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Effect of high temperature on feeding behaviour and heat production in group-housed young pigs

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To assess the acclimation of pigs to heat stress, the effects of high (33°C) or thermoneutral (23°C) constant temperatures on feeding behaviour and components of energy balance were studied in group-housed young pigs. Three groups of five pigs were used at each temperature. After 1 week of adaptation, voluntary feed intake (VFI) and heat production (HP) were recorded for thirteen consecutive days. Animals were fed *ad libitum*. Fasting HP was measured on the last day. Average initial body weights (BW) were 21·4 and 20·9 kg at 23 and 33°C respectively. Feeding behaviour was measured individually and rate of feed intake and characteristics of feeding behaviour were calculated. The O_2 consumption, CO_2 production and physical activity of the group were used to calculate total HP (HP_{tot}) and its components, i.e. fasting HP (HP_{fas}), HP due to physical activity (HP_{act}) and thermic effect of feed (TEF). The BW gain and VFI were reduced by 37 and 30 % respectively at 33°C. The decrease in VFI corresponded to reduced consumption time (−34 %) and size of the meals (−32 %). Feeding behaviour was mostly diurnal (66 % of the VFI), and the rate of feed intake (28 g/min) was not affected by temperature. Daily HP_{tot}, HP_{fas} and TEF, expressed per kg metabolic weight ($BW^{0·60}$), were significantly decreased at 33°C by 22, 18 and 35 % respectively, whereas HP_{act} was not affected; TEF expressed per g feed was not affected (2 kJ/g). The decrease in HP_{tot} at 33°C was caused by a reduction in TEF and HP_{fas} (kJ/d per/kg $BW^{0·60}$), which are both related to reduction in VFI.

Pig: High temperature: Heat production: Feeding behaviour

Within the thermoneutral zone, dietary energy is used for growth, maintenance and physical activity. Below thermoneutrality, additional energy may need to be diverted from productive processes in order to maintain homeothermy. Under warm conditions, all heat produced has to be evacuated. Pigs exposed to warm environments acclimate by increasing (evaporative) heat loss and by reducing heat production, to maintain body temperature within narrow limits. However, they have a limited capacity to lose heat by water evaporation (Ingram, 1965) and acclimation to warm climatic conditions mainly occurs by reducing heat production (Nienaber & Hahn, 1982; Quiniou *et al.* 2001). Reduction in voluntary feed intake (VFI) and the associated thermic effect of feeding (or heat increment; TEF) is an efficient mechanism to reduce heat production (Quiniou *et al.* 2001). Heat production may also be reduced by a decrease in physical activity or BMR. Although there is information about the effect of temperature on the total heat production (HP_{tot}) in pigs (Nienaber & Hahn, 1982; Nienaber *et al.* 1987; Quiniou *et al.* 2001), little is known about the change in the components of heat production at high temperature. Moreover, these phenomena have been studied mainly in growing pigs and sows. A previous study showed that VFI was at a maximum between 19 and 25°C in young pigs weighing about 20 kg, decreased regularly between 25 and 33°C and was severely depressed above 33°C, suggesting that young pigs are heat stressed above 25°C (Collin *et al.* 2001). Based on these results, two temperatures were chosen, representing temperatures within the thermoneutral zone (23°C) or causing severe heat stress (33°C). The present study is part of a larger programme in which the effects of high *v.* thermoneutral temperatures are studied in young pigs. The programme includes studies on the physiological (fractional distribution of blood flow) and metabolic and nutritional (mitochondrial metabolism, heat production, feeding

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Abbreviations: BW, body weight; $BW^{0·60}$, metabolic body weight; HP_{act}, heat production due to physical activity; HP_{fas}, fasting heat production; HP_{tot}, total heat production; TEF, thermic effect of feed; VFI, voluntary feed intake.

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behaviour) consequences of exposure to high temperatures. The present paper focuses on the effects of a high constant temperature on VFI, heat production and its components in 20–30 kg pigs.

Materials and methods

Animals and husbandry

Crossbred (Large White×Landrace)×Piétrain male pigs, castrated at about 14 d of age and weaned at 28 ± 1 d of age were used for the experiment. After weaning, pigs were reared in groups of twelve animals in a conventional nursery room and offered *ad libitum* a starter diet providing 213 g crude protein (N × 6·25)/kg, 14·0 g lysine/kg and 13·6 MJ metabolisable energy (ME)/kg. At 2 weeks after weaning a group of six pigs of similar body weight (BW) and age, but from different litters, was constituted and placed for adaptation on a 2·3 × 1·6 m flat-deck in a room controlled for temperature and relative humidity. The temperature was initially set at 25°C, and was then progressively decreased or increased within 4 d to either 23 or 33°C. At the beginning of the adaptation period, the pigs, BW was 15·2 (SD 1·6) kg and their age was 46 (SD 1) d. Three groups of pigs were used successively at each temperature.

Rectal temperature and feed intake attain a new constant value within 96 h after exposure to high temperatures (Rafaï, 1974; Giles, 1992). Consequently, 1 week was considered to be sufficient to adapt the pig to their new environment (at least for the criterion of interest). Five pigs were selected (day 0) from the group on the basis of a similar BW and placed in a pen (2·3 × 1·6 m) in a respiration chamber (12 m^3) equipped with a metal slatted floor and a slurry pit allowing storage of urine, faeces and water spillage. The slurry pit was emptied on days 6 and 13. A feed dispenser and a drinking station allowed measurement of water and feed intakes during the experiment. Each pig had an ear tag in order to be detected when close to the trough. A fence prevented two pigs from being present at the same time near the trough. Pigs were weighed in the morning of days 1, 6, 13 and 14. At the start of the measurement period (day 1), the average BW was 21·2 (SD 1·4) kg. Animals were offered *ad libitum* a standard pelleted diet (Table 1) over the adaptation period and the first 12 d of the measurement period and fasted over day 13. The photoperiod was set at 12 h light (08.00–20.00 hours). Water was available from a nipple drinker located at a distance of 2 m opposite the trough.

The experiment consisted of measuring the feeding behaviour and heat production at one of the two temperatures over twelve and thirteen consecutive days respectively. Values for day 1 and day 6 (weighing days) were excluded from the data set. Three periods (days 2–5, 7–9 and 10–12) were distinguished, to account for the rapidly changing BW of the pigs during the experimental period.

Behaviour

Measurements. The equipment was the same as that described by Quiniou *et al.* (2000). Brief, variables concerning feed intake behaviour were recorded daily and included pig number, times at the initiation and the end of the instability of weight of the trough (i.e. visit), and feed consumption during each visit. Physical activity of the group was recorded using force sensors (type 9104A; Kistler, Winterthur, Switzerland) on which the metabolism cage was mounted.

Table 1. Ingredients and chemical composition of the diet offered to group-housed pigs

Ingredients (g/kg)	
Maize	280·5
Soyabean meal	255·0
Wheat	232·5
Barley	145·0
Fish meal	50·0
Dicalcium phosphate	18·0
Calcium carbonate	9·0
Mineral and vitamin mixture	5·0
Salt	4·0
Lysine hydrochloride	0·5
Fungicide	0·5
DM (g/kg)	884
Analysed levels (g/kg DM)	
Ash	78
Crude protein (N × 6·25)	248
Crude fibre	31
Starch	437
Fat	29
Energy values (MJ/kg DM)	
Gross energy	18·3
Metabolisable energy*	16·1
Net energy†	11·8

* Determined in a 6 d balanced trial with six pigs averaging 17·2 (SD 1·3) kg and kept at an environmental temperature of 25°C.

† Calculated from equations of Noblet *et al.* (1994).

Calculations. Several visits can occur within the same meal, with short pauses detected by the computer as a 'steady weight' of the trough. To allow comparisons to be made between studies carried out under various conditions, successive visits were combined according to a meal criterion (Bigelow & Houpt, 1988; Labroue *et al.* 1994). Two successive visits, separated by an interval longer than the meal criterion, were considered as belonging to two different meals. Based on data of the present experiment, 91 % of the individual estimated meal criteria was below 2 min. This value, also reported by Quiniou *et al.* (2000) in heavier pigs, was used as the meal criterion in further calculations.

The feeding behaviour was described for each pig by the daily number of meals, the duration and amount of feed consumed and the feeding rate. Ingestion time was calculated as the cumulative duration of visits, and consumption time as the cumulative duration of meals. These calculations were carried out for the day and the night periods.

The recorded physical activity was based on the average signal of the force sensors during a 10 s interval. Data were analysed to distinguish different types of activity such as long periods of relative calm (e.g. resting) from short, intense movements (e.g. fighting or locomotion). Five arbitrary classes of activity (based on the signal of the force sensors) were defined, allowing quantification of the intensity of physical activity for each class of activity.

Heat production

Measurements. An open-circuit respiration chamber (12 m^3) based on a design similar to that of Vermorel *et al.* (1973) was used. Both temperature and relative humidity were maintained constant (23 or 33°C and 70 or 60 % relative humidity respectively) during the experiment. Gas (CO_2 and O_2) contents of ingoing and outgoing air and ventilation rate (and weight of the trough and physical activity, see earlier) were continuously and simultaneously recorded over 10 s intervals during the 13 d experimental period.

Calculations. Calculations were carried out according to the model of van Milgen *et al.* (1997). This relates observed changes in O_2 and CO_2 concentrations in the respiration chamber to physical aspects of gas exchange and to O_2 consumption and CO_2 production by the animals; the ACSL/Optimize software (version 2.4; AEgis Simulation, Inc., Hurtsuille, AL, USA) was used. Heat production was calculated from gas exchanges according to the formula of Brouwer (1965). In the present experiment a large number of visits to the trough were recorded (on average 240/d and group) and they were strongly correlated with peaks of physical activity. It was therefore impossible to estimate simultaneously heat production associated with physical activity (HP_{act}) and the short term TEF. To circumvent this problem, the heat production per unit force was estimated only during fasting and it was assumed that this value was independent of BW and feeding status. The product of this variable and the actual daily force measured in fed pigs provided an estimate of daily HP_{act}. Measurements of heat production in fasting animals allowed the calculation of fasting heat production (HP_{fas}). It was assumed that the HP_{fas} value obtained on the last measurement day was applicable to fed animals during the previous 12 d (based on the estimated BW for each day and assuming a constant HP_{fas} on a per kg metabolic BW ($BW^{0\cdot60}$) basis). TEF was the difference between HP_{tot} and the sum of HP_{act} and HP_{fas}. Energy balance data were expressed as MJ/d or per kg $BW^{0\cdot60}$ (according to Noblet *et al.* 1999).

Statistics

Some data were measured in individual animals (e.g. feeding behaviour, feed intake), whereas other data were measured for a group of animals (e.g. heat production). In the analysis all results are reported on a ‘per pig’ basis. Performance data (BW, BW gain, VFI, voluntary water intake and feed conversion ratio), as measured between days 1 and 12, and individual feeding behaviour were analysed using the general linear models procedure of Statistical Analysis Systems (release 6·07; SAS Institute Inc., Cary, NC, USA). To account for the rapidly-changing BW of the animals, the experimental period was divided in to three sub-periods (period 1, days 2–5, period 2, days 7–9; period 3; days 10–12). The individual components of feeding behaviour (per period) were subjected to ANOVA with temperature, period, their interaction, the interaction of temperature and the group, and the interaction of temperature, group and animal as main effects, and using temperature×group as the error term for testing temperature, and temperature×group×animal as the error term for testing temperature×group. The diurnal percentage of total activity was calculated from the measurements per group and analysed with temperature, period, temperature×period and temperature group as main effects, and temperature×group as the error term for testing temperature.

The overall effect of temperature (for the whole experimental period) on mean VFI, heat production and its components, retained energy and RQ was analysed by ANOVA. To account for the changing BW during the experiment, data (per period) were analysed using temperature, period, their interaction and the temperature× group interaction as main effects. The latter term was used as the error term to test the effect of temperature.

Results

Performance

As expected, VFI was reduced at 33°C (Table 2), being 30 % lower than at 23°C with subsequent lower BW gain at 33°C than at 23°C (621 g/d *v.* 987 g/d). In addition, the feed conversion ratio was significantly lower at 23°C than at 33°C (1·50 *v.* 1·68; $P < 0\cdot05$). Despite the lower feed intake, there was a tendency for increased water consumption at 33°C.

Table 2. Effect of temperature (T) on performance of group-housed young pigs over the experimental period†
(values are expressed per pig)

	T (°C)			
	23	33	Residual SD	Statistical significance of effect of T
No. of observations‡	3	3		
Initial body weight (kg)§	21·4	20·9	0·4	
Final body weight (kg)§	33·2	28·4	0·8	**
Fasting body weight (kg)§	30·8	26·9	1·0	**
Body weight gain (g/d)	987	621	49	**
Voluntary feed intake (g/d)	1483	1045	74	**
Voluntary water intake (g/d)	4408	5863	2595	
Feed: gain	1·50	1·68	0·07	*

$^*P < 0\cdot05$, $^{**}P < 0\cdot01$.

† Performance from day 1 to day 12; for details of animals and procedures, see p. 64.

‡ Group of five pigs per observation.

§ Initial and final body weights were measured in fed pig (morning of days 1 and 13) and fasting body weight on the morning of day 14 (after 1 d without feed).

Table 3. Effects of temperature (T) and period (P) on individual components of the feeding behaviour of group-housed young pigs†

T (°C)	23			33					Statistical significance of effect of†††			
P‡	1	2	3	1	2	3	σ_1‖‖	σ_2¶¶	T	P	T × P	T × G
No. of observations§	15	15	15	15	15	15						
Duration of *P* (d)	4	3	3	4	3	3						
Mean body weight (kg)	23·6	28·0	31·5	22·7	25·5	27·4	0·4	3·0	*	**	**	
Mean components of daily feeding behaviour												
No. of visits‖	55	58	57	38	40	39	9	53				
No. of meals¶	14·8	14·0	14·2	14·7	15·8	13·8	2·2	9·9				
Feed intake (g)	1290	1576	1710	967	1129	1095	174	250	**	**	**	
Feed intake (g/kg BW$^{0·60}$)	194	214	215	148	161	150	24	30	**	*		
Ingestion time††(min)	56	57	59	43	43	40	6	5	**			
Consumption time‡‡ (min)	77	81	80	53	55	51	8	38	*			
Rate of feed intake (g/min)	23	28	30	23	27	28	3	9		**		
Rate of feed intake (g/min per kg BW$^{0·60}$)	3·5	3·8	3·7	3·6	3·9	3·8	0·4	1·2		**		
Characteristics of the meal												
Meal size (g)	93	123	132	69	78	86	16	60	*	**	*	
Meal size (g/kg BW$^{0·60}$)	13·9	16·6	16·6	10·7	11·2	11·8	2·1	8·9		**		
Ingestion time (min)	4·1	4·5	4·6	3·1	3·0	3·1	0·5	2·8				
Consumption time (min)	5·5	6·3	6·1	3·9	3·7	4·0	0·7	5·2				**
Diurnal feeding behaviour (% total)												
No. of meals	67	66	65	64	66	67	7	9				
Feed intake	67	66	66	64	68	70	6	13				
Ingestion time	67	66	65	63	69	69	7	13				
Diurnal physical activity (% total)§§	68	66	65	61	55	49	8	5	*			

BW$^{0·60}$, metabolic body weight; G, group.

*$P < 0·05$, **$P < 0·01$.

† For details of animals and procedures, see p. 64.

‡ P 1 included days 2–5, P 2 included days 7–9, P 3 included days 10–12. Days 1 and 6 were not taken into account (weighing days).

§ Each observation was the mean over 3 or 4 d for one pig (five pigs per group).

‖ Duration of instability of the trough.

¶ One meal corresponded to a group of successive visits separated by <2 min (i.e. meal criterion).

†† Cumulative duration of the visits.

‡‡ Cumulative duration of the eating and non-eating sessions within meals.

§§ Observation was physical activity of the group and the model included the effects of T, P, their interaction (T × P) and the effect of the group within temperature (G(T)); the error for testing T effect was G(T).

‖‖ Residual standard error for testing the effect of P.

¶¶ Residual standard error for testing the effect of T.

††† The model included the effects of T, P, their interaction (T × P), the interaction of T with G (T × G) and the interaction of G with T and animal (A; T × G × A); the errors for testing T and T × G effects were T × G and T × G × A, respectively. The effect of T × G × A was significant whatever the component of feeding behaviour considered ($P < 0·01$), except for the percentage of diurnal ingestion time ($P > 0·05$).

Behaviour

The effects of temperature, period and their interaction on components of feeding behaviour are given in Table 3. The decrease of 30 % in feed intake at 33°C was associated with shorter daily ingestion time (−28 %) and consumption time (−34 %) at 33°C. However, the daily number of meals and the rate of feed intake were not affected by temperature, so that meal size was significantly lower at 33°C ($P < 0·05$). The difference between consumption time and ingestion time was smaller at 33°C, which suggests that pigs spent more time near the trough at thermoneutrality than at high temperature. The duration of the meals (consumption time) was numerically decreased at 33°C (3·9 min *v.* 5·9 min, on average).

The partitioning of feeding activity between day (67 %) and night (33 %) was not affected by temperature. Two-thirds of physical activity (force) was recorded during the day at 23°C. At 33°C there was a more uniform partitioning between diurnal and nocturnal activity. Even though heat production associated with physical activity was not affected by ambient temperature, the characteristics of physical activity differed between the two temperatures (Fig. 1). The physical activity in pigs kept at 23°C appeared to be more extreme (either very calm or very active) compared with that of pigs kept at 33°C. It can be assumed that the highest levels corresponded to the standing position and locomotion, while the lower levels corresponded mainly to respiration in the lying position.

As anticipated, period affected VFI (g/d), but there was a significant interaction between period and temperature (Table 3). In other words, VFI increased regularly over successive periods at 23°C, whereas the increase was quite small at 33°C. These changes in daily VFI over the experiment were achieved through an increased meal size. The rate of feed intake increased from 23 to 29 g/min on average between period 1 and period 3, irrespective of the temperature.

Meal size and VFI, when expressed as g/kg BW$^{0·60}$, increased slightly over the experiment. However, the interaction previously observed between temperature and period for VFI and meal size was not significant.

Heat production and its components

Data on heat production in the fed and fasting states over the experimental period are given in Table 4. Pigs exposed at 33°C had a lower fasting heat production expressed per kg BW$^{0·60}$ (−14 %) than those kept at 23°C. In fed pigs the

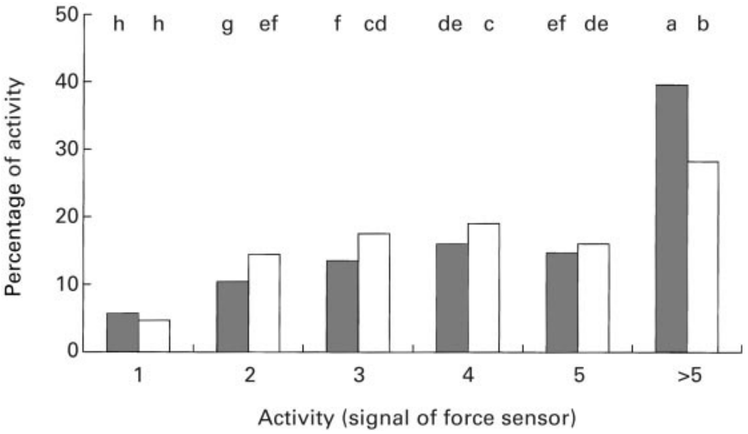

Fig. 1. Repartitioning of physical activity (signal of force sensor) at 23°C (■) or 33°C (□) in group-housed young pigs. ^{a,b,c,d,e,f,g}Mean values with unlike superscript letters were significantly different ($P < 0{\cdot}05$). For details of animals and procedures, see p. 64.

increase in ambient temperature from 23 to 33°C resulted in a 22 % decrease in HP_{tot}. The contributions of HP_{act}, TEF and HP_{fas} variations to the decrease in HP_{tot} with temperature rise were 10, 45 and 45 % respectively; the reductions were significant for TEF and HP_{fas} only ($P < 0{\cdot}05$ in both cases). The reduction in TEF was not due to a decrease in TEF per g feed (2 kJ/g at both temperatures), but essentially to the effect of VFI reduction. The RQ was significantly lower at 33°C (1·08 *v.* 1·12; $P < 0{\cdot}05$).

As indicated in Table 5, total metabolisable energy intake, HP_{tot}, HP_{act} and retained energy increased over the experiment, but the variation was smaller at 33°C than at 23°C for total metabolisable energy intake and retained energy. When expressed per kg $BW^{0{\cdot}60}$, total metabolisable energy intake, HP_{tot}, its components (except HP_{act}) and retained energy were reduced at 33°C (Table 5).

Discussion

Performance

The results of the present experiment demonstrate a clear decrease in VFI and, subsequently, in BW gain at 33°C. The comparison of results obtained at 23 and 33°C indicates that VFI declined by 45 g/d per °C, which is similar to the 39 g/d per °C calculated from a previous study (Collin *et al.* 2001), and to results of Sugahara *et al.* (1970; 42 g/d per °C) in young growing pigs. However, this decrease is greater than that reported by Rinaldo & Le

Table 4. Effect of temperature on voluntary feed intake, heat production and its components in group-housed young pigs†

	T (°C)			
	23	33	Residual SD	Statistical significance of effect of temperature††
No. of observations‡	3	3		
Body weight (BW; kg)	27·3	24·9	0·8	*
Fed state				
Voluntary feed intake (g/d)	1502	1054	69	**
Metabolisable energy intake (MEI; MJ/d)	21·69	15·13	0·99	**
Heat production (MJ/d)				
Activity	2·01	1·76	0·19	
Thermic effect of feed	3·10	2·00	0·34	*
Fasting heat production§	6·12	5·01	0·34	*
Total	11·23	8·77	0·43	**
Retained energy (MJ/d)	10·45	6·36	0·59	**
RQ	1·12	1·08	0·01	*
Thermic effect of feed (kJ)				
/kg feed	2·05	1·87	0·27	
/kJ ME	0·14	0·13	0·02	
/kJ MEI_0‖	0·17	0·15	0·03	
Fasting heat production¶, (kJ/d per kg $BW^{0{\cdot}60}$)	849	728	49	*

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$.
† For details of animals and procedures, see p. 64.
‡ One observation corresponds to data measured in a group of five pigs; the data is expressed per pig.
§ Estimated from fasting heat production measured on day 14.
‖ MEI − heat production for activity.
¶ Calculated with BW of fed pigs (morning of day 13) as reference.
†† Days 1 and 6 were not taken into account (weighing days).

Table 5. Effect of temperature (T) and period (P) on heat production and its components in group-housed young pigs†

T (°C)	23			33					Statistical significance of effect of¶:			
P‡	1	2	3	1	2	3	σ_1§	σ_2‖	T	P	T × P	G(T)
Mean body weight (kg)	23·6	28·0	31·5	22·7	25·5	27·4	0·3	1·3	*	**	**	**
Voluntary feed intake (g/d)	1290	1576	1711	967	1128	1095	72	111	**	**	*	
Metabolisable energy intake (MEI; MJ/d)	18·62	22·76	24·71	13·88	16·20	15·72	1·05	1·61	**	**	*	
Heat production (MJ/d)												
Activity	1·81	2·07	2·21	1·57	1·86	1·93	0·07	0·32		**		**
Thermic effect of feed	2·44	3·34	3·74	1·72	2·23	2·15	0·38	0·55	*	**		
Fasting heat production	5·62	6·23	6·69	4·73	5·07	5·30						
Total	9·87	11·64	12·64	8·02	9·16	9·38	0·43	0·72	**	**		
Retained energy (MJ/d)	8·75	11·12	12·07	5·86	7·04	6·34	0·66	0·94	**	**	*	
Energy balance (kJ/kg BW$^{0·60}$ per d)												
MEI	2744	3030	3103	2132	2328	2168	147	174	**			
Heat production												
Activity	271	281	279	241	266	265	11	38		*		**
Thermic effect of feed	367	452	473	262	319	294	54	79	*			
Total	1482	1577	1595	1231	1312	1286	59	68	**			
Retained energy	1312	1507	1523	900	1009	869	95	114	**			
RQ	1·10	1·11	1·14	1·08	1·09	1·08	0·01	0·02	*			

*$P < 0·05$, **$P < 0·01$.

† For details of animals and procedures, see p. 64.

‡ P 1 included days 2–5, 3–5, P 2 included days 7–9, P 3 included days 10–12. One observation corresponds to data measured in a group of five pigs; data is expressed per pig.

§ Residual standard error for testing the P effect.

‖ Residual standard error for testing the T effect.

¶ The model included the effects of T, P, group within-T G(T), the error being G(T).

Dividich (1991*a*; 28 g/d per °C) between 25 and 31·5°C in young pigs between 9 and 30 kg. The reduction in BW gain due to temperature (or feed intake) corresponded to 37 g/d per °C, which is greater than that reported in other studies in young pigs (20 g/d per °C according to Sugahara *et al.* (1970) and Rinaldo & Le Dividich (1991*a*)). The reasons for this discrepancy could be the higher initial BW (21 kg *v.* 9 kg) in the present experiment. Also, in the present experiment pigs were housed in groups, which may stimulate feed intake, at least at thermoneutrality. In addition, the relatively high BW gain and VFI recorded at 23°C could also have induced accentuated effects of heat exposure.

Feeding behaviour

Feed intake and feeding patterns in growing pigs are affected not only by physiological, genetic and social factors (Bigelow & Houpt, 1988; Labroue *et al.* 1994), but also by environmental factors (Nienaber & Hahn, 1982; Le Dividich *et al.* 1998; Quiniou *et al.* 2000). In the present study, pigs acclimatised to the hot environment by reducing their feed intake (−3·0 %/°C), which is consistent with the decrease described by Quiniou *et al.* (2000) in heavier pigs (−3·4 %/°C). Chronic exposure to 33°C also affected other components of feeding behaviour in pigs. Ingestion time per d and occupation time of the feeding station were reduced, and the duration of non-eating sessions within meals at 23°C (22 min) was twice that at 33°C (11 min). Temperature did not seem to affect the daily number of meals, which is consistent with results of Nienaber *et al.* (1993) and Quiniou *et al.* (2000), also obtained in group-housed animals.

The reduction in VFI at 33°C can be partly explained by a reduction in BW, which is the combined result of the hot environment and the decrease in VFI. Consistent with results reported by Bigelow & Houpt (1988) in young growing pigs, and by Nienaber *et al.* (1990), Labroue *et al.* (1994) and Quiniou *et al.* (2000) in heavier pigs, ingestion time and consumption time remained relatively constant during the trial, whereas the rate of feed intake increased. Meal size increased with BW (period), whereas the number of meals remained constant, so that the total VFI increased. The number of meals calculated from the present experiment (fifteen meals/d) is higher than the nine to eleven daily meals calculated in heavier pigs (Xin & DeShazer, 1991; Nienaber *et al.* 1996; Quiniou *et al.* 2000). It is consistent with results of Quiniou *et al.* (1999), who found a decrease in the number of meals with increasing BW. The period effect on feed intake (Table 5) was mainly due to the increased BW over successive periods. The significant interaction between temperature and period on feed intake ($P < 0·05$) illustrates the smaller increase at the highest temperature, which may suggest a long-term acclimation effect to high temperature.

Feeding behaviour was mainly diurnal, with two-thirds of the feed consumed during the day, and was not affected by ambient temperature. This value is similar to that reported by Labroue *et al.* (1994) and Quiniou *et al.* (2000*a*) in growing pigs kept under similar conditions. Studies converge to show that the main factor determining the partitioning of VFI between day and night on a given light pattern is BW, feeding behaviour of pigs becoming more diurnal with increasing BW (Bigelow & Houpt, 1988; Labroue *et al.* 1994; Quiniou *et al.* 1999). Although high temperature induced a decrease in the diurnal percentage of number of meals in the study of Quiniou *et al.* (2000), it did not change the partitioning between day and night in our study. It appears that, as a result of heat stress, heavier pigs shift a part of their meals to the night, which has been described in studies with cyclic temperatures mimicking real daily temperatures (Feddes *et al.* 1989; Xin & DeShazer, 1991).

Acclimation to high temperatures

Acclimation to high temperature results in both increased evaporative heat loss and decreased heat production. The first mechanism is limited in pigs, owing to the low capacity for cutaneous evaporative heat loss. As expected, results of the present experiment indicated a great reduction in heat production when pigs were exposed to 33°C, which agrees with the findings of studies by Stombaugh & Grifo (1977), Nienaber & Hahn (1982), Nienaber *et al.* (1987) and Quiniou *et al.* (2001) in heavier pigs. Gray & McCracken (1974) in 22 kg pigs obtained similar heat production values at 22 and 29°C, but their experiment was carried out to ensure similar daily intakes.

The reduced TEF contributed to 45 % of the decrease in HP_{tot} at 33°C, resulting directly from the decreased VFI. The second factor contributing to the decrease in HP_{tot} was the HP_{fas} (45 %). This finding conflicts with data from Holmes (1974), who did not observe such a decrease in heavier pigs during a 48 h fast, despite different preceding feeding levels. It can be hypothesised that, in our study, HP_{fas} was overestimated at 23°C because pigs suffered from cold. However, Bernier *et al.* (1996) showed that HP_{fas} was constant at and above 24°C in individually-housed 30–50 kg pigs fed at constant feeding levels before HP_{fas} measurements. An alternative explanation for decreased HP_{fas} at 33°C is the decrease in the viscera mass (Rinaldo & Le Dividich, 1991*a*) and the associated decrease in heat production (Koong *et al.* 1983; van Milgen *et al.* 1998) resulting from the lower feeding level. Viscera make an important contribution to HP_{fas}, and 24 h of fasting may not be sufficient to attenuate differences in visceral mass and heat production. Summarising, the reduction in heat production at high ambient temperatures seems to be the result of both direct (TEF) and indirect (HP_{fas}) effects of reduced feed intake.

The contribution of HP_{act} to total metabolisable energy intake (9 %) and to HP_{tot} (18 %) at 23°C was slightly higher than results obtained by Quiniou *et al.* (2001) at thermoneutrality (8 % of the total metabolisable energy intake and 14 % of the HP_{tot}) in 30–90 kg pigs. At 33°C, corresponding values were higher (12 and 20 % respectively) partly in connection with the reduced total metabolisable energy intake at this temperature. In the present study HP_{act} was lower at 33°C and the variation contributed to 10 % of the HP_{tot} decrease. Results of Quiniou *et al.* (2001) suggested a tendency for increased HP_{act} at high ambient temperature, in connection with intense panting of animals under heat stress. The results of the present study also support this hypothesis, as shown in Fig. 1. As indicated earlier, the upper values of activity were associated with walking or standing, whereas the lower values were associated with resting or lying. Panting can be considered an intermediate level of activity. Pigs kept at 33°C seem to reduce energy expenditure by avoiding voluntary movements, as in having long intervals between visits within a meal (Quiniou *et al.* 2000; the present study). Standing appears to be very energy expensive in pigs (Dauncey, 1990; Noblet *et al.* 1993; van Milgen *et al.* 1998) and the reduction in non-essential activity can be considered as an adaptation to the hot environment. Although panting seems to cause an increase in activity, the benefit (heat loss) probably outweighs the cost (heat production).

The RQ is indicative of the proportional rates of substrates used for catabolism and anabolism. Catabolism of substrates (e.g. for ATP synthesis) results in an RQ ≤ 1, whereas fatty acid synthesis results in an RQ >1. The observed RQ is a combination of both catabolism and anabolism, and the RQ in growing pigs is almost always >1. The exposure to 33°C resulted in a reduction in both feed intake and energy retention (and thus reduced fatty acid synthesis). Similar results were found by Rinaldo & Le Dividich (1991*b*), and are probably the cause of the reduced RQ at 33°C.

In conclusion, the present study provides some evidence that the reduction in heat production in heat-stressed young pigs is essentially caused by a reduction in the TEF and HP_{fas}. Both effects are directly related to a marked reduction in VFI at high ambient temperatures. This finding implies that nutritional adjustments, such as a reduction in the fibre or protein content of the feed, could be efficient in attenuating the negative effects of hot climatic conditions. The present results also suggest that, although HP_{act} was not different between 23 and 33°C, its partitioning between voluntary movements (standing and locomotion) and breathing depends on ambient temperature.

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