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Non ruminant nutrition

Feeding level during the last week of gestation can influence performance of sows and their litters in the subsequent lactation

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Abstract

This study investigated the impact of feeding level during the last week of gestation on performance of sows and their litters in the subsequent lactation. A total of 48 sows were assigned to one of six feeding levels (1.8, 2.4, 3.1, 3.7, 4.3, or 5.0 kg/d) from day 108 of gestation until farrowing. Post-farrowing, all sows were fed similarly during lactation with a gradual increase in feed allowance in accordance with Danish recommendation until it reached the maximum allowance of 9 kg/d on day 17 of lactation. Plasma samples were collected from the sows during farrowing and lactation, and sow's body weight and backfat thickness, and milk samples were taken during lactation. Litters were standardized to have 13 to 15 piglets each and weighed once weekly during lactation. Plasma concentrations of urea, acetate, and butyrate in sows linearly increased ($P < 0.001$), while non-esterified fatty acids linearly decreased ($P < 0.001$) during farrowing with increasing feeding level. Moreover, concentrations of triglycerides ($P < 0.001$), acetate ($P = 0.007$), and succinate ($P < 0.001$) were greater in plasma collected at the onset of farrowing compared to the end of farrowing. Conversely, concentrations of glucose, urea, and butyrate ($P < 0.001$) were lower in plasma collected at the onset of farrowing than at the end. Sows fed 2.4 and 3.1 kg/d exhibited greater triglyceride concentrations than those fed 3.7 ($P = 0.03$) and 5.0 ($P = 0.02$) kg/d. Sows fed 1.8 kg/d during the last week of gestation had lower milk yield in wk 1 ($P < 0.001$) and wk 2 ($P = 0.001$) of lactation compared to the other groups. Additionally, litter weight gain ($P = 0.04$) and litter weaning weight ($P = 0.007$) were lower in sows fed 1.8 kg/d compared to the other groups. The greatest milk yield, litter growth, and litter size were observed in sows fed 3.7 kg/d during the last week of gestation, whereas the estimate generated by the regression model revealed that sows should have been provided with 4.0 to 4.1 kg/d as an adequate feeding level to maximize these performances in the subsequent lactation. Interestingly, feeding level during the last week of gestation did not influence feed intake during lactation. In conclusion, this study highlights the significance of adequate feed supply (4.0 to 4.1 kg/d) during the last week of gestation in order to maximize performance of sows in the subsequent lactation.

Lay Summary

Feeding sows at high or ad libitum level during an extended gestation period has been found to have a negative impact on the subsequent lactation performance. Conversely, in some European countries, it has been a common practice to reduce the feed allowance during the last 2 to 3 d before expected farrowing to mitigate issues like constipation and postpartum health problems such as mastitis, metritis, and agalactia. However, recent studies suggest that sows should be fed approximately 4 kg/d during transition period to improve farrowing performance. In the present study, we investigated the carry-over effects of feeding level (dose–response design) during the last week of gestation on lactation performance of sows and their litters in the subsequent lactation. The findings revealed that a lower feeding level during the last week of gestation reduced milk yield and litter size at weaning. Milk yield, litter growth, and litter size at weaning were greater in sows supplied with 3.7 kg/d during the last week of gestation. However, the estimate generated by the regression model indicates that sows should be provided with 4.0 to 4.1 kg/d during the final week of gestation to enhance their performance in the subsequent lactation. Therefore, the present results emphasize the benefits of maintaining an adequate feeding level during the last week of gestation to improve sows' lactation performance in the subsequent lactation.

Key words: adequate feeding, gestation, piglet growth, plasma metabolites, transition

Abbreviations: BW, body weight; DIM, days in milk; DM, dry matter; D2O, deuterium oxide; MY, milk yield; NEFA, non-esterified fatty acids; NSP, nonstarch polysaccharides

Introduction

The mechanisms regulating feed intake and copious milk production in lactating sows are still poorly understood. Current nutritional studies primarily focus on improving feed intake and minimizing loss of body weight (BW) in lactating sows. Previous research has examined the effects of feeding level during gestation on sows' lactation performance, with varying results; especially with regard to body fatness at farrowing (Dourmad, 1991; Weldon et al., 1994; Revell et al., 1998a). For example, Weldon et al. (1994) found that sows

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fed ad libitum during the last 55 d of gestation had lower feed intake and greater BW loss during lactation than those fed restricted (1.85 kg/d). Revell et al. (1998b) observed a 15% reduction in milk yield (**MY**) in fat sows (340 g fat/kg BW) compared to lean sows (280 g fat/kg BW) as a result of different feeding strategies during gestation to create divergent body fat at farrowing. Dourmad (1991) suggested that backfat thickness at farrowing is a more reliable predictor of the impact of gestation feeding strategies on subsequent lactation performance than the feeding level per se. Moreover, Kim et al. (2015) observed a linear decrease in feed intake and a corresponding rise in losses of backfat and BW during lactation period with increasing backfat thickness measured at day 109 of gestation. Similar results have been reported recently from 10 different trials in three Danish production herds (Hojgaard and Bruun, 2021). Collectively, these studies imply that overfeeding during gestation, leading to excessive fatness at farrowing, negatively affects the sows' lactation performance. However, there is a lack of research on the influence of short-term feeding strategies during the transition period on subsequent lactation performance of the sows. While short-term feeding may not result in excessive fatness at farrowing, the physiological requirements of sows change rapidly during this time, and feeding strategies in this period could potentially affect subsequent lactation performance. We hypothesized that providing sows with a high feeding level during the last week of gestation would not have a negative impact on their performance during the subsequent lactation. Therefore, this study aimed to investigate the effects of different feeding level in a dose-response design during the last week of gestation on sows' feed intake, milk production, and litter performance in the subsequent lactation period.

Materials and Methods

The animal experiment procedures and care of animals under study were conducted in compliance with the regulations set forth by the Ministry of Food, Agriculture and Fisheries, The Danish Veterinary and Food Administration, as outlined in act 474 of 15 May 2014 and executive order 2029 of 14 December 2020. The rearing, housing, and sampling practices adhered to the relevant Danish laws governing the care and use of animals for research purposes. The Danish Animal Experimentation Inspectorate approved the study protocol (Animal license number: 2018-15-0201-01484), which provided oversight throughout the experiment.

Handling of sows and piglets

The experiment involved 48 hybrid sows (DanBred Landrace × DanBred Yorkshire). These sows were divided into two blocks: 24 first-parity sows and 24 second-parity sows. The observation period for this data set started on the day of farrowing (blood sampling from sows) and continued until weaning on day 24 of lactation. The sows farrowed naturally without any farrowing induction. The gestation length ranged from 114 to 117 d, calculated retrospectively based on the actual farrowing date (data not shown). Performance of the sows during the transition period with respect to sows' BW and backfat thickness as well as litter characteristics at farrowing were published earlier (Feyera et al. 2021). Each sow was individually housed in farrowing pen with her litter in non-bedded farrowing crates that had a partially slatted floor. Each pen had a covered creep area with an infrared heating lamp to provide optimal climate for the litter. The litters were standardized to have 13 to 15 piglets each, based on the number of functional teats of the sows. Cross-fostering was not performed in this experiment; therefore, surplus piglets exceeding the number of available functional teats were euthanized during litter standardization. The weight of each piglet was measured individually and precisely on days 2, 7, 14, 21, and 24 of lactation to monitor the weekly litter weight gain and estimate MY of the sows. Dead piglets were accounted for in the calculation of litter gain and litter size, by using their weight at the time of dead and the number of days they survived. Standard piglet management procedures, including teeth grinding, tail docking, iron injection, and castration, were performed according to the regular practices at Aarhus University, Research Center Foulum, AU-Viborg. Body weight and backfat thickness of the sows were measured on days 2, 7, 14, 21, and 24 of lactation. Backfat thickness was measured at 65 mm from the midline at the last rib on the right side of the sows using a Renco Lean-Meater (Renco Corp., Minneapolis, MN).

Diet and feeding

From day 108 of gestation until weaning on day 24 of lactation, sows were provided with a lactation diet formulated based on the Danish recommendation (Tybirk et al., 2018). The diet primarily consisted of wheat, barley, and soybean meal. The dietary ingredients and both the calculated and analyzed diet compositions, are presented in Table 1, and a detailed description of the diet compositions has been published previously (Feyera et al., 2021). The sows used in this study were fed six different feed levels (1.8, 2.4, 3.1, 3.7, 4.3, or 5.0 kg/d; corresponds to 23.2, 31.0, 40.0, 47.7, 55.5, or 64.5 MJ ME/d, respectively; 8 sows/feeding level) from day 108 of gestation until farrowing to investigate the impact of different feeding level on farrowing kinetics and colostrum production of the sow, within the scope of another study (Feyera et al., 2021). Throughout the lactation period, all sows were fed the same lactation diet, while the feeding level was increased gradually in accordance with Danish recommendation until it reached the maximum daily allowance of 9 kg on day 17 of lactation, to determine whether the feeding strategy employed during the pre-partum transition period had any residual effect on the sows' subsequent lactation performance. The sows were fed three meals per day both during pre- and post-farrowing period at 0700, 1500, and 2300 using a Spotmix feeding system (Schauer Agrotronic GmbH, Prambachkirchen, Austria). Feed leftover was collected daily between 0900 and 1000 to calculate the realized feed intake. Once a week, feed samples were collected and stored at −20 °C until analysis. The sows had unrestricted access to drinking water.

Milk sampling and estimation of milk yield

Milk samples were collected on days 3, 10, 17, and 24 of lactation. The milk samples were primarily collected from the first two front teats on each side. To induce milk let-down, 0.30 mL of oxytocin (Oxytocin, 10 IU/mL; Intervet International B.V., Boxmeer, Holland) was injected into the ear vein. At each sampling point, 50 mL of milk sample was obtained through hand-milking, filtered using gauze, and stored at −20 °C until analysis. The weekly estimation of sow's MY was determined retrospectively, using the prediction model developed by Hansen et al. (2012), based on litter weight gain and litter size within each week.

Table 1 Dietary ingredients, calculated, and analyzed chemical compositions of the experimental diet

Item	Composition
Ingredients, g/kg feed as-fed	
Wheat	380
Barley	350
Soybean meal	138
Oat	50.0
Sugar beet pulp	30.0
Monocalcium phosphate	14.4
Vegetable oil, fat, and soy	14.1
Limestone (granulated)	11.4
Sodium chloride	5.35
L-Lys HCl	3.58
L-Thr	1.32
DL-Met	0.72
L-Val	0.07
Premix[1]	1.06
Calculated chemical composition, g/kg as-fed	
Dry matter, g/kg feed	877
ME, MJ/kg	12.9
Starch	433
Crude protein	155
Ash	56
Dietary fiber	177
Fat	38
Total Ca	7.78
Digestible P	3.90
SID Lys [2]	8,56
SID Met	2.27
SID Thr	5.56
SID Tyr	1.78
SID Val	5.90
Analyzed chemical composition, g/kg DM	
DM, g/kg feed	869
Starch	433
Dietary fiber	210
Non-starch polysaccharides	185
Lignin	24.9
Crude protein	184
Ash	56.4
Fat	47.2
Gross energy, MJ/kg DM	18.3

[1]Supplied per kilogram of diet: 8,960 IU retinol; 50 µg 25-hydroxy vitamin D3 (Hy-D, DSM Nutritional Products, Basel, Switzerland); 167 mg α-tocopherol; 2.27 mg thiamin; 5.62 mg riboflavin; 22.7 mg niacin; 167 mg pantothenic acid; 3.35 mg pyridoxine; 5.94 mg folic acid; 0.02 mg cobalamin; 0.43 mg biotin; 4.32 mg menadione; 88.99 mg iron ($FeSO_4$); 13.0 mg copper ($CuSO_4$); 45 mg manganese (MnO), 103 mg zinc (ZnO); 0.23 mg iodine ($Ca(IO_3)_2$), and 0.38 mg selenium (Na_2SeO_3).
[2]Standard ileal digestible.

Plasma sampling and deuterium oxide (D2O) enrichment

A non-surgical external indwelling jugular vein catheter was implanted on day 113 of gestation to facilitate blood sampling during farrowing, and the catheter was removed after collecting the blood sample at the end of farrowing. The catheter was filled with a catheter block solution containing saline heparin (100 IU/mL, Heparin LEO; LEO Pharma A/S, Ballerup, Denmark), benzyl alcohol (0.1%; benzyl alcohol + 99%; Sigma-Aldrich, St. Louis, MO), and benzyl penicillin (0.2%; benzylpenicillin; Panpharma, NordMedica A/S, Copenhagen, Denmark). It was then securely attached to the sow's neck using adhesive tensoplast. Before blood sampling at the onset and end of farrowing, the catheter was primed by discarding 4 mL of blood mixed with the catheter block. Subsequently, 9 mL of blood was collected into a 10-mL heparinized vacutainer tube (Greiner Bio-One GmbH, Kremsmünster, Austria) at each sampling point. The tubes with the blood samples were immediately placed on ice until centrifugation. The blood sample at the onset of farrowing was collected following birth of the first piglet, while the blood sample at the end of farrowing was collected after the expulsion of placenta. On days 3, 10, 17, and 24 of lactation, 9 mL blood sample was collected at each sampling point, 4 h after the morning meal, by puncturing the jugular vein. The blood samples were centrifuged at 1,558 × *g* for 10 min at 4 °C. The resulting plasma aliquots were then harvested into 1.5 mL tubes and stored at −20 °C until further analyses.

On days 3 and 24 of lactation, the sows were enriched with a 40% D_2O solution to determine the total D_2O space in their body as described by Theil et al. (2002). This information was used to predict the total pools of body protein and fat on days 3 and 24 of lactation, respectively, based on the method outlined by Rozeboom et al. (1994). To determine the background D_2O space and total D_2O space, blood samples were collected before and 5 h after D_2O enrichment, respectively. The blood samples were collected into 4 mL clot activator vacutainer tubes (BD, Belliver Industrial Estate, Plymouth, UK). After allowing the samples to clot undisturbed at room temperature, they were centrifuged at 1,558 × *g* for 10 min at 4 °C. The resulting serum samples were harvested into 1.5 mL tubes and stored at −20 °C until further analysis. Then, the sows' body pools of protein and fat were calculated from their BW, backfat, and D_2O space on days 3 and 24 of lactation, using the method developed by Rozeboom et al. (1994). The mobilization of protein and fat during the lactation period was determined by calculating the difference between the respective pools on days 3 and 24 of lactation as follows:

$$\text{Body protein (kg)} = 1.3 + 0.103 \times \text{live weight (kg)} + 0.092 \times D_2O\text{ (kg)} - 0.108 \times \text{backfat (mm)}$$

$$\text{Body fat (kg)} = 7.7 + 0.649 \times \text{live weight (kg)} - 0.610 \times D_2O\text{ (kg)} + 0.299 \times \text{backfat (mm)}$$

Chemical analyses and calculations

Chemical analyses were performed on the diet in duplicate, except for lignin, which was analyzed singly. The dry matter (**DM**) content was determined by drying the sample at 103 °C for 20 h in a forced air oven until a constant weight was achieved. Analysis of crude ash, nitrogen, and crude fat (EC 152/2009) followed the guidelines established by the official journal of the European-Commission (2009). Starch, nonstarch polysaccharides (**NSP**), and lignin were analyzed using the method described by Bach Knudsen (1997). The gross energy was determined using an Automatic Isoperibol Calorimetry system (Parr Instrument Company, Moline, IL). Milk samples underwent analysis for fat, protein, lactose, and DM concentrations in triplicate using infrared spectroscopy (Milkoscan 4000, FOSS, Hillerød, Denmark).

Plasma glucose, lactate, triglycerides, and urea concentrations were determined using standard procedures (Siemens Diagnostics Clinical Methods for ADVIA 1650). Plasma concentration of non-esterified fatty acids (**NEFA**) was determined using the Wako NEFA C ASA-ACOD assay method (Wako Chemicals GmbH, Neuss, Germany). The ADVIA 1650 Chemistry System (Siemens Medical Solutions, Tarrytown, NY) was used to measure these plasma metabolites. Short-chain fatty acid concentrations (acetate, propionate, butyrate, and succinate) in plasma were analyzed by liquid chromatography-mass spectrometry according to Han et al. (2015) with modifications described by Curtasu et al. (2020).

Statistical analyses

The statistical analyses were conducted using the SAS procedure (version 9.3, SAS Institute Inc., Cary, NC). The concentrations of plasma metabolites during farrowing were analyzed using the MIXED procedure of SAS. The model included fixed effects for feeding level (1.8, 2.4, 3.1, 3.7, 4.3, and 5.0 kg/d), parity (first and second), time during farrowing (onset and end), and the interaction between feeding level and time during farrowing. The average feed intake, sow BW and backfat loss, MY, litter weight gain, and litter size were analyzed on a weekly basis using the MIXED procedure of SAS. The model included fixed effects for feeding level and parity. The pools of body protein and fat on day 3 of lactation and their respective losses during lactation were analyzed similarly as in the preceding model, but not on a weekly basis. The changes in concentrations of fat, protein, lactose, and DM in milk, and concentrations of plasma metabolites during lactation, were analyzed using the MIXED procedure of SAS. Fixed effects included feeding level, parity, and days in milk (DIM; 3, 10, 17, and 24), while sow was included as a random effect. Potential interaction effect of feeding level with parity and DIM was examined. To stabilize the residual variance, log transformation was applied to plasma concentrations of triglycerides and NEFA before the statistical analyses. Orthogonal polynomial contrasts were employed to assess the linear, quadratic, and cubic effects of feeding level. Coefficients of the orthogonal polynomial contrasts were generated by the IML procedure of SAS using the realized feed level in each group. In cases where the quadratic and/or cubic polynomial contrast exhibited significance or a tendency on key response variables, adequate feeding level was estimated through regression from the cubic contrast. The data are presented as LSMEANS ± SEM, statistical significance was declared at $P < 0.05$, and a tendency was indicated at $P \leq 0.10$.

Results

Plasma metabolites during farrowing

An interaction between feeding level and time during farrowing was observed for plasma concentrations of triglycerides, propionate, and butyrate (Figure 1). Results indicated that at the onset of farrowing, sows fed 2.4, 3.1, and 4.3 kg/d exhibited greater plasma concentrations of triglycerides than at the end of farrowing ($P < 0.001$; Figure 1A). Furthermore, sows fed 2.4 kg/d displayed a greater concentration of propionate ($P = 0.01$), whereas those fed 4.3 kg/d showed a lower concentration of propionate ($P = 0.02$) at the onset of farrowing (Figure 1B). At the end of farrowing, sows fed 4.3 ($P = 0.003$) and 5.0 ($P < 0.001$) kg/d demonstrated greater plasma concentrations of butyrate (Figure 1C).

The plasma concentration of lactate was greatest in sows fed 2.4 kg/d, lowest in sows fed 1.8 kg/d, and intermediate in the remaining groups ($P = 0.005$; mean comparison; Table 2). Furthermore, plasma concentrations of urea, acetate, and butyrate increased ($P < 0.001$), while that of NEFA decreased ($P < 0.001$) with increasing feeding levels. First-parity sows had greater concentrations of glucose ($P = 0.04$), triglycerides ($P = 0.002$), and propionates ($P = 0.01$) but lower concentration of NEFA ($P = 0.005$) compared to second-parity sows. At the onset of farrowing, plasma concentrations of triglycerides ($P < 0.001$), acetate ($P = 0.01$), and succinate ($P < 0.001$) were greater, while concentrations of glucose, urea, and butyrate were lower ($P < 0.001$) compared to the end of farrowing. During farrowing, plasma lactate concentration showed a quadratic

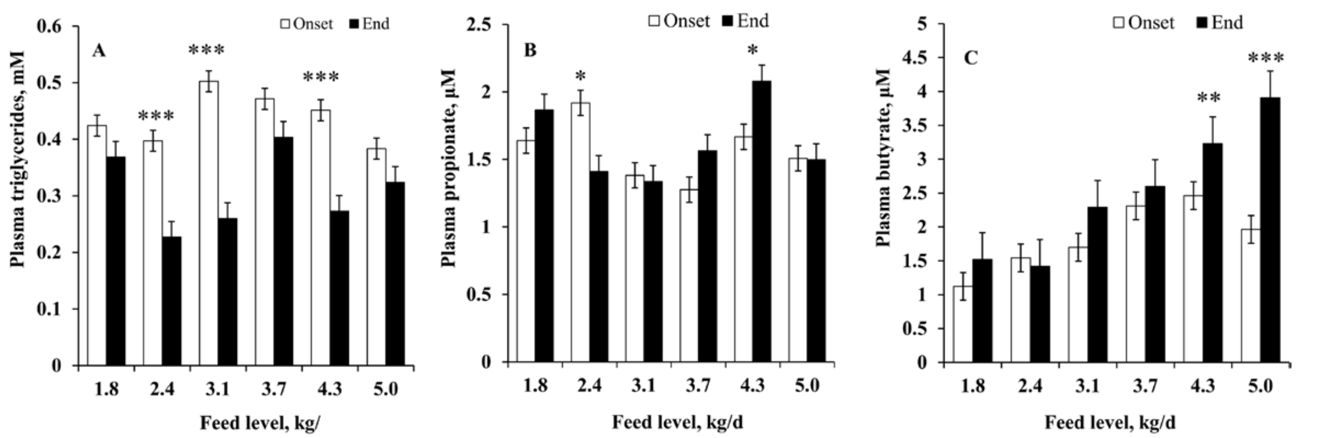

Figure 1. Interaction between feeding levels and time around farrowing for plasma concentrations of A) triglycerides, B) propionate, and C) butyrate at the onset of farrowing (white bar) and the end of farrowing (black bar) in sows fed different feeding levels from day 108 of gestation until farrowing. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, values are LSMEANS ± SEM; $n = 8$ sows/feeding level.

Table 2 Influence of feeding level during the transition period on sow plasma metabolites during farrowing (n = 8 sows/feeding level)

Item	Feeding level (FL), kg/d							Parity			Time at farrowing (time)			P-value[2]					
	1.8	2.4	3.1	3.7	4.3	5.0	SEM	First	Second	SEM	Onset	End	SEM[1]	FL	Parity	Time	Linear	Quad	Cubic
Glucose, mM	5.95	6.27	5.97	6.61	6.26	6.19	0.239	6.39	6.03	0.133	5.94	6.48	0.113	0.29	0.04	<0.001	0.30	0.33	0.57
Lactate, mM	1.08^{c}	1.74^{a}	1.51^{ab}	1.47^{ab}	1.52^{ab}	1.32^{bc}	0.122	1.53	1.35	0.068	1.47	1.41	0.058	0.002	0.06	0.51	0.51	0.003	0.06
TG, µM[3]	396	312	381	437	362	354	56.7	450	303	31.9	438	309	22.8	0.68	0.002	<0.001	0.99	0.73	0.22
NEFA, µM[4]	946^{a}	671^{b}	598^{bc}	387^{c}	369^{cd}	245^{d}	87.6	438	634	49.0	572	500	38.0	<0.001	0.005	0.09	<0.001	0.27	0.62
Urea, mM	2.24^{b}	2.27^{b}	2.61^{b}	3.17^{ab}	3.07^{ab}	3.57^{a}	0.258	2.95	2.69	0.150	2.66	2.98	0.105	0.002	0.21	<0.001	<0.001	0.69	0.71
Acetate, µM	113^{b}	121^{b}	146^{a}	151^{a}	148^{a}	151^{a}	8.3	143	133	4.4	145	132	3.7	<0.001	0.09	0.007	<0.001	0.08	0.75
Propionate, µM	1.75	1.66	1.36	1.42	1.87	1.50	0.249	1.83	1.36	0.133	1.57	1.63	0.098	0.49	0.01	0.29	0.74	0.37	0.37
Butyrate, µM	1.32^{b}	1.48^{b}	1.99^{ab}	2.45^{a}	2.84^{a}	2.94^{a}	0.302	2.29	2.05	0.161	1.85	2.49	0.129	<0.001	0.25	<0.001	<0.001	0.91	0.38
Succinate, µM	8.27	8.57	9.66	7.64	7.91	7.50	0.613	8.20	8.32	0.339	8.64	7.88	0.238	0.12	0.79	<0.001	0.08	0.15	0.24

[a–d]Means within a row with different superscript differ (P < 0.05).
[1]Standard error of the mean and the largest SEM value within the group was reported.
[2]The linear, quadratic, and cubic P-values refer to the effect of the feeding level.
[3]Triglycerides.
[4]Non-esterified fatty acids

increase (P = 0.005) and tended to show a cubic increase (P = 0.06) with increasing feeding level during the last week of gestation.

Sow and litter performance

There was no evidence to suggest that feeding level during the last week of gestation had any impact on sows' feed intake during lactation (Table 3). However, first-parity sows had greater feed intake in week 1 (P = 0.03), but had lower in week 3 (P = 0.03) of lactation compared to second-parity sows. The average weekly BW loss was highest in sows fed 4.3 kg/d during the last week of gestation, lowest in sows fed low-to-intermediate feeding level (1.8-3.1 kg/d) and intermediate in the remaining groups (P = 0.03). Notably, feeding levels during the last week of gestation did not show effect on backfat loss (P = 0.88), as well as mobilization of body protein (P = 0.53) and fat (P = 0.18) in the sows during the subsequent lactation.

Sows that were fed 3.7 kg/d during the last week of gestation had greater MY in week 1 of lactation compared to those provided 1.8 (P < 0.001), 2.4 (P = 0.001), and 3.1 (P = 0.04) kg/d during last week of gestation. Conversely, sows fed 1.8 kg/d had lower MY in week 2 (P = 0.004), week 3 (P = 0.02), and week 4 (P = 0.008) of lactation than the remaining groups. The results revealed a consistent linear increase in MY throughout the lactation period, with a quadratic increase during the first 3 wk of lactation with increasing feeding level during the last week of gestation (Table 3). Litters nursing sows fed 1.8 kg/d during the last week of gestation demonstrated lower weight gain during week 2 (P = 0.02) and overall (P = 0.04) lactation period, resulting in a lower litter weaning weight (P = 0.007) than the remaining groups. The litter size was consistently lower in sows fed 1.8 kg/d during the last week of gestation than the rest of the groups, while the average litter size at weaning was greater in sows fed 3.7 and 4.3 kg/d compared to the remaining groups (Table 3). First-parity sows had lower MY, litter size (week 1; P < 0.001), litter weight gain (week 3; P = 0.006), and litter weaning weight (P = 0.006) compared to second-parity sows.

Plasma metabolites during lactation and milk composition

The interaction between feeding level and DIM was observed for plasma concentration of urea, where sows fed 1.8, 2.4, and 3.1 kg/d during the last week of gestation displayed lower concentration of urea on d 3 of lactation (P < 0.001; Figure 2). Plasma concentrations of triglycerides were greater in sows fed 2.4 and 3.1 kg/d compared to sows fed 3.7 (P = 0.03) and 5.0 (P = 0.02) kg/d during the last week of gestation (Table 4). First-parity sows had greater concentrations of glucose and urea (P < 0.001), but lower concentrations of acetate (P = 0.03) and succinate (P < 0.001) compared to second-parity sows. On day 3 of lactation, plasma concentrations of triglycerides and NEFA were greater, while concentrations of urea, propionate, and butyrate were lower compared to the remaining DIM (P < 0.001). Plasma concentrations of glucose and succinate were lower on day 24 of lactation compared to the remaining DIM (P < 0.001). Feeding level during the last week of gestation did not affect milk composition, but first-parity sows had greater concentration of milk protein (P = 0.004) and tended to have a greater milk DM (P = 0.06) compared to second-parity sows. As lactation progressed,

Table 3 Influence of feeding level during the transition period on sow and litter performance in the subsequent lactation (*n* = 8 sows/feeding level)

Item	Week	Feeding level (FL), kg/d						SEM	Parity		SEM[1]	*P*-value[2]					Optimum[3]
		1.8	2.4	3.1	3.7	4.3	5.0		First	Second		FL	Parity	Linear	Quadratic	Cubic	
Daily feed intake, kg/d	1	4.06	4.51	4.32	4.32	4.36	4.05	0.145	4.42	4.12	0.107	0.13	0.03	0.69	0.02	0.25	
	2	6.41	6.60	6.64	6.61	6.34	5.76	0.313	6.31	6.47	0.230	0.30	0.58	0.13	0.06	0.65	
	3	7.14	7.65	7.67	7.49	7.38	7.37	0.296	7.15	7.74	0.201	0.68	0.03	0.91	0.18	0.32	
	4	7.72	7.28	7.42	7.52	7.64	7.62	0.356	7.32	7.75	0.262	0.93	0.19	0.81	0.47	0.46	
Overall week average		6.33	6.48	6.51	6.48	6.37	6.16	0.308	6.25	6.52	0.223	0.96	0.34	0.63	0.35	0.96	
Sow weight loss, kg	1	5.4	4.1	3.5	7.4	6.5	6.9	1.53	4.2	7.1	1.08	0.20	0.03	0.10	0.45	0.15	
	2	3.6	2.4	2.2	5.3	7.6	7.4	2.40	6.0	3.5	1.77	0.33	0.25	0.05	0.39	0.35	
	3	5.6	4.8	3.1	5.3	8.2	6.1	1.61	4.9	6.2	1.18	0.26	0.38	0.23	0.30	0.17	
	4	1.2	4.3	4.1	5.8	5.1	2.8	1.58	4.7	2.0	1.17	0.46	0.07	0.44	0.20	0.66	
Overall week average		4.0^{b}	3.9^{b}	3.2^{b}	6.0^{ab}	6.9^{a}	5.7^{ab}	0.97	5.0	4.6	0.71	0.03	0.70	0.009	0.50	0.12	
Sow backfat loss, mm	1	0.3	1.0	0.5	0.5	1.8	1.4	0.59	0.8	1.1	0.46	0.33	0.57	0.09	0.65	0.89	
	2	1.2	0.9	0.4	0.6	0.1	0.6	0.45	0.9	0.4	0.33	0.47	0.17	0.12	0.41	0.70	
	3	0.9	1.0	1.5	1.3	1.8	1.1	0.34	1.4	1.2	0.25	0.29	0.51	0.23	0.24	0.33	
	4	1.0	1.5	0.7	1.4	0.8	0.5	0.4	0.6	1.3	0.27	0.33	0.06	0.27	0.30	0.84	
Overall week average		0.9	1.1	0.8	0.9	1.1	0.9	0.25	0.9	1.0	0.18	0.88	0.82	0.80	0.89	0.91	
Protein loss days 3-24, kg		0.8	0.6	0.3	0.7	1.6	1.9	0.76	0.9	1.1	0.54	0.53	0.73	0.15	0.25	0.85	
Fat loss days 3-24.kg		10.1	10.1	3.6	15.1	8.2	16.3	4.16	7.2	14.2	2.95	0.18	0.06	0.29	0.28	0.95	
Milk yield, kg	1	8.41^{c}	8.81^{b}	8.99^{b}	9.21^{a}	9.01^{ab}	9.05^{ab}	0.094	8.65	9.18	0.065	<0.001	<0.001	<0.001	<0.001	0.67	[3.9]
	2	12.0^{b}	13.4^{a}	13.8^{a}	14.4^{a}	13.9^{a}	13.8^{a}	0.439	13.1	13.9	0.322	0.004	0.05	0.003	0.005	0.68	[3.6]
	3	13.4^{c}	14.5^{bc}	15.3^{ab}	16.5^{a}	15.9^{ab}	15.6^{ab}	0.681	14.4	16.0	0.499	0.02	0.02	0.004	0.05	0.50	[4.1]
	4	13.2^{b}	14.5^{ab}	14.7^{ab}	15.9^{a}	15.76^{a}	15.6^{a}	0.676	14.3	15.6	0.495	0.04	0.03	0.003	0.18	0.82	[4.3]
Overall week average		11.7^{b}	$12.8^{ab\dagger}$	13.2^{ab}	14.2^{a}	13.6^{a}	13.7^{a}	0.608	12.6	13.8	0.441	0.04	0.04	0.005	0.09	0.88	[4.1]
Litter weightgain, kg	1	2.19	2.59	2.69	2.82	2.62	2.65	0.191	2.57	2.61	0.141	0.20	0.82	0.09	0.07	0.59	[3.4]
	2	2.98^{b}	3.56^{a}	3.39^{a}	3.70^{a}	3.57^{a}	3.69^{a}	0.177	3.37	3.58	0.123	0.02	0.17	0.004	0.15	0.31	
	3	3.17	3.57	3.72	3.99	3.94	3.76	0.250	3.36	4.02	0.134	0.15	0.006	0.03	0.10	0.77	[4.1]
	4	3.09	3.50	2.99	2.98	3.61	3.65	0.367	3.40	3.21	0.270	0.50	0.57	0.29	0.38	0.52	
Overall week average		2.86^{b}	3.31^{a}	3.20^{a}	3.37^{a}	3.43^{a}	3.44^{a}	0.150	3.18	3.36	0.118	0.04	0.22	0.005	0.27	0.49	
Litter weaning weight, kg		82.4^{b}	94.6^{a}	93.3^{a}	98.4^{a}	98.3^{a}	98.5^{a}	3.52	89.6	98.9	2.59	0.007	0.006	<0.001	0.08	0.45	[4.1]
Litter size, *n*	1	14.0^{b}	14.4^{ab}	14.5^{a}	14.5^{a}	14.6^{a}	14.3^{ab}	0.12	13.9	14.8	0.09	0.03	<0.001	0.02	0.01	0.79	[3.9]
	2	12.9^{b}	13.7^{a}	13.7^{a}	14.0^{a}	14.0^{a}	13.6^{a}	0.21	13.5	13.8	0.15	0.002	0.07	0.003	0.002	0.69	[3.8]
	3	12.4^{b}	13.4^{a}	13.4^{a}	14.0^{a}	14.0^{a}	13.5^{a}	0.30	13.3	13.6	0.22	0.001	0.32	<0.001	0.009	0.58	[4.1]
	4	11.9^{b}	13.3^{a}	13.2^{a}	13.9^{a}	13.7^{a}	13.5^{a}	0.32	13.2	13.3	0.24	<0.001	0.61	<0.001	0.01	0.74	[4.0]
Overall week average		12.8^{c}	13.7^{b}	13.7^{b}	14.2^{a}	14.0^{a}	13.7^{b}	0.15	13.5	14.0	0.11	<0.001	0.002	<0.001	<0.001	0.83	[4.0]

[a–c]Means within a row with different superscript differ ($P < 0.05$).
[1]Standard error of the mean and the largest SEM value within the group was reported.
[2]The linear, quadratic, and cubic *P*-values refer to the effect of the feeding level.
[3]Optimal daily feeding level was estimated for cubic contrast when the quadratic and/or cubic contrast showed significance ($P < 0.05$) or a tendency ($P \le 0.10$).
[†]Tended to be low ($P = 0.07$) compared to milk yield in sows fed 3.7 kg/d.

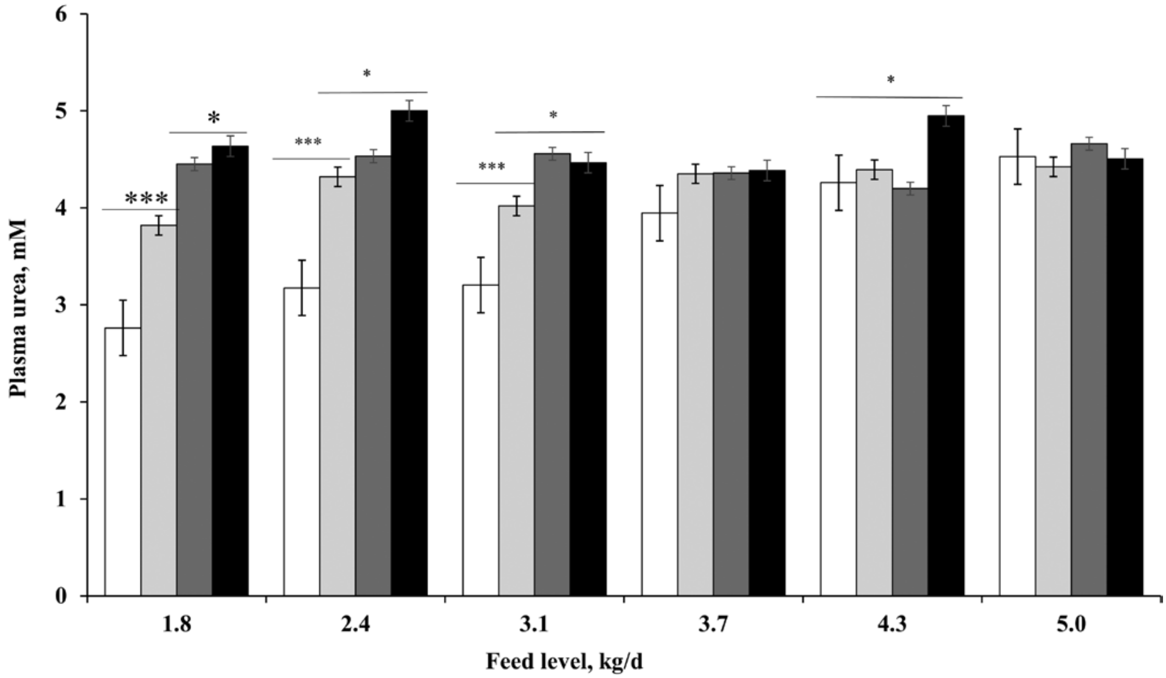

Figure 2. Interaction between feeding levels and days in milk (day 3: white bar; day 10: light gray bar; 17: gray bar; day 24: black bar) for plasma concentration of urea during the lactation period in sows fed different feeding level from day 108 of gestation until farrowing. *$P < 0.05$, ***$P < 0.001$, values are LSMEANS ± SEM; $n = 8$ sows/feeding level.

milk concentrations of lactose increased, while that of fat and DM decreased ($P < 0.001$).

Discussion

This study aimed to evaluate the potential carry-over effects of different feeding level administered to sows in the last week of gestation on the performance of both the sows and their litters during the subsequent lactation. Feeding lactating sows aims to avoid a low or a reduced feeding level to maximize milk production while avoiding excessive depletion of body reserves. A smooth transition from gestation to lactation is crucial, and feeding practice during this period plays a vital role in attaining this goal. Previous research has demonstrated that prolonged ad libitum feeding during gestation can lead to excessive body fat in sows at farrowing, thus reducing lactation feed intake (Dourmad, 1991; Weldon et al., 1994; Revell et al., 1998a). However, further investigation is needed to comprehend the impact of short-term feeding level during the transition period on the performance of sows in the subsequent lactation. The present study addresses this research gap and provides valuable insights into optimizing feeding strategies during the transition period to enhance the performance of both sows and their litter in the following lactation. The findings from this study will contribute to a better understanding of the effects of different feeding level during the last week of gestation on the performances of lactating sows and their litters.

Plasma metabolites during farrowing

The observed plasma metabolite profiles during farrowing were consistent with our expectations. The production of short-chain fatty acids is influenced by the amounts of undigested fiber that reaches the hindgut (Bach Knudsen, 2001; Flint et al., 2015). As feeding level increase, the amount of undigested fiber reaching the hindgut is expected to rise proportionally. This partly explains the observed linear increase in plasma concentrations of acetate and butyrate during farrowing in this study. Short-chain fatty acids are essential for the host's energy metabolism and provide multiple additional benefits for the animal. Butyrate, for instance, is an important fuel for the colonocytes (Layden et al., 2013) and plays a crucial role in maintaining colonic health and function (Bach Knudsen et al., 2018), but can also be considered as a biomarker for health and gut microbiota (Wei et al., 2021). Moreover, butyrate not cleared in the colonocytes will pass to the liver and further to the peripheral circulation where it also can play a role in connection with systemic inflammation (Bach Knudsen et al., 2018). Therefore, although this study did not analyze the compositions of gut microbiota, it is reasonable to believe that the linear increase in butyrate concentration in the peripheral blood, with increasing feeding levels, could have positively impacted the gut health and functionality of the sows.

In a feeding strategy where energy is not deficient, NEFA is mainly released from the breakdown of dietary triglycerides. However, when sows are provided with varying energy levels, as in the present study, the concentration of NEFA in the bloodstream reflects the energy balances of the sows. If an animal is fed below its energy requirement, elevated NEFA levels in the bloodstream indicate that the body utilizes its fat stores to compensate for the energy deficit. On the other hand, the plasma concentration of urea increased with increasing feeding level in late gestation, indicating an increased protein catabolism during farrowing due to increased protein intake above the sows' requirement. This finding is consistent with previous studies (Le Cozler et al., 1998; Mosnier et al., 2010). Pedersen et al. (2019a) likewise reported an increase in protein oxidation as the intake of standardized ileal digestible protein increased (11.8-15.6%), further supporting the findings of the present study.

Table 4 Influence of feeding level during the transition period on plasma metabolites and milk composition in the subsequent lactation (n = 8 sows/feeding level)

	Feeding level (FL), kg/d							Parity			Days in milk (DIM)					*P*-value[2]					
Item	1.8	2.4	3.1	3.7	4.3	5.0	SEM	First	Second	SEM	3	10	17	24	SEM[1]	FL	Parity	DIM	Linear	Quadratic	Cubic
Plasma metabolites																					
Glucose, mM	5.41	5.60	5.33	5.39	5.66	5.53	0.097	5.66	5.32	0.074	5.49^{b}	5.64^{a}	5.65^{a}	5.18^{c}	0.063	0.10	<0.001	<0.001	0.31	0.49	0.81
Lactate, mM	1.31	1.70	1.65	1.59	1.41	1.40	0.159	1.43	1.59	0.116	1.43	1.54	1.60	1.47	0.088	0.40	0.25	0.13	0.73	0.05	0.21
Urea, mM	3.80	4.14	3.94	4.14	4.33	4.41	0.212	4.56	3.60	0.155	3.53^{d}	4.10^{c}	4.34^{b}	4.54^{a}	0.116	0.24	<0.001	<0.001	0.03	0.85	0.65
TG[3],µM	208^{ab}	217^{a}	216^{a}	187^{b}	194^{ab}	181^{b}	53.3	193	208	39.6	233^{a}	184^{b}	185^{b}	203^{b}	40.2	<0.05	0.14	<0.001	0.007	0.32	0.32
NEFA[4], µM	210	252	241	236	249	247	0.1	214	266	0.1	311^{a}	278^{a}	199^{b}	189^{b}	0.1	0.95	0.12	<0.001	0.53	0.67	0.60
Acetate, µM	141^{a}	113^{b}	130^{a}	108^{b}	131^{a}	112^{b}	7.9	115	131	5.8	119^{b}	137^{a}	122^{b}	112^{b}	4.9	0.02	0.03	<0.001	0.07	0.27	0.10
Propionate, µM	2.02	1.97	1.94	1.94	2.11	2.02	0.149	2.01	2.00	0.109	1.55^{b}	2.06^{a}	2.22^{a}	2.17^{a}	0.093	0.96	0.86	<0.001	0.71	0.62	0.63
Butyrate, µM	4.45	3.79	4.04	3.52	4.02	3.84	0.384	3.66	4.23	0.285	2.08^{b}	4.75^{a}	4.53^{a}	4.42^{a}	0.285	0.43	0.10	<0.001	0.31	0.29	0.66
Succinate, µM	9.12	10.5	10.3	10.2	9.43	9.08	0.579	8.61	9.77	0.431	9.77^{a}	10.1^{a}	10.4^{a}	8.90^{b}	0.352	0.21	<0.001	0.001	0.46	0.02	0.33
Milk composition, % as-is																					
Fat	7.85	7.94	7.28	7.86	7.52	7.64	0.231	7.77	7.59	0.171	8.60^{a}	7.70^{b}	7.52^{b}	6.91^{c}	0.168	0.23	0.38	<0.001	0.35	0.48	0.88
Protein	5.12	5.10	5.05	5.20	5.13	5.06	0.055	5.20	5.02	0.041	5.54^{a}	4.90^{c}	4.90^{c}	5.09^{b}	0.041	0.31	0.004	<0.001	0.89	0.56	0.09
Lactose	5.23	5.17	5.20	5.19	5.22	5.24	0.031	5.19	5.22	0.023	4.93^{d}	5.25^{c}	5.31^{b}	5.35^{a}	0.018	0.54	0.25	<0.001	0.43	0.13	0.62
Dry matter	18.7	18.7	18.1	18.9	18.4	18.5	0.22	18.8	18.4	0.16	19.5^{a}	18.5^{b}	18.3^{b}	17.9^{c}	0.17	0.06	0.06	<0.001	0.55	0.70	0.39

[a–d]Means within a row with different superscript differ ($P < 0.05$).
[1]Standard error of the mean and the largest SEM value within the group was reported.
[2]The linear, quadratic, and cubic P-values refer to the effect of the feeding level.
[3]Triglycerides.
[4]Non-esterified fatty acids.

Feed intake and body weight loss

Contemporary hyper-prolific lactating sows often face challenges in obtaining sufficient energy for milk production solely from voluntary feed intake. Previous studies have indicated that feeding strategies and dietary compositions during gestation can influence the feed intake of the sows during lactation (Dourmad, 1991; Weldon et al., 1994; Le Cozler et al., 1998; Ren et al., 2017). These studies have shown that providing sows with ad libitum or high feed level during gestation can lead to excessive backfat and body fat at farrowing, negatively impacting subsequent lactation feed intake. For instance, an increase of 1 mm in backfat thickness at day 109 of gestation, regardless of parity, has been associated with a reduction of 60-120 g of daily feed intake during lactation (Kim et al., 2015). Similarly, Mullan and Williams (1990) reported that a decrease of 1 mm in backfat thickness at farrowing was associated with an increase of 100 g daily feed intake during lactation. However, Hojgaard and Bruun (2021) did not observe such a substantial impact of backfat thickness at farrowing on the lactation feed intake of the sows. The latter finding revealed that even a significant increase in backfat thickness from 9 to 26 mm at farrowing only resulted in a marginal decrease of 280 g/d in average daily feed intake during lactation. This finding suggests that the phenomenon may be attributed to genetic selection for reproductive traits and improvements in average weight gain and feed efficiency in female lines over several decades. In the present study, we investigate the impact of different feeding level during the last week of gestation. Unlike previous studies (Kim et al., 2015; Ren et al., 2017), our findings indicate that high feeding level during the final week of gestation did not adversely affect feed intake during lactation. This could be attributed to the fact that the short-term high feeding level during the last week of gestation did not increase backfat thickness and body fat of the sows (Feyera et al., 2021), or due to genetic selection for average daily weight gain and thus a high daily feed intake in hyper-prolificacy sows. Our results, especially for those sows on the high feeding level, are complementary to those of Neil et al. (1996), who reported that ad libitum feeding during the last 5 d of gestation had a beneficial effect on the lactation feed intake of the sows.

In the study conducted by Revell et al. (1998a), it was observed that sows with high level of body fat (340 g fat/kg BW) at the onset of farrowing exhibited a 30% lower lactation feed intake compared to their lean counterpart (280 g fat/kg BW). This may suggest that feeding sows 5.0 kg/d for an extended gestation period results in excessive fat accumulation before farrowing. However, during the last 2 wk of gestation, fetal growth and mammary development occur rapidly (McPherson et al., 2004; Farmer and Hurley, 2015), and sows are physically active in the last few days of gestation (Thodberg et al., 2002; Andersen et al., 2014). Therefore, sows with high or ad libitum feeding level during the last week of gestation are likely to utilize the extra energy for fetal growth, mammary gland development, and nest-building, while a minor part could be used to increase maternal body reserves. This helps mitigate the potential adverse effects of high-energy intake during late gestation on lactation feed intake. Hence, when evaluating the impact of feeding level during gestation on lactation feed intake, it is crucial to specify the stage of gestation, length of feeding, and feeding level, rather than making generalizations. This is why the present result highlights the benefits of increased feeding level during the final week of gestation, in accordance with the criteria investigated in our study, rather than reducing feed supply before the expected farrowing (Tabeling et al., 2003).

Similar to feed intake, the weekly BW loss of the sows was not affected by the feeding level during the last week of gestation, and the potential impact of this feeding level on gut fill at farrowing has been published earlier (Feyera et al., 2021). However, sows fed 4.3 kg/d during the last week of gestation had greater BW loss during the overall lactation compared to those fed ≤3.1 kg/d. Previous studies have reported negative impacts of high feeding level during longer periods, either throughout or during the last 2 months of gestation, on the sows' lactation BW loss (Dourmad, 1991; Weldon et al., 1994; Young et al., 2004). The sows in the present study lost 3.2 to 6.9 kg/wk, corresponding to 11 to 23 kg during lactation, consistent with findings from previous studies (Strathe et al., 2017; Pedersen et al., 2019b). Importantly, the observed difference in BW loss of the sows in the present study cannot be solely explained by their feed intake during the lactation period. The difference can likely be partly attributed to the difference in MY of the sows among the groups (discussed below). Supporting our findings, Neil (1996) did not observe a negative impact on BW loss of the sows during lactation when ad libitum feeding was provided during the last 5 d of gestation. This, along with our results, implies a positive impact of a high feeding level during the last week of gestation on the subsequent lactation performance of the sows.

Milk yield and litter performance

Optimizing MY is of utmost importance as it directly affects the growth and development of piglets, often at the expense of the sow's well-being. Adequate MY is essential for the survival and growth of the piglets. Research indicates that milk production can limit the effective growth rate of piglets, but also suggests that sows have the potential for greater milk synthesis than what is typically expressed under normal conditions (Harrell et al., 1993; Boyd et al., 1995). To maximize the synthesis potential of mammary epithelial cells, it is crucial to comprehend the nutritional requirements and physiological processes involved in milk production. This understanding encompasses identifying the specific nutrients necessary for milk production and the regulatory mechanisms governing milk synthesis and secretion. By realizing these factors, optimal nutritional support can be provided to lactating sows, resulting in increased quality and quantity of milk production, benefiting both the sows (through reduction of body reserve mobilization) and the piglets. Studies have suggested that manipulating the onset of transient milk production could be a potential strategy for enhancing milk production in sows (Krogh et al., 2015; Vadmand et al., 2015). However, the dietary strategies that influencing the timing of transient milk production in sows remain unknown. The nutrition of sows during the transition period can impact transient milk production, as the nutrient requirements and physiology undergo dynamic changes during this period (Feyera and Theil, 2017; Theil et al., 2022). Hence, it is crucial to consider the influence of nutrition during this critical period on the subsequent lactation performance of the sows.

The present study observed that increasing feeding level during the last week of gestation led to a linear increase in MY, litter size, litter weight gain, and litter weaning weight. Interestingly, sows fed intermediate to high feeding level (≥3.7 kg/d) exhibited higher MY and litter size than in previous

Danish studies where the sows were fed optimal dietary protein (Strathe et al., 2017; Hojgaard et al., 2019a, 2019b) or lysine concentrations (Hojgaard et al., 2019c) for milk production during lactation. Moreover, the average lactation MY of sows fed 3.7 kg/d (14.2 kg) was similar to the peak lactation MY (14.0-14.1 kg) reported for 2nd to 4th parity Danish sows (Strathe et al., 2017). Although litter weaning weight and litter weight gain did not differ between groups fed ≥2.4 kg/d, sows fed 3.7 and 4.3 kg/d exhibited larger litter sizes at weaning. However, it should be noted that sows fed ≥3.7 kg/d during the last week of gestation experienced greater lactation weight loss, indicating that nutrient intake was more constrained in these groups relative to nutrient output in the milk. Insufficient dietary nutrient intake for milk production can lead to sows relying on their body reserves (Strathe et al., 2017; Costermans et al., 2020), especially when the supplies of protein and amino acids are insufficient, which could ultimately lead to increased BW loss and decreased milk production (Strathe et al., 2020). Therefore, the present findings suggest that feeding strategy during the transition period can influence subsequent lactation performance, although the mechanism behind this effect requires further investigation.

The present study has highlighted the significant influence of feeding level during the final week of gestation on sows' performance during lactation. The findings suggest that appropriate feeding level during this period can maximize MY, litter size, and litter weaning weight, as per the regression estimate from the cubic contrast. A regression estimate from the cubic contrast revealed that sows should receive 4.1 kg/d during the last week of gestation to optimize performance in the subsequent lactation. Intriguingly, the same feeding level has been reported to improve farrowing performance of the sows based on complementary criteria i.e. farrowing duration, stillbirth rate, and the need for farrowing assistance (Feyera et al., 2021). Although MY did not show a statistical difference among sows fed ≥3.7 kg/d, feeding above 4.1 kg/d during the final week of gestation prolonged farrowing duration and compromised piglet survival (Feyera et al., 2021). Consequently, this study emphasizes the potential for strategic feeding during the last week of gestation to enhance the sow's performance in the subsequent lactation.

Conclusion

The present study demonstrated the significance of carry-over effects of feeding level during the last week of gestation on subsequent lactation performance of the sows and their litters. The study showed that the different feeding levels employed during the last week of gestation did not affect the lactation feed intake of the sows. A 4.0 to 4.1 kg/d was estimated from the regression model as an adequate feeding level during the last week of gestation to maximize MY, litter size, and litter weaning weight in the subsequent lactation. The study emphasized that strategic feeding during the final week of gestation is essential to enhance performance of the sows in the subsequent lactation period.

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Conflict of Interest Statement

The authors declared that there are no conflicts of interest.

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