Determination of net energy content of dietary lipids fed to growing pigs using indirect calorimetry¹

Enkai Li, Hu Liu, Yakui Li, Ling Liu, Fenglai Wang, Defa Li, and Shuai Zhang²

State Key Laboratory of Animal Nutrition, College of Animal Science and Technology, China Agricultural University, Beijing 100193, P.R. China

ABSTRACT: The objective of this experiment was to determine the NE content of different dietary lipids fed to growing pigs using indirect calorimetry. Thirty-six growing (initial BW: 41.1 ± 3.1 kg) barrows were allotted to 6 diets based on completely randomized design with 6 replicate pigs per diet. Diets included a corn-soybean meal basal diet and 5 test diets each containing 10% palm oil, poultry fat, fish oil, corn oil, or flaxseed oil at the expense of corn and soybean meal. During each period, pigs were individually housed in metabolism crates for 14 d, which included 7 d for adaptation to feed, metabolism crates, and environmental conditions. On day 8, pigs were transferred to the open-circuit respiration chambers and fed 1 of the 6 diets at 2.3 MJ ME/kg BW^{0.6}/day. Total feces and urine were collected and daily heat production (HP) was also

calculated from day 9 to day 13. On the last day of each period (day 14), pigs were fasted and the fasting heat production (FHP) was measured. The results show that the FHP of pigs averaged 809 kJ/kg BW^{0.6}·day⁻¹ and was not affected by diet characteristics. The DE values were 35.98, 36.84, 37.11, 38.95, and 38.38 MJ/kg DM, the ME values were 35.79, 36.56, 36.92, 37.73, and 38.11 MJ/kg DM, and the NE values were 32.42, 33.21, 33.77, 34.00, and 34.12 MJ/kg DM, for the palm oil, poultry fat, fish oil, corn oil, and flaxseed oil, respectively. Based on our result, we concluded that the DE content of dietary lipid varied from 91% to 98% of its GE content, the ME content of dietary lipid was approximately 99% of its DE content, and the NE content of dietary lipid was approximately 90% of its ME content in growing pigs.

Key words: dietary lipids, growing pigs, indirect calorimetry, net energy

© The Author(s) 2018. Published by Oxford University Press on behalf of the American Society of Animal Science. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com.

J. Anim. Sci. 2018.96:2184–2194

doi: 10.1093/jas/sky132

INTRODUCTION

Lipids, a concentrated energy source, are commonly added to swine diets, and the energy value of lipids is about 2.25 times higher than

carbohydrates (Jones et al., 1992; Lin et al., 2013). However, the energy values vary among lipid sources due to different fatty acid composition which may affect the digestion, absorption, and metabolic utilization of dietary lipids (Mendoza and van Heugten, 2014). It has also been suggested that the NE content of lipids is a more accurate parameter than the DE or ME contents to describe their productive value (Van Heugten et al., 2015). Nevertheless, Sauvant et al. (2004) suggested one single NE value of all fat sources (29.77 MJ/kg DM). In NRC (2012), the NE value of lipid was estimated to be 88% of ME based upon research by van Milgen et al. (2001). It was emphasized that the NE content

¹Financial support for this research was provided by the Modern Agricultural Industry Technology System (number CARS-36), Developing key equipment for digital management and monitoring environment in animal production (number 2013AA10230602), National Natural Science Foundation of China (number 31372317) and the 111 Project (number B16044).

²Corresponding author: zhangshuai16@cau.edu.cn

Received October 15, 2017.

Accepted April 11, 2018.

of dietary lipids needs to be determined more precisely (Kerr et al., 2015).

Several researchers have determined the NE value of lipids using comparative slaughter (CS) method (Galloway and Ewan, 1989; Kil et al., 2011). The NE value of tallow, soybean oil, and choice white grease reported in their studies were far less than those provided by Sauvant et al. (2004) and NRC (2012). The comparative slaughter method which used 179 kcal per kg metabolic BW ($\text{kg}^{0.6}$) as the NE for maintenance (NEm) may have underestimated the NE value of lipids enriched with unsaturated fatty acids since NEm would probably be higher under pen conditions and in connection with increased oxidative stress (López Bote et al., 2001; Verstegen, 2001). The measurement of antioxidant parameters can help to effectively evaluate the energy values of dietary lipids (Shurson et al., 2015).

Therefore, the objective of this experiment was to determine the NE content of lipid sources with diverse fatty acid composition when fed to growing pigs using indirect calorimetry (IC).

MATERIALS AND METHODS

The China Agricultural University Laboratory Animal Welfare and Animal Experimental Ethical Inspection Committee (Beijing, China) reviewed and approved all protocols used in this experiment.

Equipment for Indirect Calorimetry

The 6 open-circuit respiration chambers used in this experiment were previously described by Liu et al. (2014) and Li et al. (2017). The temperature was maintained at 22 °C in the fed state and was gradually increased to 24 °C during the fasted state. The relative humidity was controlled at 70%. Oxygen content was measured with a paramagnetic differential analyzer (Oxymat 6E, Siemens, Munich, Germany), whereas CO_2 and CH_4 contents were measured with infrared analyzers (Ultramat 6E, Siemens). The analyzers had a range of measurement of 19.5% to 21% for O_2 , 0% to 1% for CO_2 , and 0% to 0.1% for CH_4 with a sensitivity of 0.2% within the measurement range. Gas concentrations in each chamber were measured at 5-min intervals. We used the ethanol combustion experiment to check the accuracy of the chamber in measuring gaseous exchange.

Animals, Diets, and Experimental Design

This study was conducted at the Fengning Swine Research Unit of China Agricultural University

(Hebei, China). Thirty-six growing barrows (Duroc $\times$ Landrace $\times$ Yorkshire) with an initial BW of 41.1 ± 3.1 kg were allotted to 1 of 6 diets according to completely randomized design with 6 replicated pigs per diet. There were 6 pigs and 6 open-circuit respiration chambers used each time, resulting in 6 replicate periods. The fish oil and poultry fat used in this experiment were feed grade (free fatty acids < 5%), while other lipids were all food grade (free fatty acids < 0.2%). The fatty acid profile of the lipid sources is presented in Table 1. Diets included a corn-soybean meal basal diet (CNTR) and 5 test diets each containing 10% palm oil (PALM), poultry fat (POUF), fish oil (FISH), corn oil (CORN), or flaxseed oil (FLAX) at the expense of corn and soybean meal (Table 2). All lipid sources were provided by Zhongda Agricultural Science and Technology Co., Ltd. (Shandong province, China). Synthesized lysine, methionine, threonine, tryptophan, and valine were added in order to be above the animals requirements at all periods (NRC, 2012).

During each period, pigs were housed individually in metabolism crates for 14 d, which included 7 d for adaptation to experimental diet, metabolism crates, and environmental conditions. On day 8, pigs were transferred to the open-circuit respiration chambers and fed 1 of the 6 diets at 2.3 MJ ME/kg $\text{BW}^{0.6}/\text{day}$. Total feces and urine were collected and daily heat production (HP) was also measured from day 9 to day 13. On the last day of each period (day 14), pigs were fasted and the fasting heat production (FHP) was measured from 2200 (day 14) to 0600 h (day 15). The FHP period started then 30 h after the last meal and on animals kept in the dark to minimize their physical activity.

A standard corn-soybean meal diet was fed to pigs before the experiment. Pigs were fed equal sized meals twice daily at 0900 and 1600 h. Water was available continuously through a low-pressure nipple drinker. The chambers were opened for approximately 1 h per day to feed pigs and collect feces and urine. The O_2 consumption and CO_2 and CH_4 production during this time were not included in the calculation of daily HP. The concentration of CO_2 in the chamber increased when the door was closed. The calculation of HP began when the concentration of CO_2 in the chamber was above 2,000 ppm (Li et al., 2017). For each period, pigs were weighed on day 1, 9, 13, and 14. The average body weight for each period was used to calculate the HP.

Sample Collection

During day 9 to day 13, feed refusals and spillage were collected twice daily to be dried and weighed.

Table 1. Analyzed chemical composition of the lipid sources (% , as-fed basis)

Item	Palm oil	Poultry fat	Fish oil	Corn oil	Flaxseed oil
Fatty acids (% of total fatty acids)					
C8:0	0.1	0.1	0.1	0.1	0.1
C12:0	0.1	0.1	0.2	0.0	0.0
C14:0	0.9	0.8	7.0	0.0	0.1
C16:0	46.2	23.0	19.8	12.7	5.2
C16:1	0.1	2.7	7.3	0.1	0.1
C17:0	0.1	0.2	1.5	0.1	0.1
C18:0	5.1	8.1	4.2	1.9	3.7
C18:1 n-9	37.2	39.6	15.0	31.4	28.9
C18:2 n-6	9.1	21.9	2.0	51.9	16.3
C18:3 n-6	0.0	0.1	0.4	0.0	0.0
C18:3 n-3	0.4	1.6	1.8	0.7	43.1
C20:0	0.4	0.3	0.9	0.4	0.3
C20:1	0.1	0.5	3.1	0.3	0.8
C20:2	0.0	0.0	0.1	0.0	0.0
C20:3 n-3	ND ⁵	0.1	0.2	ND	0.1
C20:3 n-6	ND	0.1	0.2	ND	0.0
C20:4 n-6	ND	0.1	1.3	ND	0.0
C20:5 n-3	ND	0.0	12.4	ND	ND
C21:0	0.0	0.3	0.3	0.0	0.1
C22:0	0.1	0.2	0.3	0.0	0.2
C22:1 n-9	0.0	0.0	0.4	0.0	0.8
C22:2	ND	0.0	0.1	0.0	0.0
C22:6 n-3	ND	0.0	18.7	ND	ND
C23:0	0.0	0.0	0.5	0.0	0.0
C24:0	0.1	0.1	1.5	0.2	0.1
C24:1	0.0	0.0	0.7	0.0	0.1
PUFA ¹	9.4	23.9	37.1	52.7	59.5
UFA ²	46.9	66.8	63.7	84.5	90.1
SFA ³	53.1	33.2	36.2	15.4	9.8
U:S ⁴	0.9	2.0	1.8	5.5	9.2

¹PUFA = polyunsaturated fatty acids.²UFA = unsaturated fatty acids.³SFA = saturated fatty acids.⁴U: S was the ratio of unsaturated to saturated fatty acids.⁵ND = nondetectable.

Total feces and urine were collected according to the methods described by [Liu et al. \(2014\)](#). Feces were collected twice daily at 0900 and 1600 h when the chamber door was opened and immediately stored at -20°C . Urine was collected separately for each pig into plastic buckets containing 50 mL of 6 N HCl and sieved with cotton gauze. The total urinary volume produced by each pig was measured and 5% of the daily urinary excretion was stored at -20°C . Urine was also collected separately during the 24 h fasting state to calculate urinary N losses for the calculation of FHP. At the end of the experiment, feces and urine samples were thawed, and thoroughly mixed, and a sub-sample was saved for chemical analysis. Fecal samples were oven-dried for 72 h at 65°C . The feed and fecal samples were ground through a 1-mm

Table 2. Ingredient composition and chemical analysis of experimental diets (% , as-fed basis)

Item	Dietary treatment ¹					
	CNTR	PALM	POUF	FISH	CORN	FLAX
Ingredients, %						
Corn	70.37	63.13	63.13	63.13	63.13	63.13
Soybean meal	26.00	23.32	23.32	23.32	23.32	23.32
Palm oil	—	10.00	—	—	—	—
Poultry fat	—	—	10.00	—	—	—
Fish oil	—	—	—	10.00	—	—
Corn oil	—	—	—	—	10.00	—
Flaxseed oil	—	—	—	—	—	10.00
Dicalcium phosphate	1.20	1.20	1.20	1.20	1.20	1.20
Limestone	0.80	0.80	0.80	0.80	0.80	0.80
Salt	0.35	0.35	0.35	0.35	0.35	0.35
Premix ²	0.50	0.50	0.50	0.50	0.50	0.50
Lys-HCl ³	0.38	0.34	0.34	0.34	0.34	0.34
DL-Met	0.16	0.14	0.14	0.14	0.14	0.14
L-Thr	0.14	0.13	0.13	0.13	0.13	0.13
L-Trp	0.02	0.02	0.02	0.02	0.02	0.02
L-Val	0.08	0.07	0.07	0.07	0.07	0.07
Analyzed composition, %						
DM	90.07	90.70	90.31	90.36	90.53	89.65
CP	17.49	15.61	15.06	15.01	15.45	15.02
AEE ⁴	3.83	12.98	12.97	12.52	12.66	12.93
NDF	15.52	13.93	13.67	13.55	13.60	13.83
ADF	4.45	3.94	3.98	3.89	3.66	3.55
Ash	4.58	4.52	4.44	4.33	4.44	4.39

¹CNTR = basal diet; PALM = diet containing 10% palm oil; POUF = diet containing 10% poultry fat; FISH = diet containing 10% fish oil; CORN = diet containing 10% corn oil; FLAX = diet containing 10% flaxseed oil.

²Premix provided the following per kg of complete diet for growing pigs: vitamin A, 5,512 IU; vitamin D₃, 2,200 IU; vitamin E, 30 IU; vitamin K₃, 2.2 mg; vitamin B₁₂, 27.6 µg; riboflavin, 4.0 mg; pantothenic acid, 14.0 mg; niacin, 30.0 mg; choline chloride, 400.0 mg; folacin, 0.7 mg; thiamine 1.5 mg; pyridoxine 3.0 mg; biotin, 44.0 µg; Mn, 40.0 mg; Fe, 75.0 mg; Zn, 75.0 mg; Cu, 100.0 mg; I, 0.3 mg; Se, 0.3 mg.

³L-Lysine hydrochloride was provided by Dacheng Group, Changchun, China.

⁴AEE = acid hydrolyzed ether extract.

screen prior to chemical analysis. On the morning of day 14, blood samples (8 mL) were collected by anterior vena cava puncture using anticoagulant-free Vacutainer tube (Becton Dickinson Vacutainer Systems, Franklin Lakes, NJ). Serum was obtained after centrifugation (Biofuge22R; Heraeus, Hanau, Germany) at $3,000 \times g$ for 15 min at 4°C and then stored at -80°C until analysis.

Chemical Analysis

All chemical analyses were conducted in duplicate and repeated if the duplicates differed by more than 5%. Feed and fecal samples were analyzed for

DM (AOAC, 2007; Method 934.01), Ash (AOAC 2007; Method 942.15), CP (AOAC, 2007; Method 990.03), and Acid hydrolyzed ether extract (AEE, AOAC, 2007; Method 954.02). The NDF and ADF concentrations were determined using filter bags and fiber analyzer equipment (Fiber Analyzer, Ankom Technology, Macedon, NY) following a modification of the procedure of Van Soest et al. (1991). The GE in the lipid sources, diets, urine, and fecal samples was determined using an Isoperibol Calorimeter (Parr 6300 Calorimeter, Moline, IL) with benzoic acid as a standard. Fatty acid profiles of the lipid sources were determined by gas chromatography (6890 series, Agilent Technologies, Wilmington, DE) according to the procedures of Sukhija and Palmquist (1988) with slight modifications. Lipid samples were converted to fatty acid methyl esters using methanolic HCl. Undecanoic acid (C11:0) was used as the internal standard. Aliquots of 1 µL were injected into a capillary column (60 m × 250 µm × 250 nm, DB-23, Agilent) with cyanopropyl methyl silicone as the stationary phase. Column oven temperature was programmed with a 1:20 split. Injector and detector temperatures were maintained at 260 and 270 °C, respectively. Nitrogen was the carrier gas at a flow rate of 2 mL/min. Serum samples were thawed and thoroughly mixed immediately before analysis. Antioxidant parameters including superoxide dismutase (SOD), glutathione peroxidase (GSH-PX), malonaldehyde (MDA), total antioxidant capacity (T-AOC), catalase (CAT), and the ratio of oxidized glutathione (GSSH) to total glutathione (T-GSH) in serum were determined using assay kits according to the instructions of Beijing Kangjia Bioengineering Company (Beijing, China).

Calculations

The DM intake from day 9 to day 13 in each period was calculated as the product of feed intake and DM content of diets. Gross energy intake was calculated as the product of the GE content of the diet and the actual feed DM intake over the 5-d collection period from day 9 to day 13. The energy lost in feces, urine, and methane was measured for each diet and the DE and ME for the 6 diets were calculated. The ME included energy losses from both urine and methane. Methane energy was calculated using a conversion factor of 39.54 kJ/L (Brouwer, 1965).

From day 9 to day 13 of each period, O₂, CO₂, and CH₄ concentrations in both ingoing and outgoing air, and outgoing air flow rates were measured at 5 min intervals. These data were then used to calculate O₂ consumption and CO₂ and CH₄ production

during each 5 min interval and these values were averaged and extrapolated to a 24-h period. Total heat production (THP) was then calculated for each day from gas exchanges and urinary loss of N according to Brouwer (1965) using Eq. [1]:

$$\begin{aligned} \text{THP (kJ)} = & 16.18 \times \text{O}_2 (\text{L}) + 5.02 \\ & \times \text{CO}_2 (\text{L}) - 2.17 \times \text{CH}_4 (\text{L}) \\ & - 5.99 \times \text{urinary N (g)} \end{aligned} \quad (1)$$

Fasting heat production was calculated using the same equation, but 24-h FHP was predicted from the 8-h HP after a period of feed deprivation of 31 to 38 h (22:00 to 06:00 h) during the last day of each period (Li et al., 2018). To base production for the same time span as for the calculation of THP, the 8-h HP was also extrapolated to a 24-h period. The respiratory quotient (RQ) corresponds to the ratio between CO₂ production and O₂ consumption.

The oxidation of carbohydrate (OXCHO) and fat (OXF) were calculated by the method described by Chwalibog et al. (1992).

$$\begin{aligned} \text{OXCHO (kJ)} = & [-2.968 \times \text{O}_2 + 4.147 \\ & \times \text{CO}_2 - 1.761 \times \text{CH}_4 - 2.446 \\ & \times \text{Urinary N (g)}] \times 17.58 \end{aligned} \quad (2)$$

$$\begin{aligned} \text{OXF (kJ)} = & [1.719 \times \text{O}_2 - 1.719 \\ & \times \text{CO}_2 - 1.719 \times \text{CH}_4 - 1.963 \\ & \times \text{Urinary N (g)}] \times 39.76 \end{aligned} \quad (3)$$

The apparent total tract digestibility (ATTD) of nutrients in diets was calculated according to the methods of Noblet et al. (1994).

Retention of energy (RE) was calculated according to Eq. [4]:

$$\begin{aligned} \text{RE (MJ / kg DM)} = & [\text{ME intake (MJ / d)} \\ & - \text{THP (MJ / d)}] \\ & / \text{DM intake (kg / d)} \end{aligned} \quad (4)$$

Retention of energy as protein (RE_p) was calculated as N retention (g) × 6.25 × 23.86 (kJ/g). Retention of energy as lipid (RE_l) was calculated as the difference between RE and RE_p.

Net energy of each diet was calculated according to Noblet et al. (1994) as:

$$\text{NE (kJ / kg DM)} = \left[\text{RE (kJ / d)} + \text{FHP (kJ / d)} \right] / \text{DM intake (kg / d)} \quad (5)$$

The GE_c, DE_c, ME_c and NE_c values of lipid sources were calculated using the revised methods of Adeola (2001) as follows:

$$E_{\text{lipid}} = \left[E_{\text{lipid diet}} - E_{\text{basal diet}} \right] / 96.84\% \times 85.70\% / 11.19\% \quad (6)$$

in which $E_{\text{basal diet}}$ is the mean GE, DE, ME or NE value in the basal diet (MJ/kg of DM) and the ratio of $E_{\text{basal diet}}/96.84\%$ is the GE, DE, ME or NE value of the ingredients that supplied energy in the basal diet. The percentage of minerals and vitamins in the basal diet was 3.16% (DM basis) and was not a source of energy. Thus, the ingredients supplying energy (corn, SBM, and AAs) account for 96.84% in the basal diet on DM basis. It was assumed that the GE, DE, ME, and NE values of the corn, SBM, and AA mixture obtained from the basal diet was applicable to the other diets. $E_{\text{lipid diet}}$ is the mean GE, DE, ME, or NE value in the lipid diet (MJ/kg of DM). E_{lipid} is the calculated GE, DE, ME, and NE values (GE_c, DE_c, ME_c, and NE_c) for each lipid sample (MJ/kg of DM). 85.70% is the DM percentage of the ingredients (except lipid) that supplied energy (corn, SBM, and AAs) in the lipid diet, and 11.19% is the DM percentage of lipid sample in the lipid diet. The DM of ingredients was measured before the preparation of diets to calculate the DM ratio of each test ingredient in the diet. The DE_c/GE_c, ME_c/DE_c, and NE_c/ME_c ratios could then be calculated for each lipid source from these calculated GE_c, DE_c, ME_c, and NE_c values and used to estimate the final DE, ME, and NE values as the product of measured GEM and DE_c/GE_c for DE, measured GEM and DE_c/GE_c and ME_c/DE_c for ME and measured GEM and DE_c/GE_c, ME_c/DE_c and NE_c/ME_c for NE (Li et al., 2017). All calculations were done on a DM basis. Because there is only one estimated energy value for each lipid source, the statistical analysis cannot be conducted among energy values of lipid sources.

Statistical Analysis

Data were checked for normality and outliers were detected using the UNIVARIATE procedure of SAS (SAS Institute, Cary, NC). No outliers were identified. Data were then analyzed using ANOVA

with the MIXED procedure of SAS. Individual pig was treated as the experimental unit, and the statistical model included treatment diet as the only fixed effect, and period and chamber as random effects. Treatment means were calculated using the LSMEANS statement and statistical differences among treatments were separated using Tukey's HSD test. In all analyses, differences were considered significant if $P < 0.05$ and considered a trend at $P < 0.10$.

RESULTS

All pigs remained healthy and readily consumed their diets without any problems. Feces were successfully collected from all pigs. The ATTD of AEE was greater when dietary fat was added, regardless of source, in comparison with pigs fed the CNTR diet ($P < 0.01$; Table 3). However, the ATTD of DM, CP, OM, NDF, and ADF in diets were not affected by lipid content in growing pigs.

The crude protein content of the CNTR diet was higher than that in the lipid diets which results in greater ($P < 0.01$) nitrogen intake and nitrogen retention for pigs fed the CNTR diet than for pigs fed the lipid diets. In addition, pigs in the current experiment were fed a similar ME intake (2,300 kJ/kg BW^{0.6}/day), so the pigs fed the CNTR diet had greater ($P < 0.01$) DM intake compared with pigs fed the lipid diets (Table 4). The energy lost as urine for the 6 diets ranged from 1.5% to 2.1% of DE. Compared with the CNTR diet, the percentage of diet DE lost via CH₄ tended to be lower ($P = 0.06$) for the lipid diets. The NE to ME ratio among the 6 diets ranged from 77.2% to 80.6%.

The observed ME intake of pigs fed the 6 diets during the current experiment were 2,284, 2,357, 2,332, 2,341, 2,355, and 2,343 kJ/kg BW^{0.6}/day, respectively, which is similar to the expected values for the experimental design. Adding dietary fat, regardless of source, decreased average THP and adjusted THP, in comparison with pigs fed the CNTR diet ($P < 0.01$). The average adjusted THP for the 6 diets were 1,380, 1,245, 1,269, 1,238, 1,236, and 1,256 kJ/kg BW^{0.6}/day, respectively. However, the average FHP was 809 kJ/kg BW^{0.6}·d⁻¹ across all treatments and was not affected by diet characteristics. The pigs fed the basal diet in fed state had greater ($P < 0.01$) OXCHO for energy than the lipid diets. The RE and RE_L was greater when dietary fat was added, regardless of source, in comparison with pigs fed the CNTR diet ($P < 0.01$). Furthermore, adding dietary fat, regardless of source, decreased the RQ in the fed state, compared with pigs fed the

Table 3. ATTD of nutrients in experimental diets

	Dietary treatment ¹							
Item	CNTR	PALM	POUF	FISH	CORN	FLAX	SEM	<i>P</i> -value
Digestibility coefficients, %								
DM	87.3	87.7	88.4	88.2	90.2	89.4	0.78	0.13
OM	89.1	89.4	89.9	90.1	91.5	90.7	0.71	0.18
GE	87.7 ^b	88.4 ^{ab}	89.3 ^{ab}	89.8 ^{ab}	90.9 ^a	90.4 ^{ab}	0.74	0.04
CP	86.2	85.0	85.7	86.4	88.5	86.3	1.19	0.46
AEE ²	49.8 ^b	78.5 ^a	81.5 ^a	82.7 ^a	84.5 ^a	84.2 ^a	1.59	<0.01
NDF	70.3	67.6	69.2	68.4	73.3	70.3	2.40	0.63
ADF	62.7	61.9	65.3	59.1	66.9	61.9	3.72	0.73

^{a-b}Within a row means followed by the same letters are not different at $P < 0.05$.

¹CNTR = basal diet; PALM = diet containing 10% palm oil; POUF = diet containing 10% poultry fat; FISH = diet containing 10% fish oil; CORN = diet containing 10% corn oil; FLAX = diet containing 10% flaxseed oil.

²AEE = acid hydrolyzed ether extract.

ATTD = apparent total tract digestibility.

CNTR diet ($P < 0.01$), but the average RQ in the fasted state was not affected by diet characteristics.

There were no differences for any serum anti-oxidant parameters measured (SOD, GSH-PX, MDA, T-AOC, CAT, and GSSH/T-GSH ratio) among the 6 treatment groups (Table 5). Across the 5 dietary fat sources tested in our study, the determined DE to GE ratio ranged from 91% to 98%, the determined ME to DE ratio averaged 99%, the determined NE to ME ratio averaged 90%, and the determined NE values ranged from 32.42 to 34.12 MJ/kg DM. Numerically, palm oil had lower DE, ME, and NE values compared with poultry fat, fish oil, corn oil and flaxseed oil (Table 6).

DISCUSSION

Nutrients Digestibility, Energy, and Nitrogen Balance

The improved ATTD of AEE for the 5 lipid diets as a result of increasing amount of dietary fat agrees with previous observations from growing pigs (Jørgensen and Fernandez, 2000; Li et al., 2018), suggesting that the endogenous losses of lipids related to the feed DM intake exerts a stronger influence on the ATTD of AEE at low dietary levels than at higher levels, and added lipids have a greater digestibility than lipids from the basal diet (Jørgensen et al., 1993; Noblet and Perez, 1993; Kil et al., 2010).

The nitrogen retention was lower when dietary fat was added, regardless of source, in comparison with pigs fed the CNTR, largely due to lower daily nitrogen and amino acids intake. The basal diet used in the current trial had a much higher protein/ME ratio than diets supplemented with lipid

sources, and it can be assumed that the basal diet alone is used for maintenance, and protein and fat gain. The fat included in experimental diet benefits mainly for deposition, resulting in the case that 50% more energy retained as fat in our trial. Therefore, our experimental design should provide a NE value which is close to the true utilization of fat in a complete diet. No effects of lipid source on the RE_p and RE_L were observed among the 5 lipid diets. Previous work with rats and broiler chickens found diets enriched with polyunsaturated fatty acids (PUFA) have less total body fat deposition than diets containing saturated fatty acids (Shimomura et al., 1990; Sanz et al., 2000). Their findings indicated that rats and broiler chickens fed the diets rich in PUFA had a higher rate of fat catabolism. Also, endogenous fat synthesis (lipogenesis) may be reduced in rats and broiler chickens fed unsaturated fatty acids. However, Chwalibog and Thorbek (2000) demonstrated that under normal feeding conditions, the main source of energy for growing pigs is dietary carbohydrate followed by protein. Carbohydrates and protein typically could provide enough energy to satisfy requirements for maintenance and growth, therefore dietary fat is not supposed to oxidize but can be retained in the body. This could be a possible reason to explain why we failed to detect a different pattern of fat deposition in growing pigs. In the fed state, the OXF in this study was negative, which also indicated the pigs in fed state did not utilize the fat to supply energy, and the main oxidation substrate was the carbohydrate (Chwalibog et al., 1992).

Adding dietary fat, regardless of source, decreased the adjusted THP compared with pigs fed the CNTR diet. Data obtained with growing pigs in other studies also support our finding (Noblet

Table 4. Effect of diet characteristics on energy and nitrogen balance in growing pigs (DM basis)

Item	Dietary treatment ¹						SEM	P-value
	CNTR	PALM	POUF	FISH	CORN	FLAX		
BW, kg	41.67	40.14	40.50	42.40	40.95	41.04	1.10	0.74
DM intake, kg/d	1.40 ^a	1.23 ^b	1.22 ^b	1.24 ^b	1.23 ^b	1.21 ^b	0.02	<0.01
Nitrogen balance, g/d								
Intake	38.9 ^a	30.4 ^b	28.0 ^b	29.6 ^b	29.0 ^b	28.7 ^b	0.71	<0.01
Fecal output	5.4 ^a	4.6 ^{ab}	4.0 ^{ab}	4.0 ^{ab}	3.4 ^b	3.9 ^{ab}	0.38	0.02
Urine output	7.3 ^a	5.3 ^{ab}	4.8 ^{ab}	4.4 ^b	4.8 ^{ab}	5.5 ^{ab}	0.61	0.04
Retention	26.2 ^a	20.6 ^b	19.2 ^b	21.2 ^b	20.8 ^b	19.4 ^b	0.90	<0.01
Energy utilization, %								
Urinary energy, % DE	2.1	1.8	1.7	1.5	2.1	1.8	0.20	0.45
Methane energy, % DE	0.7	0.5	0.6	0.4	0.7	0.5	0.07	0.06
ME/DE	97.2	97.7	97.6	97.7	97.1	97.7	0.29	0.19
NE/ME	77.2 ^b	80.3 ^a	80.4 ^a	80.6 ^a	80.4 ^a	80.3 ^a	0.76	<0.01
Energy balance, kJ/kg BW ^{0.6} /d								
ME intake,	2,284	2,357	2,332	2,341	2,355	2,343	21.95	0.22
Total heat production	1,371 ^a	1,276 ^b	1,287 ^b	1,261 ^b	1,266 ^b	1,280 ^b	12.52	<0.01
Oxidation of carbohydrate ²	1,610 ^a	1,313 ^b	1,265 ^b	1,261 ^b	1,247 ^b	1,246 ^b	37.13	<0.01
Oxidation of fat ³	-417 ^b	-159 ^a	-95 ^a	-111 ^a	-108 ^a	-90 ^a	58.02	<0.01
Total heat production ⁴ adjusted	1,380 ^a	1,245 ^b	1,269 ^b	1,238 ^b	1,236 ^b	1,256 ^b	12.50	<0.01
RE _p ⁵	417 ^a	335 ^b	311 ^b	333 ^b	343 ^b	311 ^b	11.60	<0.01
RE _L ⁶	496 ^b	746 ^a	731 ^a	746 ^a	751 ^a	751 ^a	24.67	<0.01
Energy retention	913 ^b	1,081 ^a	1,042 ^a	1,079 ^a	1,085 ^a	1,062 ^a	25.24	<0.01
Fasting heat production	819	808	790	802	814	819	11.18	0.44
Respiratory quotient								
Fed state	1.10 ^a	1.04 ^b	1.03 ^b	1.03 ^b	1.02 ^b	1.03 ^b	0.01	<0.01
Fast state	0.82	0.83	0.82	0.83	0.82	0.82	0.01	0.77
Energy values, MJ/kg DM								
GE	18.09	20.52	20.52	20.55	20.63	20.68	—	—
DE	15.86 ^b	18.14 ^a	18.25 ^a	18.32 ^a	18.57 ^a	18.59 ^a	0.14	<0.01
ME	15.41 ^b	17.72 ^a	17.82 ^a	17.90 ^a	18.03 ^a	18.16 ^a	0.15	<0.01
NE	11.90 ^b	14.23 ^a	14.33 ^a	14.43 ^a	14.49 ^a	14.58 ^a	0.17	<0.01

^{a,b}Within a row means followed by the same letters are not different at $P < 0.05$.

¹CNTR = basal diet; PALM = diet containing 10% palm oil; POUF = diet containing 10% poultry fat; FISH = diet containing 10% fish oil; CORN = diet containing 10% corn oil; FLAX = diet containing 10% flaxseed oil.

²Oxidation of carbohydrate (kJ/kg BW^{0.6}·day⁻¹) = $[-2.968 \times \text{O}_2 + 4.147 \times \text{CO}_2 - 1.761 \times \text{CH}_4 - 2.446 \times \text{Urinal N (g)}] \times 17.58/\text{BW}^{0.6}$.

³Oxidation of fat (kJ/kg BW^{0.6}·day⁻¹) = $[1.719 \times \text{O}_2 (\text{L}) - 1.719 \times \text{CO}_2 (\text{L}) - 1.719 \times \text{CH}_4 (\text{L}) - 1.963 \times \text{UN (g)}] \times 39.76/\text{BW}^{0.6}$.

⁴Total heat production_{adjusted} = Total heat production was adjusted to the same ME intake at 2.3 MJ ME/kg BW^{0.6}/day.

⁵RE_p = Energy retention as protein (kJ/kg BW^{0.6}/day) = $[\text{N intake (g)} - \text{N in feces (g)} - \text{N in urine (g)}] \times 6.25 \times 23.86 (\text{kJ/g})/\text{BW}^{0.6}$.

⁶RE_L = Energy retention as fat (kJ/kg BW^{0.6}/day) = $[\text{RE (kJ)} - \text{energy retention as protein (kJ)}]/\text{BW}^{0.6}$.

et al., 2001; Li et al., 2018). This observation is due to the higher utilization efficiency of ME from lipid with the advantage of having a lower heat increment compared with the efficiency of ME utilization from protein, starch, or fiber (Noblet et al., 1994). Another reason for the reduced adjusted THP may be that the HP related to feeding activity decreases when lipid is added to diets fed to growing pigs, which results in decreased HP (Li et al., 2018). However, physical activity was not measured in our study and therefore we cannot verify this hypothesis. Even not quantifying physical activity, the FHP in our trial was measured under minimum expected activity (during the night, in the dark,

and adjustment of the cage, etc.) and after a long period of fasting. The FHP measured in the current study averaged 809 kJ/kg BW^{0.6}/day, which is close to the FHP values obtained from our previous work using the same method (Liu et al., 2014; Li et al., 2017), and also close to those obtained by the INRA group according to a specific methodology or those used in the large scale NE measurements of Noblet et al. (1994). In addition, in agreement with other literature data (Le Bellego et al., 2001; Li et al., 2018), the FHP was not affected by diet composition. López Bote et al. (2001) assumed that unsaturated fatty acids could increase the oxidative stress in pigs which may increase FHP. However,

Table 5. Effect of diet characteristics on serum antioxidant parameters in growing pigs

Item	Dietary treatment ¹						SEM	P-value
	CNTR	PALM	POUF	FISH	CORN	FLAX		
Antioxidant parameters ²								
SOD, U/mL	118.69	130.38	122.80	123.60	126.11	127.47	4.98	0.66
GSH-PX, U/mL	681.67	686.17	654.93	611.52	694.95	634.14	20.45	0.11
MDA, nmol/mL	5.18	4.13	5.16	4.66	4.73	4.31	0.49	0.59
T-AOC, U/mL	8.81	8.62	8.29	9.71	8.77	9.09	0.43	0.54
CAT, U/mL	5.79	4.87	4.82	4.87	5.31	5.10	0.42	0.55
GSSH/T-GSH	0.23	0.22	0.23	0.22	0.21	0.25	0.01	0.73

¹CNTR = basal diet; PALM = diet containing 10% palm oil; POUF = diet containing 10% poultry fat; FISH = diet containing 10% fish oil; CORN = diet containing 10% corn oil; FLAX = diet containing 10% flaxseed oil.

²SOD = superoxide dismutase; GSH-PX = glutathione peroxidase; MDA = malonaldehyde; T-AOC = total antioxidant capacity; CAT = catalase; GSSH/T-GSH = the ratio of oxidized glutathione (GSSH) to total glutathione (T-GSH).

Table 6. Energy utilization and energy content of dietary fat source in growing pigs (DM basis)

Item	Lipid source				
	Palm oil	Poultry fat	Fish oil	Corn oil	Flaxseed oil
Energy utilization ¹ , %					
DEc/GEc	91.0	93.4	94.4	98.1	97.5
MEc/DEc	99.5	99.2	99.5	96.9	99.3
NEc/MEc	90.6	90.8	91.5	90.1	89.5
Energy value ² , MJ/kg DM					
GEm	39.54	39.43	39.33	39.69	39.36
DE	35.98	36.84	37.11	38.95	38.38
ME	35.79	36.56	36.92	37.73	38.11
NE	32.42	33.21	33.77	34.00	34.12

¹GEc, DEc, MEc, and NEc were calculated according to the Eq. [6].

²GEm was measured using Isoperibol Calorimeter; DE = GEm × DEc/GEc; ME = DE × MEc/DEc; NE = ME × NEc/MEc.

serum antioxidant parameters were not affected by diet characteristics in this study. The decreased RQ for the 5 lipid diets as a result of increased amount of dietary fat also agrees with previous observation from growing pigs (Bruininx et al., 2011; Li et al., 2018). From a biochemical point of view, the higher RQ in the CNTR would be expected, because the RQ for lipid synthesis from glucose contributes largely to an increase in overall RQ, whereas deposition of dietary fat as body lipids does not affect overall RQ (van Milgen, 2002).

Energy Contents of Supplemental Lipids

In NRC (2012), the DE content of various lipid sources is based on studies by Wiseman et al. (1990) and Powles et al. (1993, 1994, 1995) using the ratio of unsaturated fatty acids to saturated fatty acids and the content of free fatty acids. The ME value of lipid was estimated as 98% of DE and the NE value was estimated as 88% of ME based upon research by van Milgen et al. (2001). The ME and

NE estimates in NRC (2012) assumed that the conversion ratio of DE to NE is the same across all fat sources. However, it has been emphasized that more studies are required to determine if these relationships are correct and can be broadly applied to different fat sources (Kellner and Patience, 2017). Across the 5 dietary fat sources tested in our study, the DE to GE ratio varied from 91% to 98%, while the ME to DE ratio (averaged 99%) and the NE to ME ratio (averaged 90%) were relatively stable among the 5 lipid sources. Even though the energetic efficiency from DE to NE we determined is greater than the NRC (2012) estimates, our results on ME/DE and NE/ME ratios fully agreed with those of Noblet et al. (1994), van Milgen et al. (2001) and Li et al. (2018). Boyd et al. (2015) also concluded that the energetic efficiency from DE to NE should be greater than what was reported in NRC (2012). In other species such as poultry, the synergetic effect of fat was reported, with higher calculated ME value than the GE value when fat was supplied into the basal diet (Cao and Adeola, 2016), which might be explained by better utilization of nutrients in basal diet in the presence of fat. However, no literature was found reporting digestibility of fat energy higher than 100% in growing pigs.

Accurate assessment of the energy values to dietary fat sources not only allows pork producers to judge the financial value of supplemental lipids but also supports differentiation of available fat sources (Van Heugten et al., 2015; Kellner and Patience, 2017). Kerr et al. (2015) also emphasized the need for accurate determination of the NE content of dietary lipids, because NE systems may allow for a more accurate prediction of the energy value of dietary lipids than DE and ME systems (Noblet et al., 1994). Several researchers have used comparative slaughter method to determine the NE value of lipids (Galloway and Ewan, 1989; Kil

et al., 2011), but the NE values reported in their studies (17.49, 20.19, and 25.05 MJ/kg DM, for the tallow, soybean oil, and choice white grease, respectively) were far less than estimates by Sauvant et al. (2004) and NRC (2012). However, across the 5 dietary fat sources tested in this study, the averaged determined dietary fat NE was 33.50 MJ/kg DM, and the NE content of the palm oil was numerically the lowest (32.42 MJ/kg DM) in connection with its lowest DE to GE ratio. This can be explained by the abundant saturated fatty acids in palm oil, which are less soluble when exposed to bile salts, and may decrease their incorporation into mixed micelles and retard the subsequent absorption (Stahly, 1984; Wiseman et al., 1986). Different fatty acid compositions had no numerical difference on the NE values of poultry fat, fish oil, corn oil, and flaxseed oil in this study. Theoretically, when large amounts of saturated oil are supplemented in diets, a considerable proportion of the dietary fatty acids is directly deposited as body tissues, with an energetic efficiency of 90%. While large amounts of polyunsaturated oil are included, some fatty acids can be oxidized to yield energy in the form of ATP, with an energetic efficiency of 66% (Black, 1995; Kil et al., 2011). However, Li et al. (2018) assumed that most of the dietary lipids are directly deposited in adipose tissue without any biochemical transformations after absorption, which is also supported by Bruininx et al. (2011). This hypothesis explains the lack of a numerical difference between the NE for poultry fat, fish oil, corn oil, and flaxseed oil and the relatively high NE-to-ME ratio for all lipids that was used in this experiment.

The reason for major discrepancies between IC and CS in determining the NE content of dietary lipids is that the energy retention measured by IC tends to be greater than those measured by CS (Quiniou et al., 1995). In studies using CS, pigs are housed in a more practical facility and then can move freely with more HP related to physical activity. In addition, pigs in studies using CS may sometimes be raised below their critical temperature with again an increased HP. Therefore, HP measured using CS may be highly increased in connection with increased energy for maintenance and FHP values (Verstegen, 2001), while FHP values measured in our study using IC were obtained under minimal activity, at thermoneutrality, etc. From this point of view, results using IC should be more reliable. Moreover, different feeding strategies, genetic background, and age of pigs between our study and the study from Kil et al. (2011) all

can affect the maintenance, growth, and body composition of pigs, resulting in variations in the NE values of lipids (Boisen and Verstegen, 1998). In order to confirm the NE value of dietary lipids, Boyd et al. (2015) used a growth assay to determine the NE of choice white grease and suggested that NE content of fat is not less than 32.55 MJ/kg for growing pigs, which strongly supports our present result. Obviously, further research is still needed to determine the NE of lipids across a diverse and robust range of dietary fat sources.

CONCLUSIONS

The NE values were 32.42, 33.21, 33.77, 34.00, and 34.12 MJ/kg DM, for the palm oil, poultry fat, fish oil, corn oil, and flaxseed oil, respectively. Based on our results, the ME/DE (approximately 99%) and NE/ME (approximately 90%) ratios are relatively constant for all fat sources we determined, while the DE/GE ratio is more variable among different fat sources in growing pigs. More work on digestibility of fat is needed for better utilization of diverse fat sources in swine industry.

LITERATURE CITED

- Adeola, O. 2001. Digestion and balance techniques in pigs. In: J. Lewis and L. L. Southern, editor. Swine nutrition. CRC Press, Washington, DC. p. 903–916.
- AOAC. 2007. Official methods of analysis. 18th rev. ed. AOAC Int., Gaithersburg, MD.
- Black, J. L. 1995. Modelling energy metabolism in the pig—Critical evaluation of a simple reference model. In: P. J. Moughan, M. W. A. Verstegen, and M. I. Visser-Reynevel, editors, Modelling growth in the pig. Wageningen Press, Wageningen, the Netherlands. p. 87–102.
- Boisen, S., and M. W. A. Verstegen. 1998. Evaluation of feed-stuffs and pig diets. Energy or nutrient-based evaluation? I. Limitations of present energy evaluation systems. Acta Agric. Scand., Sect. A. 48:86–94.
- Boyd, R. D., C. E. Zier-Rush, M. McGrath, R. Palan, J. Picou, and E. van Heugten. 2015. Calibration of net energy for fat by growth assay in early and late phases of growth in pigs. J. Anim. Sci. 93(Suppl. 2):73. (Abstr.)
- Brouwer, E. 1965. Report of subcommittee on constants and factors. In: Proc. 3rd EAAP Symp. Energy Metab. Troon Publ. No. 11. Academic, London. p. 441–443.
- Bruininx, E., J. van den Borne, E. van Heugten, J. van Milgen, M. Verstegen, and W. Gerrits. 2011. Oxidation of dietary stearic, oleic, and linoleic acids in growing pigs follows a biphasic pattern. J. Nutr. 141:1657–1663. doi:10.3945/jn.111.142562
- Cao, M. H., and O. Adeola. 2016. Energy value of poultry byproduct meal and animal-vegetable oil blend for broiler chickens by the regression method. Poult. Sci. 95:268–275. doi:10.3382/ps/pev317
- Chwalibog, A., K. Jakobsen, S. Henckel, and G. Thorbek. 1992. Estimation of quantitative oxidation and fat retention from carbohydrate, protein and fat in

- growing pigs. *J. Anim. Physiol. Anim. Nutr.* 68:123–135. doi:10.1111/j.1439-0396.1992.tb00652.x
- Chwalibog, A., and G. Thorbek. 2000. Estimation of net nutrient oxidation and lipogenesis in growing pigs. *Arch. Tierernähr.* 53:253–271. doi:10.1080/17450390009381951
- Galloway, S. T., and R. C. Ewan. 1989. Energy evaluation of tallow and oat groats for young swine. *J. Anim. Sci.* 67:1744–1750. doi:10.2527/jas1989.6771744x
- Jones, D. B., J. D. Hancock, D. L. Harmon, and C. E. Walker. 1992. Effects of exogenous emulsifiers and fat sources on nutrient digestibility, serum lipids, and growth performance in weanling pigs. *J. Anim. Sci.* 70:3473–3482. doi:10.2527/1992.70113473x
- Jørgensen, H., and J. A. Fernández. 2000. Chemical composition and energy value of different fat sources for growing pigs. *Acta Agric. Scand. Sect. A Anim. Sci.* 50:129–136. doi:10.1080/090647000750014250
- Jørgensen, H., K. Jakobsen, and B. O. Eggum. 1993. Determination of endogenous fat and fatty acids at the terminal ileum and on faeces in growing pigs. *Acta Agric. Scand. Sect. A Anim. Sci.* 43:101–106.
- Kellner, T. A., and J. F. Patience. 2017. The digestible energy, metabolizable energy, and net energy content of dietary fat sources in thirteen- and fifty-kilogram pigs. *J. Anim. Sci.* 95:3984–3995. doi:10.2527/jas2017.1824
- Kerr, B. J., T. A. Kellner, and G. C. Shurson. 2015. Characteristics of lipids and their feeding value in swine diets. *J. Anim. Sci. Biotechnol.* 6:30. doi:10.1186/s40104-015-0028-x
- Kil, D. Y., F. Ji, L. L. Stewart, R. B. Hinson, A. D. Beaulieu, G. L. Allee, J. F. Patience, J. E. Pettigrew, and H. H. Stein. 2011. Net energy of soybean oil and choice white grease in diets fed to growing and finishing pigs. *J. Anim. Sci.* 89:448–459. doi:10.2527/jas.2010-3233
- Kil, D. Y., T. E. Sauber, D. B. Jones, and H. H. Stein. 2010. Effect of the form of dietary fat and the concentration of dietary neutral detergent fiber on ileal and total tract endogenous losses and apparent and true digestibility of fat by growing pigs. *J. Anim. Sci.* 88:2959–2967. doi:10.2527/jas.2009-2216
- Le Bellego, L., J. van Milgen, S. Dubois, and J. Noblet. 2001. Energy utilization of low-protein diets in growing pigs. *J. Anim. Sci.* 79:1259–1271. doi:10.2527/2001.7951259x
- Li, Z. C., Y. K. Li, Z. Q. Lyu, H. Liu, J. B. Zhao, J. Noblet, F. L. Wang, C. H. Lai and D. F. Li. 2017. Net energy of corn, soybean meal, expeller-pressed rapeseed meal and solvent-extracted rapeseed meal in growing pigs. *J. Anim. Sci. Biotechnol.* 8:44. doi:10.1186/s40104-017-0169-1
- Li, E. K., Z. Q. Lv, H. Liu, L. Liu, Y. K. Li, Z. C. Li, F. L. Wang, D. F. Li, and S. Zhang. 2018. Determination of net energy content of soybean oil fed to growing pigs using indirect calorimetry. *Anim. Sci. J.* 89:149–157. doi:10.1111/asj.12888
- Lin, X., M. Azain, and J. Odle. 2013. Lipids and lipid utilization in swine. In: L. I. Chiba, editor. *Sustainable swine nutrition*. Blackwell Publishing Ltd., Oxford. p. 59–79.
- Liu, D., N. W. Jaworski, G. Zhang, Z. Li, D. Li, and F. Wang. 2014. Effect of experimental methodology on fasting heat production and the net energy content of corn and soybean meal fed to growing pigs. *Arch. Anim. Nutr.* 68:281–295. doi:10.1080/1745039X.2014.931016
- López Bote, C. J., B. Isabel, and J. M. Flores. 2001. Effect of dietary linoleic acid concentration and vitamin E supplementation on cell desquamation and susceptibility to oxidative damage of pig jejunal mucosa. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 85:22–28. doi:10.1046/j.1439-0396.2001.00298.x
- Mendoza, S. M., and E. van Heugten. 2014. Effects of dietary lipid sources on performance and apparent total tract digestibility of lipids and energy when fed to nursery pigs. *J. Anim. Sci.* 92:627–636. doi:10.2527/jas.2013-6488
- Noblet, J., H. Fortune, X. S. Shi, and S. Dubois. 1994. Prediction of net energy value of feeds for growing pigs. *J. Anim. Sci.* 72:344–354. doi:10.2527/1994.722344x
- Noblet, J., L. Le Bellego, J. van Milgen, and S. Dubois. 2001. Effects of reduced dietary protein level and fat addition on heat production and N and energy balance in growing pigs. *Anim. Res.* 50:227–238. doi:10.1051/animres:2001129
- Noblet, J., and J. M. Perez. 1993. Prediction of digestibility of nutrients and energy values of pig diets from chemical analysis. *J. Anim. Sci.* 71:3389–3398. doi:10.2527/1993.71123389x
- Noblet, J., and X. S. Shi. 1994. Effect of body weight on digestive utilization of energy and nutrients of ingredients and diets in pigs. *Livest. Prod. Sci.* 37:323–338. doi:10.1016/0301-6226(94)90126-0
- NRC. 2012. *Nutrient requirements of swine*. 11th rev. ed. Natl. Acad. Press, Washington, DC.
- Powles, J., J. Wiseman, D. J. A. Cole, and B. Hardy. 1993. Effect of chemical structure of fats upon their apparent digestible energy value when given to growing/finishing pigs. *Anim. Sci.* 57:137–146. doi:10.1017/S000335610000670X
- Powles, J., J. Wiseman, D. J. A. Cole, and B. Hardy. 1994. Effect of chemical structure of fats upon their apparent digestible energy value when given to growing/finishing pigs. *Anim. Prod.* 57:137–146. doi:10.1017/S000335610000670X
- Powles, J., J. Wiseman, D. J. A. Cole, and S. Jagger. 1995. Prediction of the apparent digestible energy value of fats given to pigs. *Anim. Sci.* 61:149–154. doi:10.1017/S1357729800013631
- Quiniou, N., S. Dubois, and J. Noblet. 1995. Effect of dietary crude protein level on protein and energy balances in growing pigs: comparison of two measurement methods. *Livest. Prod. Sci.* 41:51–61. doi:10.1016/0301-6226(94)00030-B
- Sanz, M., A. Flores, and C. J. Lopez-Bote. 2000. The metabolic use of energy from dietary fat in broilers is affected by fatty acid saturation. *Br. Poult. Sci.* 41:61–68. doi:10.1080/00071660086411
- Sauvant, D., J. M. Perez, and G. Tran. 2004. *Tables of composition and nutritional value of feed materials: pig, poultry, sheep, goats, rabbits, horses, fish*. Wageningen Academic Publishers, Wageningen, the Netherlands and INRA, Paris, France.
- Shimomura, Y., T. Tamura, and M. Suzuki. 1990. Less body fat accumulation in rats fed a safflower oil diet than in rats fed a beef tallow diet. *J. Nutr.* 120:1291–1296. doi:10.1093/jn/120.11.1291
- Shurson, G. C., B. J. Kerr, and A. R. Hanson. 2015. Evaluating the quality of feed fats and oils and their effects on pig growth performance. *J. Anim. Sci. Biotechnol.* 6:10. doi:10.1186/s40104-015-0005-4
- Stahly, T. 1984. Use of fats for growing pigs. In: J. Wiseman, editor. *Fats in animal nutrition*. Butterworths, Boston, MA. p. 313–331. doi:10.1016/B978-0-408-10864-5.50022-X
- Sukhija, P. S., and D. L. Palmquist. 1988. Rapid method for determination of total fatty acid content and composition of feedstuffs and feces. *J. Agric. Food Chem.* 36:1202–1206.

- Van Heugten, E., J. Odle, and R. D. Boyd. 2015. Feeding value of fat for Swine-Concepts and Practice. Milk Specialties Global Conference, Pre-Conference to Minnesota Nutrition Conference. Minnesota.
- van Milgen, J. 2002. Modeling biochemical aspects of energy metabolism in mammals. *J. Nutr.* 132:3195–3202. doi:10.1093/jn/131.10.3195
- van Milgen, J., J. Noblet, and S. Dubois. 2001. Energetic efficiency of starch, protein and lipid utilization in growing pigs. *J. Nutr.* 131:1309–1318. doi:10.1093/jn/131.4.1309
- Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *J. Dairy Sci.* 74:3583–3597. doi:10.3168/jds.S0022-0302(91)78551-2
- Verstegen, M. W. A. 2001. Developments towards net energy systems in feeds and animals. In: *Proc. Western Nutr. Conf.*, Saskatoon, SK, Canada. p. 170–184.
- Wiseman, J., D. J. A. Cole, and B. Hardy. 1990. The dietary energy values of soya-bean oil, tallow, and their blends for growing/finishing pigs. *Anim. Prod.* 50:513–518. doi:10.1017/S0003356100005006
- Wiseman, J., D. J. Cole, F. G. Perry, B. G. Vernon, and B. C. Cooke. 1986. Apparent metabolisable energy values of fats for broiler chicks. *Br. Poult. Sci.* 27:561–576. doi:10.1080/00071668608416915