

Major determinants of fasting heat production and energetic cost of activity in growing pigs of different body weight and breed/castration combination*

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A total of sixty-five observations on heat production during fasting and physical activity were obtained in four groups of pigs differing in breed and/or castration (Meishan (MC) and Large White (LWC) castrates and Large White (LWM) and Piétrain (PM) males) with body weight (BW) ranging between 25 and 60 kg. Pigs were fed *ad libitum* before fasting. Heat production was measured using indirect calorimetry. Fasting heat production (FHP) was proportional to the body weight raised to the power 0.55, but with group-specific proportionality parameters (810, 1200, 1220 and 1120 kJ/kg BW^{0.55} per d for MC, LWC, LWM and PM respectively). Group effects could be removed by expressing FHP as a function of muscle, viscera and fat: FHP (kJ/d) = 457(muscle)^{0.81} + 1969(viscera)^{0.81} – 644(fat)^{0.81}. It is hypothesized that different breeds with equal muscle and visceral mass, can have different FHP. The negative coefficient for fat would then be the result of a low FHP rather than a cause of it. Because a large part of the variation in tissue composition between groups was due to MC group, a separate equation for the lean groups was established. For lean pigs, FHP could be expressed as a function of muscle and viscera alone: FHP (kJ/d) = 508(muscle)^{0.66} + 2011(viscera)^{0.66}. Both type of pig and BW affected the number of bouts of physical activities (i.e. standing or sitting) per day, the duration of activity and the total cost of activity. Energetic cost of activity was proportional to the muscle mass raised to the power 0.91 (FHP_{activity} (kJ/h activity) = 21.0(muscle)^{0.91}). Physical activity represented less than 10% of the total heat production in fasting growing pigs housed alone in metabolic cages and kept in a quiet environment.

Energy metabolism: Fasting heat production: Body composition: Pigs

The cost of feed represents a large proportion of the total cost of pig production. For economic and environmental efficiency, it is important to match supply and requirement as closely as possible. Most feed energy evaluation systems are based on the concept of partitioning nutrients between maintenance and production. At maintenance, nutrient intake equals the obligatory requirements and takes into account normal physical activity of the animal. In pigs, the maintenance energy requirement is generally considered to be proportional to body weight (BW) raised either to the power of 0.75 (Agricultural Research Council, 1981) or approximately 0.60 (Noblet *et al.* 1991). However, there are indications that different breeds may have different maintenance requirements (Noblet *et al.* 1991). Because it

is impossible to measure maintenance requirements directly in producing animals, several predictors have been proposed (Agricultural Research Council, 1981; Noblet, 1996). If the efficiency of energy utilization below maintenance requirement is known, or if the efficiencies below and above maintenance requirement are assumed to be identical, fasting heat production (FHP) can be used to predict maintenance requirement.

The present study is part of a larger one, which has the objective of studying the effect of the animal characteristics (breed, body composition and weight) on growth performance variables. The effects of these animal characteristics may be mediated through feed intake behaviour or the partitioning of metabolizable energy. The latter can be

Abbreviations: ASE, asymptotic standard error; BW, body weight; FHP, fasting heat production; LWC, Large White castrates; LWM, Large White males; MC, Meishan castrates; NDF, neutral-detergent fibre; PM, Piétrain male; RSD, residual standard deviation.

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quantified by subjecting the animals to different nutritional circumstances (e.g. *ad libitum* feeding, fasting, or re-feeding after fasting). The study presented here deals with the second circumstance and was designed to study the effect of BW and body composition (through different breed and castration combinations) on the heat production due to fasting and physical activity in growing pigs.

Materials and methods

Thirty pigs of four breed and/or castration groups (six Meishan castrates (MC), eight Large White castrates (LWC), eight Large White males (LWM), and eight Piétrain males (PM)) were used in this study. At 2 weeks after weaning, animals were individually housed in metabolic cages. Environmental temperature was held constant at 25° for the first week and 24° thereafter. A 12 h lighting schedule was adopted. The experiment consisted of three measurement periods (corresponding to approximately 25, 40 and 60 kg live weight of the pigs) during which feed intake, feeding behaviour, digestibility and heat production were measured.

From weaning to the end of the first measurement period, the animals were offered *ad libitum* a starter diet containing (g/kg DM): crude protein 225, starch 427, fat 24 and neutral-detergent fibre (NDF) 133 (17.9, 15.7 and 15.3 MJ/kg DM of gross, digestible and metabolizable energy respectively). For the remainder of the experiment, and between measurement periods, the animals received *ad libitum* a growing diet (based on wheat, barley, maize and soyabean meal) containing (g/kg DM): crude protein 223, starch 435, fat 33 and NDF 170 (18.1, 15.4, and 14.9 MJ/kg DM of gross, digestible and metabolizable energy respectively). Free access to drinking water was ensured throughout the experiment.

At the beginning of each measurement, the animals (in their metabolic cages) were transferred to an open-circuit respiration chamber. Feed and water consumption behaviour was recorded continuously. After 5 d in the respiration chamber, the animals were subjected to a 30 h fast (24 h in pigs weighing 25 kg). To ensure that the animals remained within their thermoneutral zone, the temperature in the respiration chamber was gradually (but within 1 h) increased from 24° to 26° during the fasting period.

The respiration chambers were equipped with two infrared-beams (one aimed at the shoulder and the other at the front of the hip of the standing pig, which left both beams open when the pig was lying down) to detect physical activity of the animals. Interruption of an infrared beam for at least 20 s was considered to represent a physical activity (i.e. sitting or standing).

Concentrations of O₂ and CO₂ were measured continuously. O₂ consumption and CO₂ production were estimated as described in detail by van Milgen *et al.* (1997). Briefly, this method considers the respiration chamber as a compartmental system of three gases (O₂, CO₂ and other gases). The changes in gas concentrations are described by a model that accounts for the physical aspects of gas exchange (e.g. volume of the chamber, changes in temperature and pressure) as well as for the O₂

consumption and CO₂ production by the animal. The latter is further sub-divided into O₂ consumption and CO₂ production during the resting state, physical activity, and the thermic effect of feeding. It was assumed that the resting O₂ consumption in the fed animal was different to that after prolonged (24 or 30 h) fasting. This change between the fed and fasting states was described as a first-order process. Dependent variables in the model were [O₂] and [CO₂] in the respiration chamber whereas independent variables included time, time of physical activity, and (for fed animals) the time and quantity of feed intake. Model parameters were adjusted statistically to ensure maximum fit for both [O₂] and [CO₂].

In the study reported here, only O₂ consumption and CO₂ production during the fasting period were considered. For fasting animals, model parameters included the resting O₂ consumption and CO₂ production at the start of the fasting period (litres/h), the (asymptotic) resting O₂ consumption and CO₂ production after prolonged fasting (litres/h), the adaptation time between the start and end of the fasting period in resting levels of O₂ consumption and CO₂ production (h), and the O₂ consumption and CO₂ production during physical activity (litres/h of activity). Because model prediction appeared relatively insensitive to both the resting O₂ consumption and CO₂ production at the start of the fasting period and to the adaptation time when estimated only from data during the fasting period (van Milgen *et al.* 1997), those estimates will not be considered here.

Heat production values during fasting (kJ/d) and physical activity (kJ/h of activity) were calculated from the respective O₂ consumption and CO₂ production as described by Brouwer (1965) excluding the correction for urinary-N and CH₄ production. The (partial) RQ were calculated as the ratio between CO₂ production and O₂ consumption.

The animals were weighed every 14 d after a 16 h fast. The weight of the animals during the measurement period was obtained through a quadratic regression of weight *v.* age. Tissue and chemical compositions of the animals were estimated from a data set of a similar group of animals (published in part by Quiniou & Noblet, 1995) through allometric relationships between empty BW and body tissues (muscle, fat, viscera (gastrointestinal tract, liver, spleen, pancreas, kidneys, bladder, heart, reproductive organs, and lungs), skin, bone, blood, and head, feet and tail) or chemical components (water, protein, lipid, and minerals). Empty BW was obtained from an allometric relationship between empty BW and live weight.

Effects of BW, tissue components or breed/castration group on heat production were analysed using ANOVA and/or non-linear regression (Statistical Analysis Systems, 1989). Hypotheses concerning non-linear parameters in nested models were performed using the extra sum of squares principle as described by Ratkowsky (1983).

In twelve animals, calorimetry was performed during all three measurement periods (25, 40 and 60 kg). For various reasons, heat production could only be obtained at two measurement periods in ten animals; the missing measurement was obtained through a replacement animal (littermate kept under similar conditions) for nine of these pigs.

Table 1. Number of animals used and number of measurements of heat production for each period and each breed/castration type

Breed/castration type	No. of animals	Period*		
		1	2	3
Meishan castrate	6	4	5	5
Large White castrate	8	6	5	5
Large White male	8	5	7	4
Piértrain male	8	6	6	7

*Body weight 25, 40 and 60 kg.

This resulted in a total of sixty-five measurements of heat production. The number of animals used and the number of measurements for each period and breed/castration group is given in Table 1. Due to the limited number of measurements per animal, it was impossible to test statistically for an animal effect. As a result, the sixty-five calorimetric measurements were assumed to be independent.

Results

Weight and composition of the animals

Table 2 lists the age, live weight, feed intake and estimated empty BW, muscle, fat and visceral mass in the pigs. Due to a lower growth rate, MC were older than the other

groups at an equivalent weight. Although the experiment was designed to use animals of equal weight during each period, the average BW was slightly lower in MC compared with the other groups. The estimated muscle percentage in these animals was also lower whereas the fat percentage was higher than in the others. PM were the leanest animals with a relatively small visceral mass.

Resting fasting heat production

Resting FHP, heat production due to activity and RQ are given in Table 3. Resting FHP (kJ/kg^{0.75} per d) decreased with increasing BW while a significant breed/castration group effect was apparent. Parameter estimates of the non-linear model $FHP_i = a_i X^{b_i}$ (where i is breed/castration group and X is BW or muscle mass) indicated that FHP was not proportional to the metabolic BW. The exponent b was not different between breed/castration groups and differed significantly from 0.75 but not from 0.60 (Table 4). The hypothesis that a_i and b_i were equal for all breed/castration groups was rejected with both BW and muscle as predictors. A large part of the variation was due to the presence of MC in the data. Nevertheless, the hypothesis that there was a single a_i for the lean breed/castration groups (i.e. $a_{LWC} = a_{LWM} = a_{PM}$) and a separate one for MC was also rejected (results not shown). Apparently,

Table 2. Age, body weight, feed intake and estimated body composition of growing pigs

Period	MC	LWC	LWM	PM	RSD*	Significance†
Age (d)						
1	72.5	64.5	64.0	65.2		
2	106.0	82.8	82.3	88.2	6.7	P,G,P × G
3	138.8	106.6	106.0	110.3		
Body wt (kg)						
1	22.1	26.7	25.4	24.7		
2	38.9	39.4	38.8	40.5	7.6	P,G
3	56.6	59.2	58.9	60.4		
Average DM feed intake before fasting (g/d)						
1	1179	1242	1326	1075		
2	1526	1615	1493	1480	235	P,G
3	1828	2426	1996	1791		
Estimated empty body wt (percentage)						
1	90.8	93.7	93.6	94.0		
2	92.4	94.2	94.3	94.3	0.1	P,G,P × G
3	93.4	94.5	94.9	94.5		
Estimated muscle percentage in empty body wt						
1	30.8	43.0	41.3	51.4		
2	28.7	43.1	42.7	53.2	0.2	P,G,P × G
3	27.4	43.1	44.1	64.7		
Estimated fat percentage in empty body wt						
1	18.8	12.3	12.6	11.4		
2	24.6	15.4	14.3	13.1	0.5	P,G,P × G
3	29.4	19.6	16.3	14.6		
Estimated viscera percentage in empty body wt						
1	15.1	14.6	15.6	11.3		
2	13.5	12.9	13.9	9.6	0.3	P,G
3	12.6	11.4	12.4	8.4		

MC, Meishan castrates; LWC, Large White castrates; LWM, Large White male; PM, Piértrain male.

*Residual standard deviation of the model $Y_{ijk} = P_i + G_j + P_i \times G_j + e_{ijk}$, where P_i is the effect of period, G_j is the effect of breed/castration group and $P_i \times G_j$ is the interaction between period and breed/castration group.

†P, effect of period ($P < 0.05$); G, effect of breed/castration group ($P < 0.05$); P × G, interaction between period and breed/castration group ($P < 0.05$).

Table 3. Resting fasting heat production (FHP), heat production (HP) due to activity and RQ during fasting and physical activity in growing pigs

Period	MC	LWC	LWM	PM	RSD*	Significance†
Resting FHP (kJ/kg BW ^{0.75} per d)						
1	481	623	626	563		
2	370	563	577	534	47	P,G
3	352	516	533	490		
HP activity (kJ/h of activity)						
1	129	195	206	225		
2	169	246	253	318	67	P,G
3	211	342	360	545		
Fasting RQ						
1	0.71	0.77	0.78	0.75		
2	0.69	0.74	0.70	0.71	0.07	
3	0.76	0.73	0.73	0.73		
Activity RQ						
1	0.99	0.81	0.86	0.82		
2	0.96	0.70	0.87	0.83	0.16	
3	0.78	0.84	0.81	0.90		

MC, Meishan castrates; LWC, Large White castrates; LWM, Large White male; PM, Piétrain male; BW, body weight.

* Residual standard deviation of the model $Y_{ijk} = P_i + G_j + P_i \times G_j + e_{ijk}$, where P_i is the effect of period, G_j is the effect of breed/castration group and $P_i \times G_j$ is the interaction between period and breed/castration group.

†P, effect of period ($P < 0.05$); G, effect of breed/castration group ($P < 0.05$); P \times G, interaction between period and breed/castration group ($P < 0.05$).

resting FHP across breed/castration groups cannot be described adequately by a single predictor.

An alternative approach is one where resting FHP is not expressed by a single body component (with breed/castration group-specific parameters) but by multiple body components. The results in Table 5 indicate that muscle, bone and blood weights were highly correlated with the resting FHP. However, weights of these tissues were also correlated with each other. Similarly, weight of viscera and of the sum of head, feet and tail were strongly correlated with each other but had a weaker correlation with resting FHP, whereas fat and skin weight had a low correlation with resting FHP. The correlations between weight of tissues and resting FHP were used to create groups of tissues that served in the full model:

$$\begin{aligned} \text{FHP} = & a_1(\text{muscle} + \text{bone} + \text{blood})^{b_1} \\ & + a_2(\text{viscera} + \text{head} + \text{feet} + \text{tail})^{b_2} \\ & + a_3(\text{fat} + \text{skin})^{b_3}. \end{aligned} \quad (1)$$

Hypotheses concerning parameters were tested against this full model (residual standard deviation (RSD) 710 kJ/d). The hypothesis of single exponent (i.e. $b_1 = b_2 = b_3$) was not rejected. This exponent (0.83 with asymptotic standard error (ASE) 0.05) did not differ from 0.75, but differed from both 0.60 and 1.0. A simpler model based on muscle, viscera and fat alone also fitted the data well (RSD 714 kJ/d) whereas a model including only muscle and viscera did not (RSD 971 kJ/d). Again, a single exponent b for muscle, viscera and fat was sufficient to fit the data and this exponent differed from 0.60 and 1.0, but not from 0.75. The simplest model across breed/castration groups was therefore:

$$\text{FHP} = a_1(\text{muscle})^b + a_2(\text{viscera})^b + a_3(\text{fat})^b, \quad (2)$$

where $b = 0.81$ (ASE 0.05), $a_1 = 457$ (ASE 93) kJ/(kg muscle)^{0.81} per d, $a_2 = 1969$ (ASE 151) kJ/(kg viscera)^{0.81} per d, $a_3 = -644$ (ASE 88) kJ/(kg fat)^{0.81} per d, and RSD 717 kJ/d. This equation indicated that viscera contributed 4.3 times more (per kg^{0.81}) to the resting FHP than did muscle, whereas fat had a negative effect on resting FHP.

As indicated earlier, a large part of the variation in breed/castration groups may be due to the presence of MC in the data set. It may, therefore, be of interest to obtain a regression equation with separate parameters for the lean breed/castration groups (LWM, LWC and PM) and MC. The full model in this analysis included a total of twelve parameters:

$$\begin{aligned} \text{lean: FHP} &= a_{1L}(\text{muscle})^{b_{1L}} + a_{2L}(\text{viscera})^{b_{2L}} + a_{3L}(\text{fat})^{b_{3L}}, \\ \text{Meishan: FHP} &= a_M(\text{BW})^{b_M}. \end{aligned} \quad (3)$$

The RSD of this full model was 691 kJ/d. The model could be simplified without loss of precision by assuming a common exponent across tissues for the lean group. In addition, muscle and viscera were sufficient to explain the variation in the observations. The simplest equations (RSD 674 kJ/d) describing FHP were therefore:

$$\begin{aligned} \text{lean genotypes: FHP} &= a_{1L}(\text{muscle})^{b_L} + a_{2L}(\text{viscera})^{b_L}, \\ \text{Meishan: FHP} &= a_M(\text{BW})^{b_M}, \end{aligned} \quad (4)$$

where $b_L = 0.66$ (ASE 0.04), $a_{1L} = 508$ (ASE 108) kJ/(kg muscle)^{0.66} per d, and $a_{2L} = 2011$ (ASE 188) kJ/(kg viscera)^{0.66} per d, $b_M = 0.44$ (ASE 0.09), and $a_M = 1194$ (ASE 387) kJ/(kg BW)^{0.44} per d.

Both equations (2) and (4) indicate that the viscera contribute much more (per kg^{0.81} or kg^{0.66}) to the FHP than muscle. Even though the muscle mass exceeds that of viscera (Table 2), the total contribution of viscera to the FHP exceeds that of muscle. Based on equation (4), viscera

Table 4. Parameter estimates (a,b) with their asymptotic standard errors (ASE) describing heat production (HP; for breed/castration group i) during fasting or physical activity based on the equation $HP_i = aX^b$, where X is body weight or muscle mass

Hypothesis	X	RSD	P*	b			a			a _{LWC}			a _{LWM}			a _{PM}		
				Estimate	ASE	Estimate	ASE	Estimate	ASE	Estimate	ASE	Estimate	ASE	Estimate	ASE	Estimate	ASE	
Resting FHP (kJ/d)																		
equal b for all i	body wt	683	0.55	0.03	0.55	0.03	1130	260	810	100	1200	140	1220	140	1120	130		
b fixed at 0.60	body wt	694	0.29					660	20	980	20	1000	20	910	20			
b fixed at 0.75	body wt	884	<0.01					370	10	550	10	570	10	510	10			
equal a and b for all i	body wt	1365	<0.01															
HP due to physical activity (kJ/h of activity)																		
equal b for all i	muscle	672	0.98	0.03	0.52	0.03	1130	260	1780	130	2090	180	2130	180	1750	160		
b fixed at 0.60	muscle	704	0.16					1480	50	1680	30	1710	30	1370	30			
b fixed at 0.75	muscle	936	<0.01					1020	40	1080	30	1110	30	850	20			
equal a and b for all i	muscle	1016	<0.01															
equal b for all i	body wt	71.2	0.22	0.10	0.83	0.10	11.5	6.5	7.9	3.1	11.8	4.5	12.4	4.7	16.9	6.5		
b fixed at 0.60	body wt	73.8	0.05					18.9	2.1	28.2	2.0	29.6	2.0	40.7	1.8			
b fixed at 0.75	body wt	71.0	0.28					10.7	1.2	16.0	1.1	16.8	1.1	22.9	1.0			
equal a and b for all i	body wt	101.9	<0.01															
equal b for all i	muscle	70.7	0.30	0.09	0.79	0.09	11.5	6.5	26.5	6.7	28.0	7.8	29.3	8.1	33.7	10.1		
b fixed at 0.60	muscle	72.6	0.10					42.2	4.7	48.5	3.3	50.7	3.4	61.3	2.6			
b fixed at 0.75	muscle	70.3	0.43					29.2	3.1	31.4	2.1	32.9	2.1	38.2	1.6			
equal a and b for all i	muscle	72.9	0.12	0.08	0.91	0.08	21.0	5.2										

MC, Meishan castrate; LWC, Large White castrate; LWM, Large White male; PM, Piétrain male; RSD, residual standard deviation.
 * P, probability for testing the hypothesis that the residual sum of squares of the reduced model is equal to that of the full model ($HP_i = a_iX^b$). Hypotheses for which $P > 0.05$ are adequate for describing the data.

Table 5. Pearson correlation coefficients between resting fasting heat production (FHP) and weight of body tissues across four breed/castration groups of growing pigs

	Viscera	Muscle	Fat	Skin	Bone	Blood	HFT
FHP	0.60	0.85	0.35	0.08	0.85	0.85	0.56
Viscera		0.49	0.86	0.76	0.88	0.89	0.96
Muscle			0.43	0.14	0.84	0.83	0.57
Fat				0.93	0.73	0.74	0.94
Skin					0.51	0.52	0.85
Bone						1.00	0.88
Blood							0.89

HFT, head, feet and tail.

Table 6. Regression coefficients for the effect of breed/castration group (intercept) and body weight (BW; slope) v. the number of bouts of activity, total duration of activity and the total cost of activity in fasting swine

	Intercept				Slope	RSD
	MC	LWC	LWM	PM		
No. of bouts of activity*	49.3	70.0	59.1	64.3	-0.415	13.0
Total duration of activity†	4.00	2.70	2.60	3.27	-0.0123	0.86
Total cost of activity‡	269	187	219	517	6.00	187

MC, Meishan castrates; LWC, Large White castrates; LWM, Large White male; PM, Piétrain male; RSD, residual standard deviation.

*With units *n/d* for the intercept and *n/d per kg BW* for the slope.

†With units *h/d* for the intercept and *h/d per kg BW* for the slope.

‡With units *kJ/d* for the intercept and *kJ/d per kg BW* for the slope.

contributed to more than 60% of the FHP in the three lean breed/castration groups.

An analysis similar to the one described earlier using the chemical composition of the animal (i.e. protein, lipids, etc.) did not result in a suitable equation to predict resting FHP.

Physical activity during fasting

A general allometric model based on BW or muscle weight was used to describe the energetic cost of activity during fasting (kJ/h of activity; $\text{HP}_{\text{activity}} = a X^b$). With BW as predictor (X), a common exponent b could be used for the four breed/castration groups, but specific regression coefficients were needed for each breed/castration group. With muscle as predictor, the four breed/castration groups not only shared a common exponent, but also a common regression coefficient with $a = 21.0$ (ASE 5.2) kJ/h of activity per $(\text{kg muscle})^{0.91}$, $b = 0.91$ (ASE 0.08), and RSD 72.0 kJ/h of activity. The exponent b neither differed from 0.75 nor from 1.00.

Both breed/castration group and BW affected the number of bouts of physical activities per day, the total duration of activity and the total cost of activity (i.e. the product of energetic cost and the duration of activity) whereas there was no association between breed/castration group and BW (Table 6). With increasing BW, both the number of bouts and total duration of daily activity declined. Nevertheless, within the range of measurements, the daily energetic cost of activity increased with BW. This cost was the highest for PM, which is partially due to the relatively long duration of activity. For PM there was considerable individual variation between animals of the

same BW, especially at 60 kg. Over the fasting period, activity accounted for 7.9, 4.8, 4.9 and 8.3% of the total FHP (i.e. resting FHP + $\text{HP}_{\text{activity}}$) in MC, LWC, LWM and PM respectively.

Neither breed/castration group nor BW affected the $\text{RQ}_{\text{fasting}}$ and $\text{RQ}_{\text{activity}}$. However, $\text{RQ}_{\text{fasting}}$ was significantly lower than $\text{RQ}_{\text{activity}}$ (0.73 and 0.85 respectively). Both $\text{RQ}_{\text{fasting}}$ and $\text{RQ}_{\text{activity}}$ were significantly smaller than unity, indicating oxidation of fatty acids and/or amino acids.

Discussion

Mode of expression of fasting heat production

For inter-species comparisons, maintenance requirements and FHP are often expressed per kg metabolic BW ($\text{kg}^{0.75}$). Although widely adopted, several authors (Brown & Mount, 1982; Noblet *et al.* 1991) have indicated the inappropriateness of the exponent 0.75 for intra-species comparisons. Maintenance requirements and FHP per kg metabolic BW tend to decline with increasing BW and the present study further confirmed this. On average and across breed/castration groups, the model $\text{FHP} = a_1(\text{BW})^{0.75}$ underestimated FHP at 25 kg BW by 12% but overestimated FHP at 60 kg BW by 6%. In contrast, the RSE for FHP was within 4% of the observations when using the model $\text{FHP} = a_1(\text{BW})^{0.60}$ for the entire BW interval.

Fasting heat production

The FHP in lean, growing pigs fed *ad libitum* (within the thermoneutral zone) has been studied by several authors

(Sunstøl *et al.* 1979; Koong *et al.* 1982, 1983; Tess *et al.* 1984; Yen *et al.* 1991; Bernier *et al.* 1996) and ranges from 700 to 977 kJ/(kg BW)^{0.60} per d. The resting FHP for lean breed/castration groups in the current study (LWM, LWC and PM) was situated in the upper half of this range, average 962 kJ/(kg BW)^{0.60} per d. It should be noted that FHP in most studies is not corrected for physical activity during fasting, which further widens the range of values determined. Nevertheless, a large part of the variation may be due to differences in body composition. For example, the lean breed/castration groups in the present study had less body fat (14.3% of empty BW, estimated) and probably more muscle mass than animals of similar weight used by Tess *et al.* (1984; 18.9% fat; FHP 830 kJ/(kg BW)^{0.60} per d). The relationships between body components and FHP established in the present study can explain a large part of the reported differences in FHP.

The resting FHP in Meishan pigs was 660 kJ/kg^{0.60} per d which is lower than that reported by Bernier *et al.* (1996; 749 kJ/kg^{0.60} per d). Both these values are much lower than the FHP found in Meishan pigs by Yen *et al.* (1991, 1992) which averaged 860 kJ/kg^{0.60} per d. However, data from the latter studies were not corrected for physical activity. Given the observation that activity represents 8.5% of the resting FHP in MC, physical activity can explain a large part of the difference between the data reported by Bernier *et al.* (1996) and Yen *et al.* (1991, 1992). As the animals from Bernier *et al.* (1996) and those used in the present study came from the same population (and supposedly had similar body composition), we could not find an appropriate explanation for the difference in measured FHP.

Even though the total mass of visceral organs is small compared with that of muscle, the energy cost per (kg of tissue)^{0.66} is so much higher, that its total energy expenditure exceeds that of muscle. This is an important factor to consider as the plane of nutrition or the composition of feed can have a marked effect on visceral organ weight and thus on FHP (Koong *et al.* 1982, 1983). Moreover, the tissue composition can differ widely between breed/castration groups (Quiniou & Noblet, 1995). This is illustrated by the fact that the very lean Piétrain has a lower FHP than the less lean Large White due to the smaller visceral mass in the former. Among the visceral organs, the portal-drained viscera and the liver have been shown to be major contributors to the energy expenditure in animals (Baldwin *et al.* 1980; Yen *et al.* 1989).

The duration of the fasting period may also have an influence on the FHP. Close & Mount (1975) found a rapid decrease in heat production during the first day of fasting followed by a more gradual decrease during the following days. After a reduction in feed intake, it takes approximately 7 d before heat production reaches a new equilibrium (Gray & McCracken, 1980). These changes are probably due to changes in the weight of portal-drained viscera and the liver (Burrin *et al.* 1990). Provided that heat production due to residual digestive and absorptive processes can be accounted for, a short-duration of fasting is probably more representative for the producing animal than long-term fasting.

In predicting the FHP, the negative regression coefficient for body fat in equation (2) may, at first sight, be difficult to

interpret. Several authors (Baldwin *et al.* 1980; Webster, 1981) indicated the limited metabolic role of fat in FHP. Tess *et al.* (1984) found results similar to those reported in the present study and suggested that fatter pigs may be better insulated. However, the temperature during the fasting period (26°C) seemed to be within the thermoneutral range of fasting growing pigs (Bernier *et al.* 1996). In the thermoneutral zone, heat production does not increase with changes in environmental temperature and the (fasting) heat production is determined more by biochemical requirements for ATP than by a requirement for heat *per se*. As a result, fatter animals would not benefit (i.e. reduce FHP) from better insulation. Two possible explanations can be put forth for the negative regression coefficients. First, the observed relation between fat and FHP may be an artifact of the data set. Body composition was not measured in this experiment but estimated from a different group of animals. Therefore within a breed/castration group, variation in body composition was caused only by difference in BW and some of the observed effects may have been 'breed/castration group-specific' rather than 'tissue-specific'. An alternative explanation can be found by reversing the logic of cause and effect. Maybe it is not the fact that fatter animals have a lower FHP but rather that animals with lower FHP become fatter at equal feed intake. This logic implies that (genetically) different animals with equal muscle and visceral mass can have a different FHP but does not explain why this is the case.

Selection of modern breeds of pigs for lean muscle mass may have been accompanied by selection for energetically inefficient animals. Given the practice of close to *ad libitum* feeding, those animals with a high FHP (or maintenance requirement) will remain lean, whereas those with equal appetite and lower FHP will become fatter. Sundstøl *et al.* (1979) found a significantly higher FHP in pigs selected for seven to ten generations for low backfat thickness and high rate of gain compared with those selected in the opposite direction. Part of this difference is, of course, due to the greater muscle mass in lean animals. However, the fact that genetically obese animals can deposit the same quantity of lean tissue, but become more fat when restrictively fed on a protein-limited diet (Kyriazakis & Emmans, 1995) indicates that differences in FHP are not only due to differences in muscle mass. Koong *et al.* (1983) found that pigs selected for low backfat thickness had higher weights of stomach, large intestine, pancreas and spleen than those selected for high backfat thickness, although this was not accompanied by a statistically significant change in FHP. It may prove to be beneficial to develop a breed in which high energetic efficiency (low FHP) can be combined with a reduction in feed intake while ensuring maximum protein accretion.

Activity

Physical activity of pigs has been reported to depend on the type of feed (Schrama *et al.* 1996) and on feeding level (Susenbeth & Menke, 1991). Therefore, the duration and the total cost of activity reported here (fasting animals) might not reflect a situation in which the animals had been

fed. Pigs were also confined individually in metabolic cages in a quiet environment and these results may not apply to pigs housed in groups in a commercial setting. In contrast to results of Susenbeth & Menke (1991), there was a significant breed/castration group effect on the frequency of activity. The lowest frequency of standing was observed in MC. Kyriazakis & Emmans (1995) noticed that Meishan pigs were quieter and less active than Large White cross-breeds. These authors suggested that this may imply a lower maintenance requirement for energy in Meishan pigs. Although the number of activities in Meishan pigs was the lowest of the four groups, the total duration of activity was the longest (Table 6). Moreover, the total cost of activity was higher in MC than in LWM or LWC. The maintenance requirement of Meishan may be lower than in other pigs, but this is due more to a lower resting FHP than to a reduced energetic cost of activity.

The individual variation in the energetic cost of activity between heavier Piétrain pigs may be due to differences in sensitivity to stress as well as feet problems that occurred during the course of the experiment (the animals were housed in confinement with limited movements for almost 2 months). In addition, fasting can be considered an important stress factor and not all Piétrain pigs may react in the same way to this stress.

Sitting or standing is a very costly exercise in pigs compared with other species (Noblet *et al.* 1993). In a compilation of literature, Noblet *et al.* (1993) estimated the cost of activity in pigs at $17.4 \text{ kJ/kg}^{0.75}$ per h of activity. This is consistent with values for the Large White groups used here (averaging $16.7 \text{ kJ/kg}^{0.75}$ per h of activity), but different from both Meishan and Piétrain (11.2 and $22.0 \text{ kJ/kg}^{0.75}$ per h of activity respectively). The energy cost of sitting or standing (kJ/h of activity) contributed an extra 69% above resting FHP (kJ/h) in Large White and Meishan and 105% in Piétrain pigs. Hörnicke (1970) reported an 82% increase in (fed) heat production during activity whereas McDonald *et al.* (1988) reported a 95% increase compared with the FHP. The difference between the latter results and our present findings can largely be explained by a difference in the estimated FHP ($450 \text{ kJ/kg}^{0.75}$ per d reported by McDonald v. $560 \text{ kJ/kg}^{0.75}$ per d for the lean groups in the present study).

Jakobsen *et al.* (1994) found that the RQ in growing pigs declined during walking from 1.07 to 0.97. During walking, energy is diverted from lipogenesis ($\text{RQ} > 1$) to substrate oxidation ($\text{RQ} \leq 1$). In the present study, the RQ increased from 0.73 to 0.85 during activity, suggesting that the sources of energy during activity may be different between the fed and fasting states. However, the RQ for activity is based on a relatively short period of time and the CO_2 release may be influenced by the acid–base balance of the blood.

The theoretical cost of rising can be calculated as the energy required to raise the centre of gravity of the animal over a certain distance (e.g. 0.50 m). This cost is extremely small (less than 1%) compared with the energy the animals actually use for activity. Apparently, positional movements as well as the metabolic efficiency of movement contribute more to the energetic cost of activity than the act of rising itself.

Conclusion

Most (if not all) energy systems for livestock are based on the concept of division of available nutrients and energy between maintenance and production. This division has its merit (simplicity) but the concept of maintenance is difficult to interpret in the case of producing animals. It may, therefore, be more appropriate to study the dynamics of energy partitioning in producing animals, which can be related to events such as physical activity and the ingestion of a meal (van Milgen *et al.* 1997). Such partitioning is biologically more appropriate and would be easier to relate to the dynamics of nutrient absorption and metabolism. Future systems of energy partitioning could be based on this concept.

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