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Running head: Relationship between energy intake and body composition in modern pigs

Relationship between energy intake and growth performance and body composition in pigs selected for low backfat thickness

Fan Liu*[1], Christopher J. Brewster*, Samantha Gilmour*, David J. Henman*, Robert J. Smits*[2], Brian G. Luxford*, Frank R. Dunshea#§, John R. Pluske#†, Roger G. Campbell‡

* Rivalea Australia Pty Ltd, Corowa, NSW 2646, Australia

\# Faculty of Veterinary and Agricultural Sciences, University of Melbourne, Parkville, VIC, Australia, 3010.

§ Faculty of Biological Sciences, The University of Leeds, Leeds, United Kingdom, LS2 9JT.

† Australasian Pork Research Institute Ltd, Willaston, South Australia, 5118

‡ RG Campbell Advisory Pty Ltd, Semaphore, South Australia, 5019

[1] Corresponding author: fliu@rivalea.com.au

[2] Current address: Australian Pork Limited, Barton, ACT 2600, Australia

ABSTRACT

Genetic selection of pigs over recent decades has sought to reduce carcass fat content to meet consumer demands for lean meat in many countries (e.g.: Australia). Due to the impacts of genetic changes, it is unknown whether the carcass fat measures are still responsive to energy intake. Thus, the present experiment aimed to quantify the relationship between tissue composition and dietary energy intake in finisher pigs selected for low carcass backfat. Intact male and female pigs (n=56 for each sex; Primegro Genetics, Corowa, NSW, Australia) were fed seven different amounts of an amino acid adequate wheat-based diet containing 14.3 MJ digestible energy (**DE**)/kg to provide the following daily DE intakes- 25.8, 29.0, 32.6, 35.3, 38.5, 41.5 and 44.2 (*ad libitum*) MJ DE/d for males, and 25.8, 28.9, 32.0, 35.6, 38.3, 40.9 and 44.5 (*ad libitum)* MJ DE/d for females between 60 kg and 108 kg live weight. Body composition of anaesthetised pigs was measured using the Dual Energy X-ray Absorptiometry (**DXA**) method when individual pigs reached 108 kg, and protein, fat and ash deposition rates were calculated. Pigs were slaughtered on the 2nd day post-DXA scan for carcass backfat measurement. The results showed that the carcass backfat thickness (standardized at 83.7 kg carcass) increased by 0.125 mm for every MJ increase in daily DE intake in male pigs ($P = 0.004$; $R^2 = 0.130$), but carcass backfat of female pigs (standardized at 85.1 kg carcass) was not responsive to daily DE intake. Whole-body fat composition and fat deposition rate increased linearly (both $P < 0.01$) in male pigs but quadratically (both $P < 0.01$) in female pigs in response to DE intake. Every MJ increase of daily DE intake increased the rate of daily protein deposition by 3.8 g in intact male pigs ($P < 0.001$; $R^2 = 0.781$) and by 2.5 g in female pigs ($P < 0.001$; $R^2 = 0.643$). In conclusion, the selection for low backfat thickness over the last two decades has altered the response of fat deposition and backfat thickness to energy intake, particularly in female pigs. Despite this change, the linear relationship between DE intake and protein deposition rate was maintained in these modern genetics.

Key words: pig, energy, growth, lean, fat

List of Abbreviations

ADG, average daily gain; ADFI, average daily feed intake; BIC, Bayesian information criteria; DE, digestible energy; G:F, gain: feed; IGF-1, insulin-like growth factor 1; NADH, nicotinamide adenine dinucleotide; PUN, plasma urea nitrogen; SID, Standardized ileal digestible

INTRODUCTION

Reducing carcass fatness is a priority in some pig industries where price penalties apply on high carcass fatness. Controlling daily energy intake below the maximum protein deposition rate in finisher pigs has been practiced in these countries to avoid excessive carcass fatness, thus quantifying the relationship between energy intake and protein deposition potential of finisher pigs has been a key research area (Campbell et al., 1985; Bikker et al., 1996a; Milgen et al., 2016). The progress of genetic selection between 1985 and 2000 changed the relationship between protein deposition and energy intake from a linear-plateau (Campbell et al., 1985) to a linear pattern (King et al., 2004) as measured in Australian commercial genetics. However, carcass backfat still increased linearly with increased energy intake in 2000. Continuous genetic selection on low backfat has further reduced carcass backfat; for example, an annual reduction of 0.15 mm backfat was reported for the genetic trend in Australia (Hermesch et al., 2015), which may have reduced the carcass backfat variation and altered the phenotypic relationship between energy intake and carcass backfat thickness as well as fat content. The effectiveness of restricting energy intake as a strategy to manage carcass fatness should be re-evaluated given the progress of genetic selection. This experiment aimed to re-investigate the relationship between tissue deposition rate and energy intake in genetics that have been continuously selected for low backfat thickness in the past two decades. We hypothesized that carcass fatness measurements would have become less responsive to energy intake in the genetics selected for low backfat, whereas protein deposition rate would maintain a linear relationship with energy intake.

MATERIALS AND METHODS

Animals and Experimental Design

All animal procedures had prior institutional ethical approval (protocol ID:19N004C) under the requirement of the New South Wales Prevention of Cruelty to Animals Act (1979) in accordance with the National Health and Medical Research Council/Commonwealth Scientific and Industrial Research Organization/Australian Animal Commission Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (NHMRC, 2013).

Sixty-three intact male and 63 female cross-bred pigs (Large White × Landrace × Duroc; Primegro Genetics, Corowa, NSW, Australia) were selected into the experiment at 15 weeks of age [59.6 ± 2.49 kg and 59.4 ± 2.39 kg (mean ± standard deviation) for the male and female pigs respectively]. The sire line used in this study has been continuously selected for low backfat thickness as a significant part of the terminal sire selection index. The boars ranked at least top 10% based on this index were chosen as the terminal sires, and the pooled semen from these boars was used for mating the F1 cross-breed sows. Genetic correlations indicate that backfat thickness is positively correlated with growth rate and negatively correlated with feed efficiency (gain: feed) (Hermesch, 2004), thus selecting for low backfat compromises the progress of improving growth rate but facilitates superior feed efficiency (gain: feed). In a breeding program with a balanced breeding objective the genetic improvement in all three traits (backfat, growth rate, and feed efficiency) can be achieved. The relationship between the tissue deposition rate and energy intake of Primegro Genetics was quantified in 2000 (King et al., 2004).

All the experimental pigs were housed in the same shed and fed *ad libitum* using the same commercial diet before the commencement of the experiment. Seven pigs from each sex were randomly selected from the experimental pigs for estimating the initial body composition parameters using Dual Energy X-ray Absorptiometry (**DXA**). The entry body weight for the pigs used for the initial DXA scan was 59.2 ± 3.97 kg and 58.0 ± 3.23 kg (mean ± standard deviation) for male and female pigs, respectively, which were similar to other treatment groups. The scanned pigs were then removed from the experiment. The current experiment assumed that the body composition parameters obtained from the initial groups were representative of the experimental population, thus was used for calculating the initial tissue contents for other individual experimental pigs.

The remaining 56 pigs in each sex were randomly allocated into seven feeding levels ranging from 58% to 100% of the *ad libitum* amount of feed intake (n=8 pigs per sex per DE group). These pigs were housed and fed individually, so that the feed allowance could be controlled and daily feed intake could be measured individually. Prior to the start of the experiment, a relationship between the live weight of pigs and the amount of *ad libitum* digestible energy (**DE**) intake was quantified for male and female pigs separately, based on the unpublished data summarized from the research facility. This relationship was temporarily used as the reference for setting up daily DE allowance for the restricted-fed groups for each sex in the first three weeks of the experiment (when the true *ad libitum* DE intake remained unknown for this experiment). Next, the relationship between the live weight of pigs and *ad libitum* DE intake was adjusted based on the experimental record of actual feed intake of pigs and body weight from the *ad libitum* group. The feed allowance for each group was adjusted weekly and increased along with the body weight that was measured weekly.

The total amount of feed required for the whole experiment was manufactured in one consecutive run at a commercial feed mill and stored in a single silo at the experimental unit. The wheat, canola meal and soybean meal used in the experimental diets were scanned using a Near-Infrared analyzer (NIRS DS 2500, FOSS, Mulgrave, VIC, Australia) and the spectrum was submitted to AusScan (AUNIR, UK) and Evonik (SEA) Pte Ltd (Singapore) for estimating DE and amino acid levels respectively. The estimated DE and amino acids in the ingredients were then used for formulating the compound feed (Table 1). The diet was formulated to contain 14.3 MJ DE/kg and 0.57 g standardized ileal digestible (**SID**) lysine per MJ DE. The amount of SID lysine was optimized in recent experiments for achieving the maximum growth rate of boars and gilts of the same genetic line (Primegro Genetics) (Rikard-Bell et al., 2012; Rikard-Bell et al., 2013). The SID lysine level used in our diet was similar to the level optimized in an early study (50-85 kg range) (Giles et al., 2010) and the recommended level by the model developed by NRC (2012) (60-108 kg range). The experimental design assumed that the effects of feeding levels on growth rate and tissue deposition rate would reflect the effects of dietary energy intake when essential amino acids are not limited. Therefore, the seven corresponding DE intake levels were treated as a fixed factor in males and females separately (25.8, 29.0, 32.6, 35.3, 38.5, 41.5 and 44.2 MJ DE/d for male pigs, and 25.8, 28.9, 32.0, 35.6, 38.3, 40.9 and 44.5 MJ DE/d for female pigs). The actual average daily feed intake (**ADFI**) for the seven feeding levels is reported in Table 2.

Pigs were housed in individual pens in an enclosed and climatically controlled building (18 ± 2.7 ℃ for average shed temperature ± standard deviation). The pen size was 2.35 m × 1.77 m to provide 4.16 m^2 floor space to each pig. Pens consisted of half slatted plastic floor and half concrete floor. Pens were divided by a metal fence which allowed pigs to have visual and nose-to-nose contact with other experimental pigs. The feeder was located on the concrete floor and a nipple drinker was fixed on the fence above the plastic floor in each pen.

Growth Performance

Pigs were weighed weekly and feed allowances were adjusted relative to the updated body weight. Feed delivery and refusal were recorded every week and for calculating ADFI. Pigs were weighed twice per week when approaching 100 kg and the final body weight was recorded when pigs reached approximately 108 kg live weight. Average daily gain (**ADG**) was calculated using the weight gain divided by the number of days to reach 108 kg from entry. Then the body composition of pigs was measured using DXA and then slaughtered as per commercial practice 48 hours post-scan.

Plasma Urea Nitrogen Measurement

A blood sample was taken from each individual pig when it was approaching 108 kg, one day before the DXA scan. In the restricted-fed groups, pigs were fed at 07:00 h in the morning, and the blood samples were taken at 14:00 h. Blood was collected from the jugular vein using a heparinized vacutainer (BD Vacutainers, 4 mL, Item Number 367883, BD Diagnostics, Preanalytical Systems, Oxford, UK). Blood samples were centrifuged at 1600 × *g* for 10 min at 4 °C (Heraeus Megafuge 16R, Item Number. 50122064, Thermo Fisher Scientific, North Ryde, NSW, Australia) for harvesting plasma. The plasma samples were stored at −20 °C before analyzing for plasma urea nitrogen (**PUN**) using a commercial kit (Infinity Urea Liquid Stable Reagent, Thermo Scientific, Cat No. TR12421, Middletown, VA, USA). Briefly, the urea was firstly converted to ammonia after addition of urease, then the ammonia reacted with reduced nicotinamide adenine dinucleotide (**NADH**) and a-keto-glutamate in the presence of glutamate dehydrogenase. The rate of the above reactions, which is positively correlated with the initial concentration of plasma urea, was measured as the colorimetric change at 340 nm absorbance due to the disappearance of NADH. The assay was run in duplicate and the inter-assay coefficient of variation was 5.6%.

Dual Energy X-ray Absorptiometry (DXA) scan

Dual-energy X-ray absorptiometry can accurately estimate protein, water, fat and ash composition in anaesthetized pigs (Suster et al., 2003 and 2004). Pigs fasted from 15:00 h (after blood sampling for PUN measurement) until the next morning when pigs approached 108 kg. Pigs were sedated by intramuscular injection of Stresnil (0.2 mL per kg body weight, Elanco Animal Health, Kemps Creek, NSW, Australia). Once the pig was sedated, a face mask was mounted and connected to an isoflurane anesthesia machine. For rapid induction of anesthesia, 5% isoflurane (Piramal Enterprises Limited, Hyderabad, India) and 3.5 L/min medical oxygen was given for a short duration. Then, isoflurane was reduced to 1.5 to 2.0 % (depending on the depth of anesthesia of the individual pig) for maintaining the anesthesia state. Respiration rate, eyeball position, eye reflexes and conjunctiva color were checked every 5 minutes during anesthesia to ensure the depth of anesthesia was appropriate. Then, the pig was placed onto the DXA scanning platform (Hologic Discovery W, Model S/N85287, Software version 13.3.0.1, Waltham, MA) (Suster et al., 2003) with the belly facing down. A quantity control calibration (TBAR1904-NHANES BCA calibration) on the scanner was performed at the beginning of every scan day by using a step phantom made of acrylic and aluminium. Each scan took an average of seven minutes for a 108 kg pig. Pigs were returned to a recovery area after the DXA scan and a post-anesthesia health check was conducted every 10 minutes until the pig regained mobility. The outputs of each DXA scan were whole-body mass, lean mass, fat mass and bone mineral density data, and these data were converted to chemically determined water, protein, fat and ash mass using the algorithms validated for live pigs (Suster et al., 2003). The initial tissue composition (%) was assumed as the average value obtained from the seven male and female pigs that were scanned at the start of the experiment. The initial body composition (%) was used for calculating the initial tissue mass for each experimental pigs. Tissue deposition rates were calculated as the following equation:

$$Tissue\ deposition\ rate = \frac{(Final\ tissue\ mass - initial\ tissue\ compsition\ (\%) \times start\ body\ weight)}{Days\ of\ growth}$$

The deposition rate of whole-body water, protein, fat and ash is expressed as grams per day; final tissue mass is the tissue weight (grams) of a whole pig estimated using DXA method (converted to chemically measured water, protein, fat and ash values); initial tissue composition (%) was the average tissue composition from the seven female or male pigs scanned at entry as described above (randomly selected from same progeny population and had similar starting body weight as other experimental groups); start body weight (grams) is the live weight of each individual pig at entry. Energy retained as fat and protein was calculated using the factors 39.6 MJ/kg for fat (Burlacu et al., 2009) and 24.2 MJ/kg for protein (Jordan and Brown, 1970).

Measurements of Carcass Traits

Pigs were transported to a commercial abattoir on the first day after their DXA scan and housed in a lairage until killed in the morning of the second day. The hot standard carcass weight was measured after trimming off visceral organs (Ausmeat Trim 1 standard) (Australian Pork Limited, 2018). Backfat thickness and loin depth were measured at the P2 site (last rib; 65 mm from the midline) using Hennessey and Chong's grading probe. Dressing percentage was calculated as the ratio between hot standard carcass weight and live weight.

Statistical Methods

The responses of growth performance, tissue deposition and carcass traits to DE intake were first tested for both linear and quadratic effects using the nominal levels (25.8, 29.0, 32.6, 35.3, 38.5, 41.5 and 44.2 MJ DE/d for male and 25.8, 28.9, 32.0, 35.6, 38.3, 40.9 and 44.5 MJ DE/d for female pigs) using General Linear Model in SPSS (IBM SPSS Statistics for Windows, v25, Armonk, NY). Hot standard carcass weight was used as a covariate for the measurement of carcass backfat and loin depth. Furthermore, where a relationship was quadratically fitted and a change of slope (known as a "breakpoint") was visually identified, the fit of a one-knot piecewise regression model was examined (i.e.: protein deposition rate in male pigs, fat deposition rate and the ratio of fat: protein deposition rate in female pigs). The following piecewise regression model was used for describing their relationship with daily DE intake:

$$Y = a + b \times DE + c \times (DE - breakpoint) \; when \; DE > breakpoint;$$

$$Y = a + b \times DE \; when \; DE \leq breakpoint$$

Here, Y is the outcome variable, DE is the nominal level of daily DE intake, a is the constant, b is the coefficient of regression, and c is the change of regression coefficient when DE is greater than the breakpoint. The piecewise regression model was estimated using the Levenberg-Marquardt method in the Non-Linear Regression function in SPSS. The best-fitting piecewise regression model was identified by iteratively modifying the initial values for the parameters and breakpoint. The piecewise model with the highest R^2 was chosen to compare with linear and quadratic regression models.

Bayesian information criteria (**BIC**) is an index that reflects model residual errors as well as the model complexity. The BIC value was used for comparing the regression models (i.e., linear or quadratic vs the one-knot piecewise regression model) when linear and quadratic response were both significant ($P \leq 0.05$). The model with a lower BIC (the difference of BIC between models ≥ 2) was selected. If both models had a similar BIC (the difference of BIC between models < 2; no superior model), then a simpler model was chosen and reported. The equations for calculating BIC is referenced from (Burnham and Anderson, 2002):

$$BIC = n \times \ln\left(\frac{RSS}{n}\right) + K \times \ln(n)$$

Here, RSS is the residual sum of squares; ln is the natural logarithm; n is the number of samples in the data; K is the number of parameters in the model (K=2, 3 and 4 for the linear, quadratic and one-knot piecewise regression model respectively).

RESULTS

Initial Body Composition of Reference Pigs at 60 kg

The average water, protein, fat and ash composition was 63.0% ± 1.14%, 16.8% ± 0.21%, 12.6% ± 0.71% and 2.7% ± 0.10% for intact male pigs (mean ± standard deviation; n = 7) and 61.7% ± 2.23%, 16.6% ± 0.43%, 14.4% ± 1.46% and 2.8% ± 0.07% for female pigs (mean ± standard deviation; n = 7) respectively.

Growth Performance

Increasing DE intake increased ADG linearly ($P < 0.001$) and quadratically ($P = 0.014$) for intact males (Table 2). Increasing DE intake increased ADG linearly ($P = 0.021$) and quadratically ($P = 0.014$) for females (Table 3). A model comparison (linear vs quadratic) showed that adding a quadratic term in the regression model improved the R^2 from 0.817 to 0.833 (P = 0.032) in intact male pigs, but resulted in similar BIC values (-266.9 vs -267.7 for linear vs quadratic model), thus the linear model was chosen for describing the relationship between DE intake and ADG in male pigs. The quadratic model was chosen for the relationship in female pigs as the BIC value was reduced (-308.6 vs -310.6 for linear vs quadratic model). The best fit models are described as:

$$ADG\ (male) = -0.128\ (\pm\ 0.068\ s.e.) + 0.030\ (\pm\ 0.002\ s.e.) \times DE$$

$$R^2 = 0.817, P < 0.001$$

$$\begin{aligned} ADG\ (female) & \\ &= -0.680\ (\pm\ 0.300\ s.e.) + 0.0626\ (\pm\ 0.0174\ s.e.) \times DE \\ &- 0.00054\ (\pm\ 0.000249\ s.e.) \times DE^2 \end{aligned}$$

$$R^2 = 0.865, P < 0.001$$

in which DE is the daily digestible energy intake (MJ/day); s. e. is the standard error of the regression coefficients or the constant.

Increasing energy intake linearly (P < 0.001 for both sexes) and quadratically (P < 0.001 for both sexes) shortened the days from 60 kg to reach 108 kg live weight (Table 2 and Table 3).

Gain:feed responded to increased daily DE intake in both a linear (P = 0.006) and quadratic (P = 0.002) manner in intact male pigs (Table 2) with the quadratic model preferred due to the reduced BIC value from -388.6 to -395.0. In female pigs, the response of G:F to the increased DE intake was quadratic (Linear, P = 0.17; Quadratic, P = 0.004) (Table 3). The best fit models are described as:

$$
\begin{aligned}
Gain{:}feed\ (male) \\
&= -0.1269\ (\pm\ 0.1334\ s.e.) + 0.02755\ (\pm\ 0.00778\ s.e.) \times\ DE \\
&\quad - 0.000367\ (\pm\ 0.000111\ s.e.) \times DE^2
\end{aligned}
$$

$$R^2 = 0.280, P < 0.001$$

$$
\begin{aligned}
Gain{:}feed\ (female) \\
&= -0.000361\ (\pm\ 0.109\ s.e.) + 0.0192\ (\pm\ 0.0063\ s.e.) \times\ DE \\
&\quad - 0.000264\ (\pm\ 0.00090\ s.e.) \times DE^2
\end{aligned}
$$

$$R^2 = 0.167, P = 0.008$$

Whole-Body Tissue Composition

The whole-body protein composition (%) reduced linearly (P = 0.013) but not quadratically (P = 0.82) in response to the increased daily DE intake in male pigs (Table 4). The whole-body protein composition in female pigs reduced linearly (P =

0.002) but not quadratically (P = 0.15) in response to the increased DE intake (Table 5). The best-fit models are described as:

$$Whole\ body\ protein\ \%\ \ (male)$$
$$=\ 15.4\ (\pm\ 0.183\ s.e.) - 0.012\ (\pm\ 0.0051\ s.e.) \times DE$$
$$R^2 =\ 0.092, P = 0.023$$

$$Whole\ body\ protein\ \%\ \ (female)$$
$$=\ 15.0\ (\pm\ 0.210\ s.e.) - 0.015\ (\pm\ 0.0058\ s.e.) \times DE$$
$$R^2 =\ 0.106, P = 0.014$$

The whole-body fat composition (%) increased linearly (P = 0.001) but not quadratically (P = 0.99) in response to the increased daily DE intake in male pigs (Table 4). The whole-body fat composition increased linearly (P < 0.001) and quadratically (P = 0.031) in female pigs in response to the increased DE intake (Table 5). Adding the quadratic term increased (P = 0.048) R^2 from 0.164 to 0.224 and reduced BIC value (44.1 vs 41.9 for linear vs quadratic regression model), thus the quadratic regression model was chosen for describing the relationship between DE intake and whole-body fat composition in female pigs. The best-fit models are described as:

$$Whole\ body\ fat\ \%\ \ (male) =\ 12.1\ (\pm\ 0.96\ s.e.) + 0.083\ (\pm\ 0.027\ s.e.) \times DE$$
$$R^2 =\ 0.152, P = 0.003$$

$$Whole\ body\ fat\ \%\ \ (female)$$
$$=\ 16.7\ (\pm\ s.e.) + 0.90\ (\pm\ 0.396\ s.e.) \times DE$$
$$-\ 0.011\ (\pm\ 0.006\ s.e.) \times DE^2$$

$$R^2 = 0.224, P = 0.001$$

The whole-body water composition (%) reduced linearly in response to the increased daily DE intake in male (Linear, $P = 0.026$; Quadratic, $P = 0.78$) and female pigs (Linear, $P = 0.002$; Quadratic, $P = 0.15$) (Table 4). The whole-body ash composition (%) declined linearly (Linear, $P = 0.002$, Quadratic, $P = 0.091$) in response to the increased DE intake in male pigs (Table 5). Whole-body ash composition did not respond (Linear, $P = 0.58$; Quadratic, $P = 0.86$) to DE intake in female pigs.

Tissue Deposition Rate

Protein deposition rate (g/d) increased linearly (Linear, $P < 0.001$; Quadratic, $P = 0.083$) in response to the increased daily DE intake in male pigs (Table 6, Figure 1 (A)). Adding the quadratic term to the linear regression model did not improve R^2 ($P = 0.17$) but yielded a higher BIC (305.1 vs 307.1 for linear vs quadratic regression model). A piecewise regression model (breakpoint at DE = 38.5 MJ/d) achieved a slightly greater R^2 (0.735 vs 0.749) but higher BIC (305.1 vs 310.1 for linear vs piecewise regression model), thus the linear regression model was preferred for describing the relationship between DE intake and protein deposition rate in male pigs. The regression coefficient in the linear regression model suggests that every MJ increase in daily DE intake increased the protein deposition rate by 3.83 g per day. Protein deposition rate in female pigs increased linearly (Linear, $P < 0.001$; Quadratic, $P = 0.87$) in response to the increased daily DE intake (Table 7, Figure 1 (B)), thus a linear regression model was used (R^2=0.643, $P < 0.001$). Every MJ increase in DE intake increased protein deposition rate by 2.50 g per day. The best-fit models are described as:

$$Protein\ gain\ rate\ (male) = -7.65\ (\pm\ 11.230\ s.e.) + 3.83\ (\pm\ 0.314\ s.e.) \times\ DE$$

$$R^2 = 0.735, P < 0.001$$

$$Protein\ gain\ rate\ (female) = 20.94\ (\pm\ 9.96\ s.e.) + 2.50\ (\pm\ 0.254\ s.e.) \times\ DE$$

$$R^2 = 0.643, P < 0.001$$

The fat deposition rate (g/d) of males increased linearly (Linear, P < 0.001; Quadratic, P = 0.47) (Table 6, Figure 1 (A)). Every MJ increase of daily DE intake increased fat deposition rate by 7.4 g in male pigs. The fat deposition rate increased both linearly (P < 0.001) and quadratically (P = 0.004) in response to the increased DE intake in female pigs (Table 7, Figure 1 (B)). Adding a quadratic term in the regression model improved (P = 0.007) the R^2 from 0.753 to 0.786, and the BIC value was reduced from 371.1 to 363.0. A piecewise regression model achieved a slightly greater R^2 (0.796) but a similar BIC value as the quadratic model (364.4 vs 363.0 for piecewise vs quadratic regression model), so a simpler model, the quadratic regression model (R^2 = 0.785, P < 0.001) was chosen for describing the relationship between DE intake and fat deposition rate in female pigs. The best fit models are described as:

$$Fat\ gain\ rate\ (male) = -81.9\ (\pm\ 20.7\ s.e.) + 7.4\ (\pm\ 0.60\ s.e.) \times DE$$

$$R^2 = 0.750, P < 0.001$$

$$Fat\ gain\ rate\ (female) = -362.9\ (\pm\ 123.30\ s.e.) + 25.7\ (\pm\ 7.19\ s.e.) \times DE - 0.27\ (\pm\ 0.102\ s.e.) \times DE^2$$

$$R^2 = 0.786, P < 0.001$$

The ratio of fat: protein deposition rate of male pigs increased linearly (Linear, $P = 0.002$, Quadratic, $P = 1.00$) in response to the increased daily DE intake (Table 6, Figure 1 (A)). In female pigs the ratio of fat: protein deposition rate increased linearly ($P < 0.001$) and quadratically ($P = 0.023$) in response to the increased DE intake (Table 7, Figure 1 (B)). The quadratic model was chosen for describing the relationship between DE intake and the ratio of fat: protein deposition rate in female pigs due to the lower BIC value (-135.9 vs -137.9 for linear vs quadratic model). The best fit models are described as:

$$Ratio\ of\ fat{:}protein\ gain\ rate\ \ (male)$$

$$= \ 0.818\ (\pm\ 0.204\ s.e.) + 0.016\ (\pm\ 0.006\ s.e.) \times DE$$

$$R^2 = \ 0.130, P = 0.006$$

$$Ratio\ of\ fat{:}protein\ gain\ rate\ \ (female)$$

$$= \ -2.24\ (\pm\ 1.588\ s.e.) + 0.215\ (\pm\ 0.093\ s.e.) \times DE$$

$$-\ 0.003\ (\pm\ 0.0013\ s.e.) \times DE^2$$

$$R^2 = \ 0.225, P = 0.001$$

Water deposition rate (g/d) increased linearly but not quadratically with increased daily DE intake in male (Linear, $P < 0.001$, Quadratic, $P = 0.107$) (Table 6) and female pigs (Linear, $P < 0.001$, Quadratic, $P = 0.62$) (Table 7). Ash deposition rate (g/d) increased linearly ($P < 0.001$) and quadratically ($P = 0.036$) in response to increased daily DE intake in male pigs (Table 6). Ash deposition rate increased linearly ($P < 0.001$) but not quadratically ($P = 0.14$) with the increased daily DE intake in female pigs (Table 7).

Energy Retention for Protein and Fat Deposition

The calculated amount of energy retained as protein and fat deposition increased linearly (Linear, P < 0.001; Quadratic P = 0.29) in response to the increased daily DE intake in male pigs (Table 6). Every MJ increase of daily DE intake increased the amount of energy retention by 0.38 MJ in male pigs.

The calculated amount of energy retained for protein and fat deposition increased both linearly (P < 0.001) and quadratically (P = 0.005) in response to the increased daily DE intake in female pigs (Table 7). Adding a quadratic term in the regression model improved (P = 0.006) the R^2 from 0.827 to 0.850 and reduced BIC value from 2.5 to -1.6, so the quadratic regression model was chosen for describing the relationship between DE intake and the amount of energy retention in female pigs. The best-fit models are described as:

$$Amount\ of\ DE\ retained\ for\ protein\ and\ fat\ deposition\ (male)$$

$$= -3.43\ (\pm\ 0.900\ s.e.) + 0.384\ (\pm\ 0.025\ s.e.) \times DE$$

$$R^2 =\ 0.812, P < 0.001$$

$$Amount\ of\ DE\ retained\ as\ protein\ and\ fat\ (female)$$

$$= -13.57\ (\pm\ 4.372\ s.e.) + 1.058\ (\pm\ 0.255\ s.e.) \times DE$$

$$-\ 0.010\ (\pm\ 0.004\ s.e.) \times DE^2$$

$$R^2 =\ 0.850, P < 0.001$$

Efficiency of DE Retention

The efficiency (%) of DE retained as protein and fat increased linearly (P < 0.001; Quadratic, P = 0.103) in response to the increased daily DE intake in male pigs (Table 6). Every MJ increase of daily DE intake increased the DE retention efficiency (%) by 0.30 in male pigs.

The efficiency (%) of DE retained as protein and fat increased linearly ($P = 0.001$) and quadratically ($P < 0.001$) in response to the increased daily DE intake in female pigs (Table 7). Adding a quadratic term in the regression model improved ($P < 0.001$) the R^2 from 0.144 to 0.360 and reduced BIC value from 96.1 to 77.8, so the quadratic regression model was chosen for describing the relationship between DE intake and efficiency of DE retention in female pigs. The best fit models are described as:

$$Efficiency\ (\%)\ of\ DE\ retained\ as\ protein\ and\ fat\ (male)$$
$$= 17.6\ (\pm\ 2.15\ s.e.) + 0.303\ (\pm\ 0.060\ s.e.) \times DE$$
$$R^2 =\ 0.321, P < 0.001$$

$$Efficiency\ (\%)\ of\ DE\ retained\ as\ protein\ and\ fat\ (female)$$
$$= -15.0\ (\pm\ 9.38\ s.e.) + 2.45\ (\pm\ 0.547\ s.e.) \times DE$$
$$-\ 0.033\ (\pm\ 0.008\ s.e.) \times DE^2$$
$$R^2 =\ 0.360, P < 0.001$$

Plasma Urea Nitrogen

Plasma urea nitrogen concentration was not affected (Linear, P=0.63, Quadratic, P=0.90) by DE intake in intact male pigs (Table 6), but it reduced linearly (Linear, $P = 0.021$; Quadratic, $P = 0.44$) with increased daily DE intake in female pigs (Table 7).

Carcass Traits

Dressing percentage (%) of male pigs increased linearly (Linear, $P = 0.001$; Quadratic, $P = 0.38$) with increased DE intake (Table 8), whereas the dressing percentage of female pigs was not affected by DE intake (Linear, $P = 0.67$; Quadratic, $P = 0.13$) (Table 9). The best-fit model is described as:

$$Dress\ \%\ \ (male) =\ 73.6\ (\pm\ 1.07\ s.e.) + 0.100\ (\pm\ 0.0301\ s.e.) \times DE$$

$$R^2 = 0.156, P = 0.002$$

Carcass backfat thickness (at P2 site) explained 34.3% variation of the whole-body fat composition estimated by DXA in all the pigs in this experiment ($R^2 = 0.343$, $P < 0.001$, Supplementary Figure 1). The carcass backfat thickness increased linearly (Linear, $P = 0.003$; Quadratic, $P = 0.49$) with increased daily DE intake in intact males at a regression coefficient of 0.125 mm per MJ DE intake per day (Table 8, Figure 2), whereas it did not respond (Linear, $P = 0.51$; Quadratic, $P = 0.61$) to DE intake in females (Table 9, Figure 2). The best-fit model is described as:

$$Carcass\ backfat\ (P2\ site)\ \ (male)$$

$$= 7.59\ (\pm 1.477\ s.e.) + 0.125\ (\pm 0.0414\ s.e.) \times DE$$

$$R^2 = 0.130,\ P = 0.004$$

Loin depth measured in carcasses increased quadratically (Linear, $P = 0.21$; Quadratic, $P = 0.032$) with the increased daily DE intake in male pigs (Table 8), but it was not affected by DE intake in female pigs (Linear, $P = 0.24$, Quadratic, $P = 0.42$) (Table 9).

DISCUSSION

Genetic selection has reduced phenotypic backfat and whole-body fat composition

To meet consumer demand for lean pork and maximise profit under carcass price grids penalizing excessive carcass backfat thickness (i.e.: >12 mm), backfat thickness has been the most weighted selection trait for this sire line in the past two decades. The genetic selection for low backfat thickness has markedly reduced the phenotypic whole-body fat content and carcass backfat thickness in the commercial pigs used in the Australian pig industry. Specifically, the carcass backfat thickness measured in the current experiment was 22% and 15% less in intact male and female pigs respectively, compared with other Australian publications using the same genetic line (Primegro Genetics) from the same company over the past two decades (Dunshea et al., 2003; McCauley et al., 2003; Oliver et al., 2003; Suster et al., 2004; Suster et al., 2005; Suster et al., 2006a; Suster et al., 2006b) (summarized in Supplementary Table 1). The whole-body fat content of finisher pigs in the current experiment declined from 19% to 16% in intact male pigs and from 21% to 18% in female pigs compared with the same genetic line measured using the same DXA scanner in the past two decades (Supplementary Table 1). The voluntary dietary DE intake of finisher pigs was maintained at 1.59 and 1.60 MJ DE per kg metabolic body weight for male and female pigs, respectively, compared with the above Australian studies (Supplementary Table 1). The protein deposition rate of male and female pigs in the current study were both similar to pigs of a comparable weight range in previous work (Suster et al., 2004). In contrast, the fat deposition rate of male and female pigs was 10% and 20% less respectively than pigs of a similar weight range in previous studies (Dunshea et al., 2003; Suster et al., 2005; Suster et al., 2006b).

Response of carcass backfat and whole-body fat content to DE intake

The key finding from the experiment was that carcass backfat thickness increased by 0.125 mm for every MJ daily DE intake in intact male pigs but it did not respond to increasing DE intake in female pigs. In comparison, in the same genetic line from the the same company evaluated by King et al. (2004), every MJ increase in daily DE intake increased carcass backfat thickness by 0.20 mm and 0.30 mm in male and females pigs (slaughtered at 120 kg live weight), respectively. In a previously reported Australian study using less improved genetics, the maximum protein deposition rate plateaued at 33 MJ DE/d, and every MJ of daily DE intake beyond 33 MJ/d increased backfat thickness by 1.1 mm and 1.0 mm in male and female pigs (90 kg live weight), respectively (Campbell et al., 1985). The differing response of carcass backfat thickness to energy intake found herein is likely to be the outcome of the genetic selection for low backfat thickness in this sire line over the past two decades. It is important to mention that the backfat measurement on carcasses at the P2 site only explained 34% variation of whole-body fat composition measured by DXA method in the experiment, implying that pigs may have other means of meeting the demand of the genetic selection for low backfat at the P2 site; for example: adjusting body shape or redistributing where fat is deposited (Suster et al., 2003). Therefore, the response of carcass backfat and whole-body fat composition to energy intake was slightly different.

The whole-body fat composition in male pigs increased linearly in response to energy intake, whereas in females the response was quadratic (increased at a reducing rate) as reported in the current experiment. The linear response of whole-body fat composition to daily DE intake of male pigs in our study was similar to the response reported in the genetic line from the same company two decades ago (King et al., 2004), but differed from the earlier work using a less improved Australian genetic line (Campbell and Taverner, 1988). The genetic line used by Campbell and Taverner (1988) had an overall low protein deposition rate and it followed a linear-plateau relationship with daily DE intake. Consequently, in this previous study, the ratio of fat: protein deposition rate increased at a greater rate once daily DE intake passed the maximum protein deposition rate, resulting a whole-body fat composition increasing at a greater rate with increased daily DE intake. For the female pigs in current study, the response of whole-body fat composition to daily DE intake followed the same pattern (increased at a reducing rate) as the ratio of fat: protein deposition rate. Such pattern was driven by the similar response of fat deposition rate to DE. Bikker et al. (1996b) also found that the fat tissue deposition rate increased at a slightly reduced rate (small evidence of a quadratic response) with increased daily DE intake in 45-85 kg female pigs. The mechanism for such a quadratic response of fat deposition rate to DE intake in female pigs remains unknown. Considering that low fat deposition can be a consequence of higher heat production (Milgen et al., 2007) and that the thermic effect increases with energy intake (de Lange et al., 2007), we suspect that there was a greater proportion of heat production at the high levels of DE intake (above 40 MJ DE/d), possibly as a metabolic strategy of the female pigs to satisfy the selection pressure for low backfat. Previous studies have shown the association of increased heat production and lean genotype in pigs (Koong et al., 1983; Yen and Pond, 1985) and rodents (Lin et al., 1979). In contrast to the females, the male pigs in the current experiment did not demonstrate a quadratic relationship between fat deposition rate and DE intake, possibly because the overall greater protein deposition rate in male pigs enabled them to reach the selection pressures of low backfat without compromising the efficiency of DE retention when at a high level of DE intake.

Response of protein deposition rate to DE intake

Another key finding from the current experiment was that every MJ increase of daily DE intake increased the rate of protein deposition by 3.8 g/d in intact male pigs and by 2.5 g/d in female pigs throughout the tested range of daily DE intakes (25.8-44.5 MJ/d). Taking the intercept of the regression models into consideration, on average male pigs required 16% less DE than female pigs for depositing one gram of protein when fed *ad libitum*. Some early studies suggested that the selection emphasis on high lean gain rate had changed the relationship between protein deposition rate and dietary energy intake to a linear manner in British (Rao and McCracken, 1991), Australian (Dunshea et al., 1993; King et al., 2004) and Dutch (Bikker et al., 1996a) genetics. Quadratic (or linear-plateau) relationships between protein deposition rate and DE intake in male pigs were only reported in some early genetics in the 1980s and 90s in Australia (Campbell et al., 1985; Campbell and Taverner, 1988) and France (Quiniou et al., 1996). The long-term selection for reduced backfat thickness has not altered the linear relationship between protein deposition rate and energy intake in the current genetics, suggesting that maintaining such a linear relationship is a crucial prerequisite to avoid excessive fat deposition in response to high energy intake. Plasma urea nitrogen, a biomarker of excessive amino acids for protein synthesis, reduced linearly in the female pigs in response to DE intake in the current study. It supports the fact that the protein deposition rate increased linearly with the elevated energy intake in female pigs. By comparison, PUN did not respond to the energy intake in male pigs. The sex difference might be due to the higher efficiency of protein deposition thus an overall greater utilization of amino acids in the male compared with female pigs.

Response of growth performance to DE intake

Average daily gain of the current genetics exhibited a quadratic response to DE intake in female pigs. In male pigs the response was linear although there was some evidence of a quadratic response. These responses differed from the linear relationships reported in the same genetic line from the same company for both sexes two decades ago (King et al., 2004) but was similar to less improved Australian genetics reported in an earlier study (Campbell et al., 1985). The linear response of ADG to DE intake in male pigs was consistent with the linear relationships of protein as well as fat deposition rate in response to DE intake. The quadratic response of ADG to energy intake in female pigs was likely associated with the quadratic relationship between energy intake and fat deposition rate. Similarly, the ADG and fat tissue deposition rate of the Dutch genetics (45-85 kg gilts) used by Bikker et al. (1996b) both exhibited some evidence of a quadratic response (increased as a reducing rate) to energy intake. The quadratic response of G:F to energy intake for both male and female pigs differed from the linear relationship reported in the same genetic line supplied by the same company two decades ago (King et al., 2004). The G:F was overall greater in the current study than that reported two decades ago, likely as a consequence of the selection for low blood concentration of IGF-1 in the sire line. The blood IGF-1 concentration is negatively correlated with G:F in this genetic line (Bunter et al., 2005). In addition, the simultaneous selections for fast growth and low backfat may direct energy deposition towards lean tissue, which will facilitate superior G:F, because depositing lean tissue deposition (containing water) requires less energy than fat (Tess et al., 1984). In the current study, the G:F started to decrease at the high DE intakes (approximal >39 MJ/d). Such pattern was similar as the response of DE rention efficiency to the increased daily DE intake, particularly in female pigs. As limited by the experimental facility, the current experiment did not quantify the enery loss in the urine or in the form of heat production, thus we cannot definitively explain the quadratic response of G:F to the increased DE intake from the energy metabolism aspect. This highlights a future research direction.

Sex-dependent strategies to achieve low backfat

Our results suggest that female and male pigs may have two different mechanisms to meet the genetic selection pressure for reduced backfat. Female pigs, that have an intrinsically higher body fat content than entire male pigs, may respond to high dietary energy intake with a biological inefficiency such as increased heat production to limit energy available for fat deposition. Such a strategy compromises energy efficiency for tissue growth as evidenced by the quadratic relationship between DE efficiency for fat and protein retention, which peaked at 38.2 MJ DE/day in female pigs. In comparison, our data suggests that the male pigs do not need to compromise the DE efficiency for protein and fat deposition. The higher protein deposition rate allows male pig to utilize energy intake towards a protein deposition as an effective strategy to achieve lower backfat. Whilst consumer demand for lean pork and associated pricing grids penalize carcass fatness, selection indices need to evolve to avoid biologically inefficient responses to selection pressure on low backfat.

Implications to feeding commercial finisher pigs

The updated relationship between carcass backfat and energy intake from the current study provides quantitative guidance for managing carcass fatness by understanding the tissue deposition responses to energy intake in commercial pig production. Given that the carcass backfat thickness of male pigs still responds to daily DE intake, restricting daily DE intake remains a viable strategy to reduce backfat thickness in male pigs where penalties for carcass fatness are punitive. However, this strategy is less effective compared with the same genetic line from the same company 20 years ago (King et al., 2004). With regard to female pigs, *ad libitum* feeding (i.e., up to 44.5 MJ DE/day in the current study) is not likely to increase carcass backfat thickness. The protein deposition rate of females increased linearly throughout the wide range of DE intake. Future experiments should re-evaluate the economics of unrestricted and restricted feeding strategy in female and male pigs under various commercial conditions, where energy intakes are lower than under the ideal experimental conditions of the present study. Strategies other than manipulating energy intake to reduce carcass backfat thickness are required for female pigs if the market continues to penalize backfat thickness.

In conclusion, this study supported the concept that the effectiveness of restricting energy allowance to reduce fatness or backfat thickness of finisher pigs has decreased in the genetics selected for reduced backfat, particularly in female pigs. The protein deposition rate of both intact male and female pigs maintained a linear relationship with energy intake over several decades of selection, suggesting it is an important mechanism to avoid excessive fat deposition in response to high energy intake. However, female and male pigs seem to have developed different strategies for adapting to the selection pressure for low backfat over a prolonged period of time.

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Disclosures

The authors declare no real or perceived conflicts of interest.

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Tables and Figures

Table 1. Composition of the experimental diet

Ingredient	% as-fed basis
Wheat	75.1
Canola meal	10
Soybean meal	8.9
Blood meal	1.5
Tallow	1.6
Limestone	0.96
Dicalcium Phosphate	1.4
Lysine HCL	0.15
Methionine	0.02
Threonine	0.05
Salt	0.2
Copper Proteinate (24% Cu)	0.033
Vitamin Premix[1]	0.04
Mineral Premix[2]	0.07
Calculated composition	
Dry matter, %	90.2
Digestible energy, MJ/kg	14.3
Metabolizable energy[3], MJ/kg	13.8
Crude protein, %	18.8
Fat, %	3.1
Starch, %	52
Crude fibre, %	3.6
Ash, %	4.9
Total calcium, %	0.8
Available phosphorous, %	0.4
SID lysine, %	0.82
SID lysine:DE, g/MJ	0.57

[1] Supplied per kg of diet: copper, 101 mg; cobalt, 0.5 mg; manganese, 28 mg; magnesium, 1.6 g; zinc, 50 mg; iron, 70 mg; iodine, 0.5 mg; selenium, 0.2 mg; chromium 0.2 mg.

[2] Supplied per kg of diet: vitamin A, 3000 IU; vitamin D3, 600 IU; vitamin K, 0.4 mg; vitamin B-1, 0.6 mg; vitamin B-2, 2.0 mg; vitamin B-6, 1.2 mg; vitamin B-12, 4.0 µg; Niacin, 12 mg; pantothenic acid, 6 mg, Vitamin E 19 IU.

[3] Metabolizable energy of the diet was converted from digestible energy using the equation: Metabolizable energy = Digestible energy (kcal/kg) - 0.68 × Crude protein (g/kg) (Noblet and Perez, 1993)

Table 2. Growth performance of male pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE[4] intake of male, MJ/d							SE	P-values	
	25.7	29.0	32.6	35.3	38.5	41.5	44.2		Linear	Quadratic
Body weight (d 0), kg	59.6	59.6	59.6	59.6	59.6	59.6	59.6	0.93	1.00	1.00
ADFI[1], kg	1.78	2.00	2.25	2.44	2.66	2.87	3.05	0.040	<0.001	0.39
Days to reach 108 kg	81.3	68.5	57.9	52.9	46.9	44.9	42.5	2.04	<0.001	<0.001
ADG[2], kg	0.60	0.73	0.86	0.95	1.04	1.09	1.14	0.031	<0.001	0.014
G:F[3], kg:kg	0.34	0.36	0.38	0.39	0.39	0.38	0.38	0.010	0.006	0.002

[1] Average daily feed intake

[2] Average daily gain

[3] Gain: feed

[4] Digestible energy, MJ/d

Table 3. Growth performance of female pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE[4] intake of female, MJ/d							SE	*P*-values	
	25.8	28.9	32.0	35.6	38.2	40.9	44.5		Linear	Quadratic
Body weight (d 0), kg	59.4	59.4	59.4	59.4	59.4	59.4	59.4	0.89	1.00	1.00
ADFI[1], kg	1.81	2.03	2.24	2.48	2.68	2.86	3.11	0.038	<0.001	0.81
Days to reach 108 kg	87.6	71.6	64.1	56.6	53.4	51.3	48.7	1.98	<0.001	<0.001
ADG[2], kg	0.57	0.69	0.78	0.85	0.93	0.97	1.04	0.021	0.021	0.014
G:F[3], kg:kg	0.31	0.35	0.35	0.35	0.35	0.33	0.34	0.008	0.17	0.004

[1] Average daily feed intake

[2] Average daily gain

[3] Gain: feed

[4] Digestible energy, MJ/d

Table 4. Whole-body composition of male pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE[1] intake of male, MJ/d							SE	*P*-values	
	25.8	29.0	32.6	35.3	38.5	41.5	44.2		Linear	Quadratic
Protein, %	15.1	15.2	14.9	15.0	15.0	15.0	14.9	0.08	0.013	0.82
Water, %	54.3	54.4	53.4	53.8	53.8	53.5	52.9	0.39	0.026	0.78
Fat, %	14.2	14.3	15.4	15.1	15.0	15.5	16.0	0.41	<0.001	0.99
Ash, %	2.55	2.55	2.58	2.49	2.48	2.46	2.47	0.03	0.002	0.091

[1] Digestible energy, MJ/d

Table 5. Whole-body composition of female pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE[1] intake of female, MJ/d							SE	*P*-values	
	25.8	28.9	32.0	35.6	38.2	40.9	44.5		Linear	Quadratic
Protein, %	14.7	14.6	14.5	14.5	14.3	14.3	14.4	0.08	0.002	0.15
Water, %	52.1	51.5	51.1	51.0	50.4	50.4	50.7	0.41	0.002	0.15
Fat, %	16.4	17.4	17.8	18.3	18.8	18.8	18.4	0.44	<0.001	0.031
Ash, %	2.53	2.53	2.55	2.55	2.58	2.61	2.54	0.029	0.58	0.86

[1] Digestible energy, MJ/d

Table 6. Tissue accretion rate of male pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE[4] intake of male, MJ/d							SE	*P*-values	
	25.8	29.0	32.6	35.3	38.5	41.5	44.2		Linear	Quadratic
Lean gain, g/d	391	452	509	560	642	651	675	23.9	<0.001	0.103
Protein gain, g/d	89	103	117	129	148	150	157	5.1	<0.001	0.083
Water gain, g/d	300	346	388	427	491	496	513	18.7	<0.001	0.107
Fat gain, g/d	106	126	168	179	199	220	245	9.3	<0.001	0.47
Fat: protein gain	1.22	1.24	1.46	1.40	1.37	1.46	1.59	0.085	0.002	1.00
Ash gain, g/d	15.9	18.4	22.2	22.3	25.1	25.3	27.3	0.77	<0.001	0.036
DE retention[1], MJ/d	6.4	7.4	9.5	10.2	11.4	12.4	13.5	0.42	<0.001	0.29
DE efficiency[2], %	24.9	25.5	29.2	28.7	29.8	29.7	30.5	0.97	<0.001	0.103
PUN[3], mM	18.7	18.9	19.0	18.4	18.9	19.2	18.8	0.34	0.63	0.90

[1] Energy (MJ/d) retained for protein and fat deposition

[2] Efficiency (%) of DE retained for protein and fat deposition

[3] Plasma urea nitrogen

[4] Digestible energy, MJ/d

Table 7. Tissue accretion rate of female pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE intake of female, MJ/d							SE	*P*-values	
	25.8	28.9	32.0	35.6	38.2	40.9	44.5		Linear	Quadratic
Lean gain, g/d	372	400	450	456	492	510	563	17.2	<0.001	0.88
Protein gain, g/d	85	93	105	107	116	121	132	3.6	<0.001	0.87
Water gain, g/d	284	304	341	345	371	385	426	13.6	<0.001	0.62
Fat gain, g/d	121	155	184	204	235	245	249	8.0	<0.001	0.004
Fat: protein gain	1.48	1.70	1.77	1.93	2.03	2.05	1.92	0.10	<0.001	0.023
Ash gain, g/d	15.1	16.8	19.5	20.3	22.9	24.5	24.7	0.70	<0.001	0.14
DE retention[1], MJ/d	6.9	8.4	9.8	10.6	12.1	12.7	13.0	0.33	<0.001	0.005
DE efficiency[2], %	26.4	28.4	30.3	29.6	31.2	30.6	28.8	0.69	0.001	<0.001
PUN[3], mM	19.3	19.5	19.6	19.2	19.2	18.8	19.0	0.19	0.021	0.44

[1] Energy (MJ/d) retained for protein and fat deposition

[2] Efficiency (%) of DE retained for protein and fat deposition

[3] Plasma urea nitrogen

[4] Digestible energy, MJ/d

Table 8. Carcass traits of male pigs on various daily digestible energy allowance between 60 to 108 kg

Variables	DE[3] intake of male, MJ/d							SE	*P*-values	
	25.8	29.0	32.6	35.3	38.5	41.5	44.2		Linear	Quadratic
Dressing, %	76.3	76.8	76.8	76.6	77.5	77.9	78.3	0.49	0.001	0.38
Carcass weight, kg	82.8	83.5	83.4	83.3	84.0	84.1	84.9	0.49	0.004	0.49
Backfat[1], mm	10.7	11.6	11.7	11.8	12.2	13.1	12.8	0.57	0.003	0.86
Loin depth[2], mm	52.6	54.3	51.9	46.9	48.7	50.6	52.2	1.77	0.21	0.032

[1] Carcass weight (83.7 kg) and backfat at entry (7.17 mm) were used as co-variates

[2] Carcass weight (83.7 kg) and backfat at entry (7.17 mm) were used as co-variates

[3] Digestible energy, MJ/d

Table 9. Carcass traits of female pigs on various daily digestible energy allowance between 60 to 108 kg

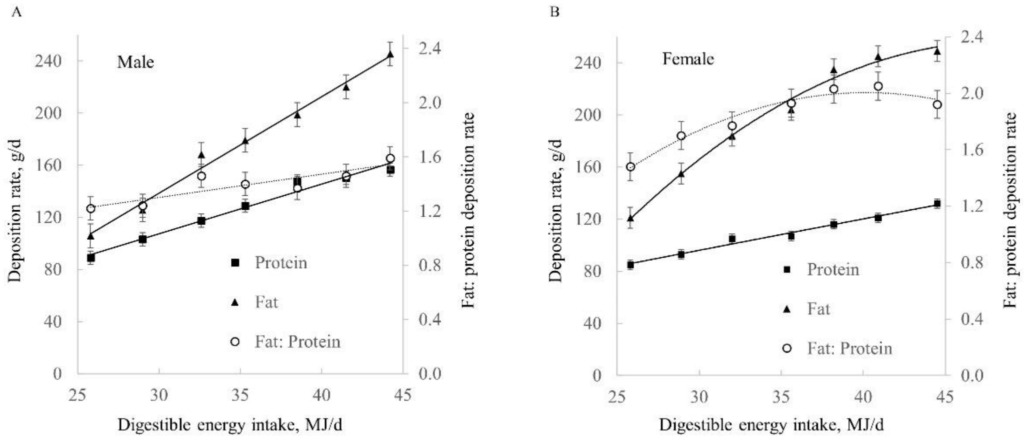
Variables	DE intake of female[3], MJ/d							SE	P-values	
	25.8	28.9	32.0	35.6	38.2	40.9	44.5		Linear	Quadratic
Dressing, %	79.4	77.5	77.3	77.7	78.7	78.6	78.8	0.66	0.67	0.13
Carcass weight, kg	86.4	84.3	84.1	84.6	85.7	85.5	85.7	0.71	0.61	0.055
Backfat[1], mm	12.4	13.5	13.0	13.4	13.3	13.2	13.0	0.84	0.68	0.82
Loin depth[2], mm	56.1	54.7	56.0	55.4	59.5	54.0	57.4	2.20	0.24	0.42

[1] Carcass weight (85.1 kg) and backfat at entry (7.05 mm) were used as co-variates

[2] Carcass weight (85.1 kg) and backfat at entry (7.05 mm) were used as co-variates

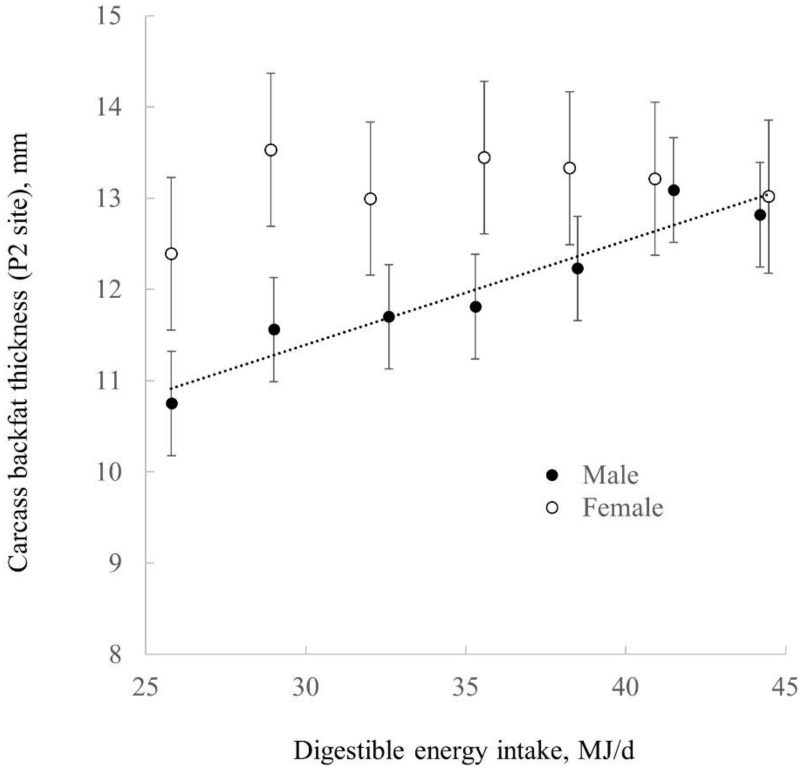
[3] Digestible energy, MJ/d

Fig. 1. Relationship between daily digestible energy (DE) intake and rate of protein deposition, rate of fat deposition, and the ratio between fat: protein deposition rate in intact male (A) and female pigs (B) (60 to 108 kg) selected for low backfat.



Mean ± standard error (s. e.) is reported for each data point. The best-fit regression models are: Protein gain rate (male) = -7.65 (± 11.230 s.e.) + 3.83 (± 0.314 s.e.) × DE, $R^2 = 0.735$, $P < 0.001$; Protein gain rate (female) = 20.94 (± 9.96 s.e.) + 2.50 (± 0.254 s.e.) × DE, $R^2 = 0.643$, $P < 0.001$; Fat gain rate (male) = -81.9 (± 20.7 s.e.) + 7.4 (± 0.60 s.e.) × DE, $R^2 = 0.750$, $P<0.001$; Fat gain rate (female)= -362.9 (± 123.30 s.e.) + 25.7 (± 7.19 s.e.) × DE - 0.27 (± 0.102 s.e.) × DE^2, $R^2= 0.786$, $P < 0.001$; Ratio of fat: protein gain rate (male) = 0.818 (± 0.204 s.e.) + 0.016 (± 0.006 s.e.) × DE, $R^2= 0.130$, $P = 0.006$; Ratio of fat: protein gain rate (female) = -2.24 (± 1.588 s.e.) + 0.215 (± 0.093 s.e.) × DE - 0.003 (± 0.0013 s.e.) × DE^2, $R^2 = 0.225$, $P = 0.001$.

Fig. 2. Relationship between daily digestible energy (DE) intake and carcass backfat thickness of pigs selected for low backfat.



Carcass backfat was measured on P2 site when pigs reached 108 kg live weight. Mean ± standard error is reported for each data point. The best-fit regression model is: Carcass backfat (intact male) = 7.59 (± 1.477 s.e.) + 0.125 (± 0.0414 s.e.) × DE, $R^2 = 0.130$, $P = 0.004$. Carcass backfat of female pigs was not affected by digestible energy intake.