Variation in faecal digestibility values related to feed efficiency traits of grower-finisher pigs

L. M. G. Verschuren, D. Schokker, R. Bergsma, Jaap van Milgen, F. Molist, M. P. L. Calus, A. J. M. Jansman

Animal 15 (2021) 100211

Contents lists available at ScienceDirect

Animal

The international journal of animal biosciences

Variation in faecal digestibility values related to feed efficiency traits of grower-finisher pigs

L.M.G. Verschuren [a,b,c,*], D. Schokker [b], R. Bergsma [a], J. van Milgen [c], F. Molist [d], M.P.L. Calus [e], A.J.M. Jansman [b]

[a] Topigs Norsvin Research Center B.V., P.O. Box 43, 6640 AA Beuningen, the Netherlands
[b] Wageningen University and Research, Wageningen Livestock Research, P.O. Box 338, 6700 AH Wageningen, the Netherlands
[c] PEGASE, INRAE, Institut Agro, 35590, Saint-Gilles, France
[d] Schothorst Feed Research B.V., P.O. Box 533, 8200 AM Lelystad, the Netherlands
[e] Wageningen University and Research, Animal Breeding and Genomics, P.O. Box 338, 6700 AH Wageningen, the Netherlands

A R T I C L E I N F O

Article history:
Received 29 June 2020
Revised 15 February 2021
Accepted 18 February 2021
Available online 17 August 2021

Keywords:
Digestion
Feed efficiency
Feed intake
Genetics
Swine

A B S T R A C T

Providing pigs a diet that matches their nutrient requirements involves optimizing the diet based on the nutrient digestibility values of the considered feed ingredients. Feeding the same quantity of a diet to pigs with similar BW but with different requirements, however, can result in a different average daily gain (**ADG**) and backfat thickness (**BF**) between pigs. Digestibility may contribute to this variation in efficiency. We investigated variation in feed efficiency traits in grower-finisher pigs associated with variation in faecal digestibility values, independent of feed intake at the time of measuring faecal digestibility. Considered traits were ADG, average daily feed intake (**ADFI**), feed conversion ratio (**FCR**), BF and residual feed intake (**RFI**). Feed intake, BW, and BF data of one hundred and sixty three-way crossbreed grower-finisher pigs (eighty female and eighty male) were collected during two phases, from day 0 of the experiment (mean BW 23 kg) till day 56 (mean BW 70 kg) and from day 56 to slaughter (mean BW 121 kg). Pigs were either fed a diet based on corn/soybean meal or a more fibrous diet based on wheat/barley/by-products, with titanium dioxide as indigestible marker. Faecal samples of one hundred and five pigs were collected on the day before slaughter and used to determine apparent faecal digestibility of DM, ash, organic matter (**OM**), CP, crude fat (**CFat**), crude fibre (**CF**), and to calculate the digestibility of nonstarch polysaccharides (**NSPs**) and energy (**E**). The effects of diet, sex and covariate feed intake at sampling (**FIs**) on faecal digestibility values were estimated and were significant for all except for CFat. Faecal digestibility values of each individual pig determined at the day before slaughter, corrected for diet, sex and FIs, were used to estimate their association with ADG, ADFI, FCR, BF, and RFI. In the first phase, a one percent unit increase in faecal digestibility of DM, ash, OM, E, CP, CFat, CF, NSP, and Ash individually was related to 0.01–0.03 unit reduction in FCR and 6–23 g/day reduction in RFI. A unit increase in CP digestibility was related to 0.1 mm increase in BF and 10 g/day increase in ADG. In the second phase, a one percent unit increase in faecal digestibility of DM, CP and Ash was related to a decrease of 16–20 g/day in RFI. In conclusion, the relationship between variation in feed efficiency traits and faecal digestibility values is different across the developmental stages of a pig.

Implications

This study shows the importance of measuring feed efficiency traits at several timepoints in the life of a grower-finisher pig, especially when differences in nutrient digestion underlying variation in feed efficiency traits are studied. Differences in faecal nutrient digestibility between sexes can be used to further support the conceptual development of precision feeding in pig production, especially in systems where boars or barrows and gilts are housed separately.

Introduction

Both nutritionists and geneticists aim to increase feed efficiency in grower-finisher pigs, as feed comprises the main cost of production. In swine nutrition, increased feed efficiency is achieved by formulating diets that are balanced in terms of nutrient supply rel-

* Corresponding author at: Topigs Norsvin Research Center B.V., P.O. Box 43, 6640 AA Beuningen, the Netherlands.
E-mail address: lisanne.verschuren@topigsnorsvin.com (L.M.G. Verschuren).

https://doi.org/10.1016/j.animal.2021.100211
1751-7311/

ative to the nutrient requirements of the animal, using different dietary ingredients and considering their nutrient composition and digestibility at ileal or faecal level. Although diet ingredient composition is the main source of variation in nutrient digestibility between pigs, there is also variation in the capability to digest nutrients between individual pigs that are fed the same diet (Ouweltjes et al., 2018). Variation among pigs for a wide range of performance traits is the main focus of study in pig genetics. In selection experiments, several generations of divergent selection for feed efficiency resulted in lines of pigs showing not only differences in feed efficiency but also sometimes in differences in faecal digestibility of nutrients (Harris et al., 2012; Mauch et al., 2018). The increase in feed efficiency was mainly the result of a decrease in feed intake, while body weight gain was similar between the genetic lines. A lower feed intake, either restricted or voluntary, results in increased faecal digestibility values (Cunningham et al., 1962; De Haer and De Vries, 1993). Even after correction for the level of feed intake, differences in digestibility of dietary energy were noticed between feed efficiency lines (Harris et al., 2012). Still, the difference in faecal digestibility of DM and nitrogen between the selection lines disappeared when correcting for differences in voluntary feed intake between lines. Therefore, the question remains whether an increased digestive capacity of pigs leads to an increased feed efficiency.

The aim of this study was to investigate the variation in feed efficiency traits of grower-finishers pigs associated with the variation in faecal digestibility values, independent of variation in feed intake. Considered traits were average daily gain (**ADG**), average daily feed intake (**ADFI**), feed conversion ratio (**FCR**), backfat thickness (**BF**) and residual feed intake (**RFI**).

Material and methods

Animals and experimental design

Pigs used in this study were part of a larger experiment described by Godinho et al. (2018) and originated from a three-way cross, i.e. Synthetic boar × (Large White × Landrace) sow. Part of the data used in the present study has been described previously and was used to predict faecal digestibility values based on faecal microbiota composition (Verschuren et al., 2020). Phenotypic data were available for one hundred and sixty pigs, eighty intact boars and eighty gilts, originating from twenty one litters. Due to death (six animals) and insufficient faecal sample volume (fourty nine animals), data of one hundred and five pigs were used for the present study. All pigs were kept under commercial conditions at the experimental facilities of Schothorst Feed Research B.V. (Lelystad, The Netherlands). Before the start of the study, pigs were housed per litter, with approximately 20% of the pigs being cross-fostered. All pigs were fed the same diet in this period. The pigs entered the study at 59–67 days of age (day 0 of the experiment) in two groups and the groups entered the study 20 days apart. Ten pigs were housed per pen and each pig was allowed a minimal space of 1 m^2. Floors of the pens were 60% concrete and 40% slatted. There were eight pens per room and one room was used per entrance date. Littermates were randomly distributed over the two diets and males and females were housed in separate pens. Erroneously, due to the random distribution of littermates, there was one litter that was completely allocated to a single pen. The pigs were kept in the facilities until they reached a live weight at slaughter of approximately 120 kg (mean age 167 days).

Feeding strategy

Two diets were used in the study, a diet based on corn/soybean meal (**CS**) as typically fed to commercial grower-finisher pigs in The Americas and a more fibrous diet based on wheat/barley/by-products (**WB**) as typically fed in Europe (Table 1). The pigs were fed *ad libitum* throughout the study, where seventeen boars and thirty two gilts were fed the CS diet, and twenty four boars and thirty three gilts were fed the WB diet. The pigs were fed a starter diet from day 0 to day 25, a grower diet from day 25 to day 67, and a finisher diet from day 67 until they reached slaughter weight. The diets were formulated on a fixed ratio of standardized ileal digestible lysine to net energy. The standardized ileal digestible lysine to net energy ratio changed over time, being 1.12 g/MJ in the starter diet, 0.94 g/MJ in the grower diet and 0.73 g/MJ in the finisher diet. The decrease of standardized ileal digestible lysine to net energy ratio in grower and finisher diets was mainly achieved by exchanging soybean meal with corn for the CS diet, and peas with wheat for the WB diets. An additional premix was added to the finisher diets containing titanium dioxide as inert marker (2.5 g/kg at the level of the diet). The experimental diets were pelleted and produced by ABZ Diervoeding, Leusden, The Netherlands.

Measurements and sampling

The experimental facilities were equipped with IVOG feeding stations (INSENTEC, Marknesse, The Netherlands) that register individual feed intake of group housed pigs. All pigs had ear tags with unique numbering; therefore, individual feed intake records were available for all pigs for each day on test. Pigs were weighted at day 0 (mean age 64 days), day 56 (mean age 120 days) and at the end of the study (104 ± 6.7 days in the experiment, mean age 167 days), dividing the experimental period in two phases, the first one being from day 0 till day 56 of the experiment, and the second one being from day 56 till the end of the experiment (Fig. 1). The BF measurements were recorded at day 56 of the trial and at the end of the trial using an ultrasound device (Renco Lean Meater; Renco Corp., Minneapolis, USA). The ADFI was calculated as the cumulative individual daily feed intake records divided by the timespan over which the feed intake records were recorded. In addition, the feed intake at sampling (**FIs**) was calculated as the ADFI over the final three days of the experiment, excluding the day of faecal sample collection due to preventive effects of animal handling during faeces collection on feed intake. The ADG was calculated as the difference between BW measurements divided by the timespan between the measurements, whereas the FCR was calculated as the ratio between ADFI and ADG. The RFI was obtained for each phase separately as the residual term of the regression (Cai et al., 2008):

$$ADFI = \mu + b_1 BW_{on} + b_2 BW_{off} + b_3 BF + b_4 ADG + b_5 O_{age} + e$$

in which ADFI, BF, and ADG are described previously, μ is the mean ADFI of the pigs, BW_{on} is the BW at the start of either phase, BW_{off} is the BW at the end of either phase, O_{age} is the age at the start of either phase, b_1, b_2, b_3, b_4, and b_5 are the linear coefficients of the regression on covariates, and e is the RFI. The mixed procedure (SAS 9.3; SAS Inst. Inc., Cary, NC) was used to obtain the RFI.

One day before slaughter, individual faecal grab samples were collected, stored at 4 °C, freeze-dried and milled over a 1 mm sieve prior to chemical analyses. Faecal samples were analysed from one hundred and five out of one hundred and sixty pigs, related to death of a few pigs (six animals) or availability of insufficient sample material (forty nine animal). Diets and faecal samples were analysed in duplicate for moisture, ash, CP, crude fat (**CFat**), crude fibre (**CF**), and titanium oxide as marker using the following methods, respectively: ISO 6496, NEN 3329, ISO/CD 15670, ISO/FDIS 6492 method B, ISO-6865:2001, and EEG 26-11-1992 nr.L344/35-37 (Method based on Short et al. (1996)). Diets were also analysed in duplicate for starch (NEN-ISO 15914:2005 en), whereas, based

Table 1
Ingredient and calculated composition of the diets fed to the grower-finisher pigs, as-fed basis.

Item	Starter (day 0–25)		Grower (day 25–67)		Finisher[1] (day 67 to end)	
	CS	WB	CS	WB	CS	WB
Ingredient, g/kg						
Corn	647.1	–	698.4	–	755.1	–
Corn gluten feed	18.1	–	25.0	50.0	50.0	50.0
Soybean meal (48% CP)	240.5	100.0	180.5	21.5	98.3	–
Soybean hulls	–	–	–	14.3	–	50.0
Soybean oil	–	25.0	–	0.3	–	–
Barley	–	200.0	–	100.0	–	150.0
Wheat	–	321.9	–	400.0	–	350.0
Wheat middlings	–	–	–	50.0	–	125.0
Rapeseed meal	–	63.0	–	80.0	–	100.0
Sunflower seed meal	–	80.0	–	80.0	–	21.9
Palmkernel meal	–	–	–	50.0	–	50.0
Palm oil	5.0	17.3	5.0	16.0	5.0	5.0
Field peas	–	120.0	–	29.4	–	–
Sugarcane molasses	40.0	30.0	50.0	50.0	50.0	50.0
Poultry fat	–	–	–	27.5	–	29.4
Monocalcium phosphate	6.7	5.3	2.0	–	0.7	–
Salt	2.7	2.1	2.4	1.8	1.8	2.1
Sodium bicarbonate	–	1.1	1.0	1.0	3.4	–
Phytase[2]	5.0	5.0	5.0	5.0	5.0	1.9
Limestone	11.6	10.9	9.4	8.9	9.9	4.0
AA premix[3]	17.3	12.5	17.3	10.2	16.7	6.7
Lys + Trp premix	7.8	4.3	8.3	3.6	9.2	–
Lys HCl (L 79%)	2.4	3.8	2.2	4.3	1.9	3.3
Met (DL 99%)	1.6	1.3	1.4	0.7	0.8	0.1
Thr (L 98%)	1.5	1.7	1.5	1.6	1.5	0.9
Val (L 10%)	–	1.4	–	–	–	–
Vitamin premix[4]	1.0	1.0				
Vitamin-trace mineral premix 1[5]	1.0	1.0				
Vitamin-trace mineral premix 2[6]	4.0	4.0	4.0	4.0	4.0	4.0
Nutrient composition, g/kg[7]						
NE, MJ/kg	9.9	9.9	10.1	9.7	10.3	9.3
Moisture	127	126	130	126	122 (130)*	110 (129)*
Ash	51	52	42	47	38 (38)*	43 (42)*
CP	182	190	159	166	122 (128)*	140 (147)*
Crude fat	34	58	35	64	39 (36)*	61 (57)*
Crude fibre	24	45	24	60	29 (25)*	82 (71)*
Starch	437	360	471	335	493 (512)*	323 (334)*
Sugar	44	50	46	58	42	59
NSP	135	170	130	216	126	246
Ca	6.9	6.9	5.2	5.5	5.0	3.8
P	4.8	5.5	3.6	4.7	3.2	4.7
SID Lys	11.1	11.1	9.5	9.1	7.5	6.8
SID Met + Cys	6.6	6.6	5.9	5.6	4.6	4.6
SID Thr	7.1	7.1	6.3	6.0	5.2	4.7
SID Trp	2.1	2.1	1.8	1.7	1.4	1.3

CS = a diet based on corn/soybean meal; WB = a diet based on wheat/barley/by-products; AA = amino acid; Lys = Lysine; Trp = Tryptophan; Met = Methionine; Thr = Threonine, Val = Valine; NE = Net energy, NSPs = Nonstarch polysaccharides; SID = Standardized ileal digestible; Cys = Cystine.

[1] An additional premix was added to the finisher diets containing titanium dioxide as inert marker (2.5 g/kg at the level of the diet)

[2] Phyzyme XP (Dupont, Wilmington, DE, USA)/ Assumed P released 500 FTU: 1.12 g digestible P/kg.

[3] Mixture of free Lys, Met, Thr, Trp, and Val to equalize dietary levels of SID amino acids relative to the net energy value of the diet.

[4] Supplied per kilogram of feed: 2 500 IU of vitamin A, 500 IU of vitamin D3, and 5 IU of vitamin E (Mervit AD3E; PreMervo, Utrecht, the Netherlands).

[5] Supplied per kilogram of feed: 12 mg of Fe (ferrous sulphate), 10 mg of Mn (manganous oxide), 0.04 mg of Co (cobalt oxide), 0.12 g of Ca, 0.0501 g of P, 0.04 mg of I (potassium iodide), 1 000 IU of vitamin A, 100 IU of vitamin D3, 5 IU of vitamin E, 0.4 mg of vitamin B1, 0.8 mg of vitamin B2, 2 mg of pantothenic acid, 4 mg of niacin, 0.4 mg of vitamin B6, 0.2 mg of folate, 0.003 mg of vitamin B12, 10 mg of vitamin C, 0.01 mg of biotin, 0.2 mg of vitamin K3, and 40 mg of choline (Mervit Sporavit; PreMervo, Utrecht, the Netherlands).

[6] Supplied per kilogram of premix: 0.4 g of Ca, 15 mg of Cu (copper sulphate), 80 mg of Fe (ferrous sulphate), 24 mg of Mn (manganous oxide), 62 mg of Zn (zinc oxide), 0.04 mg of Co (cobalt oxide), 0.4 mg of I (potassium iodide), 0.2 mg of Se (sodium selenite), 7 500 IU of vitamin A, 1 500 IU of vitamin D3, 25 IU of vitamin E, 4 mg of vitamin B2, 6 mg of pantothenate, 30 mg of niacin, 0.02 mg of vitamin B12, and 0.752 mg of vitamin K3 (Mervit START M220; PreMervo, Utrecht, the Netherlands).

[7] Based on chemical composition, digestibility, and energy values for pigs from the Centraal Veevoeder Bureau Livestock Feed Table (Centraal Veevoeder Bureau, 2019).

* Based on wet chemistry analysis, with values based on chemical composition within brackets.

on the faecal starch digestibility of the main dietary ingredients (Centraal Veevoeder Bureau, 2019), no starch was assumed to be present in faeces.

The concentrations of DM, organic matter (**OM**), nonstarch polysaccharides (**NSP**) and energy (**E**) of the diets and faeces samples were calculated as indicated below.

DM (g/kg) was calculated as:

$$1000 - moisture\ \ (g/kg)$$

OM (g/kg) was calculated as:

$$DM\ \ (g/kg) - Ash\ \ (g/kg)$$

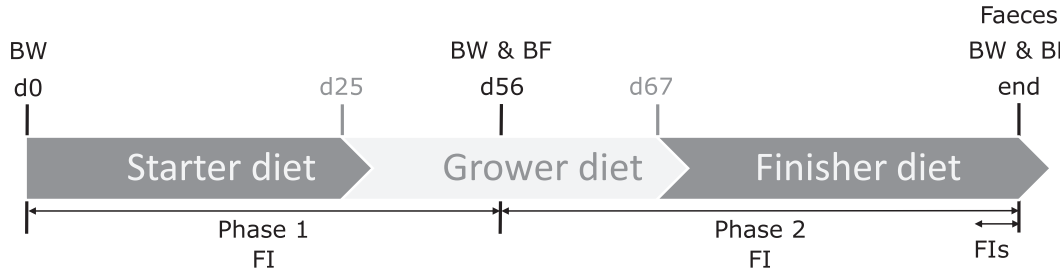

Fig. 1. Experimental design and measurements according to the experimental phase and diet fed to the grower-finisher pigs. At onset of the experiment (d0) body weight (BW) was recorded and individual feed intake registration (FI) started. One day before slaughter (end), BW and backfat thickness (BF) were recorded and faecal samples were collected. Feed intake at sampling (FIs) was calculated as feed intake over the last 3 days of the experiment.

The NSP fraction (g/kg) was calculated as:

$$DM\ (g/kg) - ((Ash\ (g/kg) + CP\ (g/kg) + CFat\ (g/kg) + starch\ (g/kg)),$$

and the **E** (kJ/kg DM) was calculated as (Centraal Veevoeder Bureau, 2019):

$$24.14 \times CP\ (g/kg) + 36.57 \times CFat\ (g/kg) + 20.92 \times CF\ (g/kg) + 16.99 \times \text{nitrogen} - \text{freeextract}\ (g/kg),$$

with nitrogen-free extract (g/kg) calculated as:

$$DM\ (g/kg) - ((Ash\ (g/kg) + CFat\ (g/kg) + CP\ (g/kg) + CF\ (g/kg))$$

Apparent faecal digestibility values, also known as apparent total tract digestibility values, were calculated in percentages based on concentrations of the marker and the nutrient in the diet and faeces as:

$$\left[1 - \left(\frac{conc.\ of\ marker\ in\ the\ diet\ (mg/kg\ DM)}{conc.\ of\ marker\ in\ the\ faeces\ (mg/kg\ DM)}\right) \times \left(\frac{conc.\ of\ nutrient\ in\ the\ faeces\ (g/kg\ DM)}{conc.\ of\ nutrient\ in\ the\ diet\ (g/kg\ DM)}\right)\right] \times 100\%$$

Statistical analysis

The experimental set-up followed a split-plot design in a 2 × 2 factorial arrangement, the two factors being diet (CS vs. WB diets) and sex (intact boars vs. gilts). Individual pigs were considered the experimental unit. First, we investigated the difference in ADG, ADFI, FCR, BF and RFI between the two diets and sexes, and obtained their residual variation after correction for these factors (model 1). Second, we investigated the relationship of faecal digestibility values with diet, sex and feed intake, and obtained their residual variation after correction for these factors (model 2). Third, we investigated to which extent variation in feed efficiency traits across individual pigs was related to variation in their faecal digestibility values, corrected for diet, sex and feed intake (model 3). The three statistical models were as follows:

$$X_{ijklm} = \mu + sex_i + diet_j + sex_i \cdot diet_j + group_k + b_a BW_l + pen_m + e_{ijklm} \quad (1)$$

$$Y_{ijklm} = \mu + sex_i + diet_j + sex_i \cdot diet_j + group_k + b_b FIs_{(jl)} + pen_m + \varepsilon_{ijklm} \quad (2)$$

$$X_{ijklm} = \mu + sex_i + diet_j + sex_i \cdot diet_j + group_k + b_a BW_l + b_c CFD_l + pen_m + \epsilon_{ijklm} \quad (3)$$

where X_{ijklm} is observed ADG, ADFI, FCR, BF, or RFI from either phase of the experiment and Y_{ijklm} is observed faecal DM, OM, E, CP, CFat, CF, NSP or ash digestibility for each pig l ($l = 1 \cdots 105$) with known *group* (k = 1 or 2), *sex* i (i = gilt or boar) and *diet* j (j = CS or WB diets). μ is the mean across pigs. b_a is the regression coefficient for BW_l, which is birth weight for ADG, live BW at start of either phase for ADFI, FCR and RFI, or live BW at moment of measuring for BF. b_b is the regression coefficient for FIs and has an interaction term between FIs and diet for faecal ash digestibility. b_c is the regression coefficient for corrected faecal digestibility (CFD_l) of each nutrient individually (DM, OM, E, CP, CFat, CF, NSP or ash), and CFD_l is obtained as the random residual term ε_{ijklm} of model 2. Thus, model 3 was applied eight times, i.e. once for each nutrient, for ADG, ADFI, FCR, BF, and RFI in either phase. Pen_m is the random effect of the m^{th} housing pen assumed to be normally distributed $N\left(0, \mathbf{I}\sigma^2_{\text{pen}}\right)$, and e_{ijklm}, ε_{ijklm}, and ϵ_{ijklm} are random residual terms assumed to be normally distributed $N(0, \mathbf{I}\sigma^2_{\text{e}})$. The mixed procedure (SAS 9.3; SAS Inst. Inc., Cary, NC) was used to fit the models. Hereafter, variance will be used as the statistical term for variation. Total variance in X_{ijklm} and Y_{ijklm}, i.e. $Var(X_{ijklm})$ and $Var(Y_{ijklm})$, were calculated and consecutively explained variance by the models was calculated as:

$$\frac{Var(X_{ijklm}) - Var(e_{ijklm})}{Var(X_{ijklm})} \times 100\%,$$

$$\frac{Var(Y_{ijklm}) - Var(\varepsilon_{ijklm})}{Var(Y_{ijklm})} \times 100\%.$$

Least squares means of model 1 and 2 were calculated per factor, and statistical differences between least square means for diet, sex, and diet by sex combinations were calculated using a posthoc Tukey test. Any differences in least square means and estimated coefficients of regression on CFD_l (i.e. $\widehat{b}_c$) were declared to be significant at $P < 0.05$ and P-values between 0.05 and 0.10 were considered indicative of a trend. Difference between diets or sexes in feed efficiency traits might partly be due to the differences in nutrient digestibility between diets and sexes, so only considering the difference in explained variance between models 1 and 3 could give biased estimates. Hence, variance in feed efficiency traits related to variance in corrected faecal digestibility values was calculated using the estimated regression coefficient from model 3 and total variance in feed efficiency traits as:

$$\frac{Var\left(\widehat{b}_c \times CFD_l\right)}{Var(X_{ijklm})} \times 100\%.$$

Results

Feed efficiency traits

Pigs on different diets and pigs from different sexes showed some differences in ADG, ADFI, FCR, BF and RFI during both phases and the overall phase (Table 2). Mean BW at start of the first phase

Table 2
Performance of male and female grower-finisher pigs fed one out of two experimental diets and the explained variance by the models.[1]

Trait[2]	CS[3]		WB[3]		*P-value*			Variance	
	B	G	B	G	Diet	Sex	D*S	RMSE	Exp
Phase 1									
ADFI, g/day	1 564	1 713	1 640	1 676	0.695	0.075	0.266	212	43.1
ADG, g/day	761[a]	871[b]	849[ab]	838[ab]	0.361	0.102	0.046	101	20.9
FCR, g/g	1.93	2.01	1.92	2.03	0.822	0.017	0.752	0.17	19.8
BF, mm	7.4	7.0	7.1	6.8	0.073	0.036	0.796	0.8	28.1
RFI, g/day	−48.0	27.8	−51.9	34.9	0.957	0.009	0.859	143	2.2
Phase 2									
ADFI, g/day	2 873	3 044	2 943	2 832	0.478	0.771	0.170	296	52.6
ADG, g/day	1066[ab]	1147[a]	1127[a]	1031[b]	0.375	0.803	0.006	139	16.0
FCR, g/g	2.60	2.68	2.66	2.77	0.181	0.069	0.754	0.21	31.5
BF, mm	10.6	11.8	9.8	10.2	<0.001	0.017	0.173	1.5	37.5
RFI, g/day	−73.8	−5.8	1.2	54.3	0.179	0.232	0.882	162	18.2
Total									
ADFI, g/day	2 164	2 299	2 237	2 198	0.788	0.357	0.089	225	40.0
ADG, g/day	912[a]	991[b]	976[b]	927[a]	0.980	0.426	0.001	93	15.9
FCR, g/g	2.28	2.35	2.29	2.40	0.449	0.018	0.585	0.1	33.8
RFI, g/day	−52.9	−7.1	−21.2	51.0	0.128	0.049	0.640	125	5.8

CS = a diet based on corn/soybean meal; WB = a diet based on wheat/barley/by-products; B = boars; G = gilts; D*S = interaction between diet and sex effects; Exp = explained variance (%) by the statistical model;
[1] Statistical model 1 including the effect of diet, sex, the interaction between diet and sex, group, body weight (birth weight for ADG, live body weight at start of each phase for ADFI, FCR and RFI, or live body weight at moment of measuring for BF), and pen;
[2] Phase 1 = from d0 till d56 of the experiment; Phase 2 = from d56 till the end of the experiment; Total = from d0 till the end of the experiment; ADFI = Average daily feed intake; ADG = Average daily gain; FCR = Feed conversion ratio; BF = Backfat thickness; RFI = Residual feed intake;
[3] Values are least square means;
[a,b] Values within a row with different superscripts differ significantly at $P < 0.05$.

was 22.6 kg, at start of the second phase 70.2 kg, and at the end of the experiment 121.1 kg (data not shown). The BW covariates in model 1 were significant for all traits except for RFI. There was a tendency for boars having a lower BW than gilts at start of the first phase of the experiment ($P = 0.097$) and at the start of the second phase ($P = 0.085$) (data not shown). Boars had a lower FCR and RFI than gilts in the first phase ($P = 0.017$ and $P = 0.009$, respectively) and in the second phase there was a tendency in the same direction for FCR but not for RFI ($P = 0.069$ and $P = 0.232$, respectively). Gilts tended to have a higher ADFI than boars in the first phase of the experiment ($P = 0.075$), which resulted in a higher ADG for gilts fed the CS diet compared to boars fed that diet ($P = 0.015$). In contrast, there was no significant difference between the sexes in ADFI during the second phase ($P = 0.771$), and boars fed the WB diet had a higher ADG than gilts fed the same diet ($P = 0.02$). Whereas at the end of the first phase of the experiment, the boars have a higher BF ($P = 0.036$), at the end of the second phase, gilts had the highest BF ($P = 0.017$). The BF of pigs fed the WB diet was lower than pigs fed the CS diet at the end of the second phase ($P < 0.001$), which was the only significant effect of diet on the feed efficiency traits. Over the total period the males had a lower FCR and RFI ($P = 0.018$ and $P = 0.049$, respectively). The explained variance by the models estimating the effects of diet, sex, the interaction between diet and sex, group and BW on feed efficiency traits ranged from 2.2% for RFI during the first phase to 52.6% for ADFI during the second phase.

Apparent faecal digestibility

Diet, sex, and FIs showed a clear effect on faecal digestibility values (Table 3). The faecal digestibility values were lower for pigs fed the WB diet compared to pigs fed the CS diet. Boars fed the WB diet had lower faecal digestibility values compared to gilts, except for CFat and ash, which were not different between sexes. All faecal digestibility values decreased with increasing FIs, except for CFat, which was not affected by FIs. There was no interaction between FIs and sex, and there was only a significant interaction between FIs and diet for faecal ash digestibility. The models estimating

Table 3
Digestibility values of the diets and sexes, the effect of feed intake at sampling on faecal digestibility, the total residual variance in faecal digestibility and explained variance as proportion of total variance (%) in faecal digestibility of grower-finisher pigs by the statistical models.[1]

Nutrient[2] (%)	CS[3]		WB[3]			*P*-value				Variance	
	B	G	B	G	FIs	Diet	Sex	D*S	FIs	RMSE	Exp
DM	86.7	87.6	73.3	75.4	−0.96	<0.001	<0.001	0.083	0.002	1.6	93.8
OM	88.0	89.0	74.9	77.0	−0.98	<0.001	<0.001	0.104	0.002	1.7	93.4
E	86.4	87.4	72.9	75.1	−1.05	<0.001	<0.001	0.120	0.002	1.8	92.8
CP	79.9	82.6	67.0	69.6	−2.50	<0.001	<0.001	0.943	<0.001	2.6	86.2
CFat	81.1	81.0	76.4	77.0	−0.24	<0.001	0.643	0.446	0.501	1.9	57.2
CF	49.7	54.8	29.8	38.1	−2.81	<0.001	<0.001	0.259	0.022	6.7	67.2
NSP	63.2	65.4	52.7	57.2	−1.72	<0.001	<0.001	0.191	0.016	3.8	61.4
Ash	58.4	57.4	42.4	43.0	–	<0.001	0.779	0.252	0.029	2.9	86.9

CS = a diet based on corn/soybean meal; WB = a diet based on wheat/barley/by-products; B = boars; G = gilts; D*S = interaction between diet and sex effects; FIs = feed intake at sampling (g/day); Exp = explained variance (%) by the statistical model.
[1] Statistical model 2 including the effect of diet, sex, the interaction between diet and sex, group, feed intake at sampling, and pen.
[2] OM = Organic matter, E = Energy, CFat = Crude fat, CF = Crude fibre, NSPs = Nonstarch polysaccharides.
[3] Values are least square means.

the effect of diet, sex, diet by sex interaction, group and FIs on faecal digestibility explained 57.2% of the variance in faecal CFat digestibility to 93.8% of the variance in faecal DM digestibility.

Feed efficiency traits and faecal digestibility

Faecal digestibility values were corrected for group, FIs, sex, diet and the interaction between sex and diet using model 2, and after this correction tested for its relationship with feed efficiency traits using model 3 (Table 4). Results comparing model 1 to model 3 are provided in supplementary Table S1, and paint a similar picture as the results in Table 4. In the first phase of the experiment, 3.7–7.6% of the variance in FCR and 4.3–7.0% of the variance in RFI was associated with all corrected faecal digestibility values. An increase in faecal digestibility values was related to a decrease in FCR and RFI in the first phase of the experiment, with the strongest relationship for DM: per percent unit of increased faecal DM digestibility a decrease of 0.03 units in FCR and 23 g/day in RFI was observed (Table 5). Variance in BF at the end of the first phase was associated with corrected CP digestibility, with a unit increase in faecal digestibility of CP relating to an increase of 0.1 mm of BF. During the first phase of the experiment, 5.5% of the variance in ADG was associated with CP digestibility, and a unit increase in CP digestibility was related to an increase of 10 g/day in ADG. There

Table 4
Variance (%) in performance traits of grower-finisher pigs explained by corrected faecal digestibility values,[1] with significant values depicted as is ($P < 0.05$), trends indicated as values with an asterisk ($P < 0.1$ and $P > 0.05$) and nonsignificant associations as values in brackets ($P > 0.1$).[2]

Trait[3]	DM	OM	E	CP	CFat	CF	NSP	Ash
Phase 1								
ADFI, g/day	(0.5)	(0.4)	(0.5)	(0.1)	(1.3)	1.6*	(0.5)	(0.8)
ADG, g/day	2.7*	3.0*	2.8*	5.5	(0.7)	(0.8)	(1.1)	(0.0)
FCR, g/g	6.8	6.4	6.3	7.6	6.6	6.3	4.2	3.7
BF, mm	2.5*	2.3*	2.3*	2.9	(0.0)	(1.5)	(1.8)	(0.7)
RFI, g/day	6.6	6.2	6.3	6.1	6.3	7.0	4.5	4.3
Phase 2								
ADFI, g/day	1.7*	1.6*	1.5*	1.7*	(0.5)	1.9	1.4*	(0.8)
ADG, g/day	(0.7)	(0.7)	(0.4)	(0.1)	(0.0)	(2.2)	(1.7)	(0.1)
FCR, g/g	(0.0)	(0.0)	(0.0)	(1.4)	(0.7)	(0.2)	(0.3)	2.4*
BF, mm	(0.2)	(0.3)	(0.4)	(0.1)	(0.2)	(0.8)	(0.4)	(0.0)
RFI, g/day	3.3	2.7*	3.0*	8.3	2.5*	2.6*	(1.7)	6.4
Total								
ADFI, g/day	(0.6)	(0.5)	(0.5)	(0.1)	(0.5)	1.7*	(0.7)	(1.0)
ADG, g/day	(0.2)	(0.3)	(0.3)	2.8*	(0.4)	(0.2)	(0.0)	(0.0)
FCR, g/g	(1.6)	(1.4)	(1.5)	4.8	2.7	(1.0)	(0.4)	3.4
RFI, g/day	4.5	3.9	4.3	6.7	3.9	4.9	2.5*	6.1

OM = Organic matter, E = Energy, CFat = Crude fat, CF = Crude fibre, NSPs = Nonstarch polysaccharides.
[1] Statistical model 3 including the effect of diet, sex, the interaction between diet and sex, group, body weight (birth weight for ADG, live body weight at start of each phase for ADFI, FCR and RFI, or live body weight at moment of measuring for BF), pen and corrected faecal digestibility. Variance in feed efficiency traits related to variance in corrected faecal digestibility values was calculated using the estimated regression coefficient of corrected faecal digestibility from model 3 and total variance in feed efficiency traits.
[2] *P*-values of regression coefficients for corrected faecal digestibility values.
[3] Phase 1 = from d0 till d56 of the experiment; Phase 2 = from d56 till the end of the experiment; Total = from d0 till the end of the experiment; ADFI = Average daily feed intake; ADG = Average daily gain; FCR = Feed conversion ratio; BF = Backfat thickness; RFI = Residual feed intake.

Table 5
Coefficients of regression relating the performance of grower-finisher pigs and corrected faecal digestibility values,[1] with significant values depicted as is ($P < 0.05$), trends indicated as values with an asterisk ($P < 0.1$ and $P > 0.05$) and nonsignificant associations as values in brackets ($P > 0.1$).[2]

Trait[3]	DM	OM	E	CP	CFat	CF	NSP	Ash
Phase 1								
ADFI, g/day	(−11.8)	(−10.5)	(−11.2)	(−2.8)	(−17.1)	−5.4*	(−5.5)	(−9.1)
ADG, g/day	11.8*	12.2*	10.9*	10.4	(5.2)	(1.6)	(3.3)	(−0.4)
FCR, g/g	−0.031	−0.030	−0.028	−0.021	−0.027	−0.007	−0.011	−0.013
BF, mm	0.09*	0.09*	0.08*	0.06	(0.01)	(0.02)	(0.03)	(0.03)
RFI, kg/day	−23.4	−22.3	−20.9	−13.9	−19.7	−5.9	−8.3	−10.6
Phase 2								
ADFI, g/day	−34.9*	−33.6*	−30.7*	−21.6*	(−16.6)	−9.0	−13.9*	(−13.9)
ADG, g/day	(−7.7)	(−7.6)	(−5.7)	(2.2)	(0.8)	(−3.5)	(−5.3)	(−1.5)
FCR, g/g	(0.001)	(0.003)	(0.002)	(−0.011)	(−0.011)	(0.002)	(0.004)	−0.014*
BF, mm	(0.06)	(0.06)	(0.07)	(−0.03)	(−0.04)	(0.03)	(0.03)	(−0.01)
RFI, g/day	−20.4	−18.4*	−17.8*	−20.1	−15.3*	−4.5*	(−6.4)	−16.1
Total								
ADFI, g/day	(−13.8)	(−12.4)	(−11.9)	(−4.4)	(−11.4)	(−5.9)	(−6.5)	(−10.4)
ADG, g/day	(3.1)	(3.3)	(3.4)	6.6*	(3.3)	(−0.7)	(−0.5)	(−0.2)
FCR, g/g	(−0.014)	(−0.013)	(−0.012)	−0.015	−0.015	(−0.003)	(−0.003)	−0.011
RFI, g/day	−17.2	−15.9	−15.4	−12.9	−13.7	−4.4	−5.5*	−11.3

OM = Organic matter, E = Energy, CFat = Crude fat, CF = Crude fibre, NSPs = Nonstarch polysaccharides.
[1] Statistical model 3 including the effect of diet, sex, the interaction between diet and sex, group, body weight (birth weight for ADG, live body weight at start of each phase for ADFI, FCR and RFI, or live body weight at moment of measuring for BF), pen and corrected faecal digestibility.
[2] *P*-values of regression coefficients for corrected faecal digestibility values.
[3] Phase 1 = from d0 till d56 of the experiment; Phase 2 = from d56 till the end of the experiment; Total = from d0 till the end of the experiment; ADFI = Average daily feed intake; ADG = Average daily gain; FCR = Feed conversion ratio; BF = Backfat thickness; RFI = Residual feed intake.

was no relationship between corrected faecal digestibility values and ADFI during the first phase of the experiment.

In the second phase of the experiment, there was a significant effect for 1.9% of the variance in ADFI being associated with corrected faecal digestibility of CF, and tendencies for DM, OM, E, and CP, with a one percent unit increase in digestibility being related to a decrease of up to 35 g/day in ADFI. Up to 8.3% of the variance in RFI was associated with corrected DM, CP and ash digestibility, and tendencies for OM, E, CFat, and CF digestibility, for which an increase in faecal digestibility values was related to a decrease of up to 20 g/day in RFI. There was no significant relationship between any tested corrected faecal digestibility values and ADG, FCR or BF during the second phase of the experiment.

Over the total period, there was no effect of any of the tested corrected faecal digestibility values and ADFI, ADG or FCR. There were, however, significant effects for all tested corrected faecal digestibility values with RFI, with an increase in digestibility being related to a decrease of up to 17 g/day in RFI. Of all corrected faecal digestibility relationships tested, CP was related to the highest percentage of variance in the feed efficiency traits in both phases, whereas corrected faecal DM digestibility had the strongest relationship with the traits.

Discussion

Variation in faecal digestibility

In this study, we investigated the variation in ADG, ADFI, FCR, BF, and RFI in grower-finisher pigs associated with faecal digestibility of DM, OM, E, CP, CFat, CF, and ash determined at the end of the fattening period. The variation in faecal digestibility values was for the largest part explained by diet. In literature, it is well established that dietary ingredients and nutrient composition affect faecal digestibility of nutrients (Le Goff and Noblet, 2001; Sauvant et al., 2004; Ouweltjes et al., 2018). Feed intake level affects faecal digestibility values as well (Cunningham et al., 1962; De Haer and De Vries, 1993). We estimated the effect of feed intake level on variation in faecal digestibility values and, even though the CS and WB diets had different calculated net energy values, an increase in FIs was associated with a reduction in faecal digestibility of all nutrients, except ash, to the same extent in both diets. The observed variation in faecal digestibility values between pigs fed the same diet could have been influenced by the method of collection of faeces samples (grab sampling on a single day), as it was shown that grab sampling of faeces over multiple days per animal provides more accurate estimates for nutrient digestibility values (Moughan et al., 1991; Agudelo et al., 2010). Between animal variation in faecal digestibility values, however, has been observed previously (Wilfart et al., 2007; Le Gall et al., 2009; Ouweltjes et al., 2018). Furthermore, Vigors et al. (2016) observed that pigs with a low RFI do not only have a higher faecal DM, E, and CP digestibility compared to high RFI pigs fed the same diet, but also show an increased expression in intestinal tissue of the gene encoding for the enzyme sucrase–isomaltase, and for the genes SGLT1, FABP2, and GLUT2, which are related to intestinal nutrient transport. They also found a lower weight of the tissue of the total intestinal tract and a different faecal microbiota composition in pigs having a low compared to high RFI (Vigors et al., 2016). These results suggest that between animal variation in faecal digestibility values may be related to differences in absorptive capacity of the intestinal tract, and to composition and activity of its residing microbiota in pigs.

Sex explained a large part of the variation in faecal digestibility values, with gilts showing higher digestibility values on both diets compared to intact males. The estimated higher digestibility of nutrients in gilts was not due to a lower feed intake in this sex, as feed intake was included as co-variable in the statistical model to explain variation in nutrient digestibility. Contradicting results on the effect of sex on nutrient digestibility in pigs have been reported in the literature. Noblet et al. (1993) found a higher faecal energy digestibility in gilts and no difference in nitrogen digestibility, whereas De Haer and De Vries (1993) observed no effect of sex on faecal energy digestibility and a higher faecal nitrogen digestibility in gilts when housed individually. Boars, however, had a higher faecal nitrogen digestibility than gilts when housed in groups (De Haer and De Vries, 1993). The higher faecal digestibility values of gilts might be due to differences in digestive capacity of the gut, as weaner gilts showed higher villus heights and higher small intestinal and pancreatic digestive enzyme activity compared to boars (Pluske et al., 2003). Effects of sex hormones might also play a role, since female steroid hormones are, amongst others, linked to intestinal hypomotility, inhibited gastric emptying, and increased bicarbonate production of the duodenal mucosa in humans (Freire et al., 2011). Differences in gut microbiota composition and fermentation activity, in particular in the hindgut, might explain part of the difference in faecal digestibility values between the sexes as well, because faecal microbiota composition is different between male and female pigs (Xiao et al., 2016; Verschuren et al., 2018). Although results in our study showed that the faecal digestibility of most nutrients was higher in gilts, FCR and RFI values were lower in boars. This indicates that differences in postabsorptive metabolism of nutrients in organs and tissues explain the difference between sexes in feed efficiency in grower-finisher pigs and even overcome the differences in faecal digestibility between sexes.

Variation in feed efficiency traits related to faecal digestibility

We found an association between feed efficiency traits and faecal digestibility of DM, OM, E, CP, CFat, CF, NSP, and Ash. It might be possible that the faecal digestibility values, measured at the end of the grower-finisher period, are not fully representative for the whole grower-finisher period, as faecal digestibility of DM, OM, E, CP, CFat, NDF, hemicellulose, cellulose, lignin and NSP increases with age (Noblet et al., 2013; Le Sciellour et al., 2018; Ouweltjes et al., 2018). The increase in faecal digestibility values with age might differ between individual pigs. For instance, Le Sciellour et al. (2018) showed an interaction between breed and age on faecal digestibility of NDF, hemicellulose, and cellulose, but found no such effect on the faecal digestibility of OM, E, CP or lignin of pigs being 11–22 weeks of age. Also Noblet et al. (2013) found no interaction between sire effect and age on faecal digestibility of DM, OM, E and CP of pigs weighing 36–90 kg. Therefore, our results on the relationship between the feed efficiency traits and faecal digestibility of DM, OM, E and CP are most likely representative for the entire grower-finisher period of the pig, whereas some caution should be taken when using and interpreting the relationship with faecal digestibility of CFat, CF, NSP and ash.

In the first phase of the experiment, increases in ADG and BF, and decreases in FCR and RFI, were associated with an increase in corrected faecal digestibility values. In contrast, in the second phase, only decreases in ADFI and RFI were associated with an increase in corrected faecal digestibility values. A possible explanation may lie in the regulation of feed intake in different growth stages. Young pigs (<50 kg BW) do not compensate for a decrease in dietary NE level by increasing feed intake when diets have a NE value below 10.5 MJ/kg, whereas older pigs tend to maintain energy intake at a fixed level (Black et al., 1986; Fagundes et al., 2009; Quiniou and Noblet, 2012). Other factors, such as the physical capacity of the gut, are most likely limiting dietary feed intake in pigs that do not compensate for a lower NE value of the diet (Li and Patience, 2017). Also, when pigs are fed diets containing a fixed energy level, an increase in dietary protein level reduces feed intake (Henry et al., 1992; Le Bellego and Noblet, 2002), and an imbalanced amino acid profile reduces feed intake as well (Gloaguen et al., 2011; 2012). Increased levels of the microbial fermentation product acetate in the blood can also reduce feed intake (Frost et al., 2014). Pigs showing a higher faecal nutrient digestibility have more dietary nutrients available for maintenance and growth compared to pigs with a lower faecal nutrient digestibility. However, if excess of a dietary nutrient or fermentation product is limiting feed intake of pigs, an increase in uptake of that nutrient or fermentation product would lead to a decreased feed intake. This provides a possible explanation for the reduced ADFI and RFI associated with an increased corrected faecal digestibility of DM, OM, E, CP, CF and NSP during the second phase of our experiment. In contrast, during the first phase of the experiment other factors than dietary nutrient composition or fermentation products were most likely limiting feed intake of the pigs and, therefore, an increased availability of nutrients due to an increased nutrient digestibility resulted in a higher ADG and BF, and a lower FCR and RFI. Hence, the relationship between feed efficiency traits and nutrient digestibility most likely changes depending on nutrient composition of the diet and the developmental stage of the pig.

In this study, a higher faecal digestibility was related to a lower FCR in the first phase and a lower RFI in both phases of the experiment. This is in line with literature, as pigs with a high feed efficiency have been shown to either have the same or a higher faecal digestibility of DM, nitrogen, energy, and neutral detergent fibre compared to pigs with a low efficiency (Harris et al., 2012; Montagne et al., 2014; Vigors et al., 2016; Mauch et al., 2018). Corrected faecal digestibility was related to up to 5.5% of the variation in ADG, 7.6% of the variation in FCR, 2.9% of the variation in BF, 1.9% of the variation in ADFI, and 8.3% of the variation in RFI. In comparison, within population genetic variation of pigs explained up to 34% of the variation in ADG, 34% of the variation in FCR, 23% of the variation in lipid deposition, 42% of the variation in ADFI, and 29% of the variation in RFI in a study of which our pigs are a subsample (Godinho et al., 2018). Pigs with a different sire have different faecal digestibility of DM, OM, CP, and E (Noblet et al., 2013), suggesting that it might be possible to increase faecal digestibility by means of breeding. First results indicate that OM, E and nitrogen digestibility are moderately to highly heritable and have a negative genetic correlation with FCR, ADFI, ADG, and RFI (Déru et al., 2021). These results are in line with our study, except for the unfavourable genetic correlation between faecal N digestibility and ADG, which is in contrast to our positive phenotypic correlation between faecal CP digestibility and ADG over the total grower-finisher period. The added value of measuring faecal digestibility on top of measuring ADG, ADFI and BF as selection parameter to genetically improve feed efficiency in pigs, therefore, is still uncertain. Since our dataset was too small to estimate such an added value, more research is needed to evaluate the possibility of improving feed efficiency of pigs by breeding for increased faecal digestibility.

Conclusion

There is substantial variation in faecal digestibility values between pigs fed a diet based on corn/soybean meal or wheat/barley/by-products. Part of the observed variation in feed efficiency traits was associated with variation in faecal digestibility values, but the results differed between young and older animals. Nevertheless, an increase in faecal digestibility values was related to a decrease in RFI over the entire grower-finisher period. In conclusion, the relationship between variation in feed efficiency traits and faecal digestibility values most likely differed between the developmental stages of a pig.

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2021.100211.

Ethics approval

This study was carried out in strict accordance with the recommendations in the European Guidelines for accommodation and care of animals. The protocol was approved by the Animal Care and Use Committee of Schothorst Feed Research, The Netherlands (Protocol Number: AVD 246002015120/132).

Data and model availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request. None of the data were deposited in an official repository.

Author ORCIDs

L.M.G. Verschuren: https://orcid.org/0000-0001-5428-4174.
D. Schokker: https://orcid.org/0000-0001-6082-7227.
R. Bergsma: https://orcid.org/0000-0002-8254-5535.
J. van Milgen: https://orcid.org/0000-0002-6131-5255.
F. Molist: https://orcid.org/0000-0002-7915-3098.
M.P.L. Calus: https://orcid.org/0000-0002-3213-704X.
A.J.M. Jansman: https://orcid.org/0000-0002-5104-8261.

Author contributions

L.M.G. Verschuren: Conceptualization, Formal Analysis, Methodology, Writing - original draft, Writing - review & editing.

D. Schokker: Conceptualization, Data curation, Funding acquisition, Methodology, Writing - original draft, Writing - review & editing.

R. Bergsma: Data curation, Project administration, Writing - original draft, Writing - review & editing.

J. van Milgen: Formal analysis, Methodology, Supervision, Writing - review & editing.

F. Molist: Data curation, Project administration, Writing - original draft, writing -review & editing.

M.P.L. Calus: Conceptualization, Formal analysis, Methodology, Supervision, Writing - original draft, Writing - review & editing.

A.J.M. Jansman: Conceptualization, Methodology, Supervision, Writing - original draft, Writing - review & editing.

Declaration of interest

The authors declare no conflict of interest.

Acknowledgements

We like to thank Schothorst Feed Research and Topigs Norsvin for providing data.

Financial support statement

This study was financially supported by the Dutch Ministry of Economic Affairs (TKI Agri & Food project 12039; Public–private partnership “Breed&Feed4Food” code BO-22.04-010-001).

References

Agudelo, J.H., Lindemann, M.D., Cromwell, G.L., 2010. A comparison of two methods to assess nutrient digestibility in pigs. Livestock Science 133, 74–77.

Black, J., Campbell, R., Williams, I., James, K., Davies, G., 1986. Simulation of energy and amino acid utilisation in the pig. Research and Development in Agriculture 3, 121–145.

Cai, W., Casey, D., Dekkers, J.C.M., 2008. Selection response and genetic parameters for residual feed intake in Yorkshire swine. Journal of Animal Science 86, 287–298.

Centraal Veevoeder Bureau, 2019. Chemical Compositions and Nutritional Values of Feed Ingredients. Centraal Veevoeder Bureau, Lelystad, the Netherlands.

Cunningham, H., Friend, D., Nicholson, J., 1962. The effect of age, body weight, feed intake and adaptability of pigs on the digestibility and nutritive value of cellulose. Canadian Journal of Animal Science 42, 167–175.

De Haer, L., De Vries, A., 1993. Feed intake patterns and feed digestibility in growing pigs housed individually or in groups. Livestock Production Science 33, 277–292.

Déru, V., Bouquet, A., Labussière, E., Ganier, P., Blanchet, B., Carillier-Jacquin, C., Gilbert, H., 2021. Genetics of digestive efficiency in growing pigs fed a conventional or a high-fibre diet. Journal of Animal Breeding and Genetics 138, 246–258.

Fagundes, A.C.A., Da Silva, R.G., Gomes, J.D.F., De Oliveira Souza, L.W., Fukushima, R. S., 2009. Influence of environmental temperature, dietary energy level and sex on performance and carcass characteristics of pigs. Brazilian Journal of Veterinary Research and Animal Science 46, 32–39.

Freire, A.C., Basit, A.W., Choudhary, R., Piong, C.W., Merchant, H.A., 2011. Does sex matter? The influence of gender on gastrointestinal physiology and drug delivery. International Journal of Pharmaceutics 415, 15–28.

Frost, G., Sleeth, M.L., Sahuri-Arisoylu, M., Lizarbe, B., Cerdan, S., Brody, L., Anastasovska, J., Ghourab, S., Hankir, M., Zhang, S., 2014. The short-chain fatty acid acetate reduces appetite via a central homeostatic mechanism. Nature Communications 5, 1–11.

Gloaguen, M., Le Floc'h, N., Corrent, E., Primot, Y., van Milgen, J., 2012. Providing a diet deficient in valine but with excess leucine results in a rapid decrease in feed intake and modifies the postprandial plasma amino acid and α-keto acid concentrations in pigs. Journal of Animal Science 90, 3135–3142.

Gloaguen, M., Le Floc'h, N., Brossard, L., Barea, R., Primot, Y., Corrent, E., van Milgen, J., 2011. Response of piglets to the valine content in diet in combination with the supply of other branched-chain amino acids. Animal 5, 1734–1742.

Godinho, R., Bastiaansen, J., Sevillano, C., Silva, F., Guimarães, S., Bergsma, R., 2018. Genotype by feed interaction for feed efficiency and growth performance traits in pigs. Journal of Animal Science 96, 4125–4135.

Harris, A., Patience, J.F., Lonergan, S.M., Dekkers, J.C.M., Gabler, N.K., 2012. Improved nutrient digestibility and retention partially explains feed efficiency gains in pigs selected for low residual feed intake. Journal of Animal Science 90, 164–166.

Henry, Y., Colleaux, Y., Seve, B., 1992. Effects of dietary level of lysine and of level and source of protein on feed intake, growth performance, and plasma amino acid pattern in the finishing pig. Journal of Animal Science 70, 188–195.

Le Bellego, L., Noblet, J., 2002. Performance and utilization of dietary energy and amino acids in piglets fed low protein diets. Livestock Production Science 76, 45–58.

Le Gall, M., Warpechowski, M., Jaguelin-Peyraud, Y., Noblet, J., 2009. Influence of dietary fibre level and pelleting on the digestibility of energy and nutrients in growing pigs and adult sows. Animal 3, 352–359.

Le Goff, G., Noblet, J., 2001. Comparative total tract digestibility of dietary energy and nutrients in growing pigs and adult sows. Journal of Animal Science 79, 2418–2427.

Le Sciellour, M., Labussière, E., Zemb, O., Renaudeau, D., 2018. Effect of dietary fiber content on nutrient digestibility and fecal microbiota composition in growing-finishing pigs. PLoS One 13, e0206159.

Li, Q., Patience, J.F., 2017. Factors involved in the regulation of feed and energy intake of pigs. Animal Feed Science and Technology 233, 22–33.

Mauch, E.D., Young, J.M., Serão, N.V.L., Hsu, W.L., Patience, J.F., Kerr, B.J., Weber, T.E., Gabler, N.K., Dekkers, J.C.M., 2018. Effect of lower-energy, higher-fiber diets on pigs divergently selected for residual feed intake when fed higher-energy, lower-fiber diets. Journal of Animal Science 96, 1221–1236.

Montagne, L., Loisel, F., Le Naou, T., Gondret, F., Gilbert, H., Le Gall, M., 2014. Difference in short-term responses to a high-fiber diet in pigs divergently selected for residual feed intake. Journal of Animal Science 92, 1512–1523.

Moughan, P.J., Smith, W.C., Schrama, J., Smits, C., 1991. Chromic oxide and acid-insoluble ash as faecal markers in digestibility studies with young growing pigs. New Zealand Journal of Agricultural Research 34, 85–88.

Noblet, J., Shi, X., Karege, C., Dubois, S., 1993. Effets du type sexuel, du niveau d'alimentation, du poids vif et du stade physiologique sur l'utilisation digestive de l'énergie et des nutriments chez le porc: interactions avec la composition du régime. Journées de la Recherche Porcine en France 25, 165–180.

Noblet, J., Gilbert, H., Jaguelin-Peyraud, Y., Lebrun, T., 2013. Evidence of genetic variability for digestive efficiency in the growing pig fed a fibrous diet. Animal 7, 1259–1264.

Ouweltjes, W., Verschuren, L.M.G., Pijlman, J., Bergsma, R., Schokker, D., Knol, E.F., van der Aar, P.J., Molist, F., Calus, M.P.L., 2018. The repeatability of individual nutrient digestibility in pigs. Livestock Science 207, 63–67.

Pluske, J.E.A., Kerton, D., Cranwell, P., Campbell, R., Mullan, B., King, R., Power, G., Pierzynowski, S., Westrom, B., Rippe, C., 2003. Age, sex, and weight at weaning influence organ weight and gastrointestinal development of weanling pigs. Australian Journal of Agricultural Research 54, 515–527.

Quiniou, N., Noblet, J., 2012. Effect of the dietary net energy concentration on feed intake and performance of growing-finishing pigs housed individually. Journal of Animal Science 90, 4362–4372.

Sauvant, D., Perez, J.-M., Tran, G., 2004. Tables of Composition and Nutritional Value of Feed Materials: Pigs, Poultry, Cattle, Sheep, Goats, Rabbits, Horses and Fish. Wageningen Academic Publishers, Wageningen, the Netherlands.

Short, F.J., Gorton, P., Wiseman, J., Boorman, K.N., 1996. Determination of titanium dioxide added as an inert marker in chicken digestibility studies. Animal Feed Science and Technology 59, 215–221.

Verschuren, L.M.G., Schokker, D., Bergsma, R., Jansman, A.J.M., Molist, F., Calus, M.P. L., 2020. Prediction of nutrient digestibility in grower-finisher pigs based on faecal microbiota composition. Journal of Animal Breeding and Genetics 137, 23–35.

Verschuren, L.M.G., Calus, M.P.L., Jansman, A.J.M., Bergsma, R., Knol, E.F., Gilbert, H., Zemb, O., 2018. Fecal microbial composition associated with variation in feed efficiency in pigs depends on diet and sex. Journal of Animal Science 96, 1405–1418.

Vigors, S., Sweeney, T., O'Shea, C.J., Kelly, A.K., O'Doherty, J.V., 2016. Pigs that are divergent in feed efficiency, differ in intestinal enzyme and nutrient transporter gene expression, nutrient digestibility and microbial activity. Animal 10, 1848–1855.

Wilfart, A., van Milgen, J., Noblet, J., Montagne, L., Simmins, P.H., 2007. Sites of nutrient digestion in growing pigs: Effect of dietary fiber1. Journal of Animal Science 85, 976–983.

Xiao, L., Estellé, J., Kiilerich, P., Ramayo-Caldas, Y., Xia, Z., Feng, Q., Liang, S., Pedersen, A.Ø., Kjeldsen, N.J., Liu, C., 2016. A reference gene catalogue of the pig gut microbiome. Nature Microbiology 1, 16161.