

The effects of environmental temperature on the growth and metabolism of pigs given different amounts of food

2.* Energy metabolism

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1. Eighteen pigs were studied at environmental temperatures of 5°, 13° and 23°, with three levels of feeding at each.
2. Energy losses in the faeces and urine were measured throughout as the pigs grew from 20 to 90 kg; respiratory exchange was measured intermittently, for an average of ten 24 h periods for each pig.
3. From regressions of heat production, energy retention and water-vapour production on body-weight, estimates of these quantities were made at weights of 25, 35, 45, 55, 65, 75 and 85 kg.
4. Digestibility of energy was unaffected by daily food intake, but increased by 0.12 percentage units per degree rise of temperature. The mean urine energy loss was 30.5 kJ/MJ digestible energy. It was not significantly affected by temperature. Methane production was not affected by temperature but fell by 0.086 ± 0.027 kJ/MJ apparent metabolizable energy (ME) with each $g/kg^{0.73}$ increase in daily food intake.
5. Heat production increased with body-weight and daily food intake and with falling temperature. There was a significant interaction between the last two factors. These effects were summarized in a general equation.
6. Total heat production during the experiment fell by 13.6 ± 2.2 MJ (3.24 ± 0.52 Mcal) per $g/kg^{0.73}$ increase in daily food intake. This corresponded to a reduction of 1.4 d in the time taken to grow from 20 to 90 kg.
7. Total energy retention throughout the experiment, estimated from energy balance results, was in close agreement with that estimated by comparative slaughter.
8. The net availability of ME was 72% at 23°: at lower temperatures it increased with body-weight to values in excess of 80%.
9. Estimates of the energy maintenance requirement at 23° were in good agreement with others in the literature. In terms of body-weight, W , measured in kg, the mean values (kJ/d) were $1761 W^{0.57}$ at 5°, $1473 W^{0.57}$ at 13° and $891 W^{0.57}$ at 23°; in units of kcal/d the corresponding coefficients of $W^{0.57}$ were 421, 352 and 213.

Of the large farm animals kept in temperate and cold climates, the pig is particularly sensitive to cold. Early studies of the effect of low temperature on the pig were concerned with the fasting animal (Tangl, 1912; Capstick & Wood, 1922; Deighton, 1929). Of more importance in animal nutrition is the effect of cold on the pig eating a normal diet, and recent work has been concerned with this situation (Holmes & Mount, 1967; Close, Mount & Start, 1971; Verstegen, 1971). Of great importance also is the interaction between environmental temperature and the animal's daily food intake. The work of Graham, Wainman, Blaxter & Armstrong (1959) with sheep showed that the animal's response to its climatic environment can be modified by its current food intake. Only recently have similar experiments been begun with pigs (Close *et al.* 1971).

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Table 1. *Design of the experiment, in terms of the three environmental temperatures and planned food intakes. The food intakes actually achieved are given in parentheses*

| Feeding level | Daily food intake (g.kg ^{-0.73} .d ⁻¹) | | |
|---------------|---|-------------|-------------|
| | At 5° | At 13° | At 23° |
| High | 160 (156.2) | 140 (135.8) | 120 (116.3) |
| Medium | 140 (137.6) | 120 (117.7) | 100 (95.8) |
| Low | 120 (117.0) | 100 (98.3) | 80 (78.7) |

In the experiment described in the first paper of this series (Fuller & Boyne, 1971), the interaction between environmental temperature and food intake on the growth and nitrogen metabolism of the pig was investigated. In two replicates of that experiment measurements of energy exchange were made, and these are the subject of this paper.

EXPERIMENTAL

Measurements made. The measurements presented here were made on eighteen pigs in the third and fourth replicates of the experiment described by Fuller & Boyne (1971), where details of the animals, diets, environmental conditions and procedures are given. The design of the experiment, which included three temperatures with three levels of feeding at each, is shown in Table 1. Body-weight, W , was measured in kg and metabolic live weight, M , was taken as $W^{0.73}$; to obtain the units of food intake used in this experiment daily food intake, measured in g, was divided by M . This convention has been adopted to minimize use of the clumsy expression 'food intake g/kg^{0.73}', throughout the paper—subsequently in the text this expression is referred to as units.

The experiment was divided into seven periods, each spanning a weight interval of 10 kg. In each period the losses of energy in faeces and in urine were measured by complete collections. The measurements of respiratory exchange (oxygen consumption, carbon dioxide, methane and water-vapour production) were made over periods of 24 h duration at intervals timed to cover as evenly as possible the weight range 20–90 kg. The total number of measurements was 182, an average of approximately ten for each animal.

At the end of the experiment, when the pigs weighed approximately 90 kg, they were slaughtered and homogenized for chemical analysis. The total energy content in joules of each ingesta-free carcass was estimated from its N and fat contents, using the factors 148.0 and 39.6 respectively (Franke & Weniger, 1958).

Measurement of respiratory exchange. One of the closed-circuit chambers described by Wainman & Blaxter (1969) was used to measure the respiratory exchange of the pigs. The chamber was equipped with aspirated wet and dry thermocouples with which temperature and humidity were monitored.

The animal's environment and daily routine in the respiration chamber and in the climatic room in which it was normally kept were made as similar as possible. The pigs were kept at all times in the same metabolism cages, which were designed to fit into the respiration chambers. The temperature in the respiration chamber was ad-

justed before the pig entered to that in the climatic room from which it came. The respiration chamber was equipped with two food troughs with lids so that the animal could be fed at the normal times (08.00 and 16.00 hours) when in the chamber.

Correction for basal evaporation in the chamber. The water-vapour collected in the absorption vessels of the apparatus arose in part from the insensible water loss of the pig, and in part from the wet food, faeces, urine and the wet thermocouple wick. The amount of water arising from these extraneous sources was estimated in a series of preliminary measurements in which the conditions of an experiment were simulated as nearly as possible. This was done by releasing predetermined quantities of water at 37° at intervals on to the urine collecting funnel. At the same time fresh faeces were left on the faeces tray and wet food was left in the food troughs. From a total of twenty-one 24 h measurements, made at different temperatures, the amount of water-vapour collected was found to be independent of the amount of water released. There was no evidence that the water loss varied with temperature, or with the saturation deficit of the air, although the tests were too limited to establish this firmly. The results were therefore taken together and a mean correction of -69 g/d was applied to all measurements made during the experiment.

Bomb calorimetry. The heats of combustion of food, faeces and urine samples were determined in an adiabatic bomb calorimeter (Gallenkamp Ltd, London). Samples of each batch of food were taken at frequent intervals and a composite sample of each batch was analysed. Faeces samples were freeze-dried, and urine was prepared for bomb calorimetry by the modification described by Fuller & Cadenhead (1969) of Nijkamp's (1965) method.

Heat production. The formula of Brouwer (1965), converted to joules, was used to calculate heat production from gaseous exchange and urinary N excretion.

RESULTS

Digestibility of energy. The digestibility of energy did not change significantly with increasing body-weight. An average value for digestibility throughout the experiment was therefore calculated for each pig, and the effects of temperature and food intake on these values were examined. There was no significant effect of increasing daily food intake, but there was a significant increase ($P < 0.05$) in the digestibility of energy with increasing temperature. The mean values are given in Table 2.

Urinary energy loss. The mean loss of energy in urine was 30.5 kJ/MJ digestible energy. There was no significant effect of increasing daily food intake on this loss, and although the loss tended to be greater at 5° than at higher temperatures, this effect was not significant.

Methane production. The calorific value of the methane produced during each measurement of respiratory exchange was expressed as a fraction of the pig's intake of apparent metabolizable energy (ME) (i.e. digestible energy - urine energy) during that day. There was no evidence of any effect of temperature on this quantity, but there was a highly significant ($P < 0.01$) linear regression on daily food intake. At the mean daily food intake of 117 units the mean energy loss as methane was 8.3kJ/MJ

Table 2. *Apparent digestibility of energy by pigs at three environmental temperatures and their urinary energy excretion expressed per MJ* of apparent digestible energy (DE). The resulting values of apparent metabolizable energy (ME) (i.e. not corrected for methane production), per g food (86% dry matter), are also given*

| | At 5° | At 13° | At 23° | SE of difference |
|---|-------|--------|--------|------------------|
| Food intake (g.kg ^{-0.73} .d ⁻¹) | 96.3 | 116.7 | 136.9 | — |
| Apparent digestibility of energy (%) | 80.9 | 81.2 | 83.0 | 0.67 |
| Urine energy loss (kJ/MJ apparent DE) | 32.6 | 29.6 | 29.5 | 3.82 |
| ME (kJ/g food) | 12.43 | 12.43 | 12.68 | 0.146 |

* 1 J = 0.239 cal.

Table 3. *Estimates of the heat production (MJ*|d) of pigs given different amounts of food at three environmental temperatures, when at different body-weights. The values are derived from equations relating intermittent measurements of heat production to body-weight, and each is the mean of two animals*

| Food intake (g.kg ^{-0.73} .d ⁻¹)... | At 5° | | | At 13° | | | At 23° | | | SE of mean (8 df) |
|---|-------|------|------|--------|------|------|--------|------|------|----------------------|
| | 117 | 138 | 156 | 98 | 118 | 136 | 79 | 96 | 116 | |
| Body-weight (kg) | | | | | | | | | | |
| 25 | 12.2 | 14.0 | 13.9 | 10.2 | 11.3 | 11.4 | 7.1 | 7.3 | 8.6 | 0.40 |
| 35 | 14.9 | 16.4 | 16.6 | 12.3 | 13.4 | 13.7 | 8.8 | 9.2 | 10.6 | 0.24 |
| 45 | 17.2 | 18.5 | 19.0 | 14.3 | 15.3 | 15.8 | 10.2 | 11.0 | 12.4 | 0.16 |
| 55 | 19.4 | 20.3 | 21.0 | 16.1 | 17.0 | 17.7 | 11.5 | 12.6 | 14.0 | 0.11 |
| 65 | 21.3 | 22.0 | 23.0 | 17.7 | 18.5 | 19.4 | 12.8 | 14.1 | 15.6 | 0.15 |
| 75 | 23.2 | 23.5 | 24.8 | 19.2 | 20.0 | 21.0 | 13.9 | 15.6 | 17.0 | 0.24 |
| 85 | 24.9 | 24.9 | 26.4 | 20.7 | 21.3 | 22.5 | 15.1 | 17.1 | 18.4 | 0.31 |

* 1 J = 0.239 cal.

apparent ME. With each unit increase in daily food intake, this value fell by 0.086 ± 0.027 kJ/MJ.

ME per g food. Although there were no significant differences in ME between temperatures, the mean values reflected those for apparent digestibility of energy. The mean values are given in Table 2.

Heat production. From individual measurements of heat production and from the animal's weight at the time of measurement, the regression of log heat production on log body-weight was calculated for each pig. From these equations, estimates were made of heat production at each weight in the series 25, 35, 45, 55, 65, 75 and 85 kg. The means for the two replicates are given in Table 3.

In an over-all covariance analysis of the original measurements of log heat production and log body-weight it was found that the regression coefficients did not differ significantly with food intake, temperature or replicate. The pooled regression coefficient was therefore calculated and found to be 0.57 ± 0.019 , indicating the power of body-weight to which heat production was proportional. Using this pooled coefficient, the intercepts in the regressions of log heat production on log body-weight were found to vary significantly with temperature ($P < 0.001$) and with daily food

Table 4. Estimates of the heat production (MJ*/d) of pigs of 30, 55 and 80 kg, and of their total heat production (MJ) during their growth from 20 to 90 kg at three environmental temperatures. The values are adjusted to a common daily food intake of 117 g/kg^{0.73} by means of the regressions given below. Each estimate is the mean of six animals

| Body-weight (kg) | At 5° | At 13° | At 23° | Approximate SE of difference between: | |
|---------------------|-------|--------|--------|--|-------------------------|
| | | | | Adjacent temperatures | Extreme temperatures |
| 30 | 14.6 | 12.3 | 9.5 | 0.33 | 0.42 |
| 55 | 19.1 | 16.9 | 13.7 | 0.17 | 0.22 |
| 80 | 24.8 | 21.0 | 18.5 | 0.42 | 0.51 |
| Total: 20-90 | 2506 | 1728 | 1088 | 129.7 | 166.5 |

* 1 J = 0.239 cal.

intake ($P < 0.001$); there was also a significant interaction between these two factors. These effects are summarized in the following equation:

$$H = \exp [7.582 - 0.040T + 0.008I + 0.00018IT] W^{0.574},$$

where H is heat production (kJ/d), W is body-weight (kg), T is temperature (°C) and I is daily food intake (g/kg^{0.73}). The standard errors of the coefficients of T , I , and IT were 0.0031, 0.00042 and 0.00003, respectively. The residual standard deviation in $\log_e H$ was 0.045, corresponding to an error of about 5% in H .

Effects of temperature and food intake on heat production at different body-weights. Estimates of heat production at 30, 55 and 80 kg, made from the original regression equations, were analysed. Heat production increased with each unit increase of daily food intake by 36.4 ± 7.5 kJ/d at 30 kg, and at 55 kg by 54.4 ± 3.8 kJ/d. These regressions did not change significantly with temperature. At 80 kg the regressions did vary significantly with temperature. The increase in heat production associated with unit increase in daily food intake was 15.9 ± 31.0 kJ/d at 5°, 46.4 ± 14.6 at 13° and 96.7 ± 24.7 at 23°. In Table 4 are given the values of heat production at these weights adjusted to the mean food intake by the appropriate regressions.

Total heat production during the experiment. From the individual measurements of heat production, an empirical regression of heat production on time was calculated for each animal. Each equation was then integrated with respect to time between limits corresponding to weights of 20 and 90 kg, to estimate the animal's total heat production throughout the experiment. Analysis of these values showed that total heat production decreased by 13.6 ± 2.2 MJ with each unit increase in daily food intake. The regression coefficient did not vary significantly with temperature. This decrease in total heat production was related to an average decrease of 1.39 d in the time taken by the pigs to grow from 20 to 90 kg. That is, for each day by which that time was reduced, total energy expenditure decreased by 9.75 MJ. There were significant differences between temperatures in the unadjusted values of heat production, and these differences were increased when the values were adjusted to the common food intake. These results are given in Table 4.

Table 5. *Estimates of the daily energy retention (MJ*) of pigs given different amounts of food at three environmental temperatures, when at different body-weights. Each estimate is the mean of two animals*

| Food intake (g/kg ^{0.75}) ... | At 5° | | | At 13° | | | At 23° | | | SE of mean (8 df) |
|--|-------|------|------|--------|------|------|--------|------|------|-------------------------|
| | 117 | 138 | 156 | 98 | 118 | 136 | 79 | 96 | 116 | |
| Body-weight (kg) | | | | | | | | | | |
| 25 | 3.1 | 4.0 | 6.2 | 2.9 | 4.1 | 6.4 | 3.5 | 5.0 | 6.7 | 0.26 |
| 35 | 5.1 | 6.2 | 8.9 | 4.2 | 6.4 | 8.9 | 4.8 | 7.5 | 9.2 | 0.21 |
| 45 | 6.5 | 9.0 | 11.8 | 5.8 | 8.1 | 11.8 | 6.1 | 8.7 | 12.0 | 0.14 |
| 55 | 7.3 | 9.8 | 14.5 | 7.2 | 10.0 | 13.8 | 7.4 | 10.4 | 13.8 | 0.25 |
| 65 | 9.9 | 13.8 | 17.5 | 8.4 | 12.6 | 16.1 | 8.4 | 11.4 | 15.6 | 0.25 |
| 75 | 11.9 | 15.7 | 19.5 | 10.0 | 14.0 | 18.0 | 9.7 | 12.3 | 17.9 | 0.42 |
| 85 | 12.9 | 19.7 | 21.0 | 11.4 | 14.8 | 19.8 | 9.8 | 13.6 | 19.5 | 0.47 |

* 1 J = 0.239 cal.

Table 6. *Regression coefficients of energy retention on metabolizable energy in pigs at three environmental temperatures when at different body-weights. Values in the sets underlined do not differ significantly*

| Body-weight (kg) | At 5° | At 13° | At 23° |
|---------------------|-------------|-------------|-------------|
| 25 | 0.63 ± 0.12 | 0.75 ± 0.13 | 0.67 ± 0.11 |
| 35 | 0.69 ± 0.10 | 0.77 ± 0.07 | 0.71 ± 0.08 |
| 45 | 0.76 ± 0.04 | 0.81 ± 0.03 | 0.73 ± 0.02 |
| 55 | 0.82 ± 0.03 | 0.81 ± 0.02 | 0.72 ± 0.02 |
| 65 | 0.82 ± 0.02 | 0.82 ± 0.02 | 0.73 ± 0.04 |
| 75 | 0.83 ± 0.04 | 0.82 ± 0.04 | 0.73 ± 0.04 |
| 85 | 0.88 ± 0.08 | 0.82 ± 0.05 | 0.75 ± 0.06 |

Daily energy retention. The daily energy retention at each of the weights in the series 25, 35, 45, 55, 65, 75 and 85 kg was calculated by subtracting the estimate of heat production given in Table 3 from the mean daily ME intake for the period of which the chosen weight was the mean. The values so derived are given in Table 5.

Total energy retention during the experiment. The total energy retention of each animal throughout the experiment was calculated in two separate ways; firstly, by subtracting from its total ME intake the estimate of total heat production described above; secondly, from the comparative slaughter results. The general mean value from the balance results was 1038 MJ and from the comparative slaughter results 1079 MJ; the difference of 41 MJ had a standard error of 30 MJ.

Net utilization of ME. For each temperature and at each of the chosen weights the regression of energy retention on ME in each replicate was calculated; in this way the experiment resembled a 'simultaneous difference trial' (Zausch, 1969). The mean values for the two replicates are given in Table 6. The standard errors at the smaller weights are rather large, but it is clear that at the lower temperatures the value of the coefficient rose with increasing body-weight whereas at 23° it tended to remain constant.

Maintenance requirements at different temperatures and body-weights. At each weight

Table 7. Estimates of the maintenance energy requirements (MJ*/d) of pigs at three environmental temperatures when at different body-weights. Estimates of other workers are given for comparison

| Body-weight (W) (kg) | Estimated maintenance energy requirements | | | Estimates from equations of: | | | |
|----------------------------|---|--------|--------|------------------------------|--------------------|-----------------------------|-----------|
| | At 5° | At 13° | At 23° | Kotarbinska (1969)† | Breirem (1939)‡ | Sharma <i>et al.</i> (1971) | |
| | | | | | | Lacombe§ | Yorkshire |
| 25 | 10.8 | 9.5 | 5.1 | 4.7 | 6.0 | 4.7 | 5.7 |
| 35 | 12.9 | 11.3 | 6.6 | 6.1 | 7.2 | 5.6 | 6.8 |
| 45 | 15.2 | 13.1 | 7.9 | 7.3 | 8.3 | 6.5 | 7.9 |
| 55 | 17.9 | 14.0 | 8.6 | 8.5 | 9.3 | 7.3 | 8.8 |
| 65 | 19.2 | 15.9 | 9.7 | 9.7 | 10.2 | 8.0 | 9.7 |
| 75 | 20.6 | 17.1 | 10.7 | 10.8 | 11.0 | 8.7 | 10.5 |
| 85 | 22.9 | 18.2 | 12.1 | 11.8 | 11.8 | 9.3 | 11.2 |

* 1 J = 0.239 cal. † 0.423W^{0.75}. ‡ 0.986W^{0.56}. § 0.771W^{0.56}. || 0.934W^{0.56}.

Table 8. Estimates of the water-vapour production (kg/d) of pigs given different amounts of food at three environmental temperatures when at different body-weights. Each estimate is the mean of two animals

| Food intake (g.kg ⁻¹ .d ⁻¹)... | At 5° | | | At 13° | | | At 23° | | | SE of mean (8df) |
|--|-------|------|------|--------|------|------|--------|------|------|------------------------|
| | 117 | 138 | 156 | 98 | 118 | 136 | 79 | 96 | 116 | |
| Body weight (kg) | | | | | | | | | | |
| 25 | 0.90 | 1.05 | 1.12 | 0.85 | 0.88 | 1.01 | 0.69 | 0.66 | 0.88 | 0.044 |
| 35 | 1.00 | 1.16 | 1.20 | 1.04 | 1.00 | 1.13 | 0.88 | 0.83 | 1.12 | 0.035 |
| 45 | 1.10 | 1.26 | 1.28 | 1.12 | 1.12 | 1.26 | 1.08 | 1.03 | 1.36 | 0.045 |
| 55 | 1.21 | 1.37 | 1.36 | 1.26 | 1.24 | 1.39 | 1.27 | 1.25 | 1.60 | 0.061 |
| 65 | 1.31 | 1.47 | 1.44 | 1.39 | 1.37 | 1.52 | 1.47 | 1.49 | 1.84 | 0.076 |
| 75 | 1.41 | 1.58 | 1.52 | 1.52 | 1.49 | 1.64 | 1.66 | 1.76 | 2.08 | 0.091 |
| 85 | 1.51 | 1.68 | 1.60 | 1.66 | 1.61 | 1.77 | 1.86 | 2.06 | 2.33 | 0.104 |

and temperature, regressions were calculated of daily heat production on the daily intake of ME. These were of the form $H = a + bU$, where H = daily heat production (in MJ) and U = daily intake of ME (in MJ). At energy equilibrium, H and U are both equal to M , the maintenance requirement, when the equation takes the form $M = a + bM$, whence $M = a / (1 - b)$. These estimates of M at each of the chosen weights and at each temperature are given in Table 7.

Water-vapour production. The weights of water-vapour produced by the pig, corrected for the basal evaporation from urine, faeces, food and the wet thermocouple wick were analysed in relation to body-weight. An empirical equation relating water-vapour production to body-weight was calculated for each animal, and from these equations estimates were made of the daily water-vapour production at each of the chosen weights. The mean values are given in Table 8.

At 30 kg, water-vapour production increased by 5.32 ± 1.17 g/d with each unit increase in daily food intake. At 55 kg the regression was 5.83 ± 1.77 g/d and at 80 kg 6.17 ± 2.51 g/d. None of these regressions varied with temperature. When adjusted to a common food intake, daily water-vapour production increased significantly with temperature at 55 and 80 kg but not at 30 kg. These results are given in Table 9.

Partition of heat loss at 30, 55 and 80 kg. The sensible and insensible components of

Table 9. *Estimates, each based on six animals, of the daily water-vapour production of pigs of different weights at three environmental temperatures, adjusted to a common daily food intake of 117 g/kg^{0.73}*

| Body-weight (kg) | Water-vapour production (g/d) | | | SE of difference between | |
|------------------|-------------------------------|--------|--------|--------------------------|----------------------|
| | At 5° | At 13° | At 23° | Adjacent temperatures | Extreme temperatures |
| 30 | 971 | 978 | 954 | 50 | 64 |
| 55 | 1200 | 1298 | 1495 | 75 | 97 |
| 80 | 1433 | 1618 | 2085 | 107 | 138 |

heat loss and the heat used in warming food and water to body temperature were calculated at weights of 30, 55 and 80 kg. These are shown in relation to environmental temperature in Fig. 1.

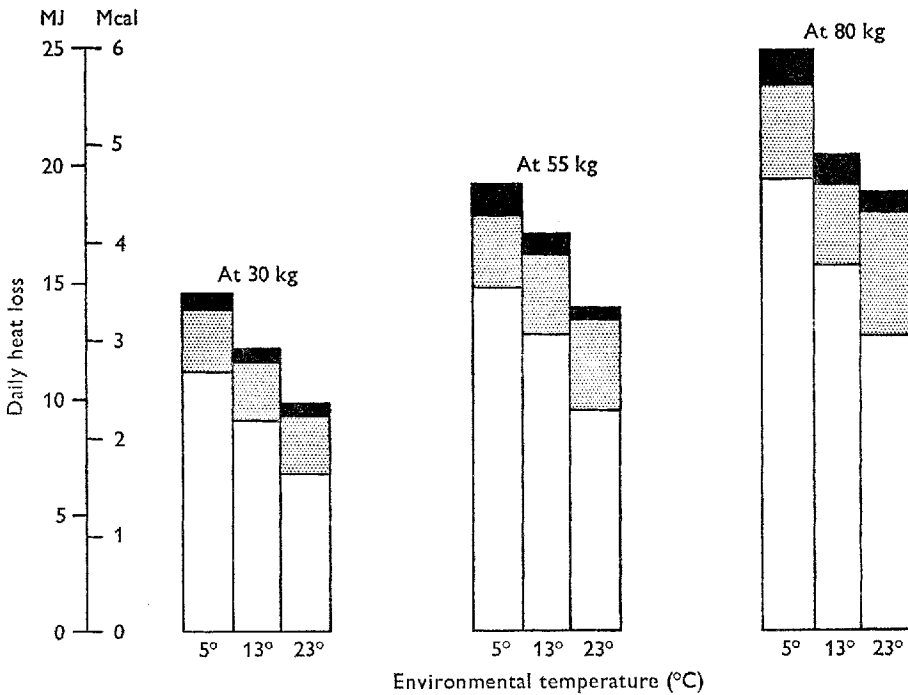


Fig. 1. Partition of heat loss by pigs weighing 30, 55 and 80 kg, at a daily food intake of 117 g/kg^{0.73}, and at environmental temperatures of 5°, 13° and 23°. Source of loss: □, sensible; ▨, insensible; ■, warming food and water.

DISCUSSION

The energy that an animal receives in its food can follow one of five courses. It can be lost in the faeces, in the urine or as methane, be emitted as heat, or be retained in the body. The results presented here show that, of these, the most seriously affected by environmental temperature is the animal's heat production. The effect of temperature on the digestibility of energy, though slight, is of some interest, as it seems to be a general finding (see Fuller & Cadenhead, 1969). The digestibility of energy fell by an average of 0.12 percentage units with each 1° fall of environmental temperature,

but was not significantly affected by the level of feeding, unlike the digestibility of N, which, at 5° and 13°, fell with increasing food intake (Fuller & Boyne, 1971).

At a constant daily food intake of 117 units, heat production increased with falling temperature by 280 kJ/d when the pigs weighed 30 kg, by 301 kJ/d when they weighed 55 kg, and by 351 kJ/d at 80 kg. As the ME of the diet was little affected by temperature, the corresponding reductions in energy retention were of virtually the same magnitude. Increasing daily food intake resulted in a higher rate of heat production at all temperatures and at all body-weights but, whereas at 30 kg and at 55 kg the regressions of heat production on food intake did not vary significantly with temperature, at 80 kg heat production increased with level of feeding much more at 23° than at 5°. Thus only at the higher body-weights did the heat increment of feeding tend to disappear in a cold environment. The same conclusion appears in the regressions of energy retention on ME (Table 6). The only comparable results with pigs seem to be those recently published by Close *et al.* (1971), who reported that the heat production of groups of pigs of 20–30 kg increased with the level of feeding at 12° and higher temperatures but not at 7°. Close (1971) obtained a similar result in an associated study of single pigs. There are, however, some problems of interpretation in these results, as in ours and as in the results which Graham *et al.* (1959) obtained with closely clipped sheep. One of the consequences of giving more food is that the animal's weight and therefore its calculated, and to a greater or lesser extent its actual, surface area increases; this in itself increases the animal's heat loss in the cold, though not in a warm environment. Expressing the results on the basis of total body-weight, or on surface area calculated therefrom, leads to two kinds of bias. Firstly, there is a systematic overestimation of the heat increment at all temperatures. This arises from the fact that at the same total body-weight pigs on a low level of feeding have a higher ingesta-free weight and therefore a higher fasting metabolism than those on a high level. Secondly, the heat increment in the cold is overestimated, relative to that in the warm, due to the effects mentioned above of the distension of the animal by food and the consequent increase in heat loss below thermal neutrality. To what extent these effects cancel out in the cold is not known. It is reasonable to conclude that some, but not all, of the heat increment of feeding can be used to replace thermoregulatory heat production in a cold environment.

From the results shown in Fig. 1, the sensitivity of the pigs to cold, as measured by the increase in their heat production with falling temperature, did not appear to change appreciably with the duration of cold exposure or the increase in body-weight which accompanied it. More precise information on this point can be obtained from a comparison of the thermal conductances of the cold-exposed pigs at different body-weights. These estimates, calculated at constant food intake, are given in Table 10. There are few comparable results with pigs in this weight range, but some estimates from other work are also given in Table 10. The estimates from the results of Bond, Kelly & Heitman (1952) resemble ours in showing little fall in conductance with increasing body-weight. The fact that they are about ten units lower than ours probably reflects the fact that they were obtained with groups of pigs. The much lower value calculated from the results of Irving, Peyton & Monson (1956) may be due to the very low

Table 10. *Estimates from the present results and from the literature of the thermal conductance of pigs between 20 and 90 kg*

| Body-wt (kg) | Temperature of measurement (°C) | Individual (I) or group (G) | Thermal conductance* (kJ.m ⁻² .d ⁻¹ .°C ⁻¹) | Critical temperature (°C) | Source |
|--------------|---------------------------------|-----------------------------|---|---------------------------|--------------------------------|
| 23 | -5 | I | 397 | 25-30 | Ingram (1964) |
| 30 | 5 | I | 397 | 19 | Present results |
| 32 | 4 | G | 335 | 16 | Bond, Kelly & Heitman (1952) |
| 46 | 9 | G | 314 | 15 | Bond, Kelly & Heitman (1952) |
| 48 | -30 | I | 176-188† | 0-5 | Irving, Peyton & Monson (1956) |
| 55 | 5 | I | 356 | 16 | Present results |
| 80 | 5 | I | 368 | 14 | Present results |

* Surface area (m²) = 0.097 $W^{0.693}$ (Brody, 1945).

† With evaporative heat loss estimated as 15 or 8% of total heat production.

temperature at which the measurements were made, for it has been shown by Mount (1963) that the thermal conductance of the pig continues to diminish with falling temperature below thermal neutrality, and may only reach its minimum value at temperatures far below the critical. The thermal conductance at very low temperatures may therefore be appreciably lower than when measured closer to thermal neutrality. It is therefore questionable whether, under normal husbandry conditions, the thermal conductance of the pig decreases significantly during its growth from 30 to 80 kg.

This does not necessarily mean that there is no change in the animal's critical temperature. Calculation of the critical temperature at 30, 55 and 80 kg has been made from the equation

$$T_c = 39.0 - \frac{H - (E_c + H_w)}{C_c},$$

where T_c is the critical temperature, H is the total heat production at thermal neutrality (taken as 23°), E_c is the evaporative heat loss in the cold, H_w is the heat used to warm food and water to body temperature, and C_c is the thermal conductance in the cold as defined above. The estimates made from this equation are also given in Table 10. Verstegen (1971) has recently used results from his experiments to estimate the critical temperature (T_{cr}) of the individual pig according to the equation

$$T_{cr} = 21 - kW,$$

where $k = 0.1$ for pigs below a body weight (W) of 50 kg and 0.15 for pigs over 50 kg. From this equation the critical temperature would be estimated as 18° for the 30 kg pig, 13° at 55 kg and 9° at 80 kg. On the other hand, Pullar (1962) measured the heat production of individual pigs during their growth from 15 to 90 kg, and found that heat production at 10° remained appreciably above that at 20° throughout the experiment, indicating that the critical temperature likewise remained above 10°, even at 90 kg. This conclusion is borne out by the fact that the optimum temperature for the growth of pigs in this weight range is also above 10° and is probably between 15 and 20° (see reviews by Mount (1968) and Fuller (1969)).

The maintenance energy requirement under thermoneutral conditions, expressed as ME, was estimated by Breirem (1939) to be

$$M \text{ (kcal)} = 196.3 W^{0.56}.$$

As this estimate was obtained under fasting conditions, Breirem suggested that it be increased by 20% to allow for activity. This gives:

$$M \text{ (kcal)} = 235.6 W^{0.56}.$$

Kotarbinska (1969), from a comprehensive series of comparative slaughter experiments, derived the equation:

$$M \text{ (kcal)} = 101 W^{0.75}.$$

Recently, Sharma, Young & Smith (1971) compared the maintenance requirements of pigs of the Lacombe and Yorkshire breeds. From the regression of heat production on ME the daily maintenance requirement of Lacombe pigs was estimated to be $771.2 W^{0.56}$ kJ and that of Yorkshire pigs $933.7 W^{0.56}$ kJ.

The maintenance energy requirements estimated by the above equations are given for comparative purposes in Table 7. Our estimates at 23° agree for the most part with those of Kotarbinska (1969) and with the results for Yorkshire pigs obtained by Sharma *et al.* (1971).

These authors found that 0.56 as the exponent of body-weight gave smaller residual variation than did 0.75. If our results at 23° are expressed per $\text{kg}^{0.56}$, the mean coefficient is 930 kJ/d, very close to the value quoted above for the Yorkshire pigs. However, in the analysis of the heat-production results given above, an over-all pooled exponent of 0.57 had been found, and this was used in an examination of the relationship between our estimates of maintenance requirements (M , in kJ) and body-weight (W , in kg), since the energy maintenance requirement can be considered as simply the heat production of the animal at a particular level of feeding (i.e. at that level of feeding which corresponds to energy equilibrium). The equations obtained were:

$$\text{at } 5^\circ M = 1761 W^{0.57};$$

$$\text{at } 13^\circ M = 1473 W^{0.57};$$

$$\text{at } 23^\circ M = 891 W^{0.57}.$$

The net utilization of ME was measured in these experiments by the regressions of energy retention at each weight and temperature. The mean value at 23° was 72%. Lund (1938) estimated the net utilization of a conventional cereal-based diet in a thermoneutral environment to be 68.3%. Breirem (1939) found a similar value, 66.2%, in growing pigs, and a higher value, 71.5%, in bigger pigs whose energy retention was largely of fat. If the equation of the Rostock workers (Nehring, 1969) is applied to our diet, a value of 71% would be predicted; direct measurement of a conventional barley-based diet at the same Institute (Nehring, Schiemann, Hoffmann & Klippel, 1960) gave a value of 73.6%. It seems therefore that, although the net utilization of the energy of any diet depends both on its composition and on the relative proportions of protein and fat synthesized from it, in practice it is unlikely

that the net utilization of the ME of the usual kind of cereal-based diets given to pigs will vary beyond the limits of 65–75%.

Finally, it is perhaps worth noting the closeness of agreement between estimates of energy retention made by comparative slaughter and balance methods. Blaxter (1967) pointed out the lack of evidence on how well these two methods agreed with one another. In this experiment the total energy retention of each animal during the experiment was estimated by the two methods; the difference between them was only $4 \pm 3\%$ of the mean total energy retention.

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