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Longitudinal pattern of growth performance and feeding behaviour in pigs fed varying dietary crude protein levels and categorised by final feed efficiency

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ABSTRACT

Feed efficiency (**FE**) estimated on pen level does not take individual feed intake or feeding behaviour into account, and thus, varying response among pen mates is impossible to quantify. This study aimed to explore the within-pen variation in FE of pigs fed one of three levels of CP. The study included 60 gilts (30–115 kg) divided into two repetitions (10 pigs/pen with an automatic feeder). Pigs were fed a low (**LCP**; 120 g SID CP/kg), standard (**SCP**; 124 g SID CP/kg) or high (**HCP**; 128 g SID CP/kg) CP diet. Pigs within diet were categorised based on their FCR in the final four growing weeks as the 30% highest (**HF**), medium 40% (**MF**), and the 30% lowest (**LF**). Weekly BW, average daily gain (**ADG**), feed conversion ratio (**FCR**), and daily and per–meal feed intake and feeding behaviour were measured per individual. Data were analysed as polynomial mixed models. Growth performance parameters except FCR had significant dietary treatment (**DT**) × time (**T**) and feed conversion category × time interactions. During weeks (**W**) 10–12, BW tended ($P \le 0.10$) to be greater in HCP compared with LCP aligning with the numerically highest intake for HCP in the preceding period. Similarly, HF intermittently had greater BW and preceding higher intake than LF or MF ($0.05 \le P \le 0.10$). The ADG of LCP pigs showed the greatest variability over time and intermittently increased faster and slower ($0.05 \le P \le 0.10$) than SCP and HCP, respectively. From W10 onwards, the HF pigs had a stable ADG while the ADG of LF and MF increased steeply and consequently was greater ($P \le 0.05$) at W13-14. In line with ADG, FCR varied significantly over time and most strongly for LCP. Overall, LF pigs had the lowest, while HF pigs had the highest FCR ($P < 0.001$). Meal size ($P < 0.001$) and duration ($P < 0.001$) had a significant DT × T interaction, being greater for HCP than LCP and occasionally SCP. In line with differences in growth rate, meal frequency decreased faster ($P < 0.05$) for HCP than LCP or SCP, resulting in longer intervals and limited differences in daily feeding duration. While meal size and duration tended ($P \le 0.10$) to be greater for HF than MF or LF pigs, differences in daily feeding behaviour were negligible. It was concluded that, independent of CP-level, a distinction in FCR categories could be attributed to differential meal feeding behaviour of HF pigs leading to higher feed intake, whereas differences in ADG changed during the growing-finishing phase.

Implications

Feed efficiency is an important trait in pig production due to its effect on the economy and environment. This study explored the growth performance and feeding behaviour of individual pigs depending on dietary CP level and feed efficiency. Over time, feed conversion ratio and average daily gain varied strongest for low CP fed pigs, indicating a need to carefully consider dietary CP levels at different ages, considering pigs did not adjust feeding behaviour. Pigs with low feed efficiency generally had the highest feed intake, reflected in higher meal size and –duration, but not consistently the highest average daily gain. This influence of intake should be considered when choosing an efficiency proxy.

Introduction

Improving feed efficiency (**FE**) in growing-finishing pigs is one of the main drivers to reduce the environmental and climate impact of the overall pig production. Fifty five percent of the total carbon dioxide emissions related to pig production stems from the feed production (Hermansen and Kristensen, 2011), while with

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respect to nitrogen efficiency, ~6.3 kg nitrogen is required for a pig to grow from 8 to 110 kg BW, which with ~46% retained nitrogen results in a substantial amount being excreted (Millet et al., 2018). The complexity of feed efficiency can be attributed to multiple animal and environmental factors as well as non-animal factors including feed processing and nutrient composition affecting energy and nutrient requirement, digestibility, absorption and utilisation. With respect to the nutrient composition, CP ingestion is a key component, which together with the dietary energy is the main driver to achieve the animal's growth performance potential (Scudder, 1902; Armsby, 1909). The common practice in Denmark is currently a one–phase feeding regimen with the dietary CP level in growing-finishing diets adjusted to fit an average pen level growth performance (Tybirk et al., 2018), resulting in exact nutrient requirements not being met for most animals (Pomar et al., 2009). Thus, it is likely that individual pigs are either being deficient or oversupplied with energy and nutrients, leading to poorer growth and FE. This has been illustrated in two studies (Andretta et al., 2016b; Andretta et al., 2018), showing that feeding growing-finishing pigs to meet their individual CP requirements greatly reduced the amount of excreted nitrogen. In addition, it has been shown that the differences in FE levels can to a great degree be ascribed to the individual variation among pigs (Pomar et al., 2003; Ouweltjes et al., 2018). Indeed, the individual variation can be distributed among several parameters, including the biological processes previously mentioned, but also parameters related to feeding behaviour have been suggested to explain some of the differences in FE observed among pen mates. However, examining the detailed feeding behaviour of the individual pig has revealed conflicting results. For example, FE has been found to correlate negatively (Andretta et al., 2016a), positively or not at all (De Haer et al., 1993; Rauw et al., 2006; Carcò et al., 2018) to feed intake and feeding pattern per day. Furthermore, it has been suggested that certain behavioural parameters are strongly associated with digestibility coefficients of DM content (De Haer and De Vries, 1993). Thus, to improve FE, accommodating individual nutrient requirements, a greater understanding of the variation in FE among individuals is needed. For this reason, feeding stations enabling registration of feed intake and feeding behaviour on the individual level are a necessary tool to manage individual nutrient requirements and for estimating FE on an individual level. The overall aim of this study was to explore the varying responses in FE among pen mates, as well as investigating the impact of dietary CP level on growth performance and feeding behaviour. Furthermore, the study was intended to generate additional hypotheses that would enable further testing of whether certain biological parameters such as the pig's microbiome, function and morphology of the small intestine, serum metabolomic and biochemistry profile, as well as pancreatic enzyme activity, could unravel possibilities of improving FE in grower-finisher pigs.

Material and methods

Animals and experimental design

Pre experimental period

A total of 60 Danish Landrace/Yorkshire × Duroc gilts (6.86 ± 1.00 kg BW) were included in the experiment which lasted from weaning (28 days of age) to slaughter (20 weeks of age). The experiment was divided into two blocks with 30 pigs in each block. The newly weaned pigs were from known litter origin and were sourced from a commercial farm. Pigs were distributed between three pens (10 pigs/pen) in each block and were balanced by BW and litter. Pigs were housed in pens with slatted concrete floor and equipped with single-space automatic feeders (Compident MLP Piglet, Schauer Agrotronic GmbH, Germany) during the first 6 weeks after weaning. Throughout the entire weaner period, pigs had *ad libitum* access to feed and water and were provided with bedding material. Pigs were, on an *ad libitum* basis, fed two standard commercial diets (DLG, Fredericia Denmark) from 7 to 15 kg BW (9.9 MJ net energy/kg, 18.8% CP, 14.6 g/kg lysine (Lys)) based on wheat, barley and extruded barley and from 15 to 30 kg BW (8.9 MJ net energy/kg, 18.3% CP, 13.1 g/kg Lys) based on barley, wheat and soybean meal, both formulated according to Danish nutrient recommendations (Tybirk et al., 2018). Feed intake and BW were monitored throughout the weaning period.

Experimental period

After 6 weeks in the weaning pens, pigs were moved to grower-finisher pens (n = 3), equipped with automatic feeders (Compident MLP Pro, Schauer Agrotronic GmbH, Germany), for the remaining growth period (10 weeks) and fed dietary treatments. Pigs (28.5 ± 4.70 kg BW) were redistributed among the grower-finisher pens to balance feed conversion ratio (**FCR**) (1.50 ± 0.09) based on the latest 3 weeks and to offset any carryover effect from the weaner to the grower-finisher pens. The three grower-finisher pens represented one of three dietary treatments corresponding to the following crude protein levels, low (**LCP**), standard (**SCP**) and high (**HCP**). The individual pig acted as the experimental unit as registration of individual feed intake was possible. The assignment of dietary treatment to the automatic feeder was altered between blocks. Throughout the entire grower-finisher period, pigs had *ad libitum* access to feed and water. Pig's health status was checked regularly during the weaner- and the grower-finisher phase. Light was on for 12 h during the weaner phase and light duration followed the natural light cycle during the grower-finisher phase. Temperature in the weaner phase was set to 24 °C during the first 2 weeks and was decreased by approximately 1° weekly until ~20 °C. Average temperature during the grower-finisher phase was 20.5 °C.

Diets and feed efficiency categorisation

During the experimental grower-finisher period, pigs were, on an *ad libitum* basis, fed either a commercial (DLG, Fredericia, Denmark) low CP (LCP, 120 g standardised ileal digestible (**SID**) CP/kg, n = 20), standard CP (SCP, 124 g SID CP/kg, n = 20), or high CP (HCP, 128 g SID CP/kg, n = 20) diet (Table 1). All three diets were formulated according to the corresponding Danish dietary CP recommendations depending on feed efficiency of grower-finisher herds and were formulated to be comparable with respect to Lys to CP ratio (LCP; 6.42, SCP; 6.45, HCP: 6.56) and with respect to the ratio between Lys and next limiting amino acids, i.e. methionine, threonine, tryptophan and valine. Diets were formulated to be isoenergetic on a net energy basis. In week 19 of age, pigs within dietary treatment were grouped into three categories (Feed conversion category) of the 30% highest (**HF**; n = 18), 40% medium (**MF**; n = 24), 30% lowest (**LF**; n = 18) FCR, based on average FCR during the final four experimental weeks. This resulted in six animals in the HF, six animals in the LF and eight animals in the MF groups within each CP level.

Feed intake and BW

Pigs were weighed weekly on an individual basis. Automatic feed intake registrations were done continuously on individual pigs. All pigs were equipped with electronic ear tag transponders enabling the feeding system to recognise each pig using radio frequency identification. After pigs were registered, a cover in front of the feeding trough would open, allowing pigs access to the feed. During the first 5 days in the weaner phase, the cover in front of the automatic feeders was open with feed visible and accessible

Table 1
Ingredient and chemical composition of low (LCP), standard (SCP) or high (HCP) CP pig diets (as–fed basis) used in the grower-finisher phase.

Item	Dietary CP level		
	LCP	SCP	HCP
Ingredient, %			
Barley	34.96	39.96	34.93
Wheat	30.00	25.00	27.00
Soybean meal	11.10	9.80	13.90
Wheat bran	5.00	1.00	2.50
Rye	5.00	5.00	5.00
Sunflower meal	3.90	8.00	5.00
Corn	2.50	3.70	4.30
Dried beet pulp	2.00	2.00	2.00
Oat	2.00	2.00	2.00
Calcium carbonate	1.25	1.25	1.15
Palm oil	0.60	0.60	0.60
NaCl	0.55	0.52	0.47
L-lysine sulphate	0.45	0.49	0.44
Monocalcium phosphate	0.20	0.20	0.21
Vitamin-mineral premix[1]	0.20	0.20	0.20
Threonine, 98%	0.13	0.13	0.13
Phytase	0.06	0.06	0.06
DL-Methionine	0.04	0.03	0.05
Xylanase	0.04	0.04	0.04
Vitamin E[2]	0.03	0.03	0.03
Calculated chemical composition			
Net energy, MJ/kg feed[3]	8.7	8.7	8.7
DM, %	92.1	91.9	91.6
CP, %	14.8	15.2	15.8
Crude fat, %	3.0	2.9	3.0
Crude fibre, %	1.9	3.0	4.9
Ash, %	3.9	3.9	4.0
Lysine, g/kg	9.2	9.5	9.9
Methionine, g/kg	2.7	2.8	3.0
Zinc, g/kg	0.087	0.087	0.087
Calcium, g/kg	6.7	6.7	6.7
Phosphorous, g/kg	4.2	4.3	4.4
Sodium, g/kg	2.3	2.1	2.1
SID[4] amino acids			
SID Lysine	7.4	7.7	8.1
SID Methionine	2.2	2.3	2.4
SID Threonine	4.8	5.1	5.3
SID Tryptophan	1.4	1.5	1.6
SID Valine	5.2	5.3	5.4

[1] Supplied per kg diet: 84 mg Fe (iron-II-sulphate monohydrate), 10 mg Cu (Copper-II-sulphate pentahydrate), 42 mg Mn (manganese-II-oxide), 55 mg Zn (zinc oxide), 0.22 mg I (calcium iodine), 0.32 mg Se (sodium selenite), 4 200 IU Vitamin A, 420 IU Vitamin D3, 60 IU Vitamin E (all-rac-α-tocopheryl acetate), 2.8 g L-Lysine sulphate, 0.3 g DL methionine, 1.3 g L-Threonine, 3.9 mg Propyl gallate, 120 mg diatomaceous earth, 5 mg silicic acid, 8.10 mg citric acid, 900 FTU 6-phytase, 3 200 U endo-1,4 beta-xylanase. Additionally, per kg diet, SCP provided 0.3 g L-Lysine sulphate, LCP provided 0.10 g DL-methionine and 0.10 mg citric acid, and HCP provided 0.2 g DL-methionine and 0.10 mg citric acid.
[2] Mixed with calcium carbonate.
[3] Re-calculated from Danish feed unit (physiological energy): 1 FE = 8,4 MJ net energy (Dutch net energy system).
[4] SID = Standardised ileal digestible.

until all pigs had started feeding from the automatic feeders. Hereafter, the cover in front of feeders was closed between feeding sessions. In case of simultaneous registration of more than one transponder, feeders would automatically close, thus preventing more than one pig from accessing the feeder at a time. The feeders registered the time of arrival and departure and trough weight immediately before and after each visit. Weight was detected by automatic lowering of the troughs onto a scale. Feed intake was calculated by taking the difference in trough weight before and after each visit. These recordings were the basis for calculating daily and weekly feed intake, FCR, as well as the parameters related to feeding behaviour by day (cumulative time spent feeding, meal frequency and postprandial correlation) or by meal. Meal behaviour variables were meal size, meal rate (g/min), meal interval (interval between two consecutive meals within pig) and meal duration. The meal criterion was defined as the minimum interval between two feeding sessions, where each session was considered a separate meal. The criterion was determined based on visual evaluation of a log-survivorship function and set at 3 min (Slater and Lester, 1982; Gloaguen et al., 2013). Troughs were automatically refilled from a small silo above each feeder when trough weight fell below a set minimum threshold. Access to the feeders was locked during refilling. On the day before the arrival of pigs, each feeder was calibrated. Throughout the experiment, discrepancy between feeder weight between each visit and before and after each visit was regularly checked for negative or excessive intake or feeding rate. Accuracy was verified regularly during the first two experimental weeks by comparing automatic registration by electronic feeders with manual scale registration of gradually increasing amounts of feed. Average correlation between manual and automatic registrations was 96.5%. Feeders were calibrated at the beginning, middle and end of each block both within the pre-experimental starter period and the grower-finisher period.

Statistical analyses

The growth performance and feeding behaviour data were analysed using a polynomial mixed model in R (Pinheiro et al., 2019) studio version 4.2.2 (R Core Team, 2021). The individual pig was used as the observational unit. Model residuals were assessed and confirmed to be normally distributed using residual plots and quantile–quantile plots. Analyses of meal feeding behaviour were performed for meals above 0 g. Meal rate, size, interval and duration were square root transformed to obtain normality of residuals. The model included up to the 4th order polynomial of time (based on exploratory plots), dietary CP level, FCR category and their two-way interactions with time as fixed effects. The BW on the day of insertion into the grower-finisher pens was included as a covariate, whereas pigs (repeated measurement) and pen within block were included as random effects including a random slope over time in the model. The covariate initial BW was only included in the model when it was found to improve model fit (BIC, AIC, logLikelihood). To allow posthoc comparison of the response variables between groups, Tukey-Kramer adjusted LS-means were calculated using the emmeans package (Lenth et al., 2023) when relevant. In case of significant time × factor interactions, additional posthoc comparisons of slopes were performed using the emtrends function in the emmeans package. A P-value < 0.05 was considered significant, whereas a value between ≤ 0.05 and $P \leq 0.10$ was considered a statistical trend.

Results

Growth performance

The FCR (avg. ± SD) across the entire growing-finishing periods was 2.53 ± 0.67, 2.33 ± 0.51 and 2.21 ± 0.54 for pigs categorised in the HF, MF and LF FCR categories, respectively. A dietary CP level × time interaction effect was found for all the measured growth performance parameters. The BW (Fig. 1A) of HCP compared with LCP pigs tended ($P \leq 0.10$) to be greater in weeks 10 (49.1 vs 47.3 kg), 11 (56.9 vs 53.0 kg) and 12 (65.0 vs 60.2 kg) and this effect persisted numerically. With respect to average daily gain (**ADG**) (Fig. 2A), up to 11 weeks after weaning, a similar trend over time across CP levels was observed. Thereafter, the LCP pigs were gaining BW faster ($P < 0.05$) during week 11 to week 13 and slower ($P < 0.10$) in week 14 to week 15 compared with SCP and HCP pigs. Daily feed intake (Fig. 3A) was numerically highest

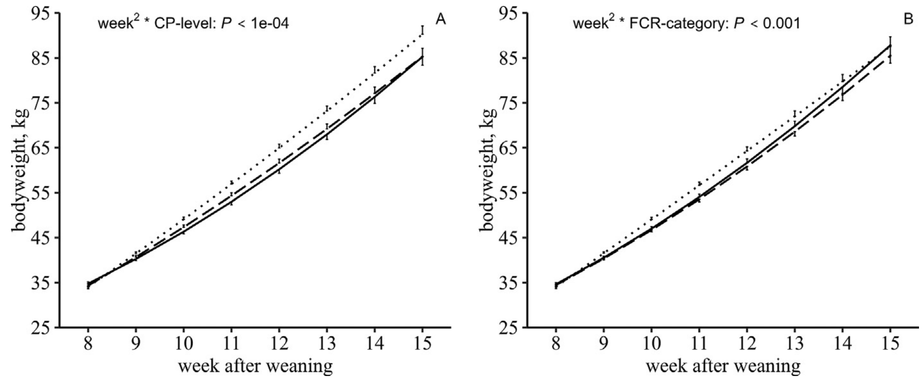

Fig. 1. Development of BW (kg) over time depending on dietary CP level (A), i.e. low (LCP ——), standard (SCP — —) or high (HCP ■■■), or on feed conversion ratio (FCR) category (B) classified by 30% lowest (LF ——), 40% intermediate (MF — —) or 30% highest (HF ■■■) feed conversion based on the final 4 growing weeks of pigs.

for HCP pigs from days 55–95 and tended to increase at a faster rate on day 75 (P = 0.08) than LCP. A negative (P < 0.0001) trend of the feed intake curve was observed for HCP from days 95–105 compared to a positive trend for LCP and SCP pigs. Concerning FCR (Fig. 4A), LCP pigs displayed a declining ($P \leq 0.05$) trend in weeks 10–12, whereas HCP and SCP pigs showed an increase ($P \leq 0.05$) trend. The inverse pattern was observed for HCP (decreasing) and LCP (increasing) from week 14 (P < 0.05). All performance parameters except for FCR had a significant FCR category × time interaction. BW (Fig. 1B) was higher for HF pigs compared with LF ($P \leq 0.01$) or MF ($P \leq 0.10$) pigs between weeks 9 and 12. Pigs in the HF group had a relatively stable ADG (Fig. 2B) from approximately 10 weeks after weaning onwards, whereas a steep increase in ADG was observed for MF and LF pigs from weeks 10 to 14. Consequently, ADG was higher for pigs in the MF ($P \leq 0.05$) and LF (P < 0.01) category in weeks 13 and 14 compared with HF. Pigs in the MF ($P \leq 0.05$) and LF ($P \leq 0.10$) categories had lower daily feed intake (Fig. 3B) than HF pigs from days 55 to 75 (approximately weeks 8–11). A significant simple effect of feed efficiency category on FCR (P < 0.001; Fig. 4B) was observed, where FCR of LF pigs was lowest and that of HF pigs highest.

Feeding behaviour

Results on the effect of CP level on feeding behaviour parameters are shown in Table 2 and Supplementary Figs. S1–S6. All feeding behaviour parameters except for feeding rate per meal were significantly affected by a time × CP level interaction. The daily feeding duration increased steeply for all CP levels and reached a peak at around days 60–65, whereafter there was a slow decrease, with the fastest decline observed for LCP and the slowest decline for SCP. Daily feeding duration of HCP pigs plateaued from days 75–90, whereas feeding duration for both LCP and SCP pigs kept declining (P < 0.05). Daily feeding duration remained close to stable after 90 days for SCP and LCP but decreased rapidly for HCP (P < 0.01). Similarly, the meal frequency pattern was affected differentially for the HCP group; the HCP group had a continuously decreasing trend as opposed to SCP and LCP, which initially had increasing and thereafter decreasing trends from day 60 onwards. There was a tendency (P = 0.09) for a lower meal frequency for HCP than LCP and SCP at days 65–70. Interval between meals increased more rapidly for HCP than the other two CP-levels and the latter two consequently had flatter trends up to day 75 (P < 0.001). Moreover, LCP tended (P < 0.10) to have shorter meal intervals than HCP between days 65–100. Meal size increased quadratically over time and tended to be larger for HCP than both LCP (P < 0.08) and SCP (P < 0.10) between days 60 and 95 due to a steeper increasing trend (P < 0.01) for the first 30 days. Meal duration (min/meal) was significantly affected by a CP × day interaction (P < 0.001). A general pattern was observed with an initial steep incline up to approximately day 60, a slower incline until day 90 and thereafter a decline. Pigs in the HCP group had a tendency ($P \leq 0.10$) to have longer meals compared with pigs within the LCP group from days 70 to 90. In line with this, the HCP had the steepest slope ($P \leq 0.05$) up to day 60 compared to either of the other two treatments. Feeding rate (g/min) for each meal increased linearly over time. There was a tendency (P = 0.07) for a simple effect of CP-level where the highest feeding rate was observed for HCP; however, Tukey-Kramer adjusted posthoc comparisons of treatments showed no tendency for statistical differences. CP level did not significantly affect postprandial correlations between meal size and interval length.

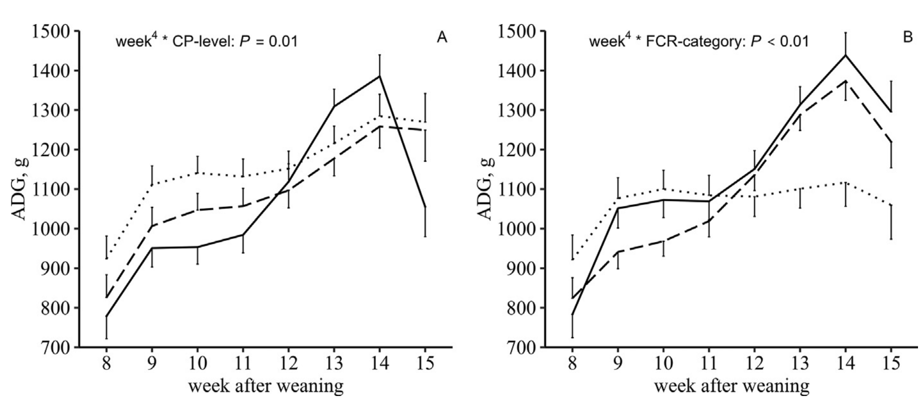

Fig. 2. Development of average daily gain (ADG, g) over time depending on dietary CP level (A), i.e. low (LCP ——), standard (SCP — —) or high (HCP ■■■), or on feed conversion ratio (FCR) category (B) classified by 30% lowest (LF ——), 40% intermediate (MF — —) or 30% highest (HF ■■■) feed conversion based on the final 4 growing weeks of pigs.

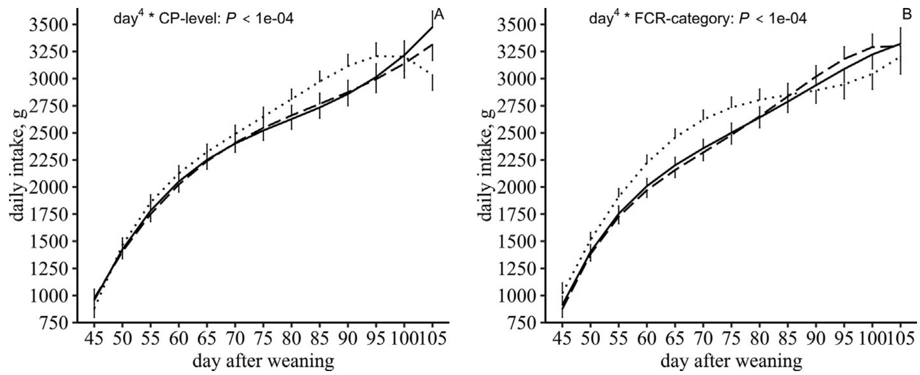

Fig. 3. Development of daily feed intake (g) over time depending on dietary CP level (A), i.e. low (LCP ——), standard (SCP — —) or high (HCP ■■■), or on feed conversion ratio (FCR) category (B) classified by 30% lowest (LF ——), 40% intermediate (MF — —) or 30% highest (HF ■■■) feed conversion based on the final 4 growing weeks of pigs.

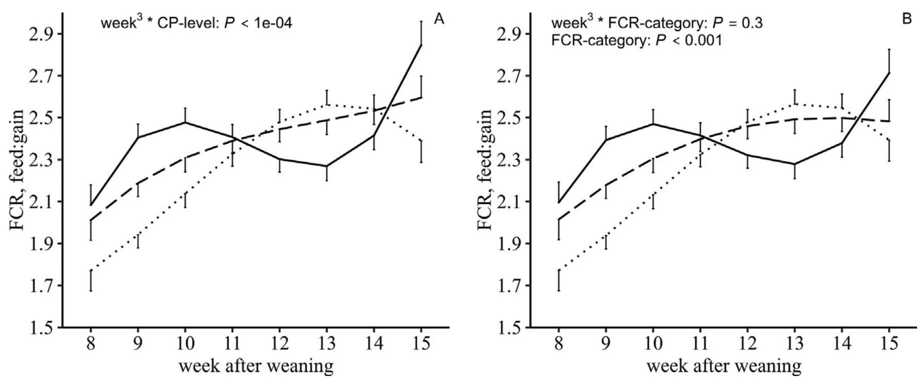

Fig. 4. Development of feed conversion ratio (FCR) over time depending on dietary CP level (A), i.e. low (LCP ——), standard (SCP — —) or high (HCP ■■■), or on feed conversion ratio (FCR) category (B) classified by 30% lowest (LF ——), 40% intermediate (MF — —) or 30% highest (HF ■■■) feed conversion based on the final 4 growing weeks of pigs.

Table 2
Effect of low (LCP), standard (SCP) or high (HCP) dietary CP level on feeding behaviour of pigs during the grower-finisher phase.

	LS-means[1]				LS-trend[1]				*P*-value					
Parameter	LCP	SCP	HCP	SEM	LCP	SCP	HCP	SEM	CP-level	CP-level × Day	Day	Day^2	Day^3	Day^4
Behaviour per day														
Meal frequency	11.7	10.3	7.70	0.72	−0.19	−0.13	−0.10	0.02	0.07	<0.01	<0.001	<0.001	<0.001	–
Duration, min	85.0	89.0	81.5	2.80	−0.74	−0.54	−0.46	0.08	0.22	0.02	0.01	<0.01	<0.001	<0.001
Prandial corr.[2]	0.19	0.12	0.20	0.03	–	–	–	–	0.25	0.10	0.75	–	–	–
Behaviour per meal														
Size, g[3]	13.2	14.1	16.6	0.48	0.18	0.19	0.25	0.01	0.18	<0.001	<0.001	<0.001	–	–
	203 ± 1.85	235 ± 2.17	311 ± 3.01											
Duration, min[3]	2.46	2.66	3.00	0.09	0.002	0.003	0.010	0.004	0.04	<0.001	<0.001	0.14	<0.001	<0.001
	6.89 ± 0.05	8.22 ± 0.06	9.75 ± 0.08											
Rate, g/min[3]	5.24	5.20	5.44	0.09	–	–	–	–	0.07	0.78	<0.001	0.45	0.56	0.05
	27.7 ± 0.09	27.7 ± 0.10	30.0 ± 0.11											
Interval, min[3]	9.26	10.0	11.6	0.38	0.05	0.04	0.09	0.008	0.07	<0.001	<0.001	0.02	–	–
	112 ± 1.08	130 ± 1.24	163 ± 1.58											

Abbreviations: LCP = Low CP; SCP = Standard CP; HCP = High CP.
[1] Least square means and trend, i.e. slope, at average day (72.2).
[2] Postprandial correlation; correlation between meal size and time to next meal.
[3] Variable is square root transformed. Values represent LS-means (upper value) of transformed variable and raw mean ± SE (lower value).

The effect of FCR category on feeding behaviour parameters over time is shown in Table 3 and Supplementary Figs. S1–S6. There was a tendency for a FCR category × time interaction to influence daily feeding duration (min/day), which decreased more rapidly ($P < 0.05$) between days 70 and 90 for HF than for LF or MF pigs. The HF group had the numerically highest feeding duration prior to day 80. Daily feeding time remained mostly stable from day 90 onwards. Meal frequency and meal interval for pigs in the different categories were similar among FCR categories during the entire experiment. An interaction of FCR category with time ($P < 0.01$) was observed for meal frequency due to a faster decrease in meal frequency for HF compared to LF (days 60–70) or MF (days

Table 3
Effect of feed conversion ratio (FCR) category[1] on feeding behaviour of pigs during the grower-finisher phase.

Parameter	LS-means[2]				LS-trend[2]				*P*-value					
	LF	MF	HF	SEM	LF	MF	HF	SEM	FCR-category	FCR-category × Day	Day	Day[2]	Day[3]	Day[4]
Behaviour per day														
Meal frequency	9.72	10.6	9.27	0.66	−0.14	−0.12	−0.16	0.02	0.12	<0.01	<0.001	<0.001	<0.001	0.34
Duration, min	81.9	85.3	88.2	3.19	−0.93	−0.48	−0.33	0.09	0.29	0.07	0.01	<0.01	<0.001	<0.001
Prandial corr.[3]	0.06	0.11	0.10	0.05	–	–	–	–	0.67	0.31	0.75	–	–	–
Behaviour per meal														
Size, min[4]	14.3 225 ± 1.97	14.0 231 ± 2.13	15.6 290 ± 3.10	0.50	0.20	0.19	0.22	0.01	0.32	0.01	<0.001	<0.001	0.86	0.67
Duration, min[4]	2.59 7.75 ± 0.06	2.63 7.80 ± 0.05	2.90 9.19 ± 0.08	0.10	0.004	0.005	0.006	0.005	0.93	0.08	<0.001	0.14	<0.001	<0.001
Rate, g/min[4]	5.28 27.8 ± 0.10	5.27 28.0 ± 0.09	5.32 29.6 ± 0.11	0.10	–	–	–	–	0.67	0.35	<0.001	0.45	0.56	0.05
Interval, min[4]	10.4 128 ± 1.25	9.93 127 ± 1.09	10.5 146 ± 1.66	0.37	–	–	–	–	0.16	0.07	<0.001	0.02	0.10	0.17

Abbreviations: LF = Low feed conversion ratio; MF = Medium feed conversion ratio; HF = High feed conversion.
[1] Feed conversion ratio (FCR) category: pigs classified into categories based on FCR in the final 4 weeks i.e. 30% lowest (LF), medium 40% (MF), and 30% highest (HF).
[2] Least square means and -trend, i.e. slope, at average day (72.2).
[3] Preprandial correlation; correlation between meal size and time to previous meal.
[4] Variable is square root transformed. Values represent LS-means (upper value) of transformed variable and raw mean ± SE (lower value).

60–65) pigs, whereas the opposite was observed from day 90 onwards. Meal interval increased nearly linearly for all treatments, and no obvious numeric differences were observed. A time × FCR-category tendency was obtained due to a steeper slope for HF than LF or MF from the start of the experimental period up to day 60 because of HF having a lower meal interval ($P < 0.05$) at day 45. Larger meal sizes were observed for pigs in the HF group between days 60 and 85 ($0.05 < P < 0.10$) compared with pigs in the MF group. This coincided with a steeper positive trend ($P < 0.01$) up to day 65 for the HF compared to the MF or LF group. A tendency for a FCR category × day interaction was found for meal duration (min/meal) due to HF pigs having longer meal durations than LF pigs (days 65–85; $P < 0.10$). Additionally, the difference between HF and MF during this period was close to a tendency ($P < 0.12$). There was no significant effect of FCR category or its interaction with time on feeding rate per meal (g/min) or postprandial correlation.

Discussion

Growth performance

Feed efficiency is the most important growth performance parameter to improve, as the production economy through variable costs (Patience et al., 2015), environmental impact through excretion of nitrogen and phosphorus (Gaillard et al., 2020), as well as the carbon footprint through feed production (McAuliffe et al., 2016) are all tightly linked to the feed. For this reason, exploring the varying response in feed efficiency between pen mates on an individual basis as well as in-detail information from a longitudinal perspective, is of great importance to further understand the background for the variation and a prerequisite for further improving this trait.

The dietary CP level had a numerical effect on the BW by the end of the grower-finisher period, a finding supported by several previous studies (Campbell et al., 1984; Kerr et al., 1995; Carpenter et al., 2004; Fang et al., 2019) performed over several decades. The dietary energy concentration remained constant across the three dietary treatments, suggesting that the increase in feed intake and consequently BW for HCP compared with SCP and LCP was driven by the dietary CP level, at least within a certain time frame of the grower-finisher period. In support of this finding, Park et al. (2020) and colleagues found that a high-energy diet did not result in increased growth. Interestingly, the curves for ADG displayed a dynamic pattern over time for LCP as evident by the faster increase in gain over time for LCP compared with the HCP group from weeks 12–14 of the experimental period. Within the same period, FCR numerically improved for LCP and worsened for HCP pigs. With respect to the LCP group, the most likely physiological mechanism behind the improved growth performance is the effect of compensatory growth, which after a period of restricted protein intake can be activated following a recovery period with a dietary protein level at or above requirements (Menegat et al., 2020). As shown in previous studies, growing-finishing pigs restricted in dietary protein for a limited period were able to compensate by displaying increased ADG and improved feed efficiency in the subsequent recovery period (Fabian et al., 2004; Chaosap et al., 2011). In this regard, it is also worth noting that CP requirements are dynamic of nature, and in general decrease over time (Tybirk et al. 2018). It is widely recognised that a supply of CP above requirements leads to a stagnated or even decreased growth due to the energy spent on the deamination processes (Fuller and Chamberlain, 1982). This is in line with the numerically greater feed intake combined with high dietary CP levels. As both protein accretion (Schinckel et al., 1996) and feed efficiency decline with age (Arthur et al., 2008), a dietary CP level above requirements may not necessarily result in continuous increased growth rates.

The basis for categorisation into the three FCR groups was on performance data during the last 4 weeks of the experiment and the categories were representative of the full experimental period. Several interactions between FCR category and week after weaning, mainly in the late phase of the experimental period, were observed. As also observed in previous studies (Arthur et al., 2009; Saintilan et al., 2015), a relation between FCR category and ADG was found. A limitation to the study was the number of replicates per dietary treatment and FCR category, and thus, it was not possible to further divide animals into subcategories reflecting whether a low FCR was the result of a high feed intake and corresponding high ADG, or a low feed intake and corresponding low ADG. From a production perspective, pigs with low FCR, as a product of low feed intake and high ADG are preferred, meeting the objective of having as many pigs as possible reaching slaughter weight within the shortest possible time while consuming the lowest amount of feed. In addition, although not covered in this study, achieving a high lean meat percentage is also desirable from a production perspective. This would reflect the partitioning of energy and protein, but only add to the complexity of understanding the interplay between the most important production traits as well as categorising these traits on individual level.

Feed efficiency measured as FCR is a well-recognised performance trait used for decades to represent the relationship between feed intake and gain. However, the duality of achieving a certain FCR, emphasises the fact that this trait is a proxy parameter and does not reflect the pig's true ability to utilise nutrients. As revealed in this study, feed efficiency is highly dynamic of nature and in line with the categorisation into low, medium, and high groups, the FCR category varied within weeks (data not shown) during the grower-finisher phase. Thus, there is a risk that some explanatory power reflecting the varying response of the pig's true ability to utilise nutrients is lost when distinction between categories is done over time, or even to a greater extent when done within the last phase of a period. On the contrary, with current modelling capabilities and practical conditions where feeding is adjusted to a pen average, categorising FCR based on the pig's performance within a limited period is acceptable and likely reflects the feed efficiency over the entire grower-finisher phase.

Feeding behaviour

The HCP–fed pigs had longer and larger meals at a slightly faster rate than LCP– and SCP–fed pigs. Similar adaptation of meal feeding behaviour is observed in the study of Hyun et al. (1997) who showed that pigs fed grower-finisher diets equal in lysine to CP ratios with four incremental CP levels between 14.3 and 19.0% CP from 27 kg up to 55 kg BW and 12.9–17.0% CP at higher BW, displayed an increase in feed intake per meal with increasing CP level up to the second highest level. Moreover, the two highest CP levels gave rise to longer feeder occupation per meal. Observed differences in meal variables suggest that sensory or postingestive feedback mechanisms control meal cessation (Smith, 1996; Gloaguen et al., 2013). The tendency for a higher feeding rate of the HCP pigs also indicates a potential difference in palatability. Since ingredient composition is similar across diets, this may be attributed to differences in nutrient composition, as for example, dietary amino acid and protein stimulate orexigenic and anorexigenic hormones involved in feed intake regulation (Müller et al., 2022a; Müller et al., 2022b; Müller et al., 2023). A substantial undersupply of protein in the early grower-finisher phase might skew the lean and fat mass homeostasis, with a tendency to favour adipose tissue accretion (Easter and Baker, 1980). As a result, this might hamper the appetite, through a negative feedback mechanism regulated by leptin (Friedman, 2016) in adipose tissue cells (Zhang et al., 1994).

Although different meal feeding patterns were observed, differences in feeding duration and intake on a daily basis were less pronounced due to adaptations in feeding frequency. Pigs adapt feeding patterns to reach desired nutrient intake, meeting demands for maintenance and nutrient accretion (Young and Lawrence, 1994; Nyachoti et al., 2004). Indeed, no differences in post- and preprandial correlations among treatments indicate a similar balance between energy uptake and meal initiation. Prandial correlations were generally low, likely because they are not only driven by physiological but also social stimuli (Fernández et al., 2011). In line with the lack of differences in prandial correlations, it has been suggested that the main determinant regulating voluntary feed intake is the dietary energy content (Henry, 1985). Hence, differences in BW may have driven differences in feeding behaviour and thus daily feed intake since maintenance energy requirements are driven by metabolic BW. Accordingly, feed intake was independent of CP level when corrected for metabolic weight.

There was a longitudinal pattern of low and medium FCR pigs eating smaller meals for a shorter duration and consequently spending less time eating on a daily basis compared with high –FCR pigs. These findings are in line with the observations of De Haer et al., 1993, Vigors et al., 2016 and Shirali et al., 2017 showing that pigs with high FE spent less time feeding per day than pigs with low FE. Moreover, Andretta et al., 2016a find a negative correlation between FE and feed intake per meal. Several studies find that increased daily feed intake is correlated with a reduced FE (Young et al., 2011; Do et al., 2013; Vigors et al., 2016). Meal size has been proposed to negatively impact nutrient digestibility (Carcò et al., 2018) due to an effect on passage rate and output of digestive enzymes (Andretta et al., 2016a). The difference in intake may also be a symptom of pigs adapting different feeding patterns because of competition. Georgsson and Svendsen, 2002 suggested that large pigs overeat when stimulated by competition leading to higher ADG and poorer FE. Several studies find that FE is affected by feeding rates (Andretta et al., 2016a; Shirali et al., 2017), but no differences in feeding rate were observed in the current study. In line with this, neither Carcò et al., 2018 nor Rauw et al., 2006 observed that feed efficiency was affected by feeding rate.

Conclusion

Only interactions between dietary CP level and week of the experimental period, as well as FCR category and week of the experimental period, were associated with changes in the growth performance and feeding behaviour. The differential patterns in ADG and FE suggest that there is a change in efficiency of nutrient utilisation over time, indicating that the response to dietary CP level is of a dynamic nature during the mid- to later stage of the grower-finisher phase. Adaptations in meal feeding behaviour indicate CP level-dependent appetite control. Moreover, the periodically higher feed intake for pigs categorised as having poor feed efficiency and changes in differences in ADG among FCR categories over time underline difficulties of using FCR as a proxy for nutrient utilisation.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101531) can be found at the foot of the online page, in the Appendix section.

Ethics approval

All the procedures in this animal experiment were conducted in accordance with the Danish Ministry of Justice, Act no. 474 of 15 May 2014, concerning experiments with animals and the care of experimental animals and a licence issued by the Danish Animal Experiments Inspectorate, the Ministry of Food, Agriculture and Fisheries, Danish Veterinary and Drug Administration.

Data and model availability statement

The data were not deposited in an official repository. The data of the subpopulation that support the study findings are available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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