The effects of plane of nutrition and environmental temperature on the energy metabolism of the growing pig

2*. Growth rate, including protein and fat deposition

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1. Measurements of energy and nitrogen balances were made on thirty-eight individually housed pigs (initial body-weights 21–38 kg) at environmental temperatures of 10, 15, 20, 25 and 30° with four levels of feeding at each temperature. Values for energy retention (ER), protein (*P*) and fat (*F*) deposition and body weight gain (ΔW) were calculated at each temperature at metabolizable energy (ME) intakes equivalent to once (M; 440 kJ/kg$^{0.75}$ per d), twice (2M), three (3M) and four (4M) times the thermoneutral maintenance energy requirement.

2. ER at each plane of nutrition increased with temperature to maximal values between approximately 20 and 25°; ER was negative at four of the five environmental temperatures at M.

3. *P* increased significantly with increase in ME intake but was dependent on environmental temperatures only at intakes of M and 2M. The increase in *P* per unit increment in ME intake decreased from 0·16 at 10° to 0·12 at 30°. The net efficiency of protein utilization also decreased with increase in environmental temperature from 0·54 at 10° to 0·39 at 30°.

4. *F* increased significantly with increase in ME intake, but was more temperature-dependent than *P*, increasing to maximum values estimated to be between 20 and 25° at each level of intake; *F* at 30° was less than that at 25°. The increase in *F* per unit increment in ME intake decreased from 0·63 at 10° to 0·51 at 30°.

5. The optimum temperature for ΔW was dependent upon ME intake, varying from above 30° at M to less than 20° at 4M. The reduction in ΔW per 1° at 15° was also dependent upon the level of intake decreasing from 1·63 g/kg$^{0.75}$ per d at M to −0·09 at 4M.

6. For a 35 kg pig the reduction in *P*, as a result of a 1° decrease in temperature at 15° at an intake corresponding to 2·5M, was equivalent to a 4 g/d reduction in food intake; the corresponding equivalent for *F* was 28 g/d.

In the mature animal, variations in food intake produce changes in body composition that are largely confined to the fat content, whereas in the growing animal the consumption of food is associated with increments in both protein and fat formation. In recent years there has been an increase in investigation into energy retention in the growing animal, with the associated importance of such investigation for meat production, for example in the pig (Kotarbinska, 1969; Fuller & Boyne, 1971; Verstegen, Close, Start & Mount, 1973; Thorbek, 1975) and for growth and development in man (Waterlow, Hill & Spady, 1976).

Energy retention (ER) in the body takes place at a rate that is dependent on the interaction between the level of intake of metabolizable energy (ME) on the one hand, and the animal's need for maintenance and thermoregulation on the other. A considerable thermal demand by the environment leads to a reduction in the ME that the animal has available for growth when it is on a given level of food intake (Blaxter, 1977).

The present work on energy retention in the growing pig has accordingly involved several planes of nutrition and levels of environmental temperature. These experiments have allowed

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Table 1. *Mean values* ($kJ/kg^{0.75}$ *per d*) *for metabolizable energy* (ME) *intake, energy retention* (*ER*), *protein* (*P*) *and fat* (*F*) *deposition for pigs on different planes of nutrition and at different environmental temperatures*

Environmental temperature (deg)	ME intake	ER	*P*	*F*
10	571	−22	14	−36
	976	216	100	116
	1446	661	170	491
	1965	956	249	707
15	504	−100	28	−128
	893	222	92	130
	1476	713	173	540
	1591	737	178	559
20	495	26	22	4
	943	342	111	231
	1412	620	154	466
	1655	792	196	596
25	455	30	32	−2
	941	353	114	239
	1494	731	177	554
	1406	692	154	538
30	455	−29	43	−72
	928	291	103	188
	1202	437	125	312

the partition of the metabolizable fraction of the food intake into those components necessary for maintenance and thermoregulation and those components associated with growth. Some of this work has been the subject of preliminary communications (Close & Mount, 1976*a*, *b*).

MATERIALS AND METHODS

Details of the animals and their feeding, and the experimental plan, routine and methods, have already been described (Close & Mount, 1978).

The animals on which the measurements were made were castrated Large White pigs, free of enzootic pneumonia, initially within the body-weight range 21–38 kg, with final weights ranging from 24 to 50 kg. Calorimetric measurements were made in duplicate during consecutive 24-hourly periods at planes of nutrition approximating to once, twice and three times the maintenance intake, and the *ad lib.* intake, at environmental temperatures of 10, 15, 20, 25 and 30 (± 0.2)°, on a total of thirty-eight pigs. The food that was used throughout provided 13·4 (± 0.1) MJ ME and 18·2 (± 0.1) g crude protein (nitrogen $\times$ 6·25) per kg dry matter.

In addition to energy balances, the N balance was estimated for two consecutive 7 d collection periods for each pig, so providing four estimates for each combination of plane of nutrition and environmental temperature. To make the N balance as accurate as possible, losses of ammonia to the air were measured by drawing samples of inlet and exhaust air through saturator bottles containing known amounts of acid (50 ml 0·05 M-sulphuric acid). The contents of each bottle were titrated against 0·1 M-sodium hydroxide at the end of each 7 d period (Verstegen *et al.* 1973). N losses to the air varied between 1 and 3 % intake, with the higher losses occurring at the higher temperature.

ER was determined as the difference between ME intake and heat loss (H) (equation no. 1

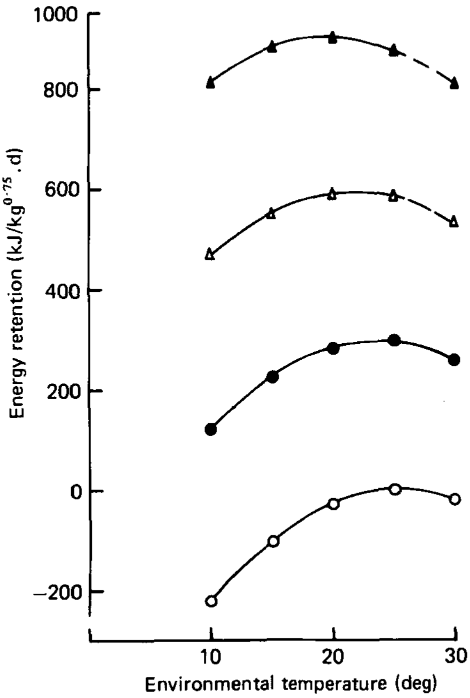

Fig. 1. Energy retention (kJ/kg$^{0.75}$ per d) of growing pigs in relation to environmental temperature (deg) and metabolizable energy (ME) intake (kJ/kg$^{0.75}$ per d). Rates of energy retention derived from the difference between ME intake and heat loss. ○—○, 440; ●—●, 880; △—△, 1320; ▲—▲, 1760 kJ ME/kg$^{0.75}$ per d. -----, Predicted values above the *ad lib.* intake of the animals.

of Close & Mount, 1978). In addition, as the N balance was determined by Kjeldahl estimates on both food and excreta, the protein deposition (*P*) was determined by assuming the N content of protein to be 160 mg/g. Taking the energy equivalent of protein as 23·8 kJ/g (Brouwer, 1965), the energy value of *P* was determined. As ER is primarily protein and fat, the energy content of fat deposition (*F*) was taken as the difference between ER and *P*. The resulting values of ER, *P* and *F* are given in Table 1. The weight of *F* was then calculated assuming fat to have an energy value of 39·8 kJ/g (Brouwer, 1965). Body-weight gain (ΔW) was calculated as g/kg$^{0.75}$ per d.

RESULTS

The results were analysed in terms of the multiple regression equation relating *P* to temperature (*T*) and ME intake with linear, quadratic and cross-product terms that gave the minimum residual variation with no redundant terms. Values for each measurement were calculated at intakes approximating to once (M; 440 kJ ME/kg$^{0.75}$ per d), twice (2M), three (3M) and four (4M) times the thermoneutral maintenance energy requirement.

ER (energy retention)

Values of ER, calculated as the difference between ME and *H*, are shown in Fig. 1. The temperature for maximum ER was dependent upon the level of feeding, decreasing from approximately 25° at M to 20° at 4M. On the lowest ME intake, ER was negative at four of the five environmental temperatures.

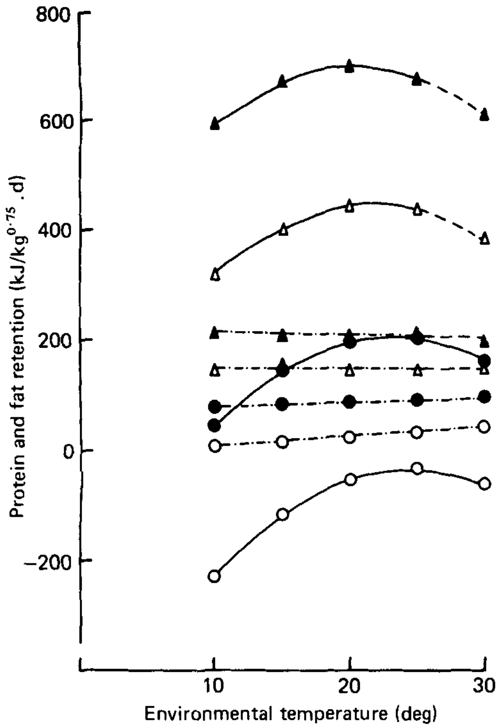

Fig. 2. Protein (kJ/kg$^{0.75}$ per d, —·—) and fat (kJ/kg$^{0.75}$ per d, ——) retention of growing pigs in relation to environmental temperature (deg) and metabolizable energy (ME) intake (kJ/kg$^{0.75}$ per d). Rates of protein retention derived from multivariate regression analysis (see p. 000). Rates of fat retention derived from the difference between energy retention and protein retention. ○—○, 440; ●—●, 880; △—△, 1320; ▲—▲, 1760 kJ ME/kg$^{0.75}$ per d. -----, Predicted values above the *ad lib.* intake of the animals.

P (*protein deposition*)

The relation of *P* to both temperature and food intake is indicated in Fig. 2. These values were derived from the equation:

$$P = -88.0 + 0.1776\,\text{ME} + 2.528\,T - 0.00184\,(\text{ME})\,(T)\,(R\ 0.958), \qquad (1)$$
$$(\pm 18.2) \quad (\pm 0.015) \quad (\pm 0.885) \quad (\pm 0.00078)$$

(residual mean square 212; 34 df), where *P* is protein retention (kJ/kg$^{0.75}$ per d), *T* is environmental temperature (deg), ME is ME intake (kJ/kg$^{0.75}$ per d).
The rates of change of *P* with ME intake and *T* are, respectively,

$$\delta P/\delta(\text{ME}) = 0.1776 - 0.00184\,T, \qquad (2)$$

$$\delta P/\delta T = 2.528 - 0.00184\,\text{ME}, \qquad (3)$$

$\delta P/\delta(\text{ME})$ was significantly positive ($P < 0.05$) at each environmental temperature (Table 2). While $\delta P/\delta T$ was significantly positive ($P < 0.05$) at M and 2M it was not significantly different from zero ($P > 0.005$) at 3M and 4M (Table 3).

Table 2. *The rate of increase in protein and fat retention (kJ/kJ* ME*) and body-weight gain (g/kJ* ME*) per unit increment in food intake at* 1100 *kJ* ME*/kg*$^{0.75}$ *per d* (2·5 *M) at several environmental temperatures*

(Values derived from equation no. 2 (p. 426). Values are mean rates with their standard errors)

Environmental temperature (deg)	Protein		Fat		Body-wt gain	
	Mean	SE	Mean	SE	Mean	SE
10	0·16	0·01	0·63	0·04	0·053	0·003
15	0·15	0·01	0·60	0·03	0·047	0·002
20	0·14	0·01	0·57	0·02	0·042	0·002
25	0·13	0·01	0·54	0·03	0·036	0·002
30	0·12	0·01	0·51	0·04	0·030	0·004

ME, metabolizable energy; M, thermoneutral maintenance energy requirement.

Table 3. *The rate of increase in protein and fat retention (kJ/kg*$^{0.75}$ *per d) and body-weight gain (g/kg*$^{0.75}$ *per d) per* 1° *increase in environmental temperature at* 15° *at several levels of food intake*

(Values derived from equation no. 3 (p. 426). Values are mean rates with their standard errors)

ME intake (kJ/kg$^{0.75}$ per d)	Protein		Fat		Body-wt gain	
	Mean	SE	Mean	SE	Mean	SE
440	1·72	0·59	17·7	4·5	1·63	0·11
880	0·91	0·38	15·1	3·7	1·06	0·24
1320	0·10	0·42	12·5	3·5	0·48	0·36
1760	−0·71	0·66	9·9	3·9	−0·09	0·48

F (fat deposition)

F, determined as the difference between ER and *P*, is shown at the different environmental temperatures and planes of nutrition in Fig. 2. At each level of food intake, *F* was estimated to increase to a maximum within the temperature range 20–25° with a subsequent reduction as temperature was increased to 30°. However the rate at which *F* increased per 1° increase in temperature at 15°, was reduced as food intake increased (Table 3). As a consequence of this, *F* appeared to become more independent of environmental temperature as level of feeding was increased. The negative fat retention at the lowest level of feeding indicated that loss of fat reserves took place at each environmental temperature, and at 10° resulted in a reduction of fat reserves of 83 g/d.

While *F* was only partially dependent on environmental temperature it was highly dependent on food intake. The rates at which *F* increased per unit increment in ME are compared with the corresponding values of *P* in Table 2.

Excluding the lowest level of feeding, energy retained as protein was, in most instances, lower than that as fat. Relative to ER, *P* at all levels of feeding decreased to a minimum between 20 and 25°. *P*:ER changed little at 3M and 4M; over the temperature range 20–25° the mean value of *P*:ER at 2M was 0·306 while at 10° it was 0·621.

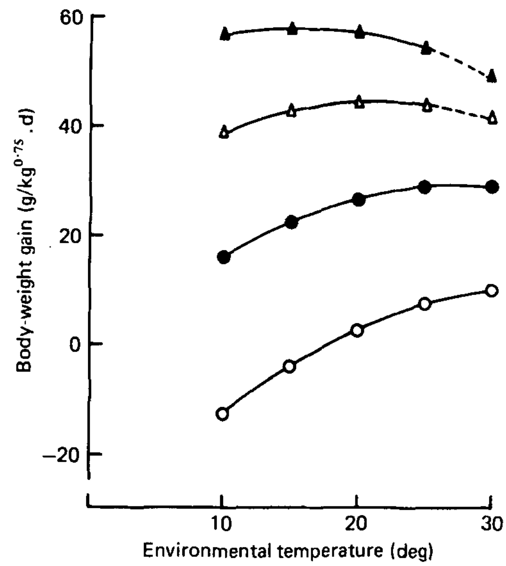

Fig. 3. Body-weight gain (g/kg$^{0.75}$ per d) of growing pigs in relation to environmental temperature (deg) and metabolizable energy (ME) intake (kJ/kg$^{0.75}$ per d). Rates of body-weight gain derived from multivariate regression analysis (see p. 428). ○—○, 440; ●—●, 880; △—△, 1320; ▲—▲, 1760 kJ ME/kg$^{0.75}$ per d. -----, Predicted values above the *ad lib.* intake of the animals.

Body-weight gain (ΔW) and its energy content

As with *P*, ΔW was subjected to a multiple regression analysis in order to determine the best-fitting equation. ΔW was best described by the equation:

$$\Delta W = -75.86 + 3.24\,T - 0.040\,T^2 + 0.0960\,\text{ME} - 0.0000144\,\text{ME}^2 - 0.00113\,(T)(\text{ME}), \quad (4)$$
$$(\pm 11.5) \quad (\pm 0.83) \quad (\pm 0.018) \quad (\pm 0.013) \quad (\pm 0.0000042) \quad (\pm 0.00028)$$
(R 0·964; residual mean square 17·6; 32 df),

where ΔW is body-weight gain (g/kg$^{0.75}$ per d), *T* is environmental temperature (deg), ME is ME intake (kJ/kg$^{0.75}$ per d). The temperature at which maximum ΔW was achieved (Fig. 3) was dependent on the level of feeding and decreased from over 30° at M to less than 20° at 4M. The rate of change in ΔW per 1° change in temperature is given by:

$$\delta(\Delta W)/\delta T = 3.24 - 0.080\,T - 0.00113\,\text{ME}. \quad (5)$$

As with protein and fat, the rate of change in ΔW at 15° was also dependent on the level of feeding (Table 3). When expressed per kg body-weight for a 35 kg animal, these represent increases of 0·67, 0·44, 0·20 and −0·04 g/d per 1°, respectively.

The mean increment in food intake required to produce unit change in ΔW (calculated from the values in Table 2) increased with increase in temperature from 1·57 at 10° to 1·77 at 15°, 1·98 at 20°, 2·31 at 25° and 2·78 g food/g increase in ΔW at 30°. This may reflect the composition of the gain as indicated by its energy content which is a measure of the contribution of *P* and *F* to the gain. At each environmental temperature, an increase in food intake above the 2M level was associated with an increase in the energy content of the gain (Fig. 4). At 20°, for example, the energy value of the gain increased from 10·77 at 2M to 13·32 at 3M and 15·79 kJ/g at 4M. In addition, at each level of food intake the results were temperature-dependent so that maximum energy values at 2M and 3M were recorded at 20° while that at 4M was recorded at 30°. At food intakes between 2M and 4M the mean energy values of the gain for all temperatures was 12·68 kJ/g.

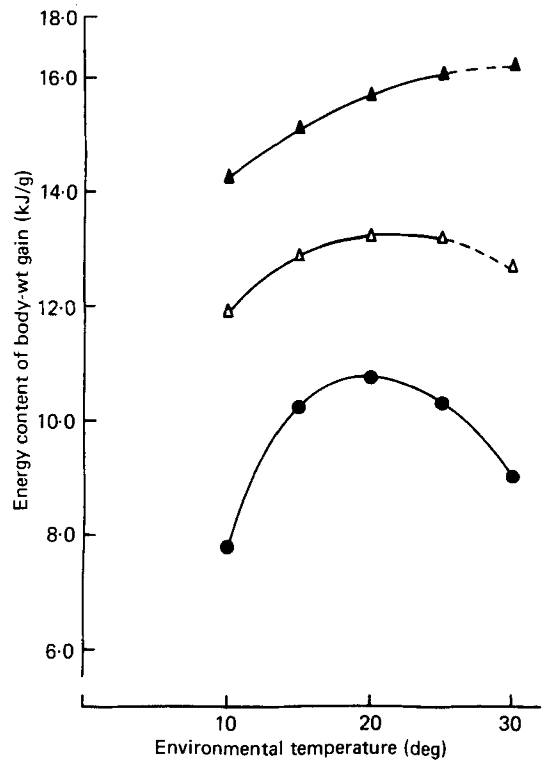

Fig. 4. The energy content of the body-weight gain (kJ/g) of growing pigs in relation to environmental temperature (deg) and metabolizable energy (ME) intake (kJ/kg$^{0.75}$ per d). Values derived from the results presented in Figs. 1 and 3. ●—●, 880; △—△, 1320; ▲—▲, 1760 kJ ME/kg$^{0.75}$ per d. -----, Predicted values above the *ad lib.* intake of the animals.

DISCUSSION

Protein and fat deposition

The results from the present investigation indicated that both *P* and *F* varied with the plane of nutrition; they also depended partly on environmental temperature (Fig. 2), with *F* being the more temperature-dependent. These interactions are in accordance with the results of Fuller (1965), Close & Mount (1971), Fuller & Boyne (1971), Verstegen *et al.* (1973) and Gray & McCracken (1974). The present results also indicated that fat retention was reduced to a greater extent than protein under cool conditions. At 10°, for example, *P* was reduced by 48 % when feeding level was decreased from 3M to 2M, whereas *F* was reduced by 85 %.

A comparison can be made between the extents to which the rates of protein and fat change in relation to both environmental temperature and level of feeding. At an environmental temperature of 15° a 1 g reduction in food intake at 2·5M resulted in a 0·076 g reduction in *P* and a 0·18 g reduction in *F*. Similarly a 1° change in temperature resulted in changes of 0·31 g/d in *P* and 5·0 g/d in *F*. The reduction in *P* as a result of a 1° decrease in temperature was equivalent to a 4 g/d reduction in food intake while that of *F* was equivalent to a 28 g/d reduction. The temperature-dependent changes in *F* were thus greater than those in *P* (see Fig. 2).

The variations in *P* and *F*, expressed as a proportion of either ME or ER, reflected changes in lean:fat deposition which is commonly used as an indicator of carcass composition. From the present rates of deposition, and assuming that the mean water content of the protein gain is 77 % (Close, 1970; Verstegen *et al.* 1973), mean values for lean:fat deposition of 2·72

Table 4. *Linear regression equations ($y = mx + c$) relating protein retention (y; $g/kg^{0.75}$ per d) to protein intake (x; $g/kg^{0.75}$ per d) at several environmental temperatures*

Environmental temperature (deg)		R
10	$y = 0.54\ (\pm 0.03)\ x - 3.04\ (\pm 0.54)$	0.988
15	$y = 0.46\ (\pm 0.03)\ x - 1.40\ (\pm 0.36)$	0.991
20	$y = 0.46\ (\pm 0.07)\ x - 1.54\ (\pm 1.13)$	0.931
25	$y = 0.46\ (\pm 0.03)\ x - 0.95\ (\pm 0.48)$	0.984
30	$y = 0.39\ (\pm 0.04)\ x - 0.32\ (\pm 0.45)$	0.980

R, correlation coefficient.

at 3M and 2.35 at 4M have been calculated over the temperature range 10–30°. At 2M, over the temperature range 20–25°, where both *P* and *F* were independent of temperature, lean:fat deposition was 3.20. Decreasing food intake results in more lean relative to fat deposition.

Previous studies (Blair, Dent, English & Raeburn, 1969; Cooke, Lodge & Lewis, 1972; Gray & McCracken, 1974) have indicated that the rate of protein retention is dependent on the level of protein intake. The net efficiency of protein utilization in the present experiments, indicated by the regression coefficients in Table 4, decreased with increase in temperature from 0.54 at 10° to 0.46 between 15 and 25° with a further reduction to 0.39 at 30°. Extrapolation to $P = 0$ provides estimates of protein maintenance at each environmental temperature equivalent to 5.63, 3.04, 3.35, 2.07 and 0.82 $g/kg^{0.75}$ per d at 10, 15, 20, 25 and 30°. For a 35 kg pig the protein requirement for maintenance is between 81 and 12 g/d for the temperature range 10–30°, with a mean value of 41 g/d over the temperature range 15–25°. Fuller, Webster, MacPherson & Smith (1976) have determined an efficiency of protein utilization of 0.56 for a 30 kg pig with a protein requirement for maintenance of 28 g/d. On the assumption that the apparent digestibility of protein is 0.80 (Fuller & Boyne, 1971; Verstegen *et al.* 1973), the maintenance requirement for apparently digested protein is 33 g/d from the present investigation and 22 g/d from that of Fuller *et al.* (1976). These values compare with those of 31–33 g/d calculated by van Es (1971) from the results of Lund (1935).

Body-weight gain

The general requirement for farm practice is to determine the range of environments and nutrition that allows maximum efficiency in the utilization of food. The optimal range of environments is then analogous to the zone of thermal neutrality but not necessarily identical with it, although estimates of the effective critical temperature on each plane of nutrition represent the minimal temperatures at which maximum efficiency is obtained on a 24-hourly basis for pigs housed under these conditions. In the present experiments the temperature corresponding to maximum growth rate was dependent upon the level of feeding, varying from above 30° at M to less than 20° at 4M, although at the higher feeding levels there was little difference in growth rate between 15 and 25°. The reduction in growth rate per 1° decrease in temperature at 15° was dependent upon the level of feeding. The reduction ranged from $-0.09\ (\pm 0.48)\ g/kg^{0.75}$ per d per 1° at 4M to $1.63\ (\pm 0.11)\ g/kg^{0.75}$ per d per 1° at M. At levels of intake normally applied in practice growth rate decreased by 0.77 $g/kg^{0.75}$ per d per 1° (mean of 2M and 3M results). For a 35 kg pig this represents a reduction in growth rate of 11 g/d per 1° decrease in temperature.

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