake integrate with plasma glucose, insulin, intestinal osmolality and enteric neurons to maintain a balance of energy intake (Cummings & Overduin, 2007).

But even taking all this into consideration, there were not enough observations to analyze how the additional fat intake affects changes on feed consumption in sows at tropical environment. Higher sow's feed intake under high temperature conditions may be due to a lower heat increment of fat compared to other nutrients (Wang *et al.*, 2022).

Other researchers demonstrated that sows fed with fat supplemented diet had higher piglet survival rate and shorter postweaning interval to estrus than those sows fed with diets that relied on starch as an energy source (Cox *et al.*, 1983; Quiniou *et al.*, 2008). In the present study, fat addition shortened the wean-to-estrus interval but did not change losses of body weight from weaning to farrowing.

Two theories exist to explain the relationship between energy balance and reproduction. The first theory, known as the metabolic fuel hypothesis, suggests that nutrient molecules and metabolites can be oxidized and serve as sensory stimuli for the reproductive axis's responses (Schneider, 2004). The second theory proposes that fat has a stimulating effect on estrogen production and sex hormone binding globulin. By supplementing fat, the production of estrogen and sex hormone binding globulin is enhanced, thereby increasing the sensitivity of the hypothalamic-pituitary-ovarian axis (Mikhael *et al.*, 2019). Maintaining reproductive function requires a certain level of adiposity. Consequently, fat serves a dual purpose as a metabolic fuel and as a means of preserving adipose tissue, thereby regulating reproductive functions.

Although fat content of the colostrum was not a measured parameter in the present study, other authors has shown the correlation between a higher calostrual fat content when fat was added in sow's diets (Farmer, 2019; Ma *et al.*, 2020). We found that the addition of fat did not have a significant impact on piglet survival rates. In a review of studies conducted between 1974 and 1979, Pettigrew & Moser (1981) observed that adding fat to sow diets improved piglet survival rates in herds with rates below 80%. However, when the piglet survival rate exceeded 80%, fat supplementation had minimal effect on improving the rate. Over the past two to three decades since Pettigrew & Moser's report in 1991, there have been significant genetic advancements in sow selection, as well as substantial improvements in pig farm facilities and management practices. With such high survival rates, sows did not respond significantly to dietary fat, indicating that the survival rate was unaffected.

In contemporary times, enhanced sow reproductive capacity leads to larger litters, but it also raises the proportion of piglets born with reduced body weights. Incorporating fat into sow diets does not alter the total weight of the litter at birth, nor does it affect the number of live piglets per litter. On the other hand, an increased ADG was observed in this study and consequently a higher weight at weaning was observed. In termoneutral conditions ADG tends to remain unaltered by fat supplementation, but this situation changes when sows were under high ambient temperatures (Christon *et al.*, 2005; Neal *et al.*, 1999; Wang *et al.*, 2022).

In recent decades, significant focus has been placed on understanding the nutritional signals that impact the hypothalamus, pituitary gland, and reproductive organs. These signals linking nutrition and reproduction can be categorized into hormones (such as insulin, leptin, growth hormone, thyroxine, triiodothyronine and glucocorticoids), growth factors (including IGF-1 and IGF-II), and metabolites (such as glucose, NEFA, BHBA, and urea). Numerous authors have examined these intermediates and their associations with reproduction (Barb *et al.*, 2001; Cosgrove & Foxcroft, 1996; Prunier & Quesnel, 2000).

In our study, we focused on insulin, glucose, luteinizing hormone and non-esterified fatty acids as nutritional signals. However, only NEFA serum levels were different between treatments. Sows fed diets with no fat added had the higher serum concentrations of NEFA. This is similar to results from studies on the effect of dietary energy source and plasma levels (Jones *et al.*, 2002; Tilton *et al.*, 1999). Carbohydrate-rich diets likely contribute to a decrease in the rise of plasma NEFA concentration during lactation. This effect is achieved by potentially limiting the availability of dietary fat and reducing the utilization of stored body fat. Although non-significant, other studies (Paterson & Pearce, 1994; Tokach *et al.*, 1992) reported higher plasma NEFA levels in sows with a prolonged WEI compared to sows with a short WEI. This may be attributed to the weak negative correlation between plasma NEFA concentration and the number of luteinizing hormone pulses in the blood.

Studies that shows a strong relationship between dietary energy source and plasma levels of insulin and glucose were performed in termoneutral conditions (Park *et al.*, 2009; van den Brand *et al.*, 2000). This is an important factor to be taken into account since most recent studies have reported an alter metabolism of insulin and glucose when the animals are under heat stress (Baumgard & Rhoads, 2013; Ross *et al.*, 2017; Seibert *et al.*, 2018). Although, the physiological mechanisms behind insulin levels and reproduction performance of pigs under heat stress remains unclear, it has been reported that high ambient temperatures negatively affect intracellular signaling pathways essential for successful reproductive function.

Fat supplementation during late gestation and lactation improved the ADFI and ADEI of sows, but no clear benefits were observed for BW change from weaning to farrowing, litter size and litter weight at birth. However, addition of fat improved subsequent reproductive performance by shortened the WEI. Moreover, supplementation of fat improved the ADG and the weight at weaning of the litter, but no differences were found for the survival rate. In the present study, no differences of serum levels of insulin, glucose and LH were observed but NEFA serum levels were higher in sows fed diets with no fat added.

References

- Barb C, Kraeling R, Barrett J, Rampacek G, Campbell R, Mowles T. 1991. Serum glucose and free fatty acids modulate growth hormone and luteinizing hormone secretion in the pig. *Proc. Soc. Exp. Biol. Med.* 198: 636-642. DOI: 10.3181/00379727-198-43301
- Barb C, Kraeling R, Rampacek G. 2001. Nutritional regulators of the hypothalamic—pituitary axis in pigs. *Reprod. Suppl.* 58: 1-15. PMID: 11980182
- Baumgard L and Rhoads Jr R. 2013. Effects of heat stress on post-absorptive metabolism and energetics. *Annu. Rev. Anim. Biosci.* 1: 311-337. DOI: 10.1146/annurev-animal-031412-103644
- Black J, Mullan B, Lorsch M, Giles L. 1993. Lactation in the sow during heat stress. *Livest. Prod. Sci.* 35: 153-170. DOI: 10.1016/0301-6226(93)90188-N
- Christon R, Saminadin G, Lionet H, Racon B. 1999. Dietary fat and climate alter food intake, performance of lactating sows and their litters and fatty acid composition of milk. *Anim. Sci.* 69: 353-365. DOI: 10.1017/S135772980005092X
- Christon R, Lionet H, Racon B, Saminadin G, Gaudru L, Schaeffer B, Cerneau P. 2005. The effect of dietary fat level on feed intake and performances of lactating sows and their litters. *Biotechnol. Anim. Husb.* 21: 195-204
- Cosgrove J and Foxcroft G. 1996. Nutrition and reproduction in the pig: ovarian aetiology. *Anim. Reprod. Sci.* 42: 131-141. DOI: 10.1016/0378-4320(96)01523-0
- Cox N, Britt J, Armstrong W, Alhusen H. 1983. Effect of feeding fat and altering weaning schedule on rebreeding in primiparous sows. *J Anim. Sci.* 56: 21-29. DOI: 10.2527/jas1983.56121x
- Cummings D and Overduin J. 2007. Gastrointestinal regulation of food intake. *J Clin. Invest.* 117: 13-23. DOI: 10.1172/JCI30227
- de Bragança M and Prunier A. 1999. Effects of low feed intake and hot environment on plasma profiles of glucose, non-esterified fatty acids, insulin, glucagon, and IGF-I in lactating sows. *Domest. Anim. Endocrinol.* 16: 89-101. DOI: 10.1016/S0739-7240(99)00002-8
- Einarsson S, Brandt Y, Lundeheim N, Madej A. 2008. Stress and its influence on reproduction in pigs: a review. *Acta Vet. Scan.* 50: 1-8. DOI: 10.1186/1751-0147-50-48
- Farmer C. 2019. Review: Mammary development in lactating sows: the importance of suckling. *Animal.* 13: 20-25. DOI: 10.1017/S1751731118003464
- Hansen P. 2009. Effects of heat stress on mammalian reproduction. *Philos. Trans. R. Soc.* 364: 3341-3350. DOI: 10.1098/rstb.2009.0131
- Hultén F, Valros A, Rundgren M, Einarsson S. 2002. Reproductive endocrinology and post-weaning performance in the multiparous sow Part 1. Influence of metabolic status during lactation. *Theriogenology.* 58: 1502-1517. DOI: 10.1016/S0093-691X(02)01059-2

- Jones G, Edwards S, Sinclair A, Gebbie F, Rooke J, Jagger S, Hoste S. 2002. The effect of maize starch or soya-bean oil as energy sources in lactation on sow and piglet performance in association with sow metabolic state around peak lactation. *Anim. Sci.* 75: 57-66. DOI: 10.1017/S1357729800052838
- Kaviani S and Cooper J. 2017. Appetite responses to high-fat meals or diets of varying fatty acid composition: a comprehensive review. *Eur. J. Clin. Nutr.* 71: 1154-1165. DOI: 10.1038/ejcn.2016.250
- Koketsu Y, Dial G, Pettigrew J, Marsh W, King V. 1996. Influence of imposed feed intake patterns during lactation on reproductive performance and on circulating levels of glucose, insulin, and luteinizing hormone in primiparous sows. *J Anim. Sci.* 74: 1036-1046. DOI: 10.2527/1996.7451036X
- Li J, Yong Y, Gong D, Shi L, Wang X, Gooneratne R, Yadnyavalkya P, Ju X. 2019. Proteomic analysis of the response of porcine adrenal gland to heat stress. *Res. Vet. Sci.* 122: 102-110. DOI: 10.1016/j.rvsc.2018.11.004
- Liu F, Zhao W, Le H, Cottrell J, Green M, Leury B, Dunshea A, Bell A. 2022. What have we learned about the effects of heat stress on the pig industry? *Animal.* 16-100349. DOI: 10.1016/j.animal.2021.100349
- Ma C, Liu Y, Liu S, Lévesque C, Zhao F, Yin J, Dong B. 2020. Branched chain amino acids alter fatty acid profile in colostrum of sows fed a high fat diet. *J Anim. Sci. Biotechnol.* 11:1-12. DOI: 10.1186/s40104-019-0423-9
- Mikhael S, Punjala-Patel A, Gavrilova-Jordan L. 2019. Hypothalamic-pituitary-ovarian axis disorders impacting female fertility. *Biomedicines.* 7: 5. DOI: 10.3390/biomedicines7010005
- National Research Council. 2012. *Nutrient Requirements of Swine: Eleventh Revised Edition.* Washington, DC: The National Academies Press. DOI: 10.17226/13298
- Neal S, Irvin K, Shurson G, Harris JrB, Hatfield E. 1999. Effect of lactation diet fat level on sow and litter performance. *PAS.* 15: 7-13. DOI: 10.15232/S1080-7446(15)31716-2
- Park M, Shinde P, Yan Y, Kim J, Choi J, Yun K, Kim Y, Lohakare J, Yang B, Lee J, Chae B. 2009. Reproductive performance, milk composition, blood metabolites and hormone profiles of lactating sows fed diets with different cereal and fat sources. *Asian Australas. J. Anim. Sci.* 23: 226-233. DOI: 10.5713/ajas.2010.90406
- Paterson A and Pearce G. 1994. Plasma hormone and metabolite concentrations and the interval from weaning to oestrus in primiparous sows. *Anim. Reprod. Sci.* 36: 261-279. DOI: 10.1016/0378-4320(94)90073-6
- Pettigrew J. 1981. Supplemental dietary fat for periparturient sows: a review. *J Anim. Sci.* 53: 107-117. DOI: 10.2527/jas1981.531107X
- Pettigrew J and Moser R. Fat in swine nutrition. 1991. In: Miller E., Ullrey D., Lewis A., editors. *Swine Nutrition.* Stoneham: Butterworths; p. 133-45
- Prunier A and Quesnel H. 2000. Nutritional influences on the hormonal control of reproduction in female pigs. *Livest. Prod. Sci.* 63: 1-16. DOI: 10.1016/S0301-6226(99)00113-X
- Quiniou N, Richard S, Mourou J, Etienne M. 2008. Effect of dietary fat or starch supply during gestation and/or lactation on the performance of sows, piglets' survival and on the performance of progeny after weaning. *Animal.* 2: 1633-1644. DOI: 10.1017/S1751731108002991
- Rosero D, Van Heugten E, Odle J, Arellano C, Boyd R. 2012a. Response of the modern lactating sow and progeny to source and level of supplemental dietary fat during high ambient temperatures. *J. Anim. Sci.* 90: 2609-2619. DOI: 10.2527/jas.2011-4242
- Rosero D, Van Heugten E, Odle J, Cabrera R, Arellano C, Boyd R. 2012b. Sow and litter response to supplemental dietary fat in lactation diets during high ambient temperatures. *J. Anim. Sci.* 90: 550-559. DOI: 10.2527/jas.2011-4049
- Ross J, Hale B, Seibert J, Romoser M, Adur M, Keating A, Baumgard L. 2017. Physiological mechanisms through which heat stress compromises reproduction in pigs. *Mol. Reprod. Dev.* 84: 934-945. DOI: 10.1002/mrd.22859
- Schneider J. 2004. Energy balance and reproduction. *Physiol. Behav.* 81: 289-317. DOI: 10.1016/j.physbeh.2004.02.007

- Schoenherr W, Stahly T, Cromwell G. 1989. The effects of dietary fat or fiber addition on energy and nitrogen digestibility in lactating, primiparous sows housed in a warm or hot environment. *J. Anim. Sci.* 67: 473-481. DOI: 10.2527/jas1989.672473x
- Seibert J, Graves K, Hale B, Keating A, Baumgard L, Ross J. 2018. Characterizing the acute heat stress response in gilts: I. Thermoregulatory and production variables. *J. Anim. Sci.* 96: 941-949. DOI: 10.1093/jas/skx036
- Seimon R, Feltrin K, Meyer J, Brennan I, Wishart J, Horowitz M, Feinle-Bisset, C. 2009. Effects of varying combinations of intraduodenal lipid and carbohydrate on antropyloroduodenal motility, hormone release, and appetite in healthy males. *J. Physiol. Regul. Integr. Comp. Physiol.* 296: 912-920. DOI: 10.1152/ajpregu.90934.2008
- Shurson G, Hogberg M, DeFever N, Radecki V, Miller E. 1986. Effects of adding fat to the sow lactation diet on lactation and rebreeding performance. *J. Anim. Sci.* 62: 672-680. DOI: 10.2527/jas1986.623672x
- Steinert R, Feinle-Bisset C, Geary N, Beglinger C. 2013. Digestive physiology of the pig symposium: secretion of gastrointestinal hormones and eating control. *J. Anim. Sci.* 91: 1963-1973. DOI: 10.2527/jas.2012-6022
- Tilton S, Miller P, Lewis A, Reese D, Ermer P. 1999. Addition of fat to the diets of lactating sows: II. Effects on hormone-sensitive lipase activity, energy mobilization in response to epinephrine, and plasma insulin and glucose concentrations. *J. Anim. Sci.* 77: 2501-2509. DOI: 10.2527/1999.7792501x
- Tokach M, Pettigrew J, Dial G, Wheaton J, Crooker B, Johnston L. 1992. Characterization of luteinizing hormone secretion in the primiparous, lactating sow: relationship to blood metabolites and return-to-estrus interval. *J. Anim. Sci.* 70: 2195-2201. DOI: 10.2527/1992.7072195x
- Tokach M, Menegat M, Courley K, Goodband R. 2019. Review: Nutrient requirements of the modern high-producing lactating sow, with an emphasis on amino acid requirements. *Animal*.13: 2967-77. DOI: 10.1017/S1751731119001253
- Tummaruk P, Sumransap P, Jiebna N. 2014. Fat and whey supplementation influence milk composition, backfat loss, and reproductive performance in lactating sows. *Trop. Anim. Health. Prod.* 46: 753-8. DOI: 10.1007/s11250-014-0559-8
- van den Brand H, Dieleman S, Soede N, Kemp B. 2000. 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. *J. Anim. Sci.* 78: 396-404. DOI: 10.2527/2000.782396x
- van den Brand H and Kemp B. 2006. Dietary fat and reproduction in the post-partum sow. *Soc. Reprod. Ferti. Suppl.* 62:177-89. PMID: 16866317
- Walsh M, Geraert P, Maillard R, Kluess J, Lawlor P. 2012. The effect of a non-starch polysaccharide hydrolysing enzyme (Rovabio® Excel) on feed intake and body condition of sows during lactation and on progeny growth performance. *Animal*. 6:1627-33. DOI: 10.1017/S1751731112000237
- Wang L, Zhang S, Johnston L, Levesque C, Yin J, Dong B. 2022. A systematic review and meta-analysis of dietary fat effects on reproductive performance of sows and growth performance of piglets. *J. Anim. Sci. Biotechnol.* 13:12. DOI: 10.1186/s40104-021-00662-3