Feeding behavior of growing and finishing pigs fed different dietary threonine levels in a group-phase feeding and individual precision feeding system

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ABSTRACT: Feeding behavior is an important aspect of pig husbandry as it can affect protein deposition (PD) in pigs. A decrease in plasma threonine (Thr) levels may influence feed intake (FI) due to amino acid imbalance. We set out to study whether different Thr inclusion rates of 70%, 85%, 100%, 115%, and 130% of the ideal Thr:lysine (Lys) ratio of 0.65 in two different feeding programs (individual precision feeding and group-phase feeding could affect pig feeding behavior and consequently PD. Two 21-d trials were performed in a 2 × 5 factorial setup (feeding systems × Thr levels) with 110 pigs in the growing phase [25.0 ± 0.8 kg of body weight (BW)] and 110 pigs in the finishing phase (110.0 ± 7.0 kg BW), which correspond to 11 pigs per treatment in each trial. Pigs were housed in the same room and fed using computerized feeding stations. The total lean content was estimated by dual x-ray absorptiometry at the beginning (day 1) and the end (day 21) of the trial. Multivariate exploratory factor analysis was performed to identify related variables. Confirmatory analysis was performed by orthogonal contrasts and Pearson correlation analysis. Graphical analysis showed no difference in feeding patterns between feeding systems during the growing or finishing phase. Pigs exhibited a predominant diurnal feeding, with most meals (73% on average) consumed between 0600 and 1800 h. Exploratory factor analysis indicated that feeding behavior was not related to growth performance or PD in growing or finishing pigs. Changes in feeding behavior were observed during the growing phase, where increasing dietary Thr resulted in a linear increase in the FI rate ($P < 0.05$). During the finishing phase, the duration of the meal and FI rate increased linearly as dietary Thr increased in the diet ($P < 0.05$). These changes in feeding behavior are, however, correlated to BW. In conclusion, the exploratory factor analysis indicated that feeding behavior had no correlation with growth performance or protein and lipid deposition in growing or finishing pigs. Dietary Thr levels and feeding systems had no direct effect on FI.

Key words: amino acids, feed intake pattern, precision feeding, precision livestock farming, precision nutrition, swine

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INTRODUCTION

Individually fed pigs in a precision feeding setup have higher amino acid (AA) efficiency of utilization than pigs fed in groups in conventional phase-feeding systems (Cloutier et al., 2015; Remus et al., 2019a). This is due to the fact that group-fed pigs receive larger and constant amounts of AA within each feeding phase to maximize herd growth performance. In contrast, precision-fed pigs receive daily individually tailored diets to concomitantly adjust the AA supply to the estimated requirements. Most of the pigs fed with precision feeding systems receive smaller amounts of AA than the group-fed pigs, and dietary AA concentration decreases as the pigs age (Andretta et al., 2014, 2016b). Precision feeding system decreases AA intake from 17% (Remus et al., 2019a, 2019b) to 27% (Andretta et al., 2014, 2016b), and further changes in dietary threonine (Thr) (Remus et al., 2019a) might impact on feeding behavior. Early studies (Yoshida et al., 1966; Benevenga et al., 1968) have proposed that drops in plasmatic Thr or histidine due to AA imbalance increased the efficiency of utilization of these AA. Additionally, the efficient incorporation into liver protein might result in plasmatic drops of the limiting AA, therefore unchaining a signal to an appetite-regulating center, which will decrease feed intake (FI).

Of the feeding behavior variables studied, meal frequency has been identified as having a potential influence on body composition (O'hea and Leveille, 1969) as shown in mice that achieved a significant fat loss without lean loss when intermittently fasted (Gotthardt et al., 2016). Likewise, intermittent feed restriction through sequential feeding in poultry led to a quick adjustment in lipogenesis and protein synthesis (Ezzine et al., 2012). In the same study, a pulse feeding of protein increased the nitrogen balance compared to ad libitum feeding. This was linked to decreased leucine oxidation and whole-body protein degradation during the postabsorptive state and greater protein synthesis in the whole body and liver during the fed state. Earlier studies (O'hea and Leveille, 1969; Allee et al., 1972) have shown that pigs fed twice a day had less fat deposition in kidneys, smaller back fat thickness, larger stomach weight, and improved feed efficiency than ad libitum-fed pigs. Pigs fed twice a day had a similar body composition but improved feed efficiency and growth as compared to ad libitum-fed pigs (Le Naou et al., 2014). Moreover, when fed ad libitum, each pig has its own feeding behavior, which might influence carcass leanness.

Previously, we demonstrated that pigs can change body composition as a function of Thr intake and feeding system (group-fed vs. individually fed pigs; Remus et al., 2019a). However, body composition in pigs was shown to change with meal frequency (Allee et al., 1972; Le Naou et al., 2014). As FI might be influenced by AA imbalance (Yoshida et al., 1966; Benevenga et al., 1968), this study was set out to establish correlations between feeding behavior, protein deposition (PD), lipid deposition (LD), and plasma concentration of Thr in growing (Remus et al., 2019a) and finishing pigs (Remus et al., 2019a). Additionally, it was assessed potential differences in the feeding pattern of group-fed or individually fed pigs receiving different levels of Thr in the diet.

MATERIAL AND METHODS

Animals were cared for according to a recommended code of practice (National Farm Animal Care Council, 2014) and to the guidelines of the Canadian Council on Animal Care (2009). Animal trials were approved by the Ethical and Animal Welfare Committee of the Sherbrooke Research and Development Centre (Agriculture and Agri-Food Canada, Sherbrooke, Quebec, Canada; case no. 478).

A total of 220 barrows of the same high-performance genotype (Fertilis 25 × G-Performer 8.0; Geneticporc Inc., St-Gilbert, Quebec, Canada) with a good health status were shipped to the Agriculture and Agri-Food Canada swine complex (Sherbrooke, Quebec, Canada) in two batches. Each batch of pigs was part of a different animal trial with a batch of 110 pigs in the finishing phase

[110–130 kg body weight (BW); November to December 2015 (Remus et al., 2020a)] and a batch of 110 pigs in the growing phase (25–50 kg BW; February to March 2016; Remus et al., 2019a). Pigs were allocated to two 76-m^2 pens each with a concrete slat floor in the same mechanically ventilated room. Pigs were fitted with an ear tag with an electronic chip granting access to the automatic precision feeders (Automatic and Intelligent Precision Feeder; University of Lleida, Lleida, Spain). A detailed description of the feeders is available in (Pomar et al., 2011; Andretta et al., 2016a). Briefly, diets are formulated daily and the feeders identify and assign individual pigs to the respective dietary treatment, mix feeds accordingly, and supply the diet according to their individual previously established requirements. The feeders record the exact time and duration of each feed demand. A time lag of 30 s during the growing phase and 15 s during the finishing phase that accounts for BW and FI was imposed between feed demands to avoid feed waste. Pigs were allowed 14 d to adapt to the environment and received a commercial feed mixture suited to their requirements (NRC, 2012). The experimental period lasted 21 d for each experiment (growing and finishing phase). Feed and water were provided ad libitum throughout the experiment. Room temperature was adjusted to 22 °C during the growing phase and 18 °C during the finishing phase.

Within each experiment, pigs were randomly assigned to two feeding systems and five levels of Thr supply according to a 2 × 5 factorial arrangement in two complete blocks. Each block consisted of 55 pigs inside a pen in the same room. Both were complete blocks with the same number of pigs from all treatments. Pigs were blocked with a time lapse of 1 wk to initiate the experimental treatment, between the two blocks, to account for the time required to complete the initial measurements. Feeding systems were an individual precision feeding (IPF) system with diets tailored daily for each pig and a conventional group-phase feeding (GPF) system. Levels of Thr supply were set to 70%, 85%, 100%, 115%, and 130% of the estimated ideal level. The individual pig was the experimental unit in both feeding systems. Each treatment had 11 replicates.

Feeding Programs, Nutritional Requirements, and Diets

Diets formulation. The requirements for AA were independently estimated for each feeding system. The four diets were formulated to have the same energy, calcium, and phosphorus concentrations (Table 1). This allowed the diets to be blended to obtain the 10 treatments resulting from the 2 × 5 factorial arrangement. Data from high-performance

Table 1. Ingredient and chemical composition of the four experimental feeds (A1, A2, B1, and B2)

Item	A1	A2	B1	B2
Ingredients (as-fed basis), g/kg				
Corn	533.4	537.9	537.1	538.3
Soybean meal (48%)	173	173	–	–
Wheat	150	150	100	100
Canola meal	47	47	–	–
AA premix[a]	33	33	–	–
Corn starch	–	–	156.3	156.3
Fat	16	16	35	35
Oat hulls	–	–	143	143
Limestone	12	12	8	8
Monocalcium phosphate	10	10	8	8
Lysine sulfate (70%)	6.7	6.7	2.8	2.8
Salt	5.5	5.5	4.8	4.8
L-threonine	4.5	–	1.2	–
Dl-methionine	2.3	2.3	0.2	0.2
L-valine (96.5%)	2.1	2.1	0.2	0.2
Micromineral premix[b]	2	2	2	2
L-tryptophan	1.1	1.1	0.3	0.3
L-isoleucine	0.7	0.7	0.2	0.2
Antimold	1	1	1	1
Cl-choline (75%)	0.2	0.2	0.2	0.2
Chemical composition, %				
Dry matter	90.85	91.25	92.99	92.67
Fat	6.79	6.74	7.88	8.44
Protein	19.85	19.88	7.50	6.88
Acid detergent fiber	3.87	4.018	6.32	6.51
Neutral detergent fiber	8.80	8.63	13.58	14.12
Total calcium	0.72	0.72	0.5	0.49
Total phosphorus	0.64	0.64	0.40	0.40
SID[c] isoleucine	0.67	0.69	0.22	0.21
SID leucine	1.34	1.39	0.64	0.59
SID lysine	1.07	1.07	0.34	0.33
SID methionine	0.53	0.53	0.16	0.14
SID methionine + cysteine	0.72	0.72	0.24	0.2
SID phenylalanine	0.75	0.77	0.28	0.26
SID serine	0.80	0.80	0.30	0.26
SID threonine	0.98	0.58	0.31	0.19
SID valine	0.89	0.89	0.29	0.27
Expected net energy, kcal/kg	3,208	3,223	3,255	3,259

[a]Mix of corn gluten meal and linseed meal (Shur-Gain, St-Hyacinthe, Quebec, Canada).

[b]Supplied per kilogram of diet (as-fed basis): vitamin A, 45,600 IU; vitamin D, 45,600 IU; vitamin E, 1,400 IU; vitamin K, 80 mg; vitamin B12, 1.2 mg; niacin, 800 mg; pantothenic acid, 600 mg; pyridoxine, 80 mg; thiamin, 80 mg; cooper, 4.9 g; iodine, 12 mg; iron, 4 mg; manganese, 2.5 g; selenium, 12 mg; and zinc, 6.1 g; supplier, manufacturer location.

[c]SID and net energy were estimated from the analyzed total AA and crude energy content in feed and from INRA-AFZ (French tables of compositionand nutritional value of feed materials) table values (Sauvant et al., 2004)

pigs from previous trials performed at Agriculture and Agri-Food Canada (Sherbrooke, Quebec, Canada) were used to simulate the Lys requirement of pigs and to formulate the feeds. Feed formulation was based on the values of total AA content corrected to the standardized ileal digestible (SID) value of each ingredient according to the digestibility values for each AA as presented in French tables of composition and nutritional value of feed materials (INRA-AFZ) tables (Sauvant et al., 2004). Feeds were formulated to contain the same AA profile (except for the Thr:Lys ratio) to keep feedstock variation small. For IPF pigs, four feeds (feeds A1 and B1 containing 130% and feeds A2 and B2 containing 70% of Thr relative to the recommended Thr:Lys levels) were mixed to meet the individual requirements calculated daily (Remus et al., 2019a, 2020a). The feeds were formulated to meet the Lys and other AA (except for Thr) requirements of the most demanding pig on the first day of the experimental period (feeds A1 and A2) and of the least demanding pig on the last day of the experimental period (feeds B1 and B2). The AA requirements, with the exception of Lys, were established using the ideal AA:Lys ratio proposed by Gloaguen et al. (2014).

Nutritional requirements within feeding programs. In the GPF system, the pigs received the same feed throughout the entire phase. The feed was a blend of feeds A and B mixed to meet the target levels of Thr and Lys for the respective treatment. For GPF pigs, Lys requirements were estimated on the basis of the assumption that requirements of a population are those of the 80th percentile pig of the group at the beginning of the phase (average of 3 d; Hauschild et al., 2010; Remus et al., 2020b). Amino acids were provided accordingly, except for Lys, which was decreased by 10% to ensure that it was the second limiting AA.

For IPF pigs, the required daily concentration of Lys for feeds was estimated with a mathematical model using information on daily individual FI (DFI) and weekly BW measures (Hauschild et al., 2012). Pigs were weighed at arrival and three times during the adaptation period to calibrate the model before the experimental period. The model consists of two components, with the first component allowing for the empirical estimation of the expected BW, DFI, and BW gain for the following day. The second model component is based on a factorial approach and uses the three estimated variables from the first model component to mechanistically determine the optimal daily concentration of Lys for each pig to meet its requirements. Daily Lys requirements (grams per day) were calculated by adding requirements of maintenance and growth as previously described (Remus et al., 2019a).

Experimental Measurements

Performance. Feed intake was registered in real time for each individual pig. Blood samples for plasma analysis were obtained after a 10-h fasting period. Total body fat and lean content were measured by dual-energy x-ray absorptiometry on days 0 and 21 of the trial with a densitometer device (Lunar Prodigy Advance; GE Healthcare, Madison, WI). Pigs were scanned in the prone position using the total body scanning mode (Lunar enCORE version 8.10.027; GE Healthcare, Madison, WI). Pigs received anesthesia induced with sevoflurane (7%) and maintained during scanning with isoflurane (5%). The duration between the beginning of anesthesia and the end of the scan (termination of anesthesia) was, on average, 20 min during the growing phase and 25 min during the finishing phase.

Data management and statistical analysis. The automatic feeders recorded 57,622 observations for the growing phase and 58,986 observations for the finishing phase over a 21-d measuring period for each respective phase. Data were imported in R (version 3.4.0; R Foundation for Statistical Computing, Vienna, Austria). The meal size was calculated by taking into account eventual short intervals between two consecutive visits registered by the feeders. Bigelow and Houpt (1988) pointed out that a short pause (e.g., used for drinking) between consecutive visits should not be considered as the start of a new meal. In the present study, because a group of pigs shared the same pen and feeders, we observed that a short pause between visits could also occur for reasons other than drinking; for instance, pigs frequently moved to and quickly resumed eating at another available feeder within the same pen (e.g., when other animals claimed the feeder). Therefore, intervals of up to 5 min between two consecutive visits were considered to pertain to the same meal consistent with literature findings (Bigelow and Houpt, 1988; Morgan et al., 2000). In the present study, a 5-min interval between visits accounted for 95% of all intervals recorded. The interval between meals was defined as the total time between the end of the previously finished meal and the start of the next meal. Feeding time per meal was defined as the average time that an animal spent eating a meal. Feed intake per meal was defined as

the average intake per meal. Feed intake rate was calculated by dividing the FI per meal by the time per meal. Total eating time per day was calculated by summing up feeding time per meal over a day. Intake of SID Lys and SID Thr were obtained for each pig by tallying the daily amount of nutrients provided by each of the feeds served.

Exploratory factor analysis was performed using the factor analysis procedure in the Minitab statistical package (version 16; Minitab Inc., State College, PA). This analysis considered only the level of ingested Thr in grams per day. Feeding system was not considered as it was encoded as a binary variable, whereas factor analysis requires variables to be continuous. Variables that were known a priori to share variance [e.g., average daily gain (ADG) is correlated with BW and gain:feed (G:F)] were not included in the analysis. Growth performance (BW, G:F, Lys, and Thr) and growth composition (LD and PD) were averages of the entire experimental period, whereas plasma composition was the final state measured on the last experimental day. Factors were extracted using principal components in order to reduce the variance of the originally considered factors to a minimum number of factors (Hair et al., 2009). Eigenvalues were selected by graphical analysis, and only those with values greater than 1 were accepted following Kaiser's criterion. The quartimax normalized rotational strategy was applied to simplify the rows of the factor loading matrix.

Feeding behavior data were analyzed as a 2 × 5 factorial arrangement using the mixed model procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC). The main effects included the feeding program (IPF vs. GPF), level of Thr (70%, 85%, 100%, 115%, and 130%), and their interaction. Blocks were considered a random effect. Assumptions for the normal distribution of residuals were tested using the Cramer-von Mises test using the univariate procedure of SAS version 9.4. The uncertainty in the estimate of the mean was expressed as the maximum standard error; $P < 0.05$ was considered to be statistically significant, and $P < 0.10$ was considered a tendency. Differences between individual treatments were analyzed by polynomial contrasts. Pearson correlation analysis was performed with the Corr procedure of SAS version 9.4 for levels within feeding systems.

RESULTS AND DISCUSSION

Detailed information on growth performance, carcass composition, and AA concentration in tissues for growing (Remus et al., 2019a) and finishing pigs (Remus et al., 2020a) was provided previously. Briefly, during the growing phase, increases in dietary Thr inclusion rate in the diet linearly increased ($P < 0.05$) growth performance (especially PD), carcass crude protein content, and AA concentration in muscles. There was no difference in growth performance between IPF and GPF pigs, but the chemical composition and AA concentration in muscle tissue differed ($P < 0.05$) for pigs in the growing phase depending on the feeding program. Thr GPF pigs had a slightly higher ($P < 0.05$) crude protein content in the longissimus dorsi and increased concentration of several AA in carcass muscles compared to IPF pigs. During the finishing phase, no effect on growth performance or muscle composition was observed for either feeding system or Thr inclusion rate. During both growing phases, no difference in fiber or energy intake was observed for either Thr inclusion rate or feeding system (data not shown).

Exploratory Analysis

The FI of pigs followed a circadian feeding pattern with a typical diurnal feeding behavior during the growing and finishing phases (Fig. 1). Most meals (73%) were consumed between 0600 and 1800 h, which corresponds to the time interval during which room lights were on. Pigs appeared to have higher FI rates between 1000 and 1800 h. A preference for diurnal eating periods has been observed for pigs (Wangsness et al., 1980; Young and Lawrence, 1994; Andretta et al., 2016a) and is likely related to the period of light in the room, which stimulated pigs to eat (Andretta et al., 2016a). During the growing and finishing phases, pigs had bigger meals during the night compared to daytime probably because fewer meals were consumed during the night. Therefore, pigs that exhibited nocturnal feeding behavior likely had longer and larger meals than pigs exhibiting diurnal feeding behavior, which seemed to consume more frequent but smaller meals.

Growing Phase

An exploratory factor analysis revealed that, for growing pigs (Table 2), variables such as PD, LD, average BW, Lys, and Thr intake presented positive high loading (>0.75) being retained in factor 1, which was named *growth*. The positive loading can be interpreted as all the variables following the same direction in the factor (or vector). It could be seen as a positive association among the variables retained in this factor. As pigs grow, energy intake

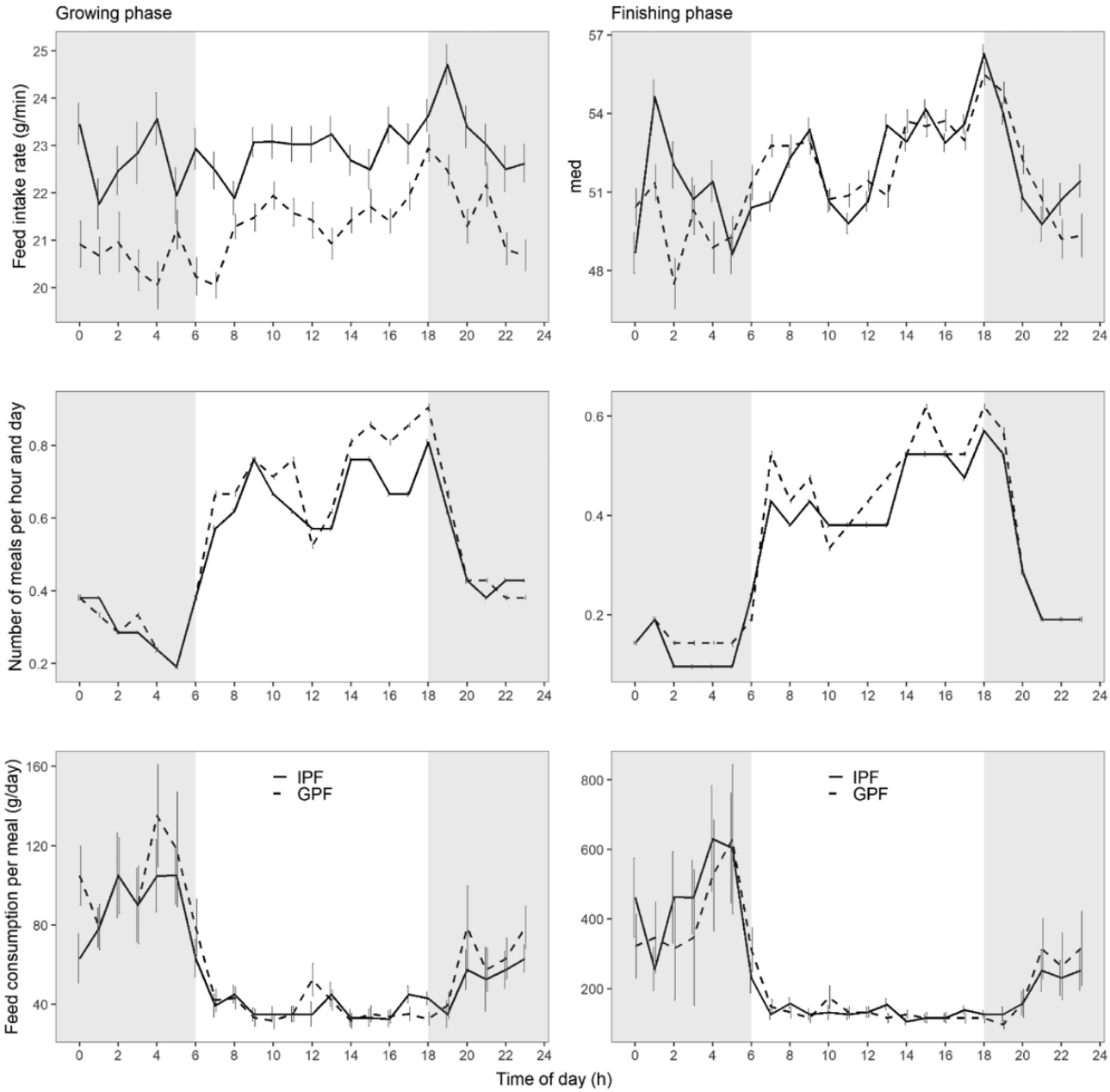

Figure 1. Circadian variation of average feed intake (FI) rate (grams of FI per minute during a meal), number of meals, and size of the meal (grams per meal) for growing (25–45 kg BW) and finishing pigs (110–130 kg BW) in a GPF or IPF program. Gray areas indicate dark period in the room.

increases with linearly increasing PD and LD until PD maximum is reached (Patience et al., 2015). Likewise, AA intake (grams per day) will increase [following the changes in average daily FI (ADFI)] as BW increases (NRC, 2012).

Factor 2 was named *feeding behavior* for retaining the variables FI per meal and time interval per meal with high negative loadings (>−0.85) and the number of meals with high positive loading (0.94). This makes feeding behavior a bipolar factor. This bipolarity can be seen as the number of meals being in the opposite direction in the factor as compared to FI per meal and time interval per meal. Regulation of meal size by pigs was shown to be an important factor in maintaining energy homeostasis (Schwartz et al., 2000). Increased meal frequency may increase fat oxidation (Smeets and Westerterp-Plantenga, 2008) and maintain glucose levels in humans, constantly decreasing hunger (Jenkins et al., 1989). However, a higher meal frequency in combination with a smaller meal size has also been shown to increase cravings and hunger in humans compared to a lower meal frequency in combination with a larger meal size (Ohkawara et al., 2013). The authors hypothesized that enhanced appetite

Table 2. Exploratory factor analysis (quartimax rotation) with correlation coefficients for growth performance, feeding behavior, and plasma response of growing pigs[a]

Variable	Factor 1: growth	Factor 2: feeding behavior	Factor 3: efficiency	Factor 4: plasma Thr	Communality
Average BW	0.88	0.01	0.15	0.00	0.80
PD, g/d	0.75	0.11	0.53	0.16	0.89
LD, g/d	0.84	0.02	0.04	−0.21	0.74
G:F efficiency	0.18	0.06	0.85	0.28	0.84
Lysine intake	0.87	−0.01	−0.34	−0.02	0.88
Threonine intake	0.75	−0.05	−0.27	0.46	0.85
Threonine efficiency of utilization	−0.08	0.12	0.83	−0.37	0.84
FI rate	0.36	0.25	−0.51	0.06	0.45
FI per meal	0.41	−0.86	−0.18	−0.01	0.94
Number of meals	0.13	0.94	0.00	−0.10	0.92
Time interval between meals	−0.16	−0.93	0.03	0.07	0.89
Plasma threonine	−0.04	−0.02	−0.01	0.88	0.77
Plasma urea	−0.26	0.17	−0.02	0.05	0.10
Variance[b]	3.84	3.44	2.20	1.29	10.77
Proportion[c]	0.27	0.25	0.16	0.09	0.77

FI, feed intake; PD, protein deposition; LD, lipid deposition.

[a]Loadings were assumed to be significant above 0.6.

[b]Variability (eingenvalue) in data explained by each factor.

[c]Proportion of variability in data explained by each factor (ranging from 0 to 1).

might prevent large drops in plasma glucose levels between meals.

Factor 3 was named *efficiency indicators* for retaining the variables G:F efficiency and Thr efficiency with high positive loadings (>0.85). Both variables are positively associated, following the same direction in the factor. Little information is available on the underlying factors determining feed efficiency. Studies with beef cattle have shown that the most feed-efficient animals had alterations in proteins related to AA transport in the liver and decreased protein turnover and presented better adaptability to oxidative stress, expending less energy in these functions (Cantalapiedra-Hijar et al., 2018; Fonseca et al., 2019). Thus, it was hypothesized that feed-efficient animals might use AA more efficiently during the growing phase. In this factor, FI rate presented its highest loading but did not reach the 0.6 threshold required to be considered highly correlated to the efficiency factor. A previous study (Rauw et al., 2006) showed that pigs eating faster had a similar G:F efficiency but a greater FI, growth, and LD in contrast to the study by Andretta et al. (2016a), which reported decreased feed and crude protein efficiency when pigs ate faster. Our data show that FI rate is poorly explained (communality = 0.45) by the sum of the factors. In this way, pigs may have a "preferred feeding rate", eating a preferred feed in a certain manner with no environmental constraints (Nielsen, 1999).

Factor 4 retained only basal plasma Thr. Threonine intake tended to share variance between the factors growth and plasma Thr, but it was rather correlated with growth than with basal plasma Thr. When critical changes in a certain AA occur, changes in the protein turnover can be observed (Swick, 1958). Such changes can result in modification (or imbalance) of the basal concentration of AA, which can ultimately lead to changes in FI (Yoshida et al., 1966; Benevenga et al., 1968). Thr factor 4, plasma Thr, presents only weak evidence that Thr intake was affecting basal plasma Thr concentrations, but it was clear that basal plasma Thr had no effect on the factor feeding behavior. Therefore, the results presented in this section do not offer a strong base to support the AA imbalance precept (Yoshida et al., 1966; Benevenga et al., 1968) in the growing phase.

Finishing Phase

During the finishing phase, the variables studied using the exploratory factor analysis accounted for 83% of the total variability observed in the data. Factor 1 accounted for most (26%) of the variance observed in the data. This factor was named *feeding behavior* for retaining the variables FI per meal and time interval per meal, both with high positive loadings (>0.90) and the number of meals with high negative loading (−0.92). The polarity in the number of meals shows that changes in this variable occur at the expense of

changes in FI per meal and the duration of the meal. Factor 2 was named *Thr* once this factor retained all the variables associated with the manipulation of this AA in the diet. The bipolarity of the factor showed that Thr intake followed an opposite direction to plasma Thr levels and Thr efficiency of utilization. This is consistent with the findings of other studies (Yoshida et al., 1966; Benevenga et al., 1968) that showed that an AA imbalance due to the restriction of one AA in the diet resulted in increased incorporation of the limiting AA into proteins. Therefore, an increase in Thr efficiency of utilization might be the result of higher incorporation of this AA in protein. The same authors (Yoshida et al., 1966; Benevenga et al., 1968) observed that AA restriction increases the incorporation of the limiting AA in the liver, contributing further to the drop in its concentration in plasma.

Factor 3 was named *LD* once this variable presented the highest loading of this factor (0.86). In this factor following the same direction in the vector than LD, with high positive loadings (>0.7) were retained average BW and Lys intake. The increase in Lys intake might be due to a possible higher ADG of the pigs with higher average BW. The model proposed by Hauschild et al. (2012) and used to estimate AA requirements in this trial assumes that pigs with higher ADG require a greater amount of Lys for PD. This probably contributed to heavier pigs receiving greater amounts of Lys. Additionally, during the finishing phase, which is normally after pigs attained maximal PD, a lower rate of PD relative to LD is normally assumed for late finishing pigs (van Milgen and Noblet, 2003) which is consistent with what was observed in this trial. Interestingly, LD was not associated with PD in the finishing phase. Factor 4 was named *PD* after the variable PD, which presented the highest loading (0.93). In the same factor, the variable feed efficiency was shown to follow the same direction as PD within this factor.

Factor 5 was named *FI rate* due to the negative high loading of this variable (−0.82). Following an opposite direction in the factor, with a positive loading (0.6), was plasma urea concentration. Basal plasma urea is well controlled, but it is affected by prolonged fasting (Veum et al., 1970) and, in this study, was not associated with crude protein intake (data not shown). A first assumption would be that pigs that go for long periods without feed present a plasma urea drop, and they will eat faster when they present themselves to the feeder once they are hungry. However, FI rate seems to be a stable characteristic of the individual over growth, and it might be due to genetics or early life experiences (Whishaw et al., 1992). Feed intake rate was independent of meal size, which is consistent with the literature (Nielsen et al., 1996). It is possible that pigs have preferences for certain feeds (Nielsen, 1999) or, in the case of this study, a certain feed mixture, which stimulates them to eat faster. In our opinion, for the specifics of this study, it is possible that an early life experience was responsible for the increase in FI rate, while the genetic background may be responsible for lower circulating levels of plasma urea (Table 3).

Confirmatory Analysis for Growing Pigs

Three crossover interactions between feeding systems and dietary Thr ($P < 0.10$) were observed for the following variables: interval between meals, feeding time per meal, and number of meals per day. These variables were not affected by any main factors alone (feeding system or dietary Thr) but rather by their crossover interactions. Therefore, an effect over these feeding behavior variables is only possible in the situation where the same feeding systems and the same dietary Thr levels as used in this study are used simultaneously. This situation is not a practice adopted by farmers or industry and only concerns this specific experiment. Therefore, these three crossover interactions (interval between meals, feeding time per meal, and number of meals per day) have no practical application and will be ignored in this study.

Average daily FI was not affected ($P > 0.10$) by feeding system or dietary Thr. Threonine intake increased linearly ($P < 0.05$) within IPF and GPF pigs, whereas Lys intake was similar among treatments (Table 4). This effect might be due to the dose–response method we used, which involved constant levels of Lys in the diet, whereas Thr was supplemented in the diet. The number of meals, FI per meal, interval between meals, and total time eating were similar across treatments. The FI rate decreased linearly ($P < 0.05$) with increasing levels of Thr in the diet. Feed intake rate can be interpreted as voracity eating (Andretta et al., 2016a). The FI rate has been associated with increasing motivation to eat in order to meet AA requirements (Schiavon et al., 2018). Our data do not support this hypothesis; the linear effect observed in our study suggests

Table 3. Exploratory factor analysis (varimax rotation) with correlation coefficients for growth performance, feeding behavior, and plasma response of finishing pigs[a]

Variable	Factor 1: feeding behavior	Factor 2: plasma Thr	Factor 3: LD	Factor 4: PD	Factor 5: FI rate	Communality
Average BW	0.10	−0.08	0.70	−0.36	0.04	0.63
PD, g/d	0.11	−0.16	−0.07	0.93	−0.14	0.94
LD, g/d	−0.04	0.01	0.86	−0.16	0.25	0.83
G:F efficiency	−0.18	0.11	−0.13	0.85	0.14	0.81
Lysine intake	−0.02	−0.45	0.74	0.20	−0.18	0.82
Threonine intake	−0.02	−0.85	0.38	0.14	−0.12	0.90
Threonine efficiency of utilization	0.05	0.73	−0.28	0.54	0.06	0.91
FI rate	0.11	−0.14	0.04	0.00	−0.82	0.70
FI per meal	0.96	−0.08	0.19	0.00	−0.05	0.97
Number of meals	−0.92	−0.05	0.12	0.01	0.11	0.88
Time interval between meals	0.94	−0.01	−0.13	−0.08	−0.07	0.92
Plasma threonine	0.07	−0.88	−0.12	0.02	0.16	0.81
Plasma urea	0.12	−0.32	0.26	0.02	0.60	0.54
Variance[b]	3.62	2.39	2.19	2.11	1.27	11.58
Proportion[c]	0.26	0.17	0.16	0.15	0.09	0.83

FI, feed intake; PD, protein deposition; LD, lipid deposition.

[a]Loadings were assumed to be significant above 0.6.

[b]The variability (eingenvalue) in the data explained by each factor.

[c]Proportion of variability in the data explained by each factor (ranging from 0 to 1).

that voracity was greater for diets with excess Thr (115% and 130% Thr). The increased voracity at higher Thr levels might be related to a higher BW. A moderate correlation was observed between average FI rate and final BW ($r = 0.5$; $P \leq 0.05$) probably due to the observed linear increase in PD and ADG with increasing Thr levels. In a previous study, FI rate, along with other feeding behavior variables, depended on the feeding phase, possibly due to a correlation with BW (Andretta et al., 2016a). The use of shorter periods of time (21 d) in this study helps to isolate the effect of BW on feeding behavior, making it possible to highlight the effects not linked to BW in a specific growing phase. (Table 4)

Confirmatory Analysis for Finishing Pigs

As with the growing period, feeding system crossover interactions with dietary Thr ($P < 0.10$) were observed for the variables number of meals per day and total time eating per day. These crossover interactions will then be ignored once the main factors did not affect these variables.

During the finishing phase, ADFI was equal between feeding programs but decreased in a quadratic manner as Thr in the diet increased ($P < 0.05$). We have previously discussed this effect (Remus et al., 2020a). Briefly, the small effect on ADFI was likely due to the numerically lower performance in terms of ADG and G:F ratio of the treatment GPF100. The difference in ADFI is reflected in the feeding time per meal, which was shortest at a dietary Thr level of 100% ($P < 0.05$). Likewise, pigs presented the greatest FI rate at a dietary Thr level of 100% ($P < 0.05$). Feeding behavior did not differ between feeding systems, despite a 16% higher SID Lys intake and a 15% higher SID Thr intake for GPF pigs relative to IPF pigs ($P < 0.05$). With the exception of one treatment (GPF100), the results of this study agree with those of Andretta et al. (2016a), who observed no effect of Lys deficiency on feeding behavior in pigs throughout the growing–finishing phases. This might be due to the fact that FI is not affected by Lys deficiency (Hrupka et al., 1999). In contrast, Thr deficiency was shown to depress FI (total amount) in rats, which was associated with a drop in plasma Thr levels (Feurte et al., 1999). Still, Thr was found to have a small impact on feeding patterns in rats (Ayaso et al., 2014) and generally no effect on FI in pigs (Edmonds and Baker, 1987). Nonetheless, a preference test suggested that pigs were capable of detecting a metabolic change caused by Thr deficiency and of modifying their feeding pattern (Ettle and Roth, 2005). In general, our results agree with the concept established by Yoshida et al. (1966) that Thr intake has no effect on FI, but a severe Thr deficiency might cause a drop in this essential AA in plasma triggering a hormonal response that modulates feeding

Table 4. Feeding behavior of growing barrow pigs (25–42 kg BW) fed different levels of threonine (70%, 85%, 100%, 115%, and 130% of the ideal Thr:Lys protein ratio; 0.65) in an IPF or a conventional GPF system

	IPF					GPF						*P*-value		
Variable	70	85	100	115	130	70	85	100	115	30	MSE	L	FS	L × FS
BW initial kg	26.0	26.2	25.6	25.2	26.0	26.7	25.7	25.8	25.7	26.2	0.8	0.40	0.49	0.84
BW final, kg	39.5	40.5	41.5	41.6	43.5	40.8	42.5	42.1	41.7	42.3	1.1	0.11	0.37	0.57
ADFI, kg/d	1.44	1.46	1.46	1.63	1.50	1.51	1.40	1.49	1.48	1.41	0.14	0.41	0.35	0.47
Lysine intake, g/d	11.6	11.8	12.4	13.6	13.1	13.3	12.7	13.0	13.0	12.4	1.0	0.48	0.31	0.19
Threonine intake, g/d	6.3	7.5	9.0	11.3	11.6	7.2	8.1	9.5	10.7	11.6	0.7	<0.0001[a]	0.31	0.45
Interval between meals, min	129	158	138	138	130	118	108	143	130	150	16	0.60	0.23	0.06[c]
Feeding time per meal, min	7	8	8	8	7	8	7	9	7	8	1	0.32	0.99	0.01[d,e]
FI per meal, g	134	164	143	168	131	132	125	151	135	152	14	0.68	0.27	0.11
FI rate, g/min	20	21	20	23	22	22	20	20	24	22	2	<0.01[b]	0.46	0.67
Number of meals per day	11	9	11	11	11	11	13	10	11	9	1	0.98	0.73	0.05[d]
Total time eating per day, min	76	79	79	79	73	80	83	78	71	68	5	0.17	0.76	0.48

FS, feeding system; L, level of threonine in the diet; L × FS = threonine level by feeding system interaction; MSE, maximum standard error.
[a]Linear effect for L ($P < 0.05$).
[b]Cubic effect for level ($P < 0.05$).
[c]Linear effect within GPF ($P < 0.05$).
[d]Fourth-degree effect within IPF ($P < 0.05$).
[e]Fourth-degree effect within GPF ($P < 0.05$).

Table 5. Feeding behavior of finishing barrow pigs (110–130 kg BW) fed different levels of threonine (70%, 85%, 100%, 115%, and 130% of the ideal Thr:Lys protein ratio; 0.65) in a conventional GPF or IPF system

	IPF					GPF						*P*-value		
	IPF70	IPF85	IPF100	IPF115	IPF130	GPF70	GPF85	GPF 100	GPF115	GPF130	MSE	L	FS	L × FS
BW initial, kg	110	109	110	110	110	108	110	110	111	109	3	0.99	0.78	0.98
BW final, kg	134	132	133	134	134	132	135	132	135	134	3	0.97	0.95	0.94
ADFI, kg/d	3.7	3.5	3.6	3.9	3.4	3.4	3.8	3.7	3.8	3.6	0.1	0.04[a]	0.71	0.13
Lysine intake, g/d	20.7	20.0	19.8	20.8	20.0	22.7	25.0	24.7	26.0	23.4	0.9	0.26	<0.0001	0.30
Threonine intake, g/d	11.6	13.1	14.6	17.2	18.0	12.6	16.1	18.2	21.3	21.3	0.7	<0.0001[b]	<0.0001	0.15
Interval between meals, min	199	235	199	215	217	229	195	179	229	213	15	0.21	0.66	0.11
Feeding time per meal, min	10	10	8	10	10	10	10	8	11	10	1	0.01[c]	0.80	0.99
FI per meal, g	543	596	537	615	540	585	580	487	626	546	43	0.11	0.95	0.86
FI rate, g/min	52	56	62	59	54	55	56	60	59	55	2	<0.0001[b]	0.80	0.46
Number of meals per day	7	6	7	7	6	6	7	8	6	7	0.4	0.17	0.23	0.01[d,e]
Total time eating per day, min	69	62	61	64	63	60	67	59	64	64	3	0.34	0.57	0.07

FS, feeding system; L, level of threonine in the diet; L × FS = threonine level by feeding system interaction; MSE, maximum standard error.
[a]Quadratic effect for level ($P < 0.05$).
[b]Linear effect for level ($P < 0.05$).
[c]Fourth-degree effect for level ($P < 0.05$).
[d]Quadratic effect within GPF ($P < 0.05$).
[e]Cubic effect within IPF ($P < 0.05$).

behavior. However, small variations in AA in the diet and, consequently, in AA intake do not affect feeding behavior (Table 5; Fig. 3).

CONCLUSION

The exploratory factor analysis indicated that feeding behavior had no correlation with growth performance or PD and LD in growing or finishing pigs. Dietary Thr levels and feeding systems had no direct effect negative impact on feeding patterns and on feeding behavior.

Conflict of interest statement. The authors declare that there is no conflict of interest.

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