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Modelling heat production and energy balance in group-housed growing pigs exposed to low or high ambient temperatures

N. Quiniou†, J. Noblet*, J. van Milgen and S. Dubois

Institut National de la Recherche Agronomique, Unité Mixte de Recherches sur le Veau et le Porc, 35590 Saint-Gilles, France

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The effects of ambient temperature (T; 12–29°C), body weight (BW; 30–90 kg) and metabolisable energy intake (ME) on components of energy balance were studied in seven groups of Piétrain × Large White barrows kept in a respiratory chamber. In Expt 1 (groups 1, 2 and 3), T varied in a cyclic way from 22°C to 12°C and then from 12°C to 22°C with three or four consecutive days at each of 22, 19, 16, 14 and 12°C. Similarly, in Expt 2 (groups 4, 5 and 6), T varied from 19 to 29°C and then from 29 to 19°C with three or four consecutive days at each of 19, 22, 25, 27 and 29°C. In both experiments, pigs were offered feed *ad libitum*. In Expt 3, pigs (group 7) were exposed to the thermic conditions of Expt 1 but their feed allowance was adjusted on a BW basis to the *ad libitum* intake recorded at 19 and 22°C in Expt 1. Groups 1, 2, 4, 5 and 7 were used over two successive cycles with initial average BW of 37 kg at cycle 1 (four pigs per group) and 63 kg at cycle 2 (three pigs per group). Groups 3 and 6 were studied at an intermediary stage of growth; their initial BW was 45 kg. The O_2 and CO_2 concentrations, physical activity and feed intake were continuously and simultaneously measured and used to calculate total heat production (HP; HP_{tot}), HP due to physical activity (HP_{act}), activity-free HP (HP_0), and thermic effect of feed. HP was modelled as a non-linear function with T, BW and ME as predictors. Results indicate that all components of HP were proportional to $BW^{0.60}$. Physical activity was minimal between 19 and 27°C (8 % ME). The estimated lower critical temperature was 24°C. Between 24 and 12°C, total thermic effect of feed decreased from 31 to 16 % ME, but the short-term thermic effect of feed (5·1 % ME) remained constant. Equations for prediction of HP_{tot}, HP_{act} and HP_0 according to BW, T and ME are proposed and evaluated according to literature values; values for the feed cost of thermoregulation in pigs are proposed.

Growing pig: Ambient temperature: Heat production: Thermoregulation: Modelling

Under thermoneutral conditions, dietary energy is used by the animal to meet its requirements for maintenance, physical activity and growth. In pigs exposed to ambient temperatures (T) below the zone of thermoneutrality, heat production (HP) increases to meet the additional requirements for thermoregulation. Under these conditions and when fed *ad libitum*, pigs may increase energy intake so that energy balance and growth performance can be maintained (Le Dividich *et al.* 1985; Massabie *et al.* 1996). On the other hand, under high T, energy intake and associated heat loss and energy retention (ER) are reduced (Rinaldo & Le Dividich, 1991; Massabie *et al.* 1996). Nutritional adaptation of pigs to changing climatic conditions seems to be a rapid process, but other short-term mechanisms are involved such as huddling in cold conditions or reduced locomotion under hot exposure. Prolonged exposure to low T also induces morphological adaptations (Le Dividich *et al.* 1998).

Previous studies have focused on the effect of T on feeding behaviour (Nienaber *et al.* 1991, 1996), performance (Massabie *et al.* 1996) or energy metabolism (Verstegen *et al.* 1973; van der Hel *et al.* 1986; Henken *et al.* 1991). The aim of the present experiments was to quantify the effects of T, body weight (BW) and

Abbreviations: BW, body weight; ECT, evaporative critical temperature; ER, energy retention; HP, HP_{tot}, HP_{act}, HP_0, heat production, total, activity-related and activity-free daily HP, respectively; LCT, lower critical temperature; ME, ME_0, total metabolisable energy intake and ME not used for physical activity, respectively; MEm, MEm_0, maintenance and activity-free maintenance ME requirements, respectively; T, ambient temperature; TEF_{tot}, TEF_{st}, total and short-term thermic effect of feed, respectively.

* **Corresponding author:** Dr J. Noblet, fax +33 2 23 48 50 80, email noblet@st-gilles.rennes.inra.fr
† On leave from the Institut Technique du Porc, BP3, 35650 Le Rheu, France.

metabolisable energy intake (ME) both on components of energy utilisation and on feeding behaviour of group-housed growing and finishing pigs over a wide range of T (12–29°C), BW (30–90 kg) and feeding levels (*ad libitum* and restricted). These results should provide a basis for modelling energy utilisation and energy requirements when pigs are exposed to variable environmental T. The 19–22°C range was assumed to be close to the zone of thermo-neutrality. The present paper will focus on heat production and energy balance. Results concerning the effect of T on feeding behaviour have been presented elsewhere (Quiniou *et al.* 2000).

Material and methods

Experimental design

Seven groups of Piétrain × Large White barrows were used. The first six groups were fed *ad libitum* (Table 1). Three groups were exposed to T ranging between 12 and 22°C (Expt 1; groups 1, 2 and 3) and a further three groups to T ranging between 19 and 29°C (Expt 2; groups 4, 5 and 6). Both energy intake and HP were expected to increase under cold exposure in *ad libitum* feeding conditions, with subsequent high correlations between HP and energy intake or T. Thus, pigs of group 7 (Expt 3) were exposed to the thermic conditions of Expt 1, but their feed allowance was adjusted on a BW basis to the *ad libitum* intake recorded at 19 and 22°C in Expt 1; at 19 and 22°C pigs of group 7 were fed *ad libitum*.

An adaptation period to the chamber and the diet was used which lasted 7 d and during which T was fixed at 22°C in Expts 1 and 3, and at 19°C in Expt 2. During the experiment T was gradually changed (Fig. 1) according to a 'V'-shaped profile in Expts 1 and 3 (22, 19, 16, 14, 12, 14, 16, 19 and 22°C) and an inverted 'V'-shaped profile in Expt 2 (19, 22, 25, 27, 29, 27, 25, 22 and 19°C). Each T level lasted 3 d, except at 12 and 29°C which lasted 4 d. After measurements at each T, the treatment was considered to be complete and the T was changed for the next treatment within 4 h. The T change was 3°C when T ranged between 16 and 25°C, and 2°C with the lower or higher T in order to obtain more accurate data under these more extreme environmental conditions. In addition, small changes in T between levels were chosen to avoid long periods for adaptation. It took 28 d to complete the cycle which corresponded to the experimental period. Relative humidity was fixed at 70 % and artificial light was provided between 08.00 and 20.00 hours.

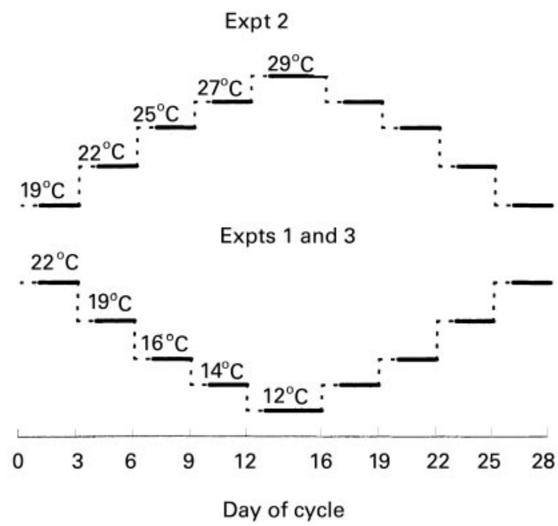

Fig. 1. Expts 1–3. Cyclic variation in temperature over the 28 d experimental period. (- - -), adaptation period; (——), measurement period.

For groups 1, 2, 4, 5 and 7, the experiment started at about 30 kg BW and these groups were studied over two consecutive cycles (cycle 1 about 30–60 kg; cycle 2 about 60–90 kg). For groups 3 and 6, the experiment started when pigs weighed about 45 kg and these animals were studied only over one cycle.

Animals and equipment

The volume of the climate-controlled open-circuit respiratory chamber (12 m^3) and the measurement range of the gas analysers limited the size of the group (four pigs in the first cycle and three in the second cycle). The surface allowance was 3·7 m^2 on a metal-slatted floor. Faeces, urine and water spillages were collected in a slurry pit. The pen was equipped with an electronic feed dispenser. A fence allowed only one pig to get in and eat at a time. The diet (Table 2) was distributed as pellets and animals had free access to water.

Table 1. Experimental design of the study

Experiment	Group	Temperature range (°C)	Body-wt range (kg)	*n*	Feeding conditions
1	1, 2	12–22	30–60	4	*Ad libitum*
	1, 2	12–22	60–90	3	*Ad libitum*
	3	12–22	45–75	4	*Ad libitum*
2	4, 5	19–29	30–60	4	*Ad libitum*
	4, 5	19–29	60–90	3	*Ad libitum*
	6	19–29	45–75	4	*Ad libitum*
3	7	12–22	30–60	4	Pair-fed below 19°C*
	7	12–22	60–90	3	Pair-fed below 19°C*

* Pigs were fed *ad libitum* at 19 and 22°C.

Table 2. Composition of the experimental diet

Ingredients (g/kg)	
Wheat	220·0
Barley	220·0
Maize	220·0
Soyabean meal (480 g crude protein*/kg)	244·5
Wheat bran	40·0
Rapeseed oil	10·0
Lysine hydrochloride	0·5
Dicalcium phosphate	20·0
$CaCO_3$	10·0
NaCl	5·0
Vitamin and trace mineral mixture	10·0
DM (g/kg)	877
Analysed composition (g/kg DM)	
Ash	68
Crude protein*	208
Crude fat	35
Crude fibre	42
Starch	490
Lysine†	11·6
Energy content (MJ/kg DM)	
Gross energy‡	18·4
Digestible energy‡	15·7
Metabolisable energy‡	15·1
Net energy§	11·2

* N × 6·25.
† Estimated from amino acid composition of raw materials. Methionine + cystine, threonine and tryptophan contents relative to lysine (100) were 62, 70 and 22, respectively.
‡ As measured on individually-kept growing pigs.
§ Estimated from digestible energy content (MJ/kg DM) and chemical components (g/kg DM) according to the relationship proposed by Noblet *et al.* (1994).

Measurements

The pigs were weighed at the beginning and end of each cycle and intermediately at the beginning of the 16°C (Expts 1 and 3) and 25°C (Expt 2) levels. The feed reservoir was filled daily with an amount of feed sufficient to meet the appetite of the group. The weight of the feeder was measured continuously. Water was supplied away from the feeder by a nipple drinker to avoid disturbing the feed intake measurements. The pen was placed on four force sensors (type 9104A; Kistler, Winterthur, Switzerland) for which the response was supposed to be proportional to the physical activity of the animals.

Every 10 s, mean values for O_2 and CO_2 concentrations were recorded as described by van Milgen *et al.* (1997). Simultaneously, over the same time span, the signal of the force sensors was recorded. When the weight of the trough was detected as unstable, the corresponding beginning and ending time and remaining amounts of feed in the feeder were recorded. The aim of these simultaneous measurements was to relate each instantaneous variation in O_2 and CO_2 concentrations to physical activity and eating events in the chamber.

A sample of feed was collected weekly and its DM content was determined. For each group all samples were pooled at the end of the experiment for further chemical analyses. Energy values for the experimental diet were assessed using a digestibility trial with four additional 60–65 kg pigs according to routine techniques (Noblet *et al.* 1994).

Calculations

The digestible energy intake corresponded to the difference between gross energy intake and energy losses in faeces. ME was calculated as the difference between the digestible energy intake and energy losses in urine (Table 2). The day of T change was considered as a transition day for adaptation to the new environmental conditions. In addition, this day was used for cleaning the chamber and weighing pigs at the beginning, middle or end of the cycle. Consequently, these data were not taken into account in the calculations. The BW at each T level was interpolated from the measured BW.

The components of HP were estimated for each group of pigs based on the 2- or 3 d remaining at each T and were subsequently expressed on a daily basis per pig. Taking into account that only one measurement per cycle was performed at 12 and 29°C (*v.* two at the other T), these data were duplicated. The model proposed by van Milgen *et al.* (1997) that allows analysing the short-term dynamics of both O_2 consumption and CO_2 production was used. This model is based on a series of differential equations describing the changes in O_2 and CO_2 concentrations due to physical aspects of gas exchange (i.e. volume of the chamber, ventilation rate, T) as well as the O_2 consumption and CO_2 production, where the latter two are related to the levels of physical activity and feed intake of animals. In practice, the model provides estimates of gas exchanges during resting (l/min), physical activity (l/unit force) and feed intake (l/g). Subsequently, the corresponding HP was calculated from the respective O_2 consumption and CO_2 production as described by Brouwer (1965), excluding the correction for urinary N and CH_4 production. The daily HP due to physical activity (HP_{act}) and due to the thermic effect of feed were calculated as the product of HP (kJ/unit force or kJ/g) and total daily physical activity (units force) or mean daily feed intake (g), respectively. As explained by van Milgen *et al.* (1998), the thermic effect of feed calculated by this model corresponds to the temporary increase in O_2 consumption and CO_2 production induced by the intake of a meal. Ingestion, digestion and absorption can therefore be considered as components of the short-term thermic effect of feed (TEF_{st}). The total daily HP (HP_{tot}) was considered as the sum of HP_{act}, TEF_{st} and resting HP, the latter considered as constant over the day. The daily HP not related to physical activity (HP_0) was obtained as the sum of TEF_{st} and resting HP. The ME not used for physical activity (ME_0) was calculated as ME minus HP_{act}. ER was calculated as the difference between ME and HP_{tot}. All calculations are summarised in the Appendix.

Statistical analyses

Data from the three experiments (groups 1–7) were used to calculate prediction equations for HP_{act} and HP_0 with T, BW and ME_0 as predictors. Two different approaches were used for HP_{tot}; it was either considered as the sum of the equations for HP_{act} and HP_0 (i.e. with T, BW and ME_0 as predictors) or a prediction equation was directly calculated with T, BW and ME as predictors. Parameter estimates were carried out using Statistical Analysis Systems PROC NLIN package, release 6.07 (SAS Institute Inc., Cary, NC, USA). It was hypothesised that HP_0 and HP_{tot} depended on the sum of two major components, the first one being proportional to a power function of BW (i.e. maintenance effect) and the second one being directly related to energy intake (i.e. total thermic effect of feed; TEF_{tot}). In addition, it was hypothesised that both components also depended on T up to a value corresponding to the lower critical temperature (LCT). Indeed, LCT is defined by Mount (1974) as the T above which the HP required to maintain homeothermia is no longer dependant on T but depends only on feed intake. The basic structure of the model is as follows.

If T ≤ LCT then:

$$HP_0 = BW^a \times (b + c \times T + d \times T^2) + ME_0 \times (e \times T + f),$$

or else

$$HP_0 = BW^a \times (b + c \times LCT + d \times LCT^2) + ME_0 \times (e \times LCT + f),$$

where a, b, c, d, e, f are coefficients. The same model was used for HP_{tot} with ME instead of ME_0 as predictor. Hypotheses concerning parameters in nested models were tested using the extra-sum-of-squares principle (F test) as described by Ratkowski (1983). In these models, the term $(e \times LCT + f)$ corresponds to the TEF_{tot}. The maintenance not related to physical activity ME requirement (MEm_0) was calculated from the prediction equation of HP_0 with HP_0 equal to ME_0 (Appendix). For calculation purposes, ME (kJ/d) was that estimated according to the prediction equation obtained in the *ad libitum*-fed pigs of the present experiment and published by Quiniou *et al.* (2000): ME (kJ/d) $= -16710 + 547 \times T - 31{\cdot}73 \times T^2 + 973{\cdot}0 \times BW - 3{\cdot}44 \times BW^2 - 12{\cdot}56 \times T \times BW$ (residual SD 4349 kJ/d).

Results

Mean values obtained in *ad libitum*-fed pigs studied over two successive cycles in Expts 1 and 2 are presented in Tables 3 and 4 respectively. BW averaged 49 and 75 kg during cycles 1 and 2 respectively, irrespective of the T and experiment considered. Results show that ME, HP_{tot} and ER at 19 and 22°C were similar in both experiments during cycle 1. In contrast, during cycle 2 ME and ER were higher in Expt 2. In Expt 1 ME increased with decreasing T; the increment was most important between 22 and 16°C in cycle 1 and only between 22 and 19°C in cycle 2. The increase in T between 19 and 29°C in Expt 2 was associated with a reduction of ME which was twice as great during cycle 2 than during cycle 1 (−12·8 *v.* −6·2 MJ/pig per d; Table 4). In Expt 3, feed allowance was similar at 12, 14 and 16°C and close to the spontaneous level of ME measured at 19 and 22°C on a BW basis in Expt 1. At these latter T, pigs compensated for the feed restriction imposed at the lowest T and ME was higher than in Expt 1.

Under *ad libitum* feeding conditions, the HP_{tot} appeared to be minimal at 29°C in light pigs (14·07 MJ/d in cycle 1; Table 4) and increased both with decreasing T and increasing BW; the maximum value was obtained at 12°C in heavy pigs (21·86 MJ/d on average in cycle 2; Table 3). In Expt 1 the highest ER was obtained at 16°C (13·59 and 15·32 MJ/d in cycles 1 and 2 respectively). In Expt 2 ER was maximal at 19°C (12·70 and 18·05 MJ/d in cycles 1 and 2, respectively) and decreased progressively up to 29°C (8·23 and 8·83 MJ/d in cycles 1 and 2, respectively). Physical activity accounted for 13 % HP_{tot} at 19 and 22°C, and increased both when T increased and decreased, to reach approximately 17 % HP_{tot} at both 12 and 29°C. The TEF_{st} represented on average 5·1 % ME between 12 and 22°C, with no important variation due to T. In Expt 2 the corresponding value was 5·3 % ME, but it was more variable; the lowest and the highest values were observed at 19 and 25°C during cycle 1 (4·8 and 5·7 % ME respectively) (Tables 3 and 4).

As expected from the experimental design, the observed Pearson correlations were low between T and BW (r −0·05) and between T and ME (r −0·24) when data from the three experiments were considered. The exponent relating BW to HP_0 and HP_{tot} was 0·59 (SE 0·01) and 0·61 (SE 0·02) respectively, which was not significantly different from 0·60. The HP_{act} was proportional to BW raised to the exponent 0·68 (SE 0·06); the accuracy of the model was similar when the exponent was fixed to 0·75 or 0·60. Consequently, in further calculations, the exponent for BW was fixed at 0·60 in the prediction equations and $BW^{0{\cdot}60}$ was considered to be the metabolic BW.

According to equation 1 (Table 5), HP_{act} was not affected by ME_0 and varied only with BW and T. The minimal value of HP_{act} was obtained at 21·8°C (191 kJ/d per kg $BW^{0{\cdot}60}$) and it increased up to 274 and 234 kJ/d per kg $BW^{0{\cdot}60}$ at 12 and 29°C respectively.

It was initially assumed that the maintenance and feed components of HP_0 were not affected by T when above the LCT. In addition, it was assumed that different values for LCT could exist for the maintenance effect and for the TEF_{tot}, and that they could vary linearly with BW. However, there was no significant effect of BW on LCT and a constant LCT was considered hereafter. Estimated values of LCT for maintenance and TEF_{tot} were very similar (24·3 (SE 3·9) and 23·1 (SE 2·6)°C, respectively) and neither differed from 24°C. Consequently, the LCT was fixed at 24°C in the equations hereafter. A model without LCT values was also calculated and compared for accuracy with the model with LCT (Table 5).

When T was below LCT, it was hypothesised according to the basic structure of the model that the maintenance and TEF_{tot} components of HP_0 varied with T according to a quadratic and linear relationship respectively. To simplify the model, coefficients that did not have a significant contribution were removed. It appeared that the coefficients c and f were not different from zero so that, below LCT, the maintenance component varied linearly with T whereas TEF_{tot} was proportional to T (equation 3; Table 5). In the model without LCT (equation 4; Table 5), the maintenance component of HP_0 varied quadratically with T whereas TEF_{tot} was proportional to T as in the former equation. From a statistical point of view, both equations were

Table 3. Expt 1. Utilisation of metabolisable energy intake (ME) in *ad libitum*-fed pigs studied over two cycles of varying ambient temperature*
(Mean values with their standard errors†)

	Cycle 1 (*n* 4)										Cycle 2 (*n* 3)									
Temperature (°C)	12		14		16		19		22		12		14		16		19		22	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Body weight (kg)	47·5	2·3	47·5	2·9	47·7	4·1	47·8	5·6	47·8	7·7	74·3	2·1	74·3	2·7	74·3	3·9	75·6	5·9	75·7	7·8
ME (MJ/pig per d)	30·24	0·64	30·22	1·09	29·92	2·40	28·35	2·09	26·41	2·91	36·79	1·13	35·21	1·10	35·46	2·70	35·58	1·52	33·91	1·92
Heat production (MJ/pig per d):																				
Total	17·62	0·52	17·00	0·70	16·33	0·85	15·93	1·36	15·17	1·77	21·86	0·08	21·27	0·45	20·13	0·42	20·59	0·79	20·02	1·10
Due to physical activity	2·88	0·10	2·54	0·16	2·38	0·24	2·26	0·27	1·87	0·26	3·80	0·15	3·25	0·11	2·85	0·12	2·57	0·12	2·52	0·23
Short-term thermic effect of feed:																				
MJ/pig per d	1·57	0·12	1·56	0·15	1·56	0·15	1·47	0·18	1·30	0·18	1·87	0·02	1·81	0·14	1·78	0·18	1·78	0·07	1·73	0·15
% ME	5·2	0·3	5·1	0·3	5·2	0·3	5·1	0·3	4·8	0·3	5·1	0·1	5·1	0·3	5·0	0·2	5·0	0·2	5·1	0·4
Energy retained (MJ/pig per d)	12·62	0·12	13·22	0·54	13·59	1·57	12·43	0·85	11·24	1·43	14·93	1·05	13·95	0·78	15·32	2·36	14·99	1·07	13·89	1·01
RQ	1·12	0·01	1·12	0·01	1·12	0·01	1·13	0·01	1·11	0·02	1·14	0·02	1·09	0·02	1·15	0·02	1·14	0·02	1·15	0·01

* For details of experimental design and procedures, see Table 1, Fig. 1 and p. 98.
† Results from groups 1 and 2 combined. Values represent mean of two values at 12°C and four values at all other temperatures (from increasing and decreasing phases of cycle for both groups 1 and 2).

Table 4. Expt 2. Utilisation of metabolisable energy intake (ME) in *ad libitum* fed pigs studied over two cycles of varying ambient temperature*
(Mean values with their standard errors†)

	Cycle 1 (*n* 4)										Cycle 2 (*n* 3)									
Temperature (°C)	19		22		25		27		29		19		22		25		27		29	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Body weight (kg)	50·3	6·8	49·6	4·7	49·3	3·4	49·1	2·4	48·9	1·7	75·3	7·8	75·4	6·0	75·3	4·4	75·3	3·2	75·2	2·6
ME (MJ/pig per d)	28·53	3·94	26·50	2·64	27·33	0·58	24·61	0·76	22·30	0·28	39·15	2·39	38·22	0·45	34·61	2·65	30·90	1·72	26·32	2·3
Heat production (MJ/pig per d)																				
Total	15·84	1·76	14·65	1·05	14·68	0·31	14·63	0·12	14·07	0·06	21·10	1·41	20·76	1·36	19·27	0·85	18·63	0·53	17·49	1·02
Due to physical activity	1·92	0·23	1·92	0·19	1·78	0·12	2·05	0·24	2·36	0·04	3·10	0·45	2·77	0·05	3·02	0·17	3·21	0·21	3·08	0·12
Short-term thermic effect of feed																				
MJ/pig per d	1·36	0·28	1·43	0·23	1·57	0·04	1·26	0·02	1·20	0·01	2·14	0·19	2·01	0·22	1·82	0·19	1·60	0·08	1·43	0·13
% ME	4·6	0·3	5·3	0·3	5·8	0·5	5·1	0·2	5·4	0·1	5·5	0·2	5·3	0·2	5·2	0·2	5·2	0·2	5·4	0·1
Energy retained (MJ/pig per d)	12·70	2·24	11·84	1·59	12·65	0·56	9·98	0·64	8·23	0·22	18·05	1·15	17·46	3·15	15·34	1·81	12·27	1·25	8·83	1·28
RQ	1·08	0·01	1·09	0·01	1·06	0·04	1·06	0·02	1·04	0·01	1·11	0·01	1·12	0·02	1·10	0·01	1·07	0·02	1·07	0·02

* For details of experimental design and procedures, see Table 1, Fig. 1 and p. 98.
† Results from groups 4 and 5 combined. Values represent mean of two values at 29°C and four values at all other temperatures (from increasing and decreasing phases of cycle for both groups 4 and 5).

Table 5. Prediction equations for heat production due to physical activity and not related to physical activity (activity-free) and total heat production in growing pigs according to ambient temperature (T), body weight (BW) and daily metabolisable energy intake (ME) or activity-free ME (ME_0) for models with and without a lower critical temperature (LCT)*

(Mean values with their standard errors)

					Coefficients										
						b		c		d		e			
Equation	Model†	Groups used	X	LCT (°C)	a	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Residual SD	CV
Heat production due to physical activity															
1		1–6	–	–	0·60	598	46	−37·2	4·7	0·85	0·11	–	–	354	13·4
2		1–6	–	–	0·75	322	24	−20·1	2·5	0·46	0·06	–	–	354	13·4
Activity-free heat production															
3	With LCT	1–7	ME_0†	24	0·60	1482	22	−39·7	1·7	NS		0·013	0·001	594	3·8
4	Without LCT	1–7	ME_0	–	0·60	1714	74	−66·4	8·8	0·74	0·20	0·013	0·001	586	3·8
Total heat production															
5	With LCT	1–7	ME	24	0·60	2317	126	−108·1	15·2	1·64	0·39	0·013	0·001	668	3·7
6	Without LCT	1–7	ME	–	0·60	2285	81	−103·5	9·7	1·50	0·22	0·013	0·001	657	3·6

NS, Intercept for thermic effect of feed was not significantly different from zero.
* If $T \leq LCT$, $Y = BW^a(b + cT + dT^2) + eXT$; if $T > LCT$, $Y = BW^a(b + cLCT + dLCT^2) + eXLCT$.
† $ME_0 = ME -$ heat production due to physical activity.

similar, with a CV < 4 %. In both cases TEF_{tot} increased from 16 to 31 % ME_0 when T varied between 12 and 24°C. Concomitantly, the efficiency of ME_0 utilisation for growth ($1-TEF_{tot}$) decreased from 84 to 69 % over this T range. The same approach as described earlier for HP_0 was used for HP_{tot} (see Fig. 2). According to the model with LCT fixed at 24°C, the TEF_{tot} was proportional to T whereas the maintenance component varied quadratically (equation 5; Table 5). The accuracy was similar when LCT was removed; CV < 4 % (equation 6; Table 5).

Discussion

The effect of T on voluntary feed intake has been discussed in detail by Quiniou *et al.* (2000) and the present discussion will focus on heat production and its components. In the literature, proposed values for daily maintenance ME requirement (MEm) under thermoneutral conditions are most often expressed as a function of $BW^{0.75}$ (420 kJ Holmes & Close, 1977; 440 kJ Close, 1978; 510 kJ Halter *et al.* 1980; 500 kJ Thorbek *et al.* 1984). Other exponents have been proposed (891 kJ/d per kg $BW^{0.57}$ Fuller & Boyne, 1972; 718 kJ/d per kg $BW^{0.569}$ Halter *et al.* 1980). According to results obtained in our laboratory (Noblet & Etienne 1987*a*,*b*; Noblet *et al.* 1991, 1999; van Milgen *et al.* 1998, 2000), 0·75 would better correspond to mature animals (gestating or lactating sows) and 0·60 to growing animals. Results of the present experiment confirm the latter value. The MEm value (970 kJ/d per kg $BW^{0.60}$) is close to that calculated by Noblet *et al.* (1999) under comparable T and experimental conditions (1014 kJ/d per $kg^{0.60}$).

The quadratic effect of T on the maintenance component of HP_{tot} is consistent with the linear effect of T for HP_0 and the quadratic effect of T found for HP_{act}. In other words, it can be suggested that the quadratic effect of T on maintenance is mainly due to the effect of T on physical activity of pigs. From a statistical point of view, prediction equations with and without an LCT were similar for HP_0 and HP_{tot}. In both cases, the same CV was obtained. However, with regard to the usual concept of critical temperatures to relate HP to T (Mount, 1974), models including a LCT value may be easier to interpret and will be used for evaluation and further calculations.

In the HP_0 prediction equations, HP for zero ME_0 corresponds to the fasting HP at zero physical activity. According to equation 3, the minimal value for fasting HP would theoretically be reached when T is equal to the LCT, i.e. 24°C in the present experiment. From measurements of fasting HP performed over the same BW range as in the present study, Bernier *et al.* (1996) obtained a constant

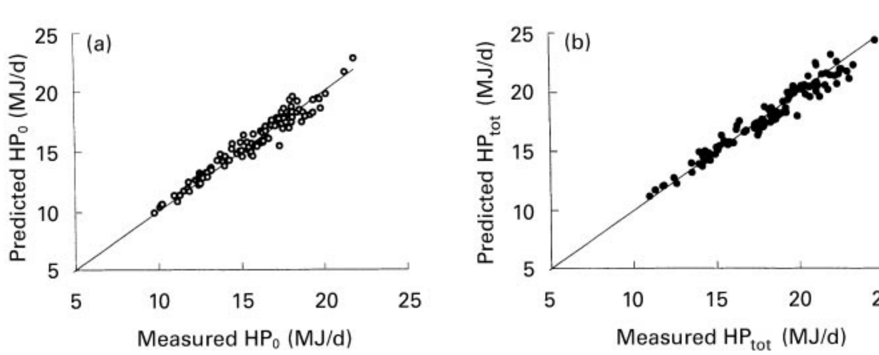

Fig. 2. Predicted *v.* measured heat production (a) unrelated to physical activity (HP_0) and (b) total (HP_{tot}) in group-housed growing pigs from the present study. Predictions were generated using equation 3 (a) and equation 5 (b) (see Table 5). (—), The bisector.

value for fasting HP at and above 24°C, which is in agreement with the value of LCT obtained in the present study. From calculations proposed by Holmes & Close (1977), the LCT of 60 kg pigs would be about 18°C. This lower value is partly due to differences in insulation of both groups of pigs (less back-fat and greater sensitivity to cold in modern pigs), but also to differences in the methods used for estimating LCT. From our equations, it can be concluded that energy expenditure starts to increase when T is below 23–24°C. Unlike the study of Holmes & Close (1977), the present study indicates that LCT does not vary with BW in growing–finishing pigs.

Little information exists on the upper limit of the thermoneutral zone. However, as discussed by Mount (1974), this T range may be split into two distinct parts, which are separated by the evaporative critical temperature (ECT). Between LCT and ECT, corresponding to the zone of thermal comfort, little thermoregulatory effort is required to maintain homeothermia. Between ECT and the upper critical temperature, minimal HP_{tot} may result from changes in relative contributions of non-evaporative and evaporative heat losses with T. This concept has been adopted by numerous authors (Black *et al.* 1986; Revell & Williams, 1993), even if it may result in a very narrow zone of thermal comfort, as predicted by Mount (1974) and as indicated by our results. Indeed, the marked depressing effect of T on feed intake above 25°C (Quiniou *et al.* 2000) combined with the increased panting activity (see later) would indicate that ECT of growing pigs is close to this value. Consequently, the zone of thermal comfort would range between 23–24°C (LCT) and 25°C (ECT).

In the present study HP_{act} represented 8 % ME (14 % HP_{tot}) under thermoneutral conditions. With the same system of measurement as in the present study, similar values have been obtained in group-housed pigs with a BW of 25 kg (9 % ME and 18 % HP_{tot}; A Collin, J van Milgen, S Dubois and J Noblet, unpublished results), whereas Ramonet *et al.* (2000) reported a higher contribution of HP_{act} to HP_{tot} or ME in gestating sows (22 and 19 %, respectively). Other results available in the literature refer to measurements performed using i.r. cells (McDonald *et al.* 1988; Noblet *et al.* 1993; van Milgen *et al.* 1998) or ultrasonic burglar devices (Gentry *et al.* 1997; Schrama *et al.* 1998). These systems detect only standing and sitting positions on the one hand, or locomotion on the other hand. Additional minor movements while standing or lying (e.g. walking or movements such as panting or shivering) are not detected by i.r. cells, whereas standing without movement is not detected by burglar devices. According to J van Milgen and J Noblet (unpublished results), HP due to standing represents 40–50 % total HP_{act} in growing pigs. However, despite differences between techniques the physical activity has been unanimously reported to have a high energy cost in pigs with, for instance, an energy expenditure of 30 kJ/kg $BW^{0·75}$ per 100 min standing in adult sows and growing pigs (Noblet *et al.* 1993; van Milgen *et al.* 1998).

In the present study, minimal contribution of HP_{act} to HP_{tot} was measured and estimated (equation 1) at 22°C, and it increased both under colder and warmer exposure. Under cold exposure van der Hel *et al.* (1986) reported the opposite effect. However, physical activity as defined by van der Hel *et al.* (1986) corresponded only to locomotion intensity and did not account for intense shivering under cold T. Increased energy expenditure for physical activity at high T is due to intense panting (not detected by burglar device or i.r. beams) while locomotion is reduced (A Collin, J van Milgen, S Dubois and J Noblet, unpublished results).

The TEF_{st}, calculated according to van Milgen *et al.* (1997), represented a constant percentage of ME_0 (5·1), and therefore appears to have no contribution to thermoregulation over the T range studied in the present experiment. In contrast, the feed component taken into account in equations 3 and 5, which can be considered as the TEF_{tot}, changed linearly with T. It decreased from 31 to 16 % ME between 24 and 12°C and, concomitantly, the efficiency of energy utilisation for growth increased from 69 to 84 %. This effect of T on TEF_{tot} or efficiency of ME utilisation has been reported by several authors (Verstegen *et al.* 1973; Stahly & Cromwell, 1979; Noblet *et al.* 1985, 1988). It indicates a partial utilisation of the thermic effect of feed, and specifically its long-term component, to meet the additional thermoregulatory heat requirement. Above LCT, TEF_{tot} needs to be dissipated and is completely lost with a subsequent constant value for the efficiency of utilisation of energy for growth.

In order to evaluate the models, it is of major interest to use the equations with other data sets. In fact, available data on HP_{act} are scarce, and it was not possible to evaluate the HP_0 equations. The evaluation was therefore performed only for HP_{tot}. Data of Verstegen (1971) obtained in various feeding and housing conditions, as well as results obtained in our laboratory on individually-kept pigs fed *ad libitum* and exposed to T ranging between 22 and 12°C (as in Expt 1; N Quiniou, J Noblet, J van Milgen and S Dubois, unpublished results) were used. From the first data set (Verstegen, 1971), utilisation of equations 5 and 6 at T below 12°C did provide accurate mean results, but with high (positive or negative) residues. Thus, data obtained under T that were outside the T range used in the present study were removed, so that 282 results were available (Table 6). Fig. 3 shows that predicted and measured values are highly correlated (*r* 0·96). It also indicates that predicted values are systematically higher than measured HP_{tot}. This difference may be due to the genetic evolution of growth characteristics over the last 30 years. Indeed, pigs available in the late 1960s were fatter than cross-bred barrows used in the present experiment, and produced less heat because of their (probably) lower maintenance requirements and their greater efficiency of ME utilisation which is higher for fat gain than for protein gain (Noblet *et al.* 1999).

From the second data set obtained in individually-kept pigs (N Quiniou, J Noblet, J van Milgen and S Dubois, unpublished results), the predicted and measured HP_{tot} are also highly correlated (*r* 0·87), as presented in Fig. 4. In contrast with the previous evaluation, both equations 5 and 6 underestimated measured HP_{tot}; the highest difference was observed at 12°C (−4 %) and may be due to housing conditions. Indeed, under low T, an individually-housed pig is assumed to produce a greater amount of additional heat

Table 6. Description of data used to develop (present study) and evaluate (Verstegen, 1971; N Quiniou, J Noblet, J van Milgen and S Dubois, unpublished results*) proposed prediction equations (equation 5, Table 5) for total heat production†

Value	Mean	Minimum	Maximum
Group size			
Present study		3	4
Verstegen (1971)		1	5
Unpublished results		1	1
Body weight (kg)			
Present study	61·6	32·2	94·1
Verstegen (1971)	44·7	15·8	103·2
Unpublished results	63·3	36·0	85·7
Temperature (°C)			
Present study	19·9	12·0	29·0
Verstegen (1971)	17·9	12·0	26·9
Unpublished results	17·2	12·0	22·0
Metabolisable energy intake (MJ/d)			
Present study	31·51	18·54	50·80
Verstegen (1971)	18·10	5·71	33·52
Unpublished results	33·67	24·07	39·68
Total heat production (MJ/d)			
Present study	18·26	10·97	24·66
Verstegen (1971)			
Measured	11·66	5·03	23·06
Predicted	13·01	6·57	23·38
Unpublished results			
Measured	19·32	13·99	22·97
Predicted	19·04	13·24	23·19
Energy retained (MJ/d)			
Present study	13·25	6·38	26·15
Verstegen (1971)			
Measured	6·39	−0·73	15·23
Predicted	5·04	−1·55	13·72
Unpublished results			
Measured	14·35	7·04	20·68
Predicted	14·63	8·88	21·00

* Obtained in our laboratory using single-housed pigs.
† Basic prediction equation: total heat production $= BW^{a'} \times (b' + c' \times T + d' \times T^2) + ME \times (e' \times T \times f')$, where BW is body weight, T is ambient temperature, ME is metabolisable energy and a′, b′, c′, d′, e′, f′ are coefficients.

than group-housed pigs to maintain homeothermia, as huddling behaviour cannot be used to limit the surface of skin in contact with ambient air.

From a practical point of view, it is of major interest to quantify the overall feed requirement for thermoregulation when animals are kept below their LCT. From the present study, the extra feed requirement for thermoregulation can be calculated at any BW over the 30–90 kg range and at any T between 12 and 24°C. From prediction equations of ME (Quiniou *et al.* 2000), and HP_{act} and HP_0, ER is calculated as the difference between ME_0 and HP_0. As HP_0 depends on ME_0, then the calculation of ER corresponds to:

$$ER = ME_0 - (BW^{0.60} \times (b + c \times T) + e \times T \times ME_0),$$

which is equivalent to:

$$ME_0 = (ER - BW^{0.60} \times (b + c \times T))/(1 - e \times T).$$

With ER fixed to the level calculated at 24°C, the first derivative of this equation (with respect to T) gives the thermoregulatory ME_0 requirement for maintenance of ER when T decreases below 24°C (Fig. 5). Our model indicates that the lower the value of T, the higher will be the thermoregulatory energy demand associated with an additional decrease of T. In addition, this extra feed requirement will increase with increasing BW, and will depend on the thermoneutral ER level. According to this approach, for 30–90 kg pigs the thermoregulatory feed requirement averages 19 g/d per °C between 12 and 24°C and 27 g/d per °C between 12 and 18°C. This latter value is

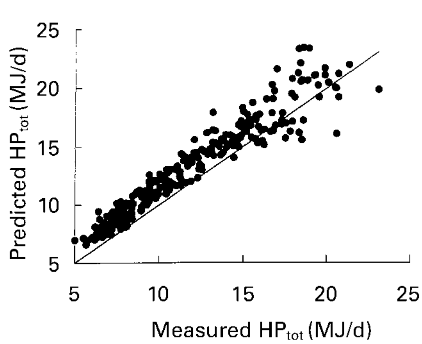

Fig. 3. Predicted (y) *v.* measured (x) total heat production (HP_{tot}) in pigs kept under various feeding and housing conditions (*n* 282; measured data from Verstegen, 1971; see Table 6). Predictions were generated using equation 5 (see Table 5). (—), The bisector. Regression equation: y = 1·889(SE 0·206) + 0·954(SE 0·017)x, CV 8·9, R^2 0·92.

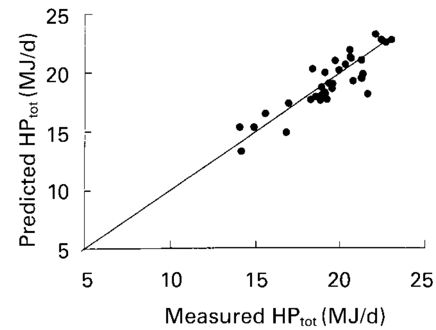

Fig. 4. Predicted *v.* measured total heat production (HP_{tot}) in individually-housed growing pigs (measured data from N Quiniou, J Noblet, J van Milgen and S Dubois, unpublished results). Predictions were generated using equation 5 (see Table 5). The fine line represents the bisector.

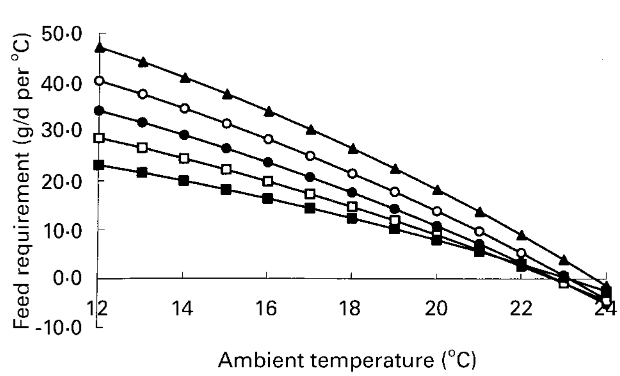

Fig. 5. Calculated daily feed requirement for thermoregulation of group-housed growing pigs according to ambient temperature and body weight (▲, 90 kg; ○, 75 kg; ●, 60 kg; □, 45 kg; ■, 30 kg). For details of calculations, see p. 100.

lower than the 33–32 g/d per °C proposed by Le Dividich *et al.* (1987; 30–97 kg BW for individually-housed pigs) and Verstegen *et al.* (1982; 25–100 kg BW for group-housed pigs) from studies performed with feeding level adjusted to maintain growth rate under various T.

Conclusion

The present study provides equations to predict HP and its components and energy gain for growing pigs under a wide range of T, BW and ME. According to our results the LCT would be approximately 24°C in 30–90 kg pigs with a higher marginal efficiency of dietary energy utilisation for growth under low T. In addition, it is suggested that the contribution of physical activity to HP_{tot} can be important. These relationships represent an advancement in modelling growth of the pig towards a better estimation of ER under various climatic environments.

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Appendix. Variables determined during the study, their calculation and analysis

Variable	Abbreviation	Calculation	Analysis
Temperature (°C)	T		
Body weight (kg)	BW		
Heat production due to physical activity	HP_{act}	Gas model*	
Resting heat production	Resting HP	Gas model*	
Short-term thermic effect of feed	TEF_{st}	Gas model*	
Metabolisable energy intake (kJ/d)	ME	In *ab libitum*-fed pigs using the equation of Quiniou *et al.* (2000): $ME = -16710 + 1547 \times T - 31{\cdot}73 \times T^2 + 973{\cdot}0 \times BW - 3{\cdot}44 \times BW^2 - 12{\cdot}56 \times T \times BW$ residual SD 4349 kJ/d	
Metabolisable energy intake not used for physical activity	ME_0	$ME_0 = ME - HP_{act}$	
Heat production not related to physical activity	HP_0	$HP_0 = \text{resting HP} + TEF_{st}$	$HP_0 = BW^a \times (b + c \times T + d \times T^2) + ME_0 \times (e \times T + f)$
Total heat production	HP_{tot}	$HP_{tot} = HP_{act} + TEF_{st} + \text{resting HP}$	$HP_{tot} = BW^a \times (b' + c' \times T + d' \times T^2) + ME \times (e' \times T + f')$
Energy retention	ER	$ER = ME - HP_{tot} = ME_0 - HP_0$	
Efficiency of energy utilization for growth	k_g	$k_g = 1 - (e \times T + f)$	
Maintenance ME requirement not related to physical activity	MEm_0	$MEm_0 = BW^a \times (b + c \times T + d \times T^2)/(1 - (e \times T + f))$	
Maintenance ME requirement	MEm	$MEm = BW^{a'} \times (b' + c' \times T + d' \times T^2)/(1 - (e' \times T + f'))$	

a, a′, b, b′, c, c′, d, d′, e, e′, f, f′ coefficients.
* van Milgen *et al.* (1997).