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Metabolic utilization of dietary energy and nutrients for maintenance energy requirements in sows: basis for a net energy system

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Digestible energy (DE), metabolizable energy (ME) and net energy for maintenance (NE_m) values of a set of fourteen diets were measured in six adult sows fed at and below their maintenance energy level. The efficiency of ME for NE_m was estimated from heat production (HP) measurements (indirect calorimetry) at these different feeding levels. HP was partitioned between HP due to physical activity, thermic effect of food (TEF) and fasting heat production (FHP). The amounts of DE digested in the small intestine or in the hindgut were measured. Equations for prediction of NE_m from dietary characteristics were calculated. HP at maintenance level averaged 400 kJ/kg body-weight$^{0.75}$, 16 and 19% of the total being due to physical activity and TEF respectively. The efficiency of ME for NE_m averaged 77·4% with higher values for digestible diethyl ether extract (100%) and starch+sugar (82%). The efficiencies of digestible crude protein (N × 6·25) and digestible residue averaged 69 and 56% respectively. The energy absorbed from the small intestine was used more efficiently than the energy fermented in the hindgut (82 *v.* 59%). These values are comparable with those obtained in growing pigs. The NE_m content of diets can be predicted accurately from equations including DE (or ME) values and some dietary chemical characteristics.

Heat production: Maintenance: Net energy: Sow

Evaluation of energy content of feeds for pigs is usually based on their digestible (DE) or metabolizable energy (ME) contents (Agricultural Research Council, 1981; INRA, 1984). But since ME is used differently according to its composition, energy evaluation systems based on the net energy (NE) concept have also been proposed (Schiemann *et al.* 1972; Just, 1982; Noblet *et al.* 1989). These NE systems were established from measurements carried out with growing or fattening pigs. The NE value was, therefore, a combination of NE for maintenance (NE_m) and NE for production (protein and/or fat deposition). However, in pig production a rather large proportion of the consumed feed is almost exclusively used for meeting maintenance energy requirements of the animals (pregnant sows, boars). So far, available scientific information has been insufficient for predicting the NE_m content of diets or, in other words, proposing relationships between the thermic effect of food (TEF) when fed at maintenance energy level and chemical characteristics of the diet. Breirem (1939) and Close & Mount (1975) reported a mean TEF equivalent to 20% of ME content for pigs, which means that the mean efficiency of ME for maintenance (k_m) averages 80%. Comparable results are available in other species; most of the information has been obtained recently with humans from studies concerning the variations of TEF in relation to diet composition (Dauncey, 1979; Dauncey & Bingham, 1983; Nair *et al.* 1983; Schutz *et al.* 1984; Kinabo & Durnin, 1990). However, in most studies with humans TEF was measured over a few hours; therefore, a fraction of the thermogenic effect was ignored (Kinabo & Durnin, 1990).

The aim of the present experiment was to determine the effect of diet composition on TEF or k_m in pigs fed at their maintenance energy level, in order to propose relationships for predicting the NE_m content of diets and ingredients. The study was based on a set of fourteen diets which were fed to adult sows at and below their energy maintenance requirement. The procedure involved continuous measurement of heat production (HP; indirect calorimetry) and its three main components: fasting heat production (FHP), TEF and energy expenditure due to physical activity. The energy expenditure for thermogenesis was assumed to be negligible since the ambient temperature (24°) was supposed to be within the thermoneutral zone of sows.

MATERIALS AND METHODS

Experimental design

Fourteen different diets which differed widely in their chemical composition were fed to six adult Large White sows (208 kg live weight on average). Sows were ovariectomized in order to avoid any effect of cycling and oestrus on heat production measurements. Each sow received eight to ten diets consecutively (eight to ten measurement periods on each animal) and each diet was measured with four different animals. The allocation of animals to diets was arranged in order to obtain similar mean live weights and similar mean measurement period numbers for all diets. Each diet was given for about 28 d, including 17 d for adaptation and 8 d in metabolism cages for collection of faeces and urine in order to measure the DE, ME and digestible nutrient contents of diets. Over these 8 d periods HP and CH_4 production were measured in open-circuit respiration chambers at two different feeding levels: the first 5 d and the last day at maintenance level (about 400 kJ ME/kg metabolic body weight ($BW^{0.75}$)) and the other 2 d at 60% of this maintenance level. Feeding level of each sow was adjusted at each measurement period in order to keep its body weight and backfat thickness constant over the experiment. The total experiment lasted about 9 months. For each sow FHP was measured four times over the experiment at the end of a balance period. The FHP measurement occurred on the third day after the end of a balance period, the sow being fed at 100% of its maintenance level for the first 2 d. Sows were fed once daily at 08.30 hours. Therefore, FHP corresponded to HP during the period starting 24 h after a meal.

The ileal digestibility of energy of the fourteen diets was measured with ileo-rectal anastomosed growing pigs (45 kg live weight on average), in order to differentiate between DE absorbed from the small intestine (DEi) and that at the hindgut level (DEh). The methodological approaches and the results have been described previously (Shi & Noblet, 1993). The same diets were also given to 45 kg pigs (Noblet & Shi, 1993).

Diets and housing

The fourteen diets were based on wheat, maize starch, cane molasses, soya-bean meal, maize-gluten feed, meat-and-bone meal, rapeseed oil, wheat middlings, sugar-beet pulp, wheat bran and wheat straw (Table 1). All diets contained (g/kg) NaCl 5, Ca_2PO_4 20, $CaCO_3$ 20, minerals and vitamins mixture 5 (Noblet *et al.* 1989). The main objective in formulating the diets was to obtain large variations in their chemical characteristics (Table 1). The diets were fed as pellets and the animals had free access to water.

During the balance period, the sows were kept individually in metabolism cages located in 10 m^3 respiration chambers. Lighting was given from 08.00 to 20.00 hours. Air velocity

Table 1. *Chemical characteristics of the diets*

(Mean values for fourteen diets)

	Minimum	Maximum	Mean
Ingredients (g/kg)			
Wheat	0	31·3	16·5
Maize starch	0	29·2	14·5
Wheat straw	0	11·2	3·7
Meat-and-bone meal	0	7·9	2·1
Rapeseed oil	0	7·8	4·5
Cane molasses	0	4·7	1·7
Maize-gluten feed	0	13·4	6·3
Sugar-beet pulp	0	11·8	4·7
Wheat middlings	0	28·0	11·6
Wheat bran	0	17·8	6·2
Soya-bean meal	10·2	35·6	22·4
Chemical composition (g/kg DM)			
Ash	79	108	92
Crude protein (N × 6·25)	159	274	204
Diethyl ether extract	16	101	64
Crude fibre	37	92	64
NDF	118	261	193
ADF	45	110	76
ADL	8	18	13
WICW	134	267	210
Starch	230	462	358
Sugar	34	81	56
Gross energy (MJ/kg DM)	17·47	19·23	18·51

* DM, dry matter; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignin; WICW, water-insoluble cell walls.

in the chamber was about 0·1 m/s and temperature and relative humidity were kept at 24° and 70% respectively.

Measurements

Sows were weighed at the beginning and at the end of the collection period. For each diet and each sow a sample of feed was collected and measured for its dry matter content. Samples of the same diet were subsequently combined for chemical analysis. Faeces and urine were collected daily, stored at 2°, weighed and subsampled at the end of the period. Faeces were freeze-dried for further chemical analysis. N losses in the air which were recovered in condensed water and outgoing air from the respiration chamber were measured according to the method described by Noblet *et al.* (1987).

Gas (CO_2, O_2 and CH_4) contents of ingoing and outgoing air were continuously recorded over 7 min intervals during the 8 d of the excreta collection period. Gas exchanges (O_2, CO_2 and CH_4) were calculated for each 7 min interval according to the method described by Vermorel *et al.* (1973); values were corrected in order to take into account the changes in gas contents of air in the chamber during the measurement interval. HP was calculated for each interval and over the 24 h period from gas exchanges according to the formula of Brouwer (1965). Duration of standing was also recorded in the respiration chamber at 7 min intervals by using two i.r. barriers located at the front and the back of the cage.

Chemical analyses

Chemical analyses on diets were performed by four different laboratories. The values reported in Table 1 correspond to the mean of the four values. Faeces and urine were analysed by one laboratory. For feed samples the Association of Official Agricultural Chemists (1975) methods were used for measuring moisture, ash, crude protein (N × 6·25; CP), Weende crude fibre (CF) and diethyl ether extract (EE). Gross energy (GE) content was measured using an adiabatic bomb calorimeter. Cell-wall fractions (neutral-detergent fibre (NDF), acid-detergent fibre (ADF), acid-detergent lignin ADL)) were determined according to the methods of Van Soest & Wine (1967), with previous amylase hydrolysis (Termamyl 300L, Novo Biolabs, Denmark). Water-insoluble cell walls (WICW) were measured according to the method of Carré & Brillouet (1989). Starch content was estimated from the Ewers polarimetric method (EEC, 1972) and sugar correspond to alcohol-soluble carbohydrates obtained by the method of Luff-Schoorl (Perez, 1991). Similar analyses were carried out on each sample of faeces but EE was measured after HCl hydrolysis; WICW, starch and sugar contents were not measured. N in urine, condensed water and outgoing air were determined on fresh material whereas the energy content of urine was obtained after freeze-drying approximately 50 ml in polyethylene bags.

Calculations and statistical analysis

DE, ME and digestible nutrient contents of diets were calculated according to routine procedures (Noblet *et al.* 1989). ME included energy losses as both urine and methane. Starch and sugar were assumed to be completely digestible. The mean results for the fourteen diets are reported in Table 2.

For each balance period, HP and activity (i.e. percentage of time while standing) were measured simultaneously at 7 min intervals over 24 h after the morning meal and during five consecutive days at maintenance level. These findings (about 1000 values for one sow given one diet) were included in a regression model where HP was related to time after the beginning of the meal and activity. The best model was a linear one where the coefficient attributed to activity corresponded to the mean energy expenditure while standing, so called activity HP (AHP). A typical activity and HP daily pattern recorded on one sow is given in Fig. 1. Differences between animals were due to the level of activity occurring after the inevitable meal activity. In addition, AHP (kJ/min standing activity) was particularly constant for each sow over the total experiment (Noblet *et al.* 1993). Total mean AHP over 24 h (MJ/d) of each 5 d period was obtained by multiplying the total duration of activity by the mean energy cost obtained from the regression equation. Resting HP (RHP; MJ/d) was then calculated as the difference between total HP and AHP. The mean values of daily AHP and RHP obtained for each sow over the total experiment are given in Table 3. RHP during the 2 d at the low feeding level (60 % of maintenance level) was similarly calculated; the coefficient used for estimating AHP was the value obtained from the regression calculated over the previous 5 d at maintenance level. A more comprehensive description of the approach has been reported by Noblet *et al.* (1993).

Three different methods were used to estimate FHP. The first one involved measurement of RHP during 1 d the sow did not receive any food in the morning. The second method resulted from the regression equation between RHP at high (mean of 5 d at 100 % maintenance level) and at low (second day at 60 % of maintenance) feeding levels and corresponding ME intakes (MJ/d). The first day at the low feeding level was supposed to be an adaptation day. ME intake considered in the regression (MEc) was equivalent to actual ME intake minus AHP, since a proportion of dietary energy (equal to AHP) was lost directly for activity energy requirements. The regression was calculated for each sow, the

Table 2. *Digestible nutrients and energy values of diets**

(Mean values for fourteen diets)

	Minimum	Maximum	Mean
Body wt (kg)	195	227	208
Dry matter (DM) intake (g/d)*	1394	1770	1580
Digestible nutrients (g/kg DM)			
Dry matter	762	871	821
Organic matter	725	833	787
Crude protein (N × 6·25)	134	239	175
Diethyl ether extract	5·3	78·7	47·3
Crude fibre	26	55	40
NDF	89	176	135
ADF	30	64	45
Residue†	105	219	151
ME/DE (%)	89·3	93·7	92·3
Energy (MJ/kg DM) as:			
Methane	0·16	0·31	0·21
Urine	0·78	1·33	0·99
Energy values (MJ/kg DM)			
Faecal DE	13·85	17·01	15·62
Ileal DE	9·67	13·63	11·79
Hindgut DE	2·67	5·67	3·84
ME	12·87	15·74	14·43
NE$_{\rm m}$	9·66	12·59	11·61
k_{m1} (NE$_{\rm m}$/DE; %)	66·0	74·6	71·4
k_m (NE$_{\rm m}$/ME; %)	73·9	80·7	77·4
Respiratory quotient*	0·86	0·91	0·88

NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ME, metabolizable energy; DE, digestible energy; NE$_{\rm m}$, net energy for maintenance; k_m, the efficiency of ME intake for maintenance requirements; k_{m1}, the efficiency of DE intake for maintenance requirements.

* At maintenance feeding level.

† Residue = digestible organic matter – (digestible crude protein + digestible diethyl ether extract + starch + sugar).

number of observations varying between sixteen and twenty (i.e. eight to ten diets). The extrapolation to zero energy intake provided an estimate of FHP. The third method was comparable with the second one but the analysis was carried out on data from all sows. In this covariance model the covariate was the variable (MEc) involved in the regression model of method 2 and the main factor was the animal (*n* 6). FHP of each sow was obtained as the difference between adjusted HP and HP associated to MEc intake, this latter value being estimated from the slope of the covariate. Body weight and body condition (backfat thickness) of each sow were kept constant over the total experiment by adjusting feed intake. Subsequently, FHP was supposed to be constant for each sow over the 9 months of the experiment.

The TEF was estimated as the difference between RHP at the maintenance level and FHP. NE intake (MJ/d) was calculated as MEc intake (MJ/d) minus TEF (MJ/d). The efficiency of ME intake for maintenance requirements (k_m) was equivalent to the ratio (× 100) between NE and MEc. NE$_{\rm m}$ (MJ/kg dry matter) was calculated as ME content multiplied by k_m (/100). These calculations were carried out on each balance period (*n* 56). The final DE, ME and NE$_{\rm m}$ values of each diet corresponded to the mean of the four measurements carried out on each diet.

The effect of sow on HP and its main components were submitted to analysis of variance

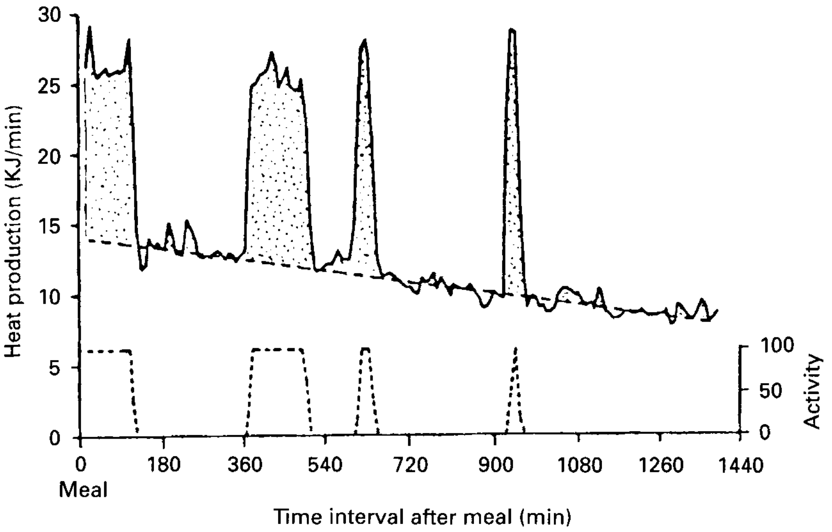

Fig. 1. Effect of time-interval after the meal (min) and physical activity (percentage of time while standing for each 7 min measurement interval; ---) on heat production (—) of a sow when fed at maintenance energy level (from Noblet *et al.* 1993).

with sow (*n* 6) and diet (*n* 14) as the main effects (Table 3). Regression equations were calculated in order to predict the NE_m content of diets from either digestible nutrient contents (Table 5) or from DE or ME contents and chemical characteristics (Table 6). Regression equations were also calculated in order to analyse the effect of diet composition on k_m. Formulation of diets was such that low correlation coefficients between variables involved in the regression equations were expected, in order to improve the accuracy and the validity of the prediction (Table 4). NE_m was also related to DEi and DEh. SAS (1988) was used for all statistical analyses.

RESULTS AND DISCUSSION

Estimation of fasting heat production

In the present experiment three approaches were used to estimate FHP. In the first method HP was measured in sows from 24 to 48 h after a meal. Under such conditions RHP declined regularly over the 24 h period with a significant CH_4 production, even 48 h after the last meal. In other words the digestion of the last meal (mainly at the hindgut level) was not completed over the day of FHP measurement. Therefore, HP included energy expenditure from the digestive and metabolic utilization of dietary energy. Consequently, the mean RHP recorded over the 24 h period was 15·47 MJ/d whereas the mean RHP over the last 6 h of the 24 h starvation period (or 42–48 h after the last meal) averaged 14·24 MJ/d for the six sows.

In the two other methods FHP was obtained either by regression (on each sow) or by covariance (on all sows) techniques with extrapolation to zero feed intake. Estimates of FHP obtained for each sow from the two statistical models were similar, the slope of the variable or the covariate being in all situations close to 0·23 (0·229 SD 0·016 in the covariance model). In addition, the values of FHP obtained by the extrapolation approach (14·56 MJ/d, on average; Table 3) were close to what was measured during the last 6 h of the fasting day (14·24 MJ/d) but lower than RHP recorded from 24 to 48 h after a meal (15·47 MJ/d).

Table 3. *Body weight (BW), dry matter (DM) intake metabolizable energy (ME) intake and heat production of sows at maintenance feeding level**

(Mean values for fourteen diets and four sows per diet)

Sow	BW (kg)	DM intake (g/d)	ME intake (MJ/d)	Heat production (MJ/d)‡			
				AHP	RHP	FHP	TEF
A	175^{f}	1430^{c}	$20·84^{c}$	$4·41^{a}$	$15·93^{c}$	12·21	$3·71^{b}$
B	191^{e}	1477^{c}	$21·11^{c}$	$4·46^{a}$	$16·87^{d}$	13·22	$3·65^{b}$
C	210^{d}	1588^{b}	$22·78^{b}$	$1·53^{e}$	$19·44^{b}$	14·65	$4·79^{a}$
D	216^{c}	1614^{b}	$23·07^{b}$	$3·88^{ab}$	$19·11^{ab}$	14·35	$4·76^{a}$
E	226^{b}	1683^{a}	$24·65^{a}$	$3·42^{bc}$	$19·00^{b}$	14·90	$4·10^{ab}$
F	232^{a}	1691^{a}	$24·69^{a}$	$2·53^{d}$	$21·34^{a}$	16·70	$4·64^{a}$
Mean	208	1580	22·74	3·34	18·64	14·36	4·27
RSD	4	46	0·97	0·93	0·97		0·81

RSD, residual SD; AHP, activity heat production; RHP, resting heat production; FHP, fasting heat production; TEF, thermic effect of food.

* For details of diets, see Tables 1 and 2 and p. 408.

† Least square means from the analysis of variance with diet (*n* 14) and sow (n 6) as the main effects; the effect of sow was significant ($P < 0·01$) for all criteria.^{a,b,c,d,e,f} Within each column mean values with the same superscript letter were not significantly different ($P > 0·05$).

‡ For details of calculation of the different components of heat production, see pp. 411–412.

The reduction of RHP over the fasting day is consistent with previous observations of Close & Mount (1975) in growing pigs whose metabolic rate continued to decrease over 3–4 d of fasting. This effect might be more important in adult sows whose hindgut is more developed and where digestion of diet is more prolonged. Consequently, even though FHP estimates obtained during the last part of the fasting day were close to the values obtained by the extrapolation methods, TEF and NE_m values were calculated from the latter estimates (mean of regression and covariance values; Table 3).

In human energy metabolism studies TEF is usually estimated as the difference between cumulated HP over a few hours after a meal and HP after an overnight fast (equivalent to FHP). But, in most studies, the duration of measurement after the meal is short, so that HP at the end of the measurement period is higher than the FHP value. Consequently, TEF is underestimated (Kinabo & Durnin, 1990). Therefore, TEF should be measured over longer periods, with subsequent higher values for TEF (Schutz *et al.* 1984). In addition, the present study shows that, for sows, FHP measured under such experimental conditions is higher than minimal HP obtained after a prolonged fasting. Furthermore, factors such as the previous feeding level (Koong *et al.* 1982), level of activity or ambient temperature affect FHP values. These different observations mean that estimates of TEF are very dependent on the experimental procedure and the method used for estimating FHP.

The daily FHP at zero activity differed between sows (Table 3). When expressed per unit $BW^{0·75}$, the variation was smaller (range 254–280 kJ/kg $BW^{0·75}$) with a mean value equivalent to 261 kJ/kg $BW^{0·75}$. Since the mean TEF averaged 22·6% of ME intake (k_m in Table 2), the mean ME requirement for maintenance at zero activity level was 337 kJ/kg $BW^{0·75}$. As reported in Table 3, the mean daily activity HP was 3·34 MJ/d, for a mean duration of standing activity of 241 min (Noblet *et al.* 1993). This quantity was equivalent to 68 kJ/kg $BW^{0·75}$, on average. Therefore, the total ME requirement for maintenance (ME_m) of the six sows used in the present experiment averaged 400 kJ/kg $BW^{0·75}$, 16 and 19% of the requirement being associated with physical activity and TEF

Table 4. *Correlation coefficients between energy values and digestible nutrient contents of the experimental diets for sows**†

(Mean values for fourteen diets)

	DE	ME	NE_m	DCP	DEE	CHO
ME	0·98	—	—	—	—	—
NE_m	0·92	0·95	—	—	—	—
DCP	0·45	0·31	0·12	—	—	—
DEE	0·51	0·52	0·61	−0·08	—	—
CHO	−0·22	0·35	0·35	−0·35	−0·33	—
Dres	−0·43	−0·58	−0·57	0·19	−0·07	−0·82

DE, digestible energy; ME, metabolizable energy; NE_m, net energy for maintenance; DCP, digestible crude protein (N × 6·25); DEE, digestible diethyl ether extract; CHO, starch + sugar; Dres, digestible residue (digestible organic matter − (DCP + DEE + CHO)).

* For details of diets, see Tables 1 and 2 and p. 408.

† Correlation coefficient whose absolute value was higher than 0·52 and 0·66 was significantly different from zero at the $P < 0·05$ and $P < 0·01$ levels respectively.

respectively. The value obtained for ME_m of sows is comparable with estimates reported by Close *et al.* (1985) and Noblet *et al.* (1990) in pregnant sows.

Energy balance data (Tables 2 and 4) show that in sows fed at their maintenance level, energy losses in faeces, urine and methane represented about 15·3, 5·3 and 1·1 % of the gross energy intake respectively. Since ME supply was slightly higher than requirements for maintenance, energy balance was positive and represented 2·6 % of gross energy intake. Total heat production, equivalent to 75·6 % of gross energy intake, had different origins: 49·4, 14·7 and 11·5 % of gross energy intake were associated with fasting heat production, thermic effect of food and physical activity, respectively. The partition of gross energy intake in sows kept on a maintenance situation is illustrated in Fig. 2.

Effect of diet composition on TEF or efficiency of utilization of ME for maintenance

k_m averaged 77·4 % for the fourteen diets (k_m in Table 2). This means that 22·6 % of ME intake was lost as HP during digestive and metabolic utilization of energy. NE_m, expressed as a percentage of DE, averaged 71·6 % (k_{m1} in Table 2). In connection with methodological differences, these values are lower than those obtained with humans where TEF represents about 10 % of energy intake (Dauncey, 1979; Golay *et al.* 1983). On the other hand, they are close to those reported by Breirem (1939) and Close & Mount (1975) in pigs, the highest k_m values obtained in the present study with high-energy diets being identical (80 %) to the value obtained by these authors.

As indicated in Table 2, k_m ranged between 74 and 81 %. Regression analysis showed that k_m increased when starch and fat (EE) or digestible diethyl ether extract (DEE) contents (g/kg dry matter) of diets were increased. The following relationships were obtained:

$$k_m = 67·2 + 0·066 \times \text{EE} + 0·016 \times \text{starch} \ (R^2\ 0·57;\ \text{residual SD (RSD) } 1·9),$$
$$k_m = 67·9 + 0·079 \times \text{DEE} + 0·016 \times \text{starch} \ (R^2\ 0·60;\ \text{RSD } 1·6).$$

Corresponding equations for k_{m1} were:

$$k_{m1} = 57·3 + 0·076 \times \text{EE} + 0·026 \times \text{starch} \ (R^2\ 0·70;\ \text{RSD } 1·6),$$
$$k_{m1} = 58·1 + 0·091 \times \text{DEE} + 0·025 \times \text{starch} \ (R^2\ 0·73;\ \text{RSD } 1·6).$$

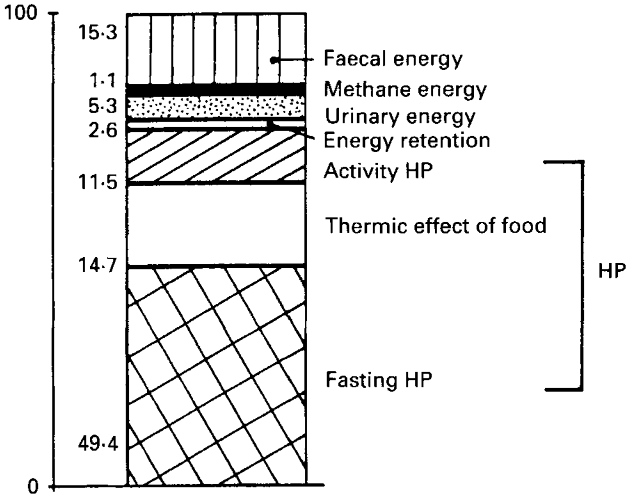

Fig. 2. Partition of gross energy intake between energy retained and energy losses in faeces, urine, methane and different components of heat production (HP), in adult sows when fed at their maintenance energy level (mean of fifty-six measurements from six different sows).

The coefficients obtained in both groups of equations indicate a higher positive effect of fat than of starch, even when expressed per unit energy. In addition, these relationships demonstrate that k_m was higher for fat or starch than for the other dietary nutrients whose efficiency averaged the intercept value (about 68%). This is confirmed by equations reported in Table 5. In order to calculate the efficiencies of digestible nutrients for NE_m, the intercept of these equations was forced to zero.

Different fractionation methods of digestible organic matter were tested, all including digestible CP (DCP) and DEE. Especially for NE, the accuracy of the prediction was not improved when the different digestible fibre estimates (digestible CF, digestible NDF, etc.) were considered. The best linear model was the combination of DCP, DEE, starch + sugar (CHO) and the digestible residue (Dres) equivalent to digestible organic matter − (DCP + DEE + CHO) (Table 5). In the DE, ME and NE_m equations calculated according to this model the intercept was not significantly different from zero ($P > 0{\cdot}05$). The efficiencies of digestible nutrients for NE_m were calculated for each nutrient as the ratio, coefficient obtained in the NE equation: corresponding coefficient in the ME (k_m) or DE (k_{m1}) equations.

First, the comparison of the coefficients obtained in the ME and DE equations indicated that the energy losses during the DE to ME step concerned DCP and Dres, corresponding schematically to energy losses in the urine and as CH_4 respectively. Second, during the ME to NE step the equations show that TEF was the highest for Dres (44% of ME intake) and the lowest (about zero) for DEE. The values for CHO (equivalent to carbohydrates degraded in the small intestine and producing mainly glucose) and DCP were intermediate (18 and 31% respectively). The value obtained for DEE is rather surprising. However, it must be noted that calculated TEF of ME or nutrients corresponds to TEF when ME or dietary nutrients replace body reserves mobilization (mainly fat) when animals are fed below their maintenance level. Therefore, k_m represents an apparent efficiency. It is then logical to obtain a negligible TEF for DEE since the energy cost of utilization of fat (or the amount of ATP that is released) is expected to be the same for DEE and mobilized body fat. In addition, we showed previously (Noblet & Shi, 1993) that the

Table 5. *Prediction of digestible energy (DE), metabolizable energy (ME) and net energy for maintenance (NE_m) (MJ/kg dry matter) from digestible nutrient contents (g/kg dry matter) of fourteen experimental diets for sows**

(Linear model without intercept)

		Regression coefficients				
Digestible nutrient...		DCP	DEE	CHO	Dres	Residual SD
DE	Mean	0·0237	0·0382	0·0172	0·0171	0·06
	SD	0·0005	0·0006	0·0001	0·0004	
ME	Mean	0·0207	0·0378	0·0169	0·0132	0·08
	SD	0·0006	0·0009	0·0002	0·0006	
NE_m	Mean	0·0142	0·0384	0·0139	0·0074	0·26
	SD	0·0021	0·0028	0·0006	0·0020	
k_{m1} (NE/DE; %)†		60	100	81	43	
k_m (NE/ME; %)†		69	102	82	56	

DCP, digestible crude protein (N × 6·25); DEE, digestible diethyl ether extract; CHO, starch + sugar; Dres, digestible residue (digestible organic matter – (DCP + DEE + CHO)); k_{m1}, efficiency of DE intake for maintenance requirements; k_m, efficiency of ME intake for maintenance requirements.

* For details of experimental diets, see Tables 1 and 2 and p. 408.

† Calculated as the ratio (× 100) between coefficients within the same column.

amount of EE actually absorbed before the end of the ileum was slightly higher than the measured DEE content at the faecal level. Indeed, this latter quantity represented an apparent value and included endogenous production of fat at the hindgut level.

On theoretical considerations (Armstrong, 1969), the TEF of infused glucose should be close to zero. The difference with the value obtained in the present study is partly explained by the fact that intake of starch (and sugar) involved additional energy cost for prehension, mastication, digestion and absorption that would reduce the apparent efficiency of utilization of CHO for maintenance. With regard to DCP, the theoretical k_m value is about 80% (Armstrong, 1969), which is again higher than the observed value in the present experiment (69%). The discrepancy can be related to the same reasons as for CHO. Finally, the k_m value obtained for Dres (56%) is also lower than the theoretical one (80–85%, according to Armstrong, 1969), the difference being consistent with the additional energy costs associated with the consumption of fibre.

The lower efficiency of Dres than for CHO is related to the nature of nutrients absorbed which are predominantly volatile fatty acids and glucose respectively. In the present experiment, DEi and DEh were estimated. Therefore, it was possible to relate ME and NE_m to DEi and DEh; the following relationships were obtained:

$$ME = 0{\cdot}97\ (\text{SD } 0{\cdot}01) \times DEi + 0{\cdot}79\ (\text{SD } 0{\cdot}02) \times DEh\ (\text{RSD } 0{\cdot}10),$$

$$NE_m = 0{\cdot}80\ (\text{SD } 0{\cdot}03) \times DEi + 0{\cdot}46\ (\text{SD } 0{\cdot}08) \times DEh\ (\text{RSD } 0{\cdot}35),$$

where energy values are expressed as MJ per kg dry matter. These equations indicate that the efficiencies of ME for NE_m were 82 and 59% when energy was degraded in the small intestine and in the hindgut respectively. The latter value is consistent with the efficiency of Dres for NE_m (56%) while the first one corresponds to the combination of efficiencies of nutrients digested at the small intestine level (DCP, DEE and CHO).

Comparable information on utilization of ME and digestible nutrients for NE_m in the literature are scarce. However, the present findings are consistent with most results

Table 6. *Prediction of net energy for maintenance (NE_m) content of fourteen experimental diets for sows* (MJ/kg dry matter (DM)) from digestible energy (DE) or metabolizable energy (ME) contents (MJ/kg DM) and/or chemical characteristics (g/kg DM)**

Equation no.		R^2	Residual SD
1	$NE_m = -4{\cdot}45 + 1{\cdot}128 \times DE - 0{\cdot}0098 \times CP$	0·95	0·22
2	$NE_m = -7{\cdot}30 + 1{\cdot}299 \times ME - 0{\cdot}0053 \times CP + 0{\cdot}0125 \times CF$	0·97	0·18
3	$NE_m = -7{\cdot}13 + 1{\cdot}291 \times ME - 0{\cdot}0054 \times CP + 0{\cdot}0101 \times ADF$	0·97	0·19
4	$NE_m = 14{\cdot}74 - 0{\cdot}0283 \times Ash + 0{\cdot}0206 \times EE - 0{\cdot}0120 \times NDF$	0·90	0·33

CP, crude protein (N × 6·25); CF; Weende crude fibre; EE, diethyl ether extract; ADF, acid-detergent fibre; NDF, neutral-detergent fibre.

* For details of experimental diets, see Tables 1 and 2 and p. 408.

obtained with humans or rats, reporting a higher TEF for protein than for carbohydrates (Dauncey & Bingham, 1983; Nair *et al.* 1983), the TEF of fat usually being lower than that for carbohydrates (Lin *et al.* 1979; Hurni *et al.* 1982). In addition, the extent of TEF measured in these studies is usually lower (less than 15% of energy intake) than has been reported with domestic animals (Van Es *et al.* 1984; present study). This difference is partly due to the methods used for estimating BMR or FHP and TEF (see pp. 411–412).

Approaches comparable to that used in the present study have been applied in growing pigs, the efficiency (k) then corresponding to the combination of efficiencies for maintenance and for energy deposition (Schiemann *et al.* 1972; Just, 1982; Noblet *et al.* 1989). The k values in 45 kg growing pigs obtained by Noblet *et al.* (1989) in the same conditions as in the present study were 54, 94, 83 and 56% for DCP, DEE, CHO and Dres respectively. The comparison of both sets of data indicates a hierarchy between digestible nutrients which is comparable when they are used either for maintenance or for maintenance + growth. However, the efficiencies of ME from DCP or DEE would be higher when they are used for maintenance only, resulting in a slightly higher overall efficiency of dietary ME for NE_m (77·4%; Table 2) than for maintenance + growth: 74% according to equations proposed by Noblet *et al.* (1989) or to direct measurements on this set of diets (J. Noblet, X. S. Shi and S. Dubois, unpublished results).

Prediction of NE content of diets for maintenance

For practical purposes, it is important to predict the NE content of feeds (ingredients or diets) in order to establish a hierarchy between feeds and adapt feed supply to energy requirements of animals. Therefore, prediction equations for NE_m were established. Similar to the report by Noblet *et al.* (1989) for growing pigs, NE_m can be estimated from a linear combination of digestible nutrient contents (Table 5), from DE (or ME) and some chemical characteristics or directly from dietary chemical characteristics (Table 6).

The accuracy of the models including DE (or ME) value was higher than the best model based on digestible nutrient contents (0·18–0·22 *v.* 0·26 MJ/kg dry matter for RSD). The prediction equation based on crude nutrient contents only had the lowest accuracy (0·33 for RSD). In all the equations including DE (or ME), CP content affected negatively the NE_m value. This should be related to the lower efficiency of DCP for NE_m; the low efficiency of Dres for NE_m was included in the negative intercept. In the equations with ME content the prediction was further improved when the fibre content (CF or ADF) was considered. The biological interpretation of the positive value of the coefficient for CF or ADF is difficult; the result is probably related to the high negative value of the intercept.

Conclusion

The present study indicates that the efficiency of ME for meeting the maintenance energy requirements of pigs averaged 77% and was reduced when the DCP or the fibre contents were increased. On the other hand, it was increased when more carbohydrates (starch) or fat were included in the diet. Similar results were obtained in growing pigs when ME was used for both maintenance and production. Equations for prediction of NE for maintenance from DE or ME values and chemical characteristics are proposed.

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