Original article

Influence of low ambient temperatures on heat production and energy balance of single-housed growing pigs fed ad libitum: a comparison with group-housed pigs

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Abstract — The effect of ambient temperature (T; 12 to 22 °C) and body weight (BW; 37 to 95 kg) on metabolisable energy intake (ME) and the components of energy balance was studied in six individually-housed barrows kept in a respiratory chamber. Each animal was fed ad libitum and was exposed successively in a cyclic manner to variable T (three days per T). The O_2 and CO_2 concentrations, feed intake and physical activity were continuously recorded and used to calculate total heat production (HP), heat production due to physical activity (HP_{act}) and the short-term thermic effect of feed (TEF_{st}). The HP and its components were modelled using non-linear equations with T, BW and ME as predictors. The results were compared to predicted values from the equations obtained in a previous experiment performed on group-housed pigs. Data indicate that adaptations of individually-housed pigs under cold exposure are more extreme when compared to group-housed animals, especially with respect to the marked increase of energy intake and physical activity. The contribution of HP_{act} to HP was on average 17 and 23% at 22 and 12 °C, respectively. Over this temperature range, the apparent efficiency of ME utilisation increased from 0.65 to 0.81. Prediction equations obtained for group-housed pigs fitted the measured HP obtained for individually-housed pigs reasonably well, which indicates that the former can be used to model energy utilisation irrespective of housing conditions (individual vs. group) when differences in feed intake under cold exposure are considered.

growing pig / ambient temperature / heat production / modelling

Résumé — Effets du froid sur la production de chaleur et le bilan énergétique du porc en croissance en loge individuelle et nourri à volonté ; comparaison avec le porc élevé en groupe. Six porcs males castrés sont utilisés afin d'étudier les effets de la température ambiante (T, entre

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12 et 22 °C) et du poids vif (PV, entre 37 et 95 kg) sur la quantité d'énergie métabolisable ingérée (EM, kJ·j^{-1}) et la production de chaleur. Les animaux sont alimentés à volonté et exposés à des T variant de façon cyclique par pallier de 3 jours au moins par T. Ils sont logés individuellement en chambre respiratoire. Les concentrations en O_2 et CO_2, la consommation d'aliment et l'intensité de l'activité physique sont mesurées en continu et utilisées afin de calculer la production de chaleur totale (HP), celle liée à l'activité physique (HP_{act}) et l'effet thermique à court terme de l'aliment (TEF_{CT}). Des équations non-linéaires sont utilisées afin de prédire HP et ses composantes en fonction de T, PV et EM. Ces résultats sont ensuite comparés à ceux obtenus à partir d'équations établies chez des porcs logés en groupe. D'après nos données, l'exposition au froid entraîne une augmentation de l'EM et de l'activité physique beaucoup plus importante chez les animaux logés individuellement que chez ceux logés en groupe. La contribution de HP_{act} est de 17 et 23 % de HP, respectivement à 22 et 12 °C. Sur cette gamme de T, l'efficacité d'utilisation de l'EM augmente de 0,65 à 0,81. L'utilisation des équations obtenues chez les porcs en groupe permet de prédire avec précision l'utilisation de l'énergie chez les porcs logés individuellement quand la différence de consommation au froid est prise en compte.

porc en croissance / température ambiante / production de chaleur / modélisation

1. INTRODUCTION

Under thermoneutral conditions, the pig heat production (HP) can be considered as the sum of three main components: HP due to feed intake or the so-called thermic effect of feed (TEF), HP due to physical activity (HP_{act}) and the zero activity fasting heat production (FHP) [19]. When temperature decreases below the lower critical temperature, HP increases to meet the additional requirement for thermoregulation. One of the main adaptations of ad libitum fed pigs to low ambient temperature is increasing the energy intake so that the energy balance and growth performance can be maintained [1, 4, 7, 8, 10, 14, 15]. Additionally, an increased contribution of physical activity to total HP at low temperatures has been reported [16], as well as an improvement of energy efficiency [2, 5, 11, 14, 16, 21].

The combined effects of both low and high temperatures, body weight (BW) and energy level on HP were studied by Quiniou et al. [16] in group-housed pigs. From these data, equations that predict HP and its components were proposed. However, under cold exposure, the behaviour of single-housed pigs differs from group-housed pigs since the latter can huddle to attenuate energy losses [9]. The aim of the present experiment was to quantify the effect of low temperatures and BW on HP and its components in single-housed pigs and to compare the results with those obtained in a study conducted on group-housed pigs that were submitted to similar temperature conditions [16].

2. MATERIALS AND METHODS

2.1. Experimental design

Six Piétrain × Large White barrows were used to investigate the effect of cold exposure on components of HP under individual housing conditions. The HP of the animals was measured in a respiration chamber using indirect calorimetry. During the 7-d adaptation period to the chamber and the diet, the temperature was fixed at 22 °C. Thereafter, the temperature was gradually changed in a cyclic way over 28 days (Fig. 1) from 22 to 12 °C and from 12 to 22 °C with three or four consecutive days at each of the following temperatures: 22, 19, 16, 14 and 12 °C. This cyclic manner with a small change in T between successive levels allows the pig to adapt to its new environment after the first day of exposure [18, 20]

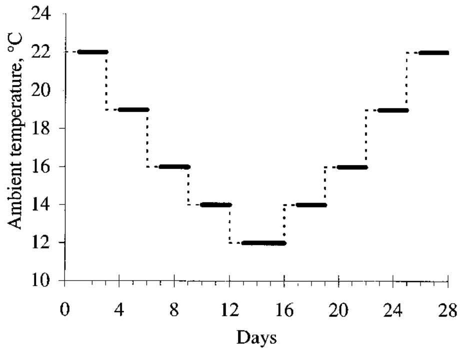

Figure 1. Cyclic variation of temperature over the 28 d experimental cycle.
------- : adaptation period, ——— : measurement period.

Table I. Composition of the experimental diet.

Composition, g·kg^{-1}	
Wheat	220.0
Barley	220.0
Corn	220.0
Soybean meal 48	244.5
Wheat bran	40.0
Oil	10.0
HCl-Lysine	0.5
Dicalcium phosphate[2]	20.0
Calcium carbonate	10.0
Salt	5.0
Vitamins and trace minerals mixture	10.0
Dry matter (DM), g·kg^{-1}	877
Chemical composition, g·kg^{-1} DM	
Ash	68
Crude protein	208
Crude fat	35
Crude fibre	42
Starch	490
Lysine[1]	11.6
Gross energy, MJ·kg^{-1} DM	18.4
Digestible energy, MJ·kg^{-1} DM[2]	15.7
Metabolisable energy, MJ·kg^{-1} DM[2]	15.1
Net energy, MJ·kg^{-1} DM[3]	11.2

[1] Estimated from amino acid composition of raw materials; methionine + cystine, threonine and tryptophan contents relative to lysine (100) were 62, 70 and 22, respectively.
[2] Measured value.
[3] Estimated from digestible energy content (DE, MJ·kg^{-1} DM) and chemical components (g·kg^{-1} DM) according to the relationship proposed by Noblet et al. [12].

and provides numerous and variable values within a reasonable trial duration. It was assumed from literature data that 22 °C was at or above the lower critical temperature of individually housed growing pigs [1]. In order to obtain a large range in BW of pigs and a subsequent high variability for regression analyses, the initial BW varied between 37 and 68 kg. Pigs were offered a pelleted cereal-based diet ad libitum (Tab. I) and had free access to water.

2.2. Measurements

The pigs were weighed at the beginning and the end of the cycle and intermediately at the beginning of the 16 °C level. During the whole experiment, the animals were housed in a metabolic crate and faeces and urine were collected daily and cumulated over the total experiment for the determination of the nutritional characteristics of the diet. The crate was mounted on four force sensors (type 9104A; Kistler, Winterthur, Switzerland) and placed in a respiration chamber (12 m^3). The response of the force sensors was supposed to be proportional to the physical activity of the animal. The crate was equipped with a feed dispenser, which consisted of a trough and a hopper. The weight of the dispenser was recorded continuously through a load cell. The hopper was filled daily with enough feed to meet the appetite of the pig. Every 10 s, mean values of O_2 and CO_2 concentrations were recorded as described by van Milgen et al. [19]. Over the same time span, the signal of the force sensors and the amount of feed consumed were recorded simultaneously in order to relate variations in O_2 and CO_2 concentration to physical activity and eating events in the chamber.

2.3. Calculations and statistical analyses

Energy values of the experimental diet were assessed according to routine techniques [12]. The day of temperature change was considered as a transition day for the adaptation to the new environment and was not considered in the calculations. Data obtained over the two or three remaining days were then pooled and used for further calculations. Mean BW at each temperature was interpolated from the BW measured regularly over the cycle. Components of HP were assessed for each day of measurements using the model proposed by van Milgen et al. [19]: it allows the calculation of HP_{act} and the contribution of short-term TEF (TEF_{st}). The latter is supposed to include HP due to ingestion, mastication, digestion and absorption. Activity-free HP (HP_0) was calculated as the difference between HP and HP_{act} and energy retention was calculated as the difference between ME intake and HP. Considering the differences in initial BW, data were expressed relative to $BW^{0.60}$ [13] and were submitted to an analysis of variance (proc GLM, [17]) with temperature and animal as the main effects; for this purpose, the data obtained for each animal at each temperature in the decreasing phase and the increasing phases were averaged.

Prediction equations were calculated according to the approach described by Quiniou et al. [16] using proc NLIN [17]. The results were compared to equations obtained for group-housed growing pigs [16]:

Equation 1: HP_{act} =

$$BW^{0.60} (598 - 37.2\ T + 0.85\ T^2) \quad (RSD = 354)$$

Equation 2: HP_0 =

$$BW^{0.60} (1482 - 39.7\ T) + 0.013\ T \cdot (ME - HP_{act}) \quad (RSD = 594)$$

Equation 3: HP =

$$BW^{0.60} (2317 - 108.1\ T + 1.64\ T^2) + 0.013\ T \cdot ME \quad (RSD = 668)$$

with HP and ME as $kJ \cdot d^{-1}$, BW as kg and T as °C (with T < 24 °C).

According to these equations, HP depends on two different components, which are thought to reflect maintenance (a function of BW) and the thermic effect of feed (TEF; a function of ME intake); 1 minus TEF is equivalent to the efficiency of ME for energy gain. In addition, both components are affected by temperature. The correlations between measured values for individual animals and predicted values obtained from the equations for group-housed animals were evaluated through proc CORR [17]. The effects of the temperature and animal on the difference between predicted and measured values were tested by analysis of variance (proc GLM).

3. RESULTS

During the whole experiment, BW ranged between 37 and 95 kg (Tab. II) and the average daily gain was 946 $g \cdot d^{-1}$. The mean BW was similar for the different temperatures. As anticipated, the Pearson correlations were low between temperature and BW (r = 0.12). However, there were significant correlations between BW and ME intake (r = 0.50) and between T and ME intake (r = –0.27).

Minimal values for ME intake, total HP and its components were obtained at 22 °C (Tab. III). A decrease of temperature induced significant differences in ME intake and its metabolic utilisation. Indeed, between 22 and 12 °C, ME intake and total HP increased linearly by 39 and 30 $kJ \cdot (kg\ BW)^{-0.60} \cdot d^{-1} \cdot °C^{-1}$, respectively. This resulted in numerically higher energy retention under the lowest temperatures (averaging 1.30 $MJ \cdot (kg\ BW)^{-0.60} \cdot d^{-1}$ at 12, 14 and 16 °C vs. 1.21 $MJ \cdot (kg\ BW)^{-0.60} \cdot d^{-1}$ at 19 and 22 °C). The contribution of HP_{act} to total HP was markedly higher at 12 than at 22 °C (23 vs. 17%). The increase of HP_0 with a decrease of temperature was not significant (P = 0.22) even though the highest (1.38 $MJ \cdot (kg\ BW)^{-0.60} \cdot d^{-1}$) and the lowest (1.23 $MJ \cdot (kg\ BW)^{-0.60} \cdot d^{-1}$) values were obtained at 12–14 and 22 °C, respectively. TEF_{st}, expressed as a percentage of ME intake, remained rather constant (8%) over

Table II. Range of values obtained and their overall mean.

	Minimum	Maximum	Overall mean
Temperature, °C	12	22	
Body weight, kg	37.2	95.2	62.3
ME intake, $MJ\cdot d^{-1}$	25.15	46.01	34.35
Total heat production (HP), $MJ\cdot d^{-1}$	13.91	26.01	19.18
Energy retained, $MJ\cdot d^{-1}$	10.25	20.11	15.15
Respiratory quotient	1.02	1.22	1.12
Components of heat production			
Short-term effect of feed, $MJ\cdot d^{-1}$	1.01	5.97	3.13
Physical activity (HP_{act})			
$MJ\cdot d^{-1}$	1.53	6.69	3.49
% of HP	8.7	28.8	18.3
Resting heat production ($HP - HP_{act}$), $MJ\cdot d^{-1}$	10.00	22.32	15.75

the temperature range considered. The respiratory quotient was not affected by temperature (Tab. III).

The prediction equations (Tab. IV) were established from the present data using the structure of equations (2) and (3) given above. For HP_0 (Eq. (4), Tab. IV), the coefficient of variation was 7.8% and it was smaller for HP (5.6%, Eq. (5), Tab. IV). The residuals, expressed relative to metabolic BW, were significantly affected by the animal but not by the temperature. In both equations, TEF decreased with decreasing temperature. Concomitantly, the efficiency of energy utilisation (k_g) calculated from equation (5) increased under cold exposure from 0.65 (22 °C) to 0.81 (12 °C). Lower k_g values were obtained using equation (4) (0.58 and 0.77, respectively).

4. DISCUSSION

From the data obtained between 12 and 29 °C in group-housed pigs, Quiniou et al. [16] found that the lower critical temperature was 23 to 24 °C. In individually-housed pigs, it can be assumed that the lower critical temperature was equal or greater than these values. If this was the case, the pigs were always exposed to cold temperatures in the current experimental conditions. The observed increase of ME intake and total HP starting at temperatures below 22 °C is consistent with this idea. Both sets of data also indicate that the lower critical temperature of growing pigs in our experimental conditions is a few degrees higher than what was proposed for instance by Close and Mount [1]. Differences in body composition (the present pigs were leaner) may partly explain these discrepancies.

Between 22 and 12 °C, the increase of voluntary feed intake was considerably greater in the present experiment than in group-housed pigs studied by Quiniou et al. [15, 16]; for 60 kg pigs, these values corresponded on average to 39 and 19 $g\cdot d^{-1}\cdot °C^{-1}$, respectively. Despite the small number of pigs in the present experiment, such a difference is consistent with the fact that, under cold exposure, individually-housed pigs cannot limit energy losses through huddling. Subsequently, cold stress is more severe and pigs are assumed to produce a greater amount of additional heat to maintain body temperature. These conclusions are quite consistent with the review of Holmes and Close [5].

Table III. Effect of ambient temperature on the utilisation of metabolisable energy (ME) intake in individually housed pigs.

	Temperature, °C					Statistics[1]		
	12	14	16	19	22	RSD	T	Animal
N observations[2]	6	12	12	11	9			
Mean body weight, kg	62.0	61.9	61.7	63.6	64.4	8.2		***
Mean metabolic body weight, $(kg\ BW)^{0.60}$	11.9	11.9	11.8	12.0	12.0	1.0		***
ME intake, $MJ \cdot d^{-1} \cdot (kg\ BW)^{-0.60}$	3.09	3.01	2.91	2.75	2.71	0.32		***
Heat production								
Total (HP), $MJ \cdot d^{-1} \cdot (kg\ BW)^{-0.60}$	1.79a	1.70b	1.61 c	1.53d	1.50d	0.08	***	***
Physical activity								
$MJ \cdot d^{-1} \cdot (kg\ BW)^{-0.60}$	0.41a	0.34b	0.28c	0.25c	0.26c	0.05	***	***
% of HP	23a	20a	18b	17b	17b	3	***	***
Resting (HP_0), $MJ \cdot d^{-1} \cdot (kg\ BW)^{-0.60}$	1.38	1.36	1.32	1.28	1.23	0.10		***
Short-term effect of feed, % ME[3]	8.6	7.7	8.0	8.2	7.1	1.3		***
Energy retained, $MJ \cdot d^{-1} \cdot (kg\ BW)^{-0.60}$	1.30	1.31	1.30	1.21	1.21	0.27		**
Respiratory quotient	1.12	1.12	1.13	1.12	1.14	0.04		**

[1] From an analysis of variance with temperature (T) and animal as the main effects.
[2] At each temperature, mean of values obtained over the two (three at 12 °C) days of measurements both during the increasing and the decreasing phases.
[3] Number of observations was 5, 9, 9, 8 and 8, at 12, 14, 16, 19 and 22 °C, respectively.

Table IV. Prediction equations[1] for activity-free heat production (HP_0) and total heat production (HP) in individually-housed growing pigs according to ambient temperature (T, °C), body weight (BW, kg) and daily metabolisable energy intake (ME, kJ·d^{-1}) (mean parameters with their asymptotic error).

No.	Equation	RSD[2]	CV[2]
4	$HP_0 = BW^{0.60}$ (1346 (± 76) – 51.6 (± 6.3) T) + 0.020 (± 0.002) T·ME_0	1217	7.8
5	HP = $BW^{0.60}$ (2762 (± 384) – 167.8 (± 46.0) T + 3.05 (± 1.32) T^2) + 0.016 (± 0.002) T·ME	1075	5.6

[1] Model: Y = $BW^{0.60}$ ($\alpha + \beta \cdot T + \chi \cdot T^2$) + $\delta \cdot X \cdot T$ where α, β, χ and δ are parameters and X corresponds to ME or ME_0 (kJ·d^{-1}); ME_0 = ME – heat production due to physical activity.
[2] RSD: residual standard deviation (kJ·d^{-1}), CV: coefficient of variation (%).

At 22 °C, HP_{act} represented 17% of total HP. Using the same measurement equipment, a similar value was obtained in 20 to 30 kg [3] and 30 to 60 kg [16] group-housed pigs (18 and 14%, respectively). This indicates that even when the animal has a limited possibility for locomotion (for example, in a metabolic crate), physical activity represents a considerable fraction of total HP. According to the prediction equation of HP_{act} (Eq. (1), [16]), the lowest level of HP_{act} occurs at about 22 °C and increases at lower temperatures (12–14 °C). The same trend was observed in the current study (Tab. III). However, equation (1) underestimates the observed HP_{act} in individually-housed pigs by approximately 20%; the highest discrepancy (30%) between the measured and predicted value is observed at 12 and 14 °C (Fig. 2). Around 19 and 22 °C, the level of physical activity was slightly higher in individually than in group-housed pigs (17 vs. 13% of HP [16], respectively), which may be attributed to the less comfortable housing conditions. At lower temperature, the increased activity may be due to both a longer duration of standing (partly related to the increased level of feeding activity) and increased moving and shivering activities when compared to group-housed pigs. Within the thermoneutral zone or under hot exposure, such a difference would not be expected since group-housed animals will behave like individual ones and avoid contact with other animals [9].

In single-housed pigs, TEF_{st} was higher than in group-housed pigs (8 vs. 5% of ME [16]) but similar to the value reported for single-housed pigs by Le Bellego et al. [6]. Experimental conditions per se influence the way the components of HP are identified by the model proposed by van Milgen et al. [19]. When only one pig is studied, different meals are clearly separated by rather long intervals, so that TEF_{st} induced by the meal can be easily detected. In

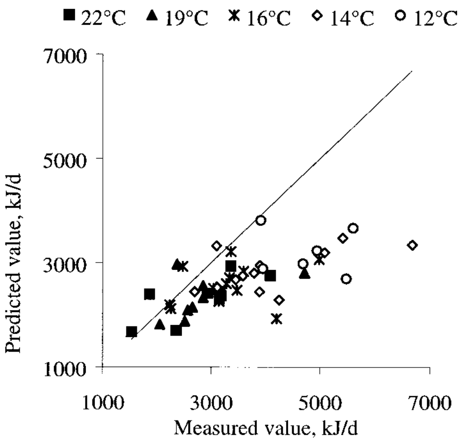

Figure 2. Comparison of measured heat production due to physical activity (HP_{act}) in individually-housed pigs and predicted HP_{act} from equation (1) [16] for group-housed pigs.

group-housed pigs, different animals eat successive meals, which results in overlapping of the post-prandial TEF_{st} of different animals. Consequently, this may result in an over-estimation of the basal HP, that is HP not related to temporary increased physical activity or feed intake. Nevertheless, according to the results obtained in the present study and in the experiment of Quiniou et al. [16], the TEF_{st} represented a constant percentage of ME intake at all T, which suggests that TEF_{st} is to be considered more as an (obligatory) energy expenditure related to the diet, than as a variable component that can be modified according to energetic needs. In contrast, the feed component given in equations (4) and (5), which can be considered as the total TEF, varied linearly with temperature. From equation (4), it can be calculated that k_g increases from 0.56 at 22 °C to 0.76 at 12 °C. The corresponding values calculated from equation (5) were 0.65 and 0.81. An improvement of k_g under cold exposure has been reported by several authors [2, 5, 11, 14, 21] and indicates that TEF is partly used to meet energy requirements for thermoregulation. In addition, the present study and our previous results in group-housed growing pigs [16] indicate that the long term component of TEF is the most concerned in the variation of TEF or k_g with ambient temperature.

Using equation (3) with the present data set provides accurate predicted HP and HP_0 as illustrated by Figure 3a. On average, predicted HP and HP_0 represented 99 and 104% of corresponding measured values (Tab. II), respectively. No significant effect of temperature on the residuals between measured and predicted values was found ($P = 0.23$), whereas the animal effect was significant. The Pearson correlation between both groups of values was $r = 0.93$ for total HP. Despite the above-mentioned discrepancy on HP_{act}, it appears that equation (2) also reasonably fitted the measured HP_0 as illustrated by Figure 3b; however, the Pearson correlation between measured and predicted HP_0 was slightly lower ($r = 0.87$) and prediction was poorer than for HP. The parameters for TEF in equation (5) was higher than the corresponding value in the equation obtained in group-housed pigs (0.016 vs. 0.013 in Eq. (4)). However, this was counterbalanced by a lower contribution of the maintenance component. For HP_0, the difference between equations (4) and (2) was even greater. The range of data obtained in the present study was narrower than that in the previous one on group-housed pigs [16] which may explain some of the difference in the adjustment of the parameters between models and a higher (× 2) coefficient of variation for equations (4) and (5) than for equations (2) and (3).

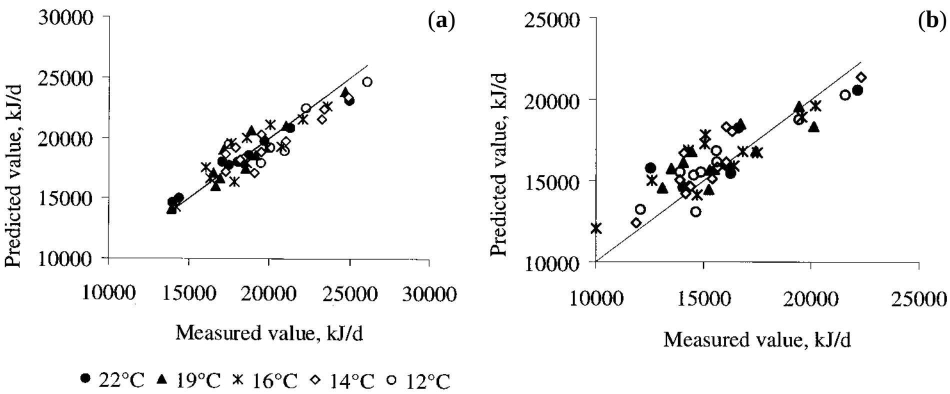

Figure 3. Comparison of measured total heat production (**a**) and activity-free heat production (**b**) in individually-housed pigs and predicted values from equations obtained for group-housed animals [16].

In conclusion, under cold exposure, the adaptation of individually-housed pigs is more extreme as compared to group-housed animals, especially with regard to the increased energy intake and physical activity. Such differences result mainly from the absence of possibilities for huddling behaviour. Equations that predict HP and resting HP (HP_0) obtained from group-housed pigs can be used for individually housed pigs with reasonable precision when differences in ME intake are considered.

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