British Journal of Nutrition (2006), **95**, 1082–1087 DOI: 10.1079/BJN20061748

Previous feeding level influences plateau heat production following a 24 h fast in growing pigs

Kees de Lange[1]*, Jaap van Milgen[2], Jean Noblet[2], Serge Dubois[2] and Stephen Birkett[1]

[1]*Department of Animal and Poultry Science, University of Guelph, Guelph, ON, Canada*

[2]*Unité Mixte de Recherches Systèmes d'Elevage, Nutrition Animale et Humaine, Institut National de la Recherche Agronomique, St Gilles, France*

(Received 24 May 2005 – Revised 6 January 2006 – Accepted 17 January 2006)

Factorial approaches to estimate energy requirements of growing pigs require estimation of maintenance energy requirements. Heat production (HP) during fasting (FHP) may provide an estimate of maintenance energy requirements. Six barrows were used to determine effects of feeding level on components of HP, including extrapolated plateau HP following a 24 h fast (FHPp). Based on a cross-over design, each pig was exposed to three feeding levels (1·55, 2·05 and 2·54 MJ metabolisable energy/kg body weight $(BW)^{0.60}$ per d) between 30 and 90 kg BW. Following a 14 d adaptation period, HP was estimated using indirect calorimetry on pigs housed individually. Dynamics of HP were recorded in pigs for 5 d during the fed state and during a subsequent 24 h fast. Metabolisable energy intake was partitioned between thermal effect of feeding (HPf), activity HP (HPa), FHPp and energy retention. Feeding level influenced ($P < 0.05$) total HP during the fed state, HPf and activity-free FHPp (609, 644 and 729 (SE 31) kJ/kg $BW^{0.60}$ per d for low, medium and high ME intakes, respectively). The value of FHPp when expressed per kg $BW^{0.60}$ did not differ ($P = 0.34$) between the three subsequent experimental periods. Feeding level did not ($P = 0.75$) influence HPa. Regression of total HP during the fed state to zero metabolisable energy intake yielded a value of 489 (SE 69) kJ/kg $BW^{0.60}$ per d, which is a lower estimate of maintenance energy requirement than FHPp. Duration of adaptation of pigs to changes in feeding level and calculation methods should be considered when measuring or estimating FHPp, maintenance energy requirements and diet net energy content.

Energy: Fasting: Heat production: Maintenance: Pigs

When using a factorial approach to establish energy requirements of growing pigs, maintenance energy requirements must be estimated (for example, Tess *et al.* 1984; Noblet *et al.* 1993, 1994; National Research Council, 1998; Birkett & de Lange, 2001*a*,*b*,*c*). These values are typically expressed on metabolisable energy (ME) or net energy (NE) bases. Conceptually, available (net) energy requirements for maintenance are best expressed as energy, or ATP, needs at the tissue level to support basic body functions in a non-producing state (basal energy requirements; Eb) (for example, van Milgen *et al.* 2001; Birkett & de Lange, 2001*a*,*b*). Maintenance energy requirements ought to be independent of animal production level and nutritional regimen and related to animal state only, which is generally not the case. Estimates of maintenance ME requirements (MEm) for growing animals are generally obtained by exposing animals to various ME intake levels and extrapolation to the ME intake level at which body energy retention is zero (for example, Quiniou *et al.* 1995). The MEm thus represents Eb and heat production (HP) associated with deriving available energy from dietary nutrients (thermal effects of feeding; HPf). Since different nutrients are utilised with varying efficiencies to generate available energy in the form of ATP, it follows that maintenance energy requirements expressed in units of digestible energy (DE), ME, and even NE, are influenced by nutrient composition from the diet (Noblet *et al.* 1993; Black, 1995; Birkett & de Lange, 2001*a*; van Milgen *et al.* 2001).

The fasting HP (FHP) is frequently used to estimate Eb (Tess *et al.* 1984; Birkett & de Lange, 2001*a*,*b*; van Milgen *et al.* 2001). FHP represents the sum of Eb and energy required to generate available energy from body nutrient stores, and is likely to be less dependent on animal production level and previous nutritional regimen than MEm. It has, however, been shown that HP in growing pigs that were fasted is influenced by previous feeding regimen (for example, Blaxter, 1989; Koong *et al.* 1983).

Van Milgen *et al.* (1997, 1998) suggested partitioning HP in growing pigs into that associated with activity (HPa), short-term HPf (HPf-st), long-term HPf (HPf-lt) and FHP, whereby FHP was standardised and mathematically derived as the plateau or asymptotic nocturnal and activity-free HP following a fast of at least 24 h (plateau FHP; FHPp). According to van

Abbreviations: BW, body weight; DE, digestible energy; Eb, basal energy requirements; FHP, fasting heat production; FHPp, plateau fasting heat production; HP, heat production; Hpa, heat production associated with activity; HPf, thermal effects of feeding; HPf-lt, long-term thermal effects of feeding; HPf-st, short-term thermal effects of feeding; HP0, extrapolated total heat production at zero energy intake; ME, metabolisable energy; MEm, maintenance metabolisable energy requirements; NE, net energy; NEm, maintenance net energy requirements; O_2, oxygen; RQ, respiration quotient.

* **Corresponding author:** Dr C. de Lange, fax +1 519 836 9873, email cdelange@uoguelph.ca

Milgen & Noblet (2000), this estimate of FHP, although measured in a catabolic state, will maintain a relationship with the animal in the anabolic state and may not be as much influenced by previous feeding level as compared with conventional estimates of FHP, including those obtained using regression techniques.

The objective of the present study was to determine effects of feeding level on plateau FHP as determined by van Milgen *et al.* (1997), as well as other main components of energy expenditure in growing–finishing pigs between 45 and 90 kg body weight (BW).

Experimental methods

General experimental design

Three sets of three littermate barrows, Piétrain × (Large White × Landrace) crosses from the INRA-St Gilles swine herd, were selected at approximately 35 kg BW and assigned to one of three feeding levels during three subsequent experimental periods according to a cross-over design. Two littermates were assigned to the same treatment sequence, while the third littermate was kept as a spare. Experimental periods consisted of 2 weeks adaptation to experimental treatments followed by indirect calorimetry and N-balance measurements in two open-circuit respiration units. An adaptation period of 2 weeks was chosen to allow the size of visceral organ, an important determinant of HP, to adjust to the new feeding level (Koong *et al.* 1983). Since measurements were made in two pigs each week, the assignment of pigs to treatments was staggered at weekly intervals, whereby measurements in littermates were made in different weeks and different respiration units. Pigs were weighed weekly and at the start and end of measuring FHP. The feeding levels represented targeted daily intakes of 1·56, 2·08 and 2·6 MJ ME/kg $BW^{0·60}$, respectively, and were adjusted every 2 or 3 d (days 1, 3 and 5 in each week) based on mean anticipated BW. During the first and second week of the adaptation period, pigs were fed manually two and three times daily, respectively. Water was freely available from low-pressure water nipple drinkers. The wheat, maize and soyabean meal-based diet (Table 1) was formulated to exceed requirements for essential nutrients for pigs with high lean growth potentials (National Research Council, 1998).

Authorisation to perform an experiment on living animals was given by the French Ministry of Agriculture and Fishery (certificates 4739 and 7704 for J. N. and J. van M., respectively).

Indirect calorimetry and nitrogen balance measurements

Pigs were maintained individually in one of the two large open-circuit respiration units at INRA-St Gilles (van Milgen *et al.* 1997) for 7 d periods. In the respiration units, pigs were fed four meals daily at 09.00, 13.00, 17.00 and 21.00 hours using a computer-controlled feed delivery system (van Milgen *et al.* 1997). The first day served as adjustment to the new environment and was not considered in the final calculations. On days 2 to 6, measurements of O_2 consumption and production of CO_2, methane and ammonia were made in pigs in the fed state; O_2 consumption and CO_2 production was measured on day 7 in fasting pigs. Changes in gas concentrations were recorded at 10 s intervals and, combined with physical aspects of gas exchanges (changes in atmospheric pressure, relative humidity, gas extraction rates), were used to calculate daily total HP (Brouwer, 1965; van Milgen *et al.* 1997). In the respiration units, animal activity (signal of force sensors underneath the metabolism cages) and ingestion of feed (measured using load cells underneath the feeder) were monitored continuously (van Milgen *et al.* 1997), while faeces and urine were collected quantitatively and removed once daily for measurement of diet DE and ME content and whole-body N balance (van Milgen *et al.* 2001).

Table 1. Composition of the experimental diet

Item	Content
Ingredient composition (%)	
Wheat	36·74
Maize	36·75
Soyabean meal	17·80
Molasses	2·00
Wheat bran	3·00
L-Lysine-HCl	0·28
DL-Methionine	0·06
L-Threonine	0·09
L-Tryptophan	0·03
Dicalcium phosphate	1·20
Calcium carbonate	1·10
Salt	0·45
Vitamins and minerals mixture*	0·50
Calculated nutrient composition†	
Crude protein (%)	16·1
Starch (%)	44·7
Crude fibre (%)	2·9
Total lysine (%)	0·94
Digestible lysine (%)‡	0·82
Digestible methionine plus cysteine (%)	0·50
Digestible threonine (%)	0·52
Digestible tryptophan (%)	0·17
Analysed nutrient composition	
Crude protein (%)	15·6
Gross energy (MJ/kg)	15·7

* van Milgen *et al.* (2001).
† Based on ingredient values according to Institut National de la Recherche Agronomique (2002).
‡ Standardised ileal digestible.

Representative feed, and pooled faeces and urine samples (pooled for days 1 to 6 during calorimetry and per pig) were analysed for energy using an adiabatic bomb calorimeter (IKA C5000; IKA, Staufen, Germany) and crude protein (N × 6·25) content (Association of Official Analytical Chemists, 1990).

Components of HP were estimated according to van Milgen *et al.* (1997, 1998) and van Milgen & Noblet (2000). In short, O_2 and CO_2 patterns were related statistically to animal activity and feed intake to generate estimates of HPa (kJ/unit of force) and HPf-st (kJ/kg feed intake). Resting HP of pigs in the fed state was calculated as total HP − HPa and HPf-st. Activity-free FHPp was estimated statistically from estimated asymptotic plateau O_2 consumption and CO_2 production following a 24 h fast. Therefore, FHPp was not measured directly. The difference between resting HP and FHPp was considered to be HPf-lt. Results concerning energy retention and HP are expressed as kJ/kg $BW^{0·60}$ per d (Noblet *et al.* 1999).

Statistical analyses

The mixed models procedure of SAS was used for statistical analyses (version 8.0; SAS Institute, Inc., Cary, NC, USA). Data (*n* 18) were subjected to ANOVA with litter (identical to treatment sequence; *n* 3), experimental period (*n* 3) and feeding level (*n* 3) as sources of variation, while animals were considered the experimental units. Period and animal were assumed to be random effects. When feeding level effects were considered significant ($P<0.05$), means per feeding level were compared using the Tukey test. Linear regression analyses were conducted to relate the various components of HP and energy retention to ME intake. In preliminary regression analyses, no pig effects on the marginal response to ME intake were observed ($P>0.10$). Therefore, only pig effects on the intercept were maintained in the linear regression models.

Results and discussion

General observations

Throughout the experiments, pigs readily consumed the feed allowances and no apparent animal health or technical problems were observed. During days 2 to 6 in the respiration units, mean observed daily ME intakes were 1552, 2053 and 2543 (SE 33) kJ/kg $BW^{0.60}$ per d (Table 2) and very similar to the targeted ME intake levels; mean BW gains were 611, 838 and 983 (SE 29) g/d, for the low, medium and high feed intake levels, respectively. The determined diet mean DE and ME contents were 14·0 and 13·5 MJ/kg, respectively, while 0·80 % of DE intake was excreted as methane; feeding level and experimental period did not influence these values ($P>0.10$). The increase in feed intake was associated with higher energy, protein and fat gains (Table 2), which is in agreement with Quiniou *et al.* (1995); the increase in RQ during the fed state is reflective of increases in body lipid gain (Brouwer, 1965).

Components of energy expenditure

Components of energy expenditure, expressed per kg $BW^{0.60}$, were not influenced by experimental period ($P>0.20$). Total HP in pigs in the fed state increased with feeding level ($P<0.001$) from 1068 kJ/kg $BW^{0.60}$ per d at the lowest feeding level to 1431 kJ/kg $BW^{0.60}$ per d at the highest feeding level (Table 2; Fig. 1). The HPa, expressed as kJ/kg $BW^{0.60}$ per d, was not affected by feeding level ($P=0.75$; Table 2). As a fraction of total HP, HPa was reduced from 18 % at the low feeding level to 14 % at the high feeding level; as a fraction of ME intake, HPa was reduced from 12 to 8 %. These values are similar to values obtained in a previous study conducted under similar conditions (van Milgen & Noblet, 2000).

Feeding level influenced both HPf-st ($P<0.001$) and HPf-lt ($P<0.001$), expressed as kJ/kg $BW^{0.60}$ per d (Table 2), while HPf-st and HPf-lt contributed nearly equally to total HPf. When expressed as kJ/kg of feed intake, feeding level influenced HPf-st as well ($P=0.04$), while it did not influence HPf-lt and HPf ($P>0.28$) (Table 3). The observed decrease in HPf-st per kg of feed intake with decreasing feeding level should be considered carefully when interpreting components of HP in growing pigs that are exposed to different feeding levels. The HPf contributed 24 and 34 % to total HP in pigs on the low and high feeding levels, respectively, which is similar to the value of 24 % obtained in previous studies (van Milgen & Noblet, 2000). Across treatments, HPf varied between 17 and 19 % of ME intake, suggesting that feeding

Table 2. Components of energy expenditure in growing pigs at three different feeding levels
(Mean values with standard errors of the treatment mean for six animals per feeding level)

Item	Feeding level			SE	P*
	Low	Medium	High		
Average BW (kg)	68·3	69·3	74·6	2·2	0·31
Feeding level (g/kg $BW^{0.60}$ per d)	113[a]	152[b]	189[c]	1	<0·001
Digestible energy intake (kJ/kg $BW^{0.60}$ per d)	1622[a]	2134[b]	2651[c]	33	<0·001
Metabolisable energy intake (kJ/kg $BW^{0.60}$ per d)	1552[a]	2053[b]	2543[c]	33	<0·001
Energy retention (kJ/kg $BW^{0.60}$ per d)					
As body protein	226[a]	319[b]	361[b]	18	<0·001
As body lipid	265[a]	513[b]	775[c]	25	<0·001
Total	491[a]	832[b]	1137[c]	29	<0·001
Heat production (kJ/kg $BW^{0.60}$ per d)					
Total, fed state	1068[a]	1232[b]	1431[c]	34	<0·001
Components, fed state					
Activity	188	185	195	11	0·75
Thermal effects of feeding					
Total	260[a]	398[b]	493[c]	23	<0·001
Short term	127[a]	195[b]	267[c]	8	<0·001
Long term	133[a]	202[b]	226[b]	17	<0·001
Ghost	9[a]	12[a,b]	18[b]	2	0·016
Resting	742[a]	846[b]	955[c]	34	<0·001
Fasting, extrapolated plateau	609[a]	644[a]	729[b]	31	0·003
RQ (fed state)	1·05[a]	1·11[b]	1·14[c]	0·01	<0·001
RQ (fasted state)	0·86	0·88	0·86	0·01	0·48

BW, body weight.
[a,b,c]Mean values within a row with unlike superscript letters were significantly different ($P<0.05$).
* Probability of energy intake level effect; measures of energy utilisation did not differ between experimental periods.

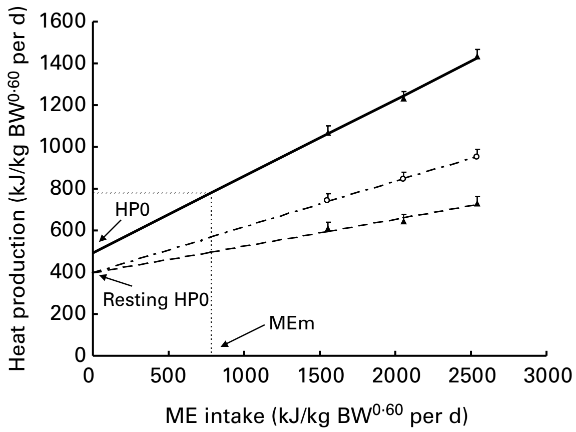

Fig. 1. Total heat production (HP;—▲—), resting HP (·–○–·) and fasting HP (– –▲– –) in growing pigs at three feeding levels, as well as extrapolated total HP at zero metabolisable energy (ME) intake (HP0), resting HP at zero ME intake (resting HP0) and estimated maintenance ME requirements (MEm, where ME intake equals heat production; 774 (SE 54) kJ/kg body weight (BW)$^{0.6}$ per d) based on linear regression analyses. Values are means, with their standard errors represented by vertical bars. Total HP = 489 (SE 69) + 0·368 ME intake; resting HP = 396 (SE 75) + 0·220 ME intake; fasting HP = 396 (SE 72) + 0·129 ME intake.

level exerts little influence on the efficiency of deriving available energy from ME intake.

In all pigs, a distinct and small increase in HP was observed over a short time period during the night. This phenomenon, previously referred to as a ghost effect (van Milgen & Noblet, 2000), is increased with feeding level ($P=0{\cdot}02$), suggesting that this HP is associated with nocturnal patterns in digestive functions, such as gut motility and pancreatic secretions (Corring *et al.* 1972).

Extrapolated FHPp, expressed as kJ/kg BW$^{0.60}$ per d, was increased with previous feeding level ($P=0{\cdot}003$) (Table 2; Fig. 1). Similarly to the conventional measure of FHP (for example, Koong *et al.* 1983), an adjustment of FHPp for previous feeding level is needed to estimate Eb from FHPp. In fasting pigs, the RQ at FHPp was not influenced by previous feeding level ($P=0{\cdot}48$; Table 2). This value was lower than unity and than those in pigs in the fed state (0·87 *v.* 1·10), indicating that pigs during the early stages of fasting mobilise some body protein or carbohydrate stores as well as body lipid stores (Brouwer, 1965). This is consistent with Chwalibog *et al.* (2004), who observed considerable oxidation of carbohydrates, based on an RQ of about 0·75, during the first day of a 4 d fast in growing pigs. Apparently, the relative contribution of the different body nutrients that are mobilised to support Eb during fasting is not influenced by previous feeding level. Variation in FHPp is probably a reflection of energy expenditure in visceral organs and sizes of visceral organs (Yen, 1997; van Milgen *et al.* 1998; Noblet *et al.* 1999; Nyachoti *et al.* 2000). Previous studies have shown that visceral organ size is influenced by (previous) nutritional regimen (Koong *et al.* 1983; Nyachoti *et al.* 2000).

Table 3. Energy expenditure per unit of feed intake in growing pigs at three different feeding levels*

(Mean values with standard errors of the treatment mean for six animals per feeding level)

	Feeding level				
Item	Low	Medium	High	SE	*P*†
Thermal effects of feeding (kJ/kg feed intake)					
Short term	1115[a]	1266[a,b]	1392[b]	81	0·04
Long term	1166	1322	1189	140	0·34
Total	2281	2588	2581	159	0·28

* Diet digestible energy (14·0 MJ/kg) and metabolisable energy (13·5 MJ/kg) contents were similar across feeding levels.

† Probability of energy intake level effect; these measures of energy utilisation did not differ between experimental periods.

[a,b]Mean values within a row with unlike superscript letters were significantly different ($P<0{\cdot}05$).

Estimates of maintenance energy requirement

As mentioned earlier, measurement of FHP may provide a more accurate estimate of Eb than MEm (Tess *et al.* 1984; Birkett & de Lange, 2001*a*,*b*; van Milgen *et al.* 2001). Traditionally, FHP production is measured as total HP in fasting animals and some time after fasting has been initiated (for example, Tess *et al.* 1984). The approach used by van Milgen *et al.* (1998, 2001) allows for estimation of activity-free and plateau FHP, eliminating the potential biases from animal activity and duration of fast.

Given the strong linear relationship between total HP and ME intake, observations from the present study may be used to obtain estimates of MEm and extrapolated total HP at zero ME intake (HP0; Fig. 1). Based on linear regression analyses, MEm was 774 (SE 54) kJ/kg BW$^{0.60}$ per d for this group of pigs (Fig. 1). The estimate of MEm for this group of pigs is at the low end of the wide range of estimates of MEm for pigs of different genotype and sex; for example, 719 kJ/kg BW$^{0.60}$ per d (Agricultural Research Council, 1981), 936 to 1122 kJ/kg BW$^{0.60}$ per d (Noblet *et al.* 1999). As discussed extensively by Noblet *et al.* (1999), van Milgen *et al.* (2001) and Birkett & de Lange (2001*a*), both experimental methodology and variability between pig groups contribute to variation in estimates of MEm.

When using regression analyses to estimate MEm and HP0 from HP at various ME intake levels, the duration of adaptation of pigs to changes in feeding levels before measuring components of HP should be considered carefully. For example, Noblet *et al.* (1994), who did not allow any time for adjustment when measuring HP following a reduction in feed intake, obtained a 50 % higher estimate of HP0 (750 kJ/kg BW$^{0.60}$ per d) as compared with the value of 489 kJ/kg BW$^{0.60}$ per d obtained in the present study. Resulting estimates of HP0 have a direct impact on diet NE contents when these are calculated as RE plus HP0 (Noblet *et al.* 1994; Birkett & de Lange, 2001*a*). Using the value of 489 kJ/kg BW$^{0.60}$ per d for HP0 as observed in the present study would have reduced the average calculated diet NE content reported by Noblet *et al.* (1994) by 15 %. Although this may change the absolute NE values (and the NE requirement), it is unlikely that the ranking of feed ingredients would be affected.

As mentioned earlier, FHPp may be used as a direct estimate of Eb or HP0. However, the present findings suggest that previous feeding level still exerts an effect on FHPp (Table 2). It is difficult to assess how long pigs should be starved before FHP will be independent of previous feeding level. For example, Chwalibog *et al.* (2004) did not observe a plateau in FHP after pigs were starved for 4 d, at which time animal wellbeing is likely to be compromised. It appears reasonable to adjust FHPp for previous energy intake level, for example by extrapolation to zero previous ME intake. This effectively increases estimates of HPf-lt. It remains to be determined, however, whether these adjustments to FHPp and HPf-lt are better related to some dietary characteristic, such as diet fibre and protein intake or extent of feed processing, rather than feeding level *per se*.

Based on linear regression analyses, extrapolated activity-free FHPp at zero previous ME intake is 396 (SE 72) kJ/kg $BW^{0.60}$ per d (Fig. 1). This value is statistically not different from HP0, i.e. extrapolated total HP at zero ME intake (489 (SE 69) kJ/kg $BW^{0.60}$ per d) and extrapolated resting HP at zero ME intake (resting HP0; 396 (SE 75) kJ/kg $BW^{0.60}$ per d). The relatively large SE values illustrate the limitations of using regression analyses to estimate accurately energy expenditure at zero ME intake. For comparison, Birkett & de Lange (2001*c*) estimated Eb, as residual energy expenditure once all other aspects of energy expenditure were accounted for, to be 360 to 420 kJ/kg $BW^{0.60}$ per d in growing pigs at normal levels of animal activity.

Since estimation of HP0 and resting HP0 requires measurements of HP at different feeding levels, the preferred method to routinely estimate Eb in different groups of pigs is to measure FHPp with corrections for the previous ME intake level (0·129 kJ/kJ ME intake; Fig. 1) and the known efficiency of using body energy stores to supply available energy for Eb, in addition to Eb itself (Birkett & de Lange, 2001*c*; van Milgen *et al.* 2001). Alternatively, Eb may be estimated indirectly as residual energy expenditure once all other aspects of energy expenditure are accounted for (Birkett & de Lange, 2001*b*,*c*).

Conclusions and implications

Feeding level influenced ($P < 0.05$) total HP during the fed state, HPf-st, HPf-lt, and FHPp. At previous ME intake levels of 1552, 2053 and 2543 kJ/$BW^{0.60}$ per d, FHPp was determined to be 609, 644, and 729 (SE 31) kJ/kg $BW^{0.60}$ per d, respectively. Under our measuring conditions, feeding level did not ($P = 0.75$) influence activity HP. Regression of resting HP during the fed state to zero ME intake yielded a value of 396 (SE 75) kJ/kg $BW^{0.60}$ per d, which is a considerably lower estimate of Eb in pigs than FHPp. Consequently, duration of adaptation of pigs to changes in feeding level should be considered when estimating Eb or maintenance energy requirements. The preferred method to routinely estimate Eb in different groups of pigs is to measure FHPp with corrections for the previous ME intake level and the known inefficiency of using body energy stores to supply available energy for Eb. This information is critical for a flexible factorial estimation of energy requirements of growing pigs.

Acknowledgements

We wish to thank Alfred Roger and Pascal Bodinier at the Animal Metabolism Research Unit and the Nutrition Laboratory at INRA-St Gilles for their assistance in animal management and chemical analyses. Financial support from INRA for the sabbatical leave of C. de Lange at INRA-St Gilles is gratefully acknowledged.

References

Agricultural Research Council (1981) *The Nutrient Requirements of Pigs*. Slough, UK: Commonwealth Agricultural Bureaux.

Association of Official Analytical Chemists (1990) *Official Methods of Analysis*, 15th ed. Washington, DC: Association of Official Analytical Chemists.

Birkett SH & de Lange CFM (2001*a*) Limitations of conventional models and a conceptual framework for a nutrient flow representation of energy utilization by animals. *Br J Nutr* **86**, 647–659.

Birkett SH & de Lange CFM (2001*b*) A computational framework for a nutrient flow representation of energy utilization by growing mono-gastric animals. *Br J Nutr* **86**, 661–674.

Birkett SH & de Lange CFM (2001*c*) Calibration of a nutrient flow model of energy utilization by growing pigs. *Br J Nutr* **86**, 675–689.

Black JL (1995) Modelling energy metabolism in the pig – critical evaluation of a simple reference model. In *Modelling Growth in the Pig*, pp. 87–102 [PJ Moughan, MWA Verstegen and M Visser-Reyneveld, editors]. Wageningen, The Netherlands: Wageningen Pers.

Blaxter K (1989) *Energy Metabolism in Animals and Man*. Cambridge, UK: Cambridge University Press.

Brouwer E (1965) Report of sub-committee on constants and factors. In *Energy Metabolism, Proceedings of the 3rd Symposium of the European Association for Animal Production*, pp. 441–443 [KL Blaxter, editor]. Troon, Scotland, May 1964, publication no. 11 London: Academic Press.

Chwalibog A, Tauson A-H & Thorbek G (2004) Energy metabolism and substrate oxidation in pigs during feeding, starvation and re-feeding. *J Anim Physiol Anim Nutr* **88**, 101–112.

Corring T, Aumaitre A & Rerat A (1972) Fistulation permanente du pancréas exocrine chez le porc. Application: réponse de la sécrétion pancréatique au repas (Permanent fistulisation of the exocrine pancreas in the pig. Application: response of pancreatic secretion to feeding). *Ann Biol Anim Biochim Biophys* **12**, 109–124.

Institut National de la Recherche Agronomique. *Tables de composition et de valeur nutritive des matiéres premiéres destinées aux animaux d'élevage: Porcs, volailles, bovins, ovins, caprins, lapins, chevaux, poissons* [D Sauvant, JM Perez and G Tran, editors]. Versailles, France: INRA Editions. (2002).

Koong LJ, Nienaber JA & Mershman HJ (1983) Effect of plane of nutrition on organ size and fasting heat production in genetically obese and lean pigs. *J Nutr* **113**, 1626–1631.

National Research Council (1998) *Nutrient Requirements of Swine*, 10th revised ed. Washington, DC: National Academic Press.

Noblet J, Fortune H, Shi XS & Dubois S (1994) Prediction of net energy value of feeds for growing pigs. *J Anim Sci* **72**, 344–354.

Noblet J, Karege C, Dubois S & van Milgen J (1999) Metabolic utilization of energy and maintenance requirements in growing pigs: effects of sex and genotype. *J Anim Sci* **77**, 1208–1216.

Noblet J, Shi XS & Dubois S (1993) Metabolic utilization of dietary energy and nutrients for maintenance energy requirements in pigs: basis for a net energy system. *Br J Nutr* **70**, 407–419.

Nyachoti CM, de Lange CFM, McBride BW, Leeson S & Schulze H (2000) Dietary influence on organ size and *in vitro* oxygen consumption by visceral organs of growing pigs. *Livest Prod Sci* **65**, 229–237.

Quiniou N, Noblet J, van Milgen J & Dourmad JY (1995) Effect of energy intake on performance, nutrient and tissue gain and protein and energy utilization in growing boars. *Anim Sci* **61**, 133–143.

Tess MW, Dickersen GE, Nienaber JA & Ferrell CL (1984) The effects of body composition on fasting heat production in pigs. *J Anim Sci* **58**, 99–110.

van Milgen J, Bernier JF, Lecozler Y, Dubois S & Noblet J (1998) Major determinants of fasting heat production and energetic cost of activity in growing pigs of different body weight and breed/castration combination. *Br J Nutr* **79**, 1–9.

van Milgen J & Noblet J (2000) Modelling energy expenditure in pigs. In *Modelling Nutrient Utilization in Farm Animals*, pp. 103–114 [JP McNamara, J France and D Beever, editors]. Wallingford: CABI Publishing.

van Milgen J, Noblet J & Dubois S (2001) Energetic efficiency of starch, protein and lipid utilization in growing pigs. *J Nutr* **131**, 1309–1318.

van Milgen J, Noblet J, Dubois S & Bernier JF (1997) Dynamic aspects of oxygen consumption and carbon dioxide production in swine. *Br J Nutr* **78**, 397–410.

Yen J-T (1997) Oxygen consumption and energy fluxes of porcine splanchnic tissues. In *Digestive Physiology in Pigs, Proceedings of the 7th International Symposium on Digestive Physiology in Pigs*, pp. 260–269 [J-P Laplace, C Fevrier and A Barbeau, editors]. EAAP publication no. 88., Paris: INRA.