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Impact of amino acid and CP restriction from 20 to 140 kg BW on performance and dynamics in empty body protein and lipid deposition of entire male, castrated and female pigs

I. Ruiz-Ascacibar[1,2], P. Stoll[1], M. Kreuzer[2], V. Boillat[3], P. Spring[3] and G. Bee[1†]

[1]Agroscope, Institute for Livestock Sciences, La Tioleyre 4, 1725 Posieux, Switzerland; [2]ETH Zurich, Institute of Agricultural Sciences, Universitätsstrasse 2, 8092 Zurich, Switzerland; [3]School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Länggasse 85, 3052 Zollikofen, Switzerland

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Breeding leaner pigs during the last decades may have changed pig's empty body (EB) composition, a key trait for elaborating feeding recommendations. This research aimed to provide new experimental data on changes in the chemical composition of the EB of pigs from 20 to 140 kg BW. In addition, the impact of a reduction in the dietary CP associated with lower lysine, methionine + cystine, threonine and tryptophan levels was determined. In total, 48 males, castrates and females weighing 20 kg BW were allocated either to a control grower–finisher diet formulated according to current Swiss feeding recommendations, or a low CP grower–finisher diet (80% of control). Feed intake was monitored and pigs were weighed weekly. The chemical composition of EB (blood, hairs and hoofs, offals, bile, carcass) was determined at 20, 40, 60, 80, 100, 120 and 140 kg BW on four pigs per gender and diet (eight pigs per gender at 20 kg). The five fractions were weighed and samples were analysed for dry matter, protein, fat and energy. Nutrient deposition rates and N efficiency were calculated by using the 20 kg BW category as reference. Analysis revealed an accurate feed optimisation for the aforementioned essential amino acids (EAA), whereas digestible isoleucine content in the low CP diet was at 70% of the control diet. Despite similar feed intake, daily gain and feed efficiency were impaired ($P < 0.01$*) from 20 to 100 kg BW in the low CP compared with the control pigs. In the same growth period, castrates had the greatest feed intake but, together with females, displayed the lowest (*$P < 0.01$*) feed efficiency. Protein deposition was reduced (*$P < 0.01$*) by up to 31% with low CP diet and was lower (*$P < 0.01$*) in castrates and females than males at 100 kg BW. The greatest fat deposition rates were found with low CP diet and castrates. N efficiency improved (*$P < 0.05$*) by 10% with the low CP diet from 100 to 140 kg. The males displayed the greatest (*$P < 0.05$*) N efficiency. These findings suggest that the CP content of finisher II diets could be reduced to 102, 102 and 104 g/kg for females, castrates and males, respectively, without a negative impact on protein deposition or growth. It remains unclear whether the negative effects found in the BW range from 20 to 100 kg on the EB deposition were due to the 20% reduction of the dietary CP and the five limiting EAA or to other EAA via an unbalanced EAA profile.*

Keywords: deposition, efficiency, empty body, growth, protein deficiency

Implications

Exact knowledge on the pig's body chemical composition and nutrient deposition rate from birth to slaughter are of great importance for elaborating accurate pig growth models and feeding recommendations. These tools help improving efficiency of pig production also in terms of the environmental impact. Because protein is an important but limiting component of pig diets, many European countries depend on imported protein sources. Thus, provided that a reduction in protein supply does not have a negative impact on carcass composition and overall growth performance, this feeding strategy would not only decrease feed costs but also increase sustainability of pork production.

Introduction

Losses of nitrogenous compounds are important contributors to the environmental impact of pig production (Gill *et al.*, 2010). Their sources are protein and non-protein N which

† E-mail: giuseppe.bee@agroscope.admin.ch

is either undigested and excreted via faeces or digested and voided through urine. The increasing concern about the environmental impact of pig production (Wood *et al.*, 2013), together with limitations in availability and high costs of dietary protein sources (Wood *et al.*, 2013; Van Milgen and Dourmad, 2015), make the reduction of the dietary protein content a priority objective in pig production. Dietary protein intake should, as far as possible, accurately cover the requirements for fully exploiting the genetic potential for growth without excessive intake. During the last decades, pig breeding programmes focussed on selection for increased carcass leanness (Brocks *et al.*, 2000). This selection process resulted in changes in the body's chemical composition and may have also led to changes in dietary protein use efficiency. Therefore, knowledge about body composition and daily nutrient deposition rate, especially of protein and fat, is of great importance for the evaluation and/or development of feeding recommendations and growth models used in software tools to predict growth performance (Nieto *et al.*, 2012). In the absence of recent experimental data on the whole body composition, current recommendations are often based on values obtained decades ago. For instance, the current Swiss nutrient recommendations (Agroscope, 2015) are based on experiments from the early 1990s (Bracher-Jakob *et al.*, 1990; Bee, 1993). Chemical analysis of the whole body or body components using the sequential slaughter technique has proven to be a reliable way for determining effects of genotype, BW and nutrition on body chemical composition (Schinckel *et al.*, 2008). Therefore, the first purpose of this study was to acquire new experimental data on temporal changes in the chemical body composition and nutrient deposition rate of modern Swiss Large White pigs in the BW range from 20 to 140 kg. Because of the increased growth rate, feed efficiency and carcass leanness, it was hypothesised that protein use efficiency markedly improved in the last decades. Possible reasons could be overestimated nutrient requirements, large safety margins in feeding recommendations or tissue-specific increased efficiency in using limiting resources. For instance, Conde-Aguilera *et al.* (2010) reported that diets deficient or not in total sulphur amino acids had dissimilar impact on the amino acid composition of different body proteins in young piglets. However, to our knowledge, there is no recent information on the dynamics in empty body (EB) protein and lipid deposition of grower–finisher pigs fed diets restricted in CP or essential amino acid (EAA) during the whole growth period. This leads to the second aim of this study, to assess the impact of a 20% reduction in dietary CP and digestible lysine (dLys), methionine + cystine, threonine and tryptophan levels compared with a standard diet composed according to the current recommendations on EB protein and lipid deposition efficiency.

Material and methods

All procedures involving animals were approved by the Swiss Cantonal Committee for Animal Care and Use (2012_14_FR 22119 and 2013_24_FR 24064).

Animals, feed and experimental design

A total of 168 pigs, 56 females, castrates and entire males each, originating from 30 litters of the Agroscope sow herd were used for this study. To obtain the number of pigs required, a total of four farrowing series were necessary. The first two farrowing series (run 1) were carried out between July 2012 and April 2013 and the second two series (run 2) from August 2013 to May 2014. Run 1 involved 84 Premo® × Large White crossbred pigs, selected from 17 litters, whereas in run 2, 84 Large White × Large White were selected from 13 litters.

For the study, a total of eight pens of equal size (17.35 m^2) each equipped with one automatic feeder and individual pig recognition system (Schauer Maschinenfabrik GmbH & Co. KG, Prambachkirchen, Austria) as described previously by Bee *et al.* (2008) were available, which allowed the determination of individual feed intake (FI) in group housed pigs. From weaning until the end of the experimental period, pigs were reared in these group pens. At the start of the grower period (21.7 ± 1.47 kg, expressed as mean ± SD), pigs were assigned within experimental treatment to one of the seven BW categories (20, 40, 60, 80, 100, 120 or 140 kg BW) such that birth weight within gender was similar. Per gender and BW category, eight pigs were allocated. In total, 16 pigs were assigned to the 20 kg BW category to have a high certainty in the basal values. To avoid the mounting because of sexual behaviour of entire males arising in the finisher period, females and castrates were housed together in pens, but separately from males.

The automatic feeders for control females and control castrates were installed in different pens than those for the low CP female and low CP castrate groups. However, all pens were accessible to all females and castrates of both treatment groups. The same was true for control males and low CP males. Per feeder a maximum of 14 pigs were allowed. All pens were in the same room, and therefore had the same environmental conditions. Pigs always had *ad libitum* access to the experimental diets and water. Pigs were weighed weekly. From weaning to the start of the grower period, all pigs were offered the same starter diet formulated according to current Swiss recommendations for pigs (Agroscope, 2015). The control CP grower (20 to 60 kg BW), finisher I (60 to 100 kg BW) and finisher II diets (100 to 140 kg BW) were formulated according to the current Swiss recommendations for swine (Agroscope, 2015) for 40, 80 and 120 kg BW, respectively. The CP and apparent dLys requirements, expressed per MJ digestible energy, were calculated as follows:

$$\text{CP (g/MJ digestible energy)} = 13.321 - 3.416 \times (\text{BW}/100)$$

$$\text{dLys (g/MJ digestible energy)} = 0.895 - 0.913 \times (\text{BW}/100) + 0.491 \times (\text{BW}/100)^2 - 0.045 \times (\text{BW}/100)^3$$

In addition, for the formulation of the standard diets the levels of the other EAA were adjusted in relation to dLys as follows: methionine = 32%; methionine + cystine = 64%; threonine = 68%; tryptophan = 20%; isoleucine = 62%; leucine = 100%; phenylalanine = 60%; phenylalanine + tyrosine = 96% and valine = 70%. The low CP grower, finisher I and finisher II diets were formulated to contain, expressed as percentage of control diet, 80% of dietary CP, and apparent ileal dLys, methionine + cystine, threonine and tryptophan. As it was intended to approach industry practice in pig feed formulation, no effort was made to adjust the levels of the other EAA in the low CP diets to recommendations. As recommended (Agroscope, 2015), all diets of the males were formulated to contain 5% higher levels of CP, lysine, methionine + cystine, threonine and tryptophan compared with the diets fed to females and castrates. The purpose of using a 20% reduction of CP and the mentioned EAA was to create clear differences in growth performance and body composition.

When the individual pig reached the initial BW of the grower, finisher I and finisher II period (greater BW than 19, 59 and 98 kg, respectively), it was allocated to the corresponding diet. Because of the duration of the study and limited feed storage capacity, feed had to be produced several times. However, because run 2 was carried out 6 months after run 1 ended, ingredients of the diets had to be adapted to obtain the same chemical composition. The main feed ingredients used were barley, wheat, oat, wheat bran, corn, soyabean meal, rapeseed meal, potato protein, sugar beet and molasses. L-Lysine-HCl, DL-methionine, L-threonine and L-tryptophan were used to achieve the desired EAA profile. Subsamples of the different experimental diets in use were collected every week. Three samples, resulting from weekly pooled subsamples, were analysed per experimental diet. In Table 1, the average chemical composition of the experimental diets used in the two runs are presented.

Table 1 *Analysed composition (g or MJ/kg as-fed) of the control and reduced protein grower, finisher I and finisher II diets*[1]

	Grower diet (20 to 60 kg BW)				Finisher I diet (60 to 100 kg BW)				Finisher II diet (100 to 140 kg BW)			
Dietary treatments	C		LP		C		LP		C		LP	
Gender	EM	CA, FE	EM	CA, FE	EM	CA, FE	EM	CA, FE	EM	CA, FE	EM	CA, FE
Dry matter	889	891	889	888	889	890	889	885	879	879	878	879
Ash	44	44	42	41	40	41	39	38	35	34	34	34
Fat	27	26	27	27	26	29	27	26	27	29	27	29
CP	167	161	137	130	141	140	119	113	129	123	104	102
Amino acids[2]												
Lysine	10.3	9.7	8.1	7.7	8.0	7.7	6.5	6.2	7.2	6.9	5.9	5.7
Methionine	3.4	3.2	2.5	2.4	2.5	2.5	1.9	1.8	2.2	2.2	1.7	2.0
Cystine	3.0	2.9	2.7	2.5	2.6	2.9	2.5	2.4	2.5	2.4	2.3	2.2
Threonine	7.6	7.3	6.0	5.7	6.1	5.9	5.0	4.7	5.4	5.3	4.4	4.0
Tryptophan	2.3	2.2	1.8	1.7	1.9	1.8	1.5	1.4	1.7	1.6	1.4	1.3
Isoleucine	6.9	6.6	5.1	4.8	5.6	5.3	4.1	3.9	5.0	4.8	3.5	3.5
Leucine	12.6	12.1	9.2	8.8	10.6	9.9	7.8	7.4	9.9	9.7	7.0	7.3
Phenylalanine	8.6	8.3	6.6	6.3	7.4	6.8	5.6	5.4	6.5	6.2	4.8	4.7
Valine	8.5	8.2	6.2	6.0	7.3	7.0	5.6	5.3	6.5	6.2	4.8	4.7
Tyrosine	6.0	5.7	4.2	3.9	5.0	4.6	3.5	3.4	4.4	4.3	3.0	3.0
Histidine	3.7	3.6	3.1	2.9	3.1	3.2	2.7	2.6	2.8	2.7	2.2	2.2
Alanine	7.1	6.8	5.4	5.2	6.0	5.8	4.7	4.4	5.6	5.5	4.1	4.3
Arginine	9.1	8.6	7.5	6.9	7.1	7.2	6.0	5.6	6.1	5.9	4.9	4.8
Asparagine	14.4	13.6	9.9	9.0	10.9	9.9	7.1	6.6	9.9	9.4	6.1	6.1
Glutamine	31.3	30.3	29.0	28.3	27.8	28.2	26.5	25.5	25.1	24.4	23.5	22.7
Glycine	7.3	7.0	5.6	5.3	6.2	6.2	5.1	4.8	5.4	5.2	4.1	4.1
Proline	12.8	12.8	11.4	11.5	12.3	12.1	11.4	11.1	11.0	10.6	10.1	9.5
Serine	7.7	7.4	6.0	5.6	6.5	6.1	5.0	4.8	5.8	5.6	4.3	4.3
Crude fibre	38	41	41	38	45	50	46	47	42	42	40	41
ADF	58	63	59	55	65	76	68	67	64	66	63	65
NDF	239	261	220	248	253	213	219	212	172	185	199	178
Calculated energy content[2]												
Digestible energy	13.2	13.2	13.2	13.2	13.2	13.2	13.2	13.2	13.2	13.2	13.2	13.2
Net energy	9.8	9.7	9.8	9.9	9.8	9.7	9.8	9.9	9.7	9.7	9.8	9.8

C = control diets formulated to meet nutrient requirements according to the Swiss feeding recommendations for growing finishing pigs in the grower, finisher I and finisher II period; LP = reduced protein diet formulated to contain, expressed as percentage of the control diets, 80% of dietary CP, lysine, methionine + cystine, threonine and tryptophan; EM = entire males; CA = castrates; FE = females.
[1]Grower, finisher I and finisher II diets were offered *ad libitum* from 20 to 60 kg BW, from 60 to 100 kg BW and from 100 to 140 kg BW, respectively.
[2]The digestible and net energy coefficients from each feed ingredient were obtained from the Swiss (Agroscope, 2015) and French (Noblet *et al.*, 2003) databases, respectively. Taking into account the relative amount of each feed ingredient in the diet, digestible and net energy content were calculated.

Slaughter and measurement of carcass composition
Pigs stayed on feed until they reached the target slaughter BW. Then they were transported individually in a trolley (100 m) to the research abattoir after withdrawal of feed for 16 h. They were stunned for 180 s using a CO_2 (87% CO_2) stunner (Samson C1 L 803; MPS Group, Holbaek, Denmark). Pigs were weighed, immediately exsanguinated and weighed again to calculate the amount of blood by weight difference. They were subsequently scalded (62°C, 3 min), hooves were removed and weighed again, so that the weight of hair and hooves portion could be calculated. Carcasses were then eviscerated. The head was removed by cutting at the occipital–atlas joint, and then split into two halves. Heart, kidneys, liver, lungs, tongue, spleen, eyes, brain, internal ear, mesentery, belly fat, full gallbladder, bladder, stomach, large intestine and small intestine were weighed separately in each animal. Gallbladder, bladder, stomach, intestine and hindgut were emptied and rinsed with clean water to remove remaining bile, urine and digesta. Before weighing, each of the before mentioned gut components was squeezed by hand to remove excess water. Empty gut and dissected organs were ground and homogenised together using a cutter (DMK 20 C; DMS Maschinensysteme, Lebensmittelmaschinen GmbH & Co. KG, Saarbrücken, Germany). The eviscerated carcasses, including the two head halves, were split longitudinally, weighed within 30 min and then chilled overnight at 2°C. The cold carcasses were weighed and the left carcass side was dissected 24 h *postmortem*. All parts from the dissected carcass were stored together in sealed plastic bags at −20°C. Before grinding, the frozen left carcasses were cleaned from excess of ice and then weighed. Afterwards, the left carcasses were ground with a shredder (Ultra-Granulator Type PS 4-5; Pallmann Maschinenfabrik GmbH & Co. KG, Zweibrücken, Germany) and further homogenised using a cutter (DMK 45 C; DMS Maschinensysteme, Lebensmittelmaschinen GmbH & Co. KG).

Subsamples were obtained from the following five homogenised portions: (1) carcass, (2) viscera and intestine, (3) hair and hoofs, (4) blood and (5) bile. Bile samples of 16 (20 kg BW) or eight (the other BW categories) pigs were pooled within treatment and BW category for later analysis. All portions were stored at −20°C until being lyophilised (Christ Delta, Newtown, UK) for 70 h. Afterwards, samples were cooled with liquid N_2 and ground using a 1 mm sieve (Grindomix GM 200; Retsch, Haan, Germany). Subsamples of hair and hoofs were ground twice, first, with a 5 mm sieve and then with a 1 mm sieve (Brabender GmbH & Co., Duisburg, Germany). These subsamples were used for compositional analysis.

Laboratory analyses
Diet and body part analyses were conducted in duplicate except when results differed by more than 5%, where up to four replicates were obtained. Dry matter in feed was determined by gravimetry, after drying at 105°C for 3 h. In the body parts, dry matter content was determined by gravimetry after lyophilisation. Ash content was determined in feed samples after 3 h at 550°C. The CP (total N $\times$ 6.25) content was analysed with a LECO FP-2000 analyser (Leco, Mönchengladbach, Germany) (International Organization for Standardization (ISO), 2008). The amino acid composition of the diets was determined after 24 h of acid hydrolysis (48 h for leucine, isoleucine and valine). Methionine and cystine were hydrolysed after peroxidation with formic acid. The amino acid profile was determined by HPLC coupled with a fluorescence detector (Alliance 2695; Waters, Milford, MA, USA) as described in the manual (Waters AccQ Tag Chemistry Package 052874 TP, rev. 1). In the diets, crude fibre and ether extract were determined according to the Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten (1997) methods 6.1.4 and 5.1.1, respectively. The ADF (Van Soest, 1963) and NDF (Van Soest and Wine, 1967) levels were also analysed. In the body parts, gross energy content was measured with an adiabatic bomb calorimetry (ISO, 1988) using a LECO AC600 (Leco, St. Joseph, MI, USA). To determine crude fat content in feeds, samples were hydrolysed in 10% HCl (v/v) for 1 h. Hydrolysate was dried and subsequently extracted with petrol ether by using the Büchi SpeedExtractor E 916 (Büchi Labortechnik AG, Flawil, Switzerland). Dry residual of fat was determined by gravimetry. Fat content in freeze-dried samples was determined using Avanti Soxtec System (2050 Extraction Unit; Foss Tecator, Hillerød, Denmark).

Calculations and statistical analysis
The amino acid digestibility coefficients for each feed ingredient were obtained from the Dutch feed database (Centraal Veevoederbureau, 1996). Using the analysed amino acid content of the diets (Table 1) and the aforementioned digestibility coefficients, the apparent and standard ileal digestible amino acid levels were calculated (Supplementary Tables S1 and S2). The digestible and net energy coefficients from each feed ingredient were obtained from the Swiss (Agroscope, 2015) and French (Noblet *et al*., 2003) feed databases, respectively. Digestible and net energy content were calculated taking into account the relative amount of each feed ingredient in the diet. The sum of the five portions (blood, hair and hooves, organs and intestines, carcass and bile) was considered as the entire EB. Data on EB were calculated from proportionate wet weights and chemical composition of each of these parts. Data from the 20 kg BW, which had not received any of the experimental diets, were used as baseline for growth performance and nutrient and energy deposition of all other pigs slaughtered at greater BW. For that purpose, the relationship between live BW and the empty BW at slaughter was calculated within each gender for the pigs in the 20 kg BW. The mentioned relationship was used to calculate the EB weight of the rest of the BW categories at the beginning of the experimental period. The chemical composition (g/kg EB) was assumed to be the same at the beginning of the experimental period within each gender. Energy and nutrient deposition rates were calculated by difference between the baseline values obtained from pigs of the 20 kg BW and the values obtained from pigs of the 40, 60, 80, 100, 120 and 140 kg BW. To calculate N efficiency,

N retention in the EB from 20 kg to the respective BW categories was divided by the total dietary N intake.

Data were analysed using the ANOVA procedure of *Systat* version 13 (2009) considering diet, gender, run and the interactions diet × gender, diet × run, gender × run, diet × gender × run as fixed effects. The pig was the experimental unit for all variables studied. Only the *P*-values of the main factors and the diet × gender interaction are reported because they were considered to be the most important for the discussion of these results. Differences among mean values within genders were determined using the Tukey's test. Significance was set at $P < 0.05$ and tendency at $P < 0.10$. Data were presented as least squares means and standard errors.

Results

Realised diet composition

The intended reduction by 20% from control to low CP diets in the contents of apparent ileal digestible CP as well as apparent ileal dLys, methionine + cystine, threonine, tryptophan was successfully achieved (Table 1). The content of CP fluctuated between 102 and 167 g/kg and digestible energy was constant at 13.2 MJ/kg (both expressed as-fed basis). The variation in dry matter was within a narrow range (88% to 89%).

Growth performance

BW measured at the beginning of the grower, finisher I and finisher II period and at slaughter did not differ between diets and among genders (Table 2). Despite similar FI, low CP pigs needed more time ($P < 0.01$) to achieve the target BW in the grower and finisher I period. As a result, average daily gain (ADG), gain-to-feed ratio and gain-to-digestible energy intake ratio was lower ($P < 0.05$) in low CP than control pigs. Regardless of the dietary treatment, females had lower ($P < 0.05$) ADG in the finisher I period compared with males and castrated pigs, and tended ($P < 0.10$) to grow at a slower rate in the grower period compared with castrates. The lower ADG is partly reflected in a lower ($P < 0.05$) FI in the grower and finisher I period by females (and males) compared with castrates. In the grower and finisher I periods, males were more ($P < 0.05$) energy efficient compared with females and castrates.

Daily protein, fat and energy deposition rate in the empty body and carcass

No diet × gender interactions were observed for protein, fat and energy deposition rates of the EB or the carcasses (Tables 3 and 4). As expected, nutrient deposition rates in the total EB and in the carcasses followed a similar pattern. Daily protein deposition was up to 31% lower ($P < 0.01$) in the low CP group in both EB and carcass than in control pigs, but this difference decreased to 10% at 140 kg BW ($P = 0.06$). At 60 kg BW low CP pigs deposited 24% more ($P < 0.05$) fat in EB compared with control pigs. Gender had an effect ($P < 0.05$) on energy deposition rate at 60, 100 and 120 kg BW in EB and carcasses, where castrates displayed the greatest fat and energy deposition rates. This was the result of corresponding differences ($P < 0.05$) in the fat deposition rates. Protein deposition rate was similar among gender, except at 100 and 140 kg BW. Compared with females, in males and castrates, protein deposition in the EB was greater ($P < 0.05$) at 100 kg BW and compared with castrates, protein deposition was faster ($P < 0.05$) in males and females at 140 kg BW. By contrast, in the carcass at the same BW category, protein deposition rates were greatest ($P < 0.05$) only in males with intermediate values for castrates. At 60, 100 and 120 kg BW, males showed the lowest EB fat deposition rate ($P < 0.05$ each), with intermediate values for females and the greatest for castrates. At 100 kg BW, castrates showed a greater ($P < 0.05$) carcass fat deposition rate compared with males and females. These differences were reflected in corresponding differences ($P < 0.05$) in carcass energy deposition rate. The castrates displayed the greatest energy deposition rates at all BW categories in the carcass, and, except for the 40 kg BW category, also in the EB.

Nitrogen efficiency

Diet did not affect the N use efficiency from 60 to 100 kg BW (Table 5). However, at 40 kg BW control pigs were 15% ($P < 0.05$) more efficient than low CP pigs. Nevertheless, at 120 and 140 kg BW low CP pigs were 10% and 11% more ($P < 0.05$) N efficient compared with control pigs. Gender affected ($P < 0.05$) N efficiency at 60, 100 and 140 kg BW. Thereby, the males displayed the greatest N efficiency rates, whereas for females and castrates, the values were similar at all the BW categories but lower ($P < 0.05$) by 15% and 12% compared with males at 60 and 140 kg BW, respectively.

Discussion

Knowledge on the quantitative deposition in the EB at various growth stages, and its relationship with FI and feed composition, are of major importance for assessing nutrient requirements (National Research Council (NRC), 2012) and developing optimal feeding strategies. There are many studies using indirect methods to estimate the body composition and changes in this composition in pigs by using either balance approaches or equations that include parameters such as back fat thickness and BW (Schinckel and De Lange, 1996; Chiba *et al.*, 2002; Reynolds and O'Doherty, 2006; Nieto *et al.*, 2012). New technologies such as computed tomography or dual-energy X-ray absorptiometry are now also available and have been proven to be suitable for estimating the body composition of pigs (Zomeño *et al.*, 2016). However, real measurements are preferable to estimates when accurate compositional data and changes in nutrient deposition with age and gender are required. Accordingly, the present study provides novel measured data on the protein, fat and energy deposition rate in the EB and carcass of entire male, castrate and female Large White pigs

Table 2 *Effect of dietary protein and essential amino acid supply and gender on growth performance of Swiss Large White pigs in the grower, finisher I and finisher II period*

		C			LP				*P*-values[3]			
Period	Item[1,2]	EM	CA	FE	EM	CA	FE	SE	D	G	R	D × G
Grower	Initial BW (kg)	21.5	21.8	21.3	21.7	21.9	21.8	0.30	0.26	0.51	0.79	0.82
Period	Final BW (kg)	61.5	62.4	62.9	62.1	61.9	62.0	0.51	0.51	0.45	0.06	0.28
	Days on diet	47.4^{bc}	48.4^{c}	50.9^{b}	55^{ab}	50.9^{b}	56.8^{a}	1.59	<0.01	0.03	<0.01	0.26
	Daily gain (kg/day)	0.85^{a}	0.85^{a}	0.83^{a}	0.74^{b}	0.80^{b}	0.72^{b}	0.019	<0.01	0.06	<0.01	0.29
	Daily feed intake (kg/day)	1.73^{b}	1.86^{a}	1.81^{b}	1.74^{b}	1.96^{a}	1.79^{b}	0.040	0.36	<0.01	<0.01	0.34
	Gain to feed (g/kg)	493^{a}	458^{b}	460^{b}	427^{c}	407^{d}	403^{d}	5.7	<0.01	<0.01	0.11	0.41
	Gain to digestible energy intake (g/MJ)	37^{a}	35^{b}	35^{b}	32^{c}	31^{d}	31^{d}	0.4	<0.01	<0.01	0.11	0.41
Finisher I	Initial BW (kg)	61.9	62.2	62.4	61.8	62.0	62.0	0.57	0.60	0.87	0.07	0.95
	Final BW (kg)	102.0	102.1	102.6	102.4	102.1	102.8	0.85	0.81	0.76	0.55	0.97
	Days on diet	37.8^{c}	37.3^{c}	40.1^{c}	40.3^{b}	40.1^{b}	48.5^{a}	1.72	<0.01	<0.01	0.56	0.16
	Daily gain (kg/day)	1.08^{a}	1.07^{a}	1.02^{b}	1.02^{b}	1.00^{b}	0.86^{c}	0.033	<0.01	<0.01	0.57	0.30
	Daily feed intake (kg/day)	2.76^{b}	3.00^{a}	2.75^{b}	2.78^{b}	3.08^{a}	2.65^{b}	0.079	0.98	<0.01	0.96	0.53
	Gain to feed (g/kg)	393^{a}	358^{b}	370^{b}	365^{b}	326^{c}	324^{c}	6.3	<0.01	<0.01	0.42	0.32
	Gain to digestible energy intake (g/MJ)	30^{a}	27^{b}	28^{b}	28^{b}	25^{c}	25^{c}	0.5	<0.01	<0.01	0.42	0.32
Finisher II	Initial BW (kg)	102.9	102.1	103.5	103.7	102.7	103.0	0.95	0.72	0.57	0.60	0.77
	Final BW (kg)	138.3^{b}	139.6^{b}	141.2^{ab}	142.9^{a}	143.1^{a}	141.0^{ab}	1.15	0.02	0.78	0.70	0.14
	Days on diet	36.8	38.5	35.0	31.5	40.3	41.8	4.22	0.76	0.44	0.32	0.39
	Daily gain (kg/day)	1.01	0.98	1.04	1.22	1.04	0.94	0.083	0.47	0.32	0.08	0.22
	Daily feed intake (kg/day)	3.21	3.67	3.60	3.85	3.52	3.23	0.209	0.81	0.69	0.54	0.08
	Gain to feed (g/kg)	315	268	291	315	295	288	14.9	0.51	0.10	0.05	0.56
	Gain to digestible energy intake (g/MJ)	24	20	22	24	22	22	1.1	0.51	0.10	0.05	0.56

C = control diet formulated to meet nutrient requirements according to the Swiss feeding requirements for grower–finisher pigs in the respective growth periods; LP = low protein formulated to contain, expressed as percentage of the control diets, 80% of dietary CP, lysine, methionine + cystine, threonine and tryptophan; EM = entire males; CA = castrates; FE = females.

[a,b,c,d]Values within a row with different superscripts differ significantly at $P < 0.05$.

[1]To calculate the average initial BW in the grower, finisher I and finisher II period, all pigs fed the respective diets in these periods were included: grower period = 144 pigs; finisher I period = 96 pigs and finisher II period = 48 pigs.

[2]To calculate the average final BW, daily gain, daily feed intake, gain to feed and gain to digestible energy intake in the grower, finisher I and finisher II period, all pigs fed the respective diets and who finished these periods were included: grower period = 120 pigs; finisher I period = 72 pigs and finisher II period = 24 pigs.

[3]Probability values for the effects of diet (D), gender (G), run (R) and D × G. None of the D × R, G × R and D × G × R interactions were significant ($P > 0.05$).

Table 3 *Effect of dietary protein and essential amino acid supply and gender on daily protein, fat and energy deposition in the empty body of pigs slaughtered at different BW*

		C			LP				*P*-values[2]			
Item[1]	BW at slaughter (kg)	EM	CA	FE	EM	CA	FE	SE	D	G	R	D × G
Protein deposition (g/day)	40	121[a]	104[a]	108[a]	79[b]	75[b]	75[b]	4.9	<0.01	0.12	<0.01	0.46
	60	133[a]	139[a]	120[a]	110[b]	107[b]	101[b]	6.1	<0.01	0.12	0.12	0.53
	80	152[a]	142[a]	127[a]	108[b]	112[b]	111[b]	11.0	<0.01	0.59	0.46	0.45
	100	162[a]	153[a]	139[b]	131[c]	131[c]	110[d]	6.5	<0.01	0.01	0.05	0.75
	120	159[a]	147[a]	148[a]	128[b]	141[ab]	125[b]	9.7	0.03	0.68	0.92	0.42
	140	168[a]	141[b]	144[b]	150[a]	129[b]	129[b]	8.5	0.06	0.03	0.29	0.93
Fat deposition (g/day)	40	105	125	119	113	111	103	10.7	0.43	0.67	0.09	0.47
	60	100[d]	154[b]	124[d]	141[c]	180[a]	149[c]	12.7	0.01	<0.01	0.40	0.78
	80	143	177	154	132	187	175	22.9	0.71	0.20	0.86	0.78
	100	171[c]	211[b]	166[c]	188[c]	254[a]	168[c]	12.7	0.07	<0.01	0.78	0.29
	120	187[b]	241[a]	220[ab]	173[b]	253[a]	212[ab]	17.4	0.82	0.01	0.85	0.73
	140	191	287	262	258	285	231	23.6	0.59	0.06	0.32	0.15
Energy deposition (MJ/day)	40	6.76[ab]	7.22[a]	7.06[a]	6.34[b]	6.16[b]	5.89[ab]	0.409	0.02	0.87	0.02	0.62
	60	7.07[b]	9.26[a]	7.75[ab]	8.16[b]	9.50[a]	8.09[ab]	0.581	0.27	0.02	0.33	0.74
	80	9.03	10.01	8.92	7.69	9.85	9.41	1.096	0.71	0.39	0.89	0.71
	100	10.31[b]	11.52[a]	9.68[b]	10.21[ab]	12.86[a]	9.00[b]	0.547	0.68	<0.01	0.94	0.21
	120	10.82[b]	12.74[a]	11.89[ab]	9.66[b]	12.96[a]	11.25[ab]	0.745	0.40	0.02	0.56	0.65
	140	11.28	14.52	13.51	13.25	13.94	12.06	1.007	0.98	0.17	0.53	0.25

C = control diet formulated to meet nutrient requirements according to the Swiss feeding requirements for grower–finisher pigs in the respective growth periods; LP = low protein formulated to contain, expressed as percentage of the control diets, 80% of dietary CP, lysine, methionine + cystine, threonine and tryptophan; EM = entire males; CA = castrates; FE = females.
[a,b,c,d]Values within a row with different superscripts differ significantly at $P<0.05$.
[1]Daily protein, fat and energy deposition was calculated by difference between the protein, fat and energy content of the empty body determined in pigs of the 20 kg BW category and the protein, fat and energy content of the empty body determined in pigs of the 40, 60, 80, 100, 120 and 140 kg BW category.
[2]Probability values for the effects of diet (D), gender (G), run (R) and D × G. None of the D × R, G × R and D × G × R interactions were significant ($P>0.05$).

from 20 to 140 kg BW. In addition, the study specifies changes in EB when dietary CP and EAA supply is reduced, as is common nowadays for environmental reasons.

Growth performance

In the current experiment, growth performance from 20 kg onwards was within the expected range for the Swiss Large White breed (SUISAG, 2014). The 11% and 12% slower growth of low CP compared with control pigs in the grower and finisher I period, respectively, points at a pronounced deficiency of dietary CP and EAA in the low CP diets. This happened despite giving all pigs *ad libitum* access to feed. These results agree with the inability of pigs in the experiment of Reynolds and O'Doherty (2006) to increase their daily consumption during the experiment (42 to 94 kg BW), when a lysine restriction was imposed, to compensate for this lack in their diet. Moreover, control pigs used the available nutrients more efficiently than low CP pigs in the present study, as was obvious from the greater gain-to-feed ratio during the grower and finisher I period. Fabian *et al.* (2002) also reported greater ADG and feed efficiencies in pigs fed diets with increasing lysine concentration (from 5 to 11 g/kg) during the grower period (21 to 50 kg BW).

The efficiency of dietary protein utilisation by the pig depends on the digestibility of the amino acids and the dietary amino acid profile itself in relation to the animal's requirements (Van Milgen and Dourmad, 2015). Some of the low CP diets had an unbalanced EAA pattern according to the Swiss feeding recommendations for pigs. For instance, the ratio of ileal digestible isoleucine to lysine was 0.53 in the grower- and finisher II low CP diets, whereas the Swiss feeding recommendations for pigs propose a ratio of 0.63.

Dietary lysine, and therefore dietary EAA recommendations, are based, to a great extent, on the maximal protein deposition rate in the EB. Consequently, differences between the various feeding guidelines are expected. American guidelines (NRC, 2012) were applied to estimate dLys requirements for Swiss Large White pigs where maximal protein deposition rate was estimated to be 8% greater than for the fast growing pigs used for the US guidelines. In this context, digestible isoleucine was not a limiting EAA in the mentioned diets.

Individual data on ADG revealed that ~ 30% of the pigs fed the low CP diets exhibited a similar growth rate compared with those fed the control diets. This illustrates individual differences either in requirements for EAA or a different genetic potential for coping with such dietary situations by utilising the dietary sources more efficiently.

The lower FI of entire males compared with castrates has already been reported to be due to the greater testosterone concentration in the serum of entire males which inhibits the appetite in pigs (Weiler *et al.*, 1998) and the greater physical activity of entire males compared with castrates (Cronin *et al.*, 2003) and females (Rydhmer *et al.*, 2006). The latter

Table 4 *Effect of dietary protein and essential amino acid supply and gender on daily protein, fat and energy deposition in the carcass of pigs slaughtered at different BW*

		C			LP				*P*-values[2]			
Item[1]	BW at slaughter (kg)	EM	CA	FE	EM	CA	FE	SE	D	G	R	D × G
Protein deposition (g/day)	40	108^{a}	92^{a}	99^{a}	69^{b}	68^{b}	67^{b}	5.1	<0.01	0.23	<0.01	0.36
	60	115^{a}	119^{a}	103^{ab}	94^{b}	90^{b}	90^{b}	5.3	<0.01	0.26	0.08	0.42
	80	128^{a}	122^{a}	107^{ab}	90^{b}	95^{b}	94^{b}	9.1	<0.01	0.59	0.42	0.40
	100	134^{a}	131^{ab}	119^{b}	111^{c}	111^{c}	94^{d}	5.6	<0.01	0.03	0.07	0.88
	120	135^{a}	126^{a}	125^{a}	108^{b}	123^{ab}	104^{b}	9.2	0.05	0.56	0.96	0.44
	140	141^{a}	120^{b}	120^{b}	125^{ab}	111^{c}	109^{c}	7.3	0.07	0.05	0.29	0.88
Fat deposition (g/day)	40	102	118	113	106	104	96	10.4	0.31	0.76	0.10	0.55
	60	93^{d}	140^{b}	112^{d}	129^{c}	165^{a}	133^{c}	11.1	0.01	<0.01	0.30	0.80
	80	128	160	139	117	168	155	20.7	0.81	0.17	0.81	0.80
	100	153^{b}	189^{a}	148^{b}	166^{b}	225^{a}	148^{b}	10.6	0.08	<0.01	0.63	0.27
	120	164^{b}	212^{a}	197^{ab}	151^{b}	225^{a}	189^{ab}	14.8	0.81	0.01	0.95	0.66
	140	171	251	230	228	247	204	20.8	0.62	0.09	0.21	0.16
Energy deposition (MJ/day)	40	6.31^{a}	6.63^{a}	6.60^{a}	5.80^{b}	5.68^{b}	5.42^{b}	0.421	0.03	0.94	0.03	0.73
	60	6.37^{b}	8.24^{a}	6.90^{b}	7.29^{b}	8.52^{a}	7.18^{b}	0.493	0.25	0.02	0.23	0.76
	80	7.89	8.87	7.86	6.66	8.69	8.23	0.963	0.67	0.33	0.84	0.71
	100	8.97^{b}	10.12^{a}	8.48^{b}	8.88^{b}	11.26^{a}	7.88^{b}	0.442	0.69	<0.01	0.91	0.17
	120	9.37^{b}	11.15^{a}	10.46^{ab}	8.34^{b}	11.4^{a}	9.86^{ab}	0.611	0.38	<0.01	0.63	0.58
	140	9.85	12.63	11.71	11.48	12.03	10.55	0.891	0.95	0.20	0.42	0.29

C = control diet formulated to meet nutrient requirements according to the Swiss feeding requirements for grower–finisher pigs in the respective growth periods; LP = low protein formulated to contain, expressed as percentage of the control diets, 80% of dietary CP, lysine, methionine + cystine, threonine and tryptophan; EM = entire males; CA = castrates; FE = females.
[a,b,c,d]Values within a row with different superscripts differ significantly at $P<0.05$.
[1]Daily protein, fat and energy deposition was calculated by difference between the protein, fat and energy content of the carcass determined in pigs of the 20 kg BW category and the protein, fat and energy content of the carcass determined in pigs of the 40, 60, 80, 100, 120 and 140 kg BW category.
[2]Probability values for the effects of diet (D), gender (G), run (R) and D × G. None of the D × R, G × R and D × G × R interactions were significant ($P>0.05$).

Table 5 *Effect of dietary protein and essential amino acid supply and gender on nitrogen efficiency (%) of pigs slaughtered at different BW*[1]

	C			LP				*P*-values[2]			
BW at slaughter (kg)	EM	CA	FE	EM	CA	FE	SE	D	G	R	D × G
40	57.5^{a}	50.5^{a}	50.2^{a}	47.0^{b}	44.4^{b}	42.9^{b}	4.40	0.05	0.40	0.01	0.88
60	54.9^{a}	47.3^{b}	43.5^{b}	50.4^{a}	44.2^{b}	46.3^{b}	1.85	0.31	<0.01	0.02	0.16
80	51.2	46.6	44.6	45.8	44.7	48.1	1.65	0.37	0.24	0.01	0.05
100	49.0^{a}	45.7^{b}	44.0^{b}	50.8^{a}	44.9^{b}	45.2^{b}	1.97	0.66	0.04	0.11	0.79
120	47.4^{a}	41.8^{b}	42.4^{b}	50.1^{a}	48.4^{a}	46.0^{a}	2.16	0.03	0.12	0.87	0.65
140	48.0^{a}	37.5^{c}	39.1^{c}	48.7^{a}	43.4^{b}	45.6^{b}	2.36	0.04	0.02	0.61	0.44

C = control diet formulated to meet nutrient requirements according to the Swiss feeding requirements for grower–finisher pigs in the respective growth periods; LP = low protein formulated to contain, expressed as percentage of the control diets, 80% of dietary CP, lysine, methionine + cystine, threonine and tryptophan; EM = entire males; CA = castrates; FE = females.
[a,b,c]Values within a row with different superscripts differ significantly at $P<0.05$.
[1]N efficiency, expressed as percentage of the N intake, was calculated by difference in the N content of the empty body determined in pigs of the 20 kg BW category and the N content of the empty body determined in pigs of the 40, 60, 80, 100, 120 and 140 kg BW category. Accordingly, N intake was determined in the correspondent periods.
[2]Probability values for the effects of diet (D), gender (G), run (R) and D × G. None of the D × R, G × R and D × G × R interactions were significant ($P>0.05$).

may have caused them to spend less time eating. By increasing the voluntary FI in the finisher II period, castrates grew at a similar rate as entire males but were less energy efficient (g of BW gain/MJ digestible energy). Because castrates and females were penned together, the dominance of castrates may have been one reason for the lower average daily FI observed in females, despite *ad libitum* feed access. Under such circumstances, it is possible that their nutrient requirements could not have been covered resulting in less efficient growth as one could have expected from females housed separately.

Differences in the response to the low CP diet among genders were manifested in the diet × gender interaction. During the finisher II period, the interaction tended to be significant for FI, in a way that entire males of the low CP group increased the FI by 20% compared with the entire males of the control group, thus managed to maintain the average daily FI. By contrast, females and castrates of the low CP group had a lower FI (−10% and −4%, respectively) compared with the females and castrates of the control pigs. According to Warnants *et al.* (2003), increased FI in growing castrates and females pigs under high supply of lysine, threonine and methionine could be due to an increased need for total protein or/and for energy. It is likely that castrates and females fed the control diet needed extra energy to eliminate an excess of protein during the finisher I period.

Tissue deposition rate

Protein, fat and energy deposition rates were calculated in relation to the data obtained at 20 kg BW. Every additional BW period effect was comprised in the subsequent BW category providing data across the whole range from 20 kg to the respective slaughter BW. The rate of protein deposition is primarily determined by the lean growth potential of the pig and the amino acid-to-digestible energy ratio of the diet, whereas the latter also influences fat deposition (Ruusunen *et al.*, 2007). Schinckel and De Lange (1996) reported a general decline in daily protein deposition after 90 kg BW, regardless of the pig genotype. In contrast, the Swiss Large White genotype tested in the present experiment with the control diet displayed a plateau-shaped curve for protein deposition in the EB and carcass only from 120 kg BW on. In agreement with previous studies (Chiba *et al.*, 2002; Ruusunen *et al.*, 2007), the low CP diet had a negative impact on protein deposition rate in the carcass and the EB. The level of differentiation between control and low CP diet decreased with increasing BW where the impact of dietary protein and amino acid supply is less important than the energy supply. Still it is also a sign that the recommendations for EAA for heavy pigs might be overstating the true requirements.

Differences in chemical body composition between genders are well known and documented (NRC, 2012). The protein deposition rate in entire males was numerically greater than for castrates and females. The greatest protein deposition rate with 168 g/day was observed at 140 kg BW in entire males fed the control diet. The mean value of protein deposition rate in entire males (159 g/day) was greater by 18% and 16% than for castrates and females, respectively. Different from Schinckel and De Lange (1996), who estimated upper level of daily protein retention for castrates at 70 kg, in the current study, castrates increased their protein deposition rate up to 120 kg BW. From 120 to 140 kg BW, protein deposition rate in the EB increased by 10% in entire males (5% and 17% in control and low CP entire males, respectively), but it remained at the same level in females and even declined by 7% in castrates (by 4% and 8% in control and low CP castrates, respectively). Fat and energy deposition displayed a linear increase with increasing BW in all three genders. As expected, the most extensive fat deposition rates were observed in castrates. Thus, the higher FI in castrates, when compared with females and entire males, was primarily used for fat and not for protein deposition. This is in agreement with results of other studies like Latorre *et al.* (2009), Rodríguez-Sánchez *et al.* (2011) and Suárez-Belloch *et al.* (2015). These results indicated that energy partitioning between protein and fat deposition depends on gender and strongly imply that gender differentiation is implemented in pig nutritional recommendations (Schinckel and De Lange, 1996; NRC, 2012). These would take into account the higher protein deposition rate of entire males compared with castrates and females, and the higher fat deposition rate of castrates compared with entire males (and females).

Nitrogen efficiency

The N efficiency found in the present study ranged between 37.5% and 57.5%. Similar efficiencies were observed by other researchers in multi-phase feeding experiments testing low dietary protein diets (Bourdon *et al.*, 1995; Pomar *et al.*, 2014). The values for N efficiency in our experiment were greater than those reported from a Swiss survey on 887 Swiss pig-fattening farms (Bracher A. and Spring P., personal communication), where estimated values ranged from 30% to 35%. In the present study, N efficiency was negatively affected by the low CP diet during the grower period. This could have been a consequence of both a lack of the limiting EAA and an imbalance in the EAA profile, which seems to be apparent when applying the Swiss recommendations (Agroscope, 2015). This assumption is confirmed by results of the study of Millet *et al.* (2011), where growing and finishing pigs used the amino acids more efficiently when fed low amino acid diets. Despite the aforementioned presumed EAA imbalances, low CP pigs were 10% more efficient than control pigs in the finisher II period. This points towards a certain overestimation of the CP and AA requirements assumed in the Swiss recommendations for pigs from 100 to 140 kg BW. An excess of dietary CP or EAA in this period, as the result of an attempt to fulfil these guidelines, would mean the need to eliminate the N excess resulting in the observed decrease N efficiency in control pigs. In this feeding phase, control pigs deposited similar amounts of protein between 120 and 140 kg BW, whereas deposition still increased by 4% in low CP pigs. This might have resulted from a gradual removal of deficiency in the low CP pigs allowing them to express compensatory protein deposition. Therefore, recommendations for the finisher II period for amino acids obviously need revision with new and compelling experimental data becoming available from the present and other studies. Greater N efficiencies were found in entire males compared with females with intermediate values for castrates. The greater FI of castrates in the grower and finisher I period compared with females, as well as the 5% greater dietary CP and EAAs supply in entire males could have enhanced this difference in N efficiency between females, entire males and castrates.

Conclusion

The data generated by the present experiment were obtained by analysis of different body fractions of pigs. Therefore, they can be used as a reference for future estimates of nutrient deposition rates, for calibrating N balance studies, and for developing and validating growth models. In the last decades, pigs have markedly increased the N efficiency, with entire males being the most efficient among the three genders. The current data show that in the finisher II period dietary CP content on as-fed basis can be reduced from 123 to 102 g for female and castrated pigs and from 129 to 104 g for entire males without a major impact on protein deposition or growth performance. The resulting revised recommendations would lead to a more efficient pig production from an economical and environmental point of view. It remains unclear whether the impact of the low CP diet on the grower and finisher I period was due to amino acid profile imbalances or deficiencies in distinct limiting EAA. This needs to be clarified in further studies.

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Supplementary material

For supplementary material/s referred to in this article, please visit http://dx.doi.org/10.1017/S1751731116001634

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