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

3*. The efficiency of energy utilization for maintenance and growth

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1. From the relation between metabolizable energy (ME) intake and heat loss (H), energy retention (ER), protein (P) and fat (F) deposition the energy costs of maintenance (ME_m) and the partial efficiencies of energy retention (k) and protein (k_P) and fat (k_F) retention were determined in growing pigs at environmental temperatures of 10, 15, 20, 25 or 30°.

2. k decreased with increase in environmental temperature from 0·79 at 10° to 0·63 at 30° with 0·67 at the thermally-neutral temperature of 25°. Each 0·04 decrease in k was associated with a 100 kJ/kg$^{0·75}$ per d decrease in ME_m. Analysis, within several ranges of environmental temperature, suggested a curvilinear relation between ER and ME intake indicating a decrease in k with increase in level of feeding, particularly at thermally-neutral temperatures.

3. Both k_P and k_F were similar at each environmental temperature and decreased from 0·78 at 10° to 0·63 at 30°. These values are discussed in relation to those predicted from experimentation and it is suggested that the wide range of predicted estimates of k_P could be attributed to differences in the rate of protein turnover.

To determine the energy requirements for growth it has been customary to partition the metabolizable energy (ME) content of the food into that required for maintenance on the one hand and that for production on the other. The maintenance energy requirement (ME_m) is that intake at which both the ME intake and the heat loss (H) of the animal are equal and therefore in energy equilibrium. The energy requirement for production (ME_p) is composed of the energy retained in tissue deposition (ER) plus the energy associated with its synthesis. The ratio ER : ME_p is the partial efficiency of energy retention (k). When both ME and k are known, estimates of the energy requirement for growth can be determined. Corresponding k values can be calculated for protein and fat retention separately. This allows estimates of k to be made either when there is a net deposition of protein (P) and fat (F), as in the young growing animal, or of F, as in the mature animal.

The energy cost of maintenance together with the energy associated with tissue synthesis represents an energy loss in the form of heat which has been shown to be dependent on both the environmental temperature (T) and plane of nutrition (Graham, Wainman, Blaxter & Armstrong, 1959; Verstegen, Close, Start & Mount, 1973; Mount, 1976; Close & Mount, 1978). In a cold environment, ME_m is larger than in a thermoneutral environment, and this leads to a reduction in ME_p if the level of food intake is constant. The question which arises is whether values of k and partial efficiencies for protein (k_P) and fat (k_F) synthesis also change with T. In the present study this problem has been approached by determining the energy costs of maintenance and production at several values for T.

Table 1. *The maintenance energy requirement* (ME_m) *and the partial efficiencies of energy retention* (k) *and protein* (k_P) *and fat* (k_F) *synthesis in the growing pig at several environmental temperatures*

Environmental temperature (deg)	ME_m (kJ/kg$^{0.75}$ per d)	k	k_P	k_F
10	723	0·79	0·78	0·78
15	577	0·75	0·75	0·75
20	480	0·71	0·71	0·71
25	440	0·67	0·68	0·67
30	469	0·63	0·63	0·63

MATERIALS AND METHODS

Measurements of H and energy and nitrogen balances were made on thirty-eight individually housed Large White pigs, initial body-weights 21–38 kg, maintained at values for T of 10, 15, 20, 25 or 30° (± 0.2) with four levels of feeding at each T value. Estimates of ME intake, H, ER, P and F were made at each T value at intakes corresponding to once, twice, three and four times the thermoneutral ME_m.

Details of the animals and their feeding, and the experimental and analytical procedures, have already been reported (Close & Mount, 1978; Close, Mount & Brown, 1978).

RESULTS

The ME_m and the corresponding value for k have been calculated at each value of T from the equation relating H to ME and T (equation no. 1 of Close & Mount, 1978) as the intake at which ME is equal to H, equivalent to zero ER (Table 1). The minimal ME_m was calculated to be 440 kJ ME/kg$^{0.75}$ per d at a thermally-neutral temperature of 25°. ME_m (kJ/kg$^{0.75}$ per d) was related to T (deg) according to the equation:

$$ME_m = 1203 \ (\pm 2.0) - 59.4 \ (\pm 19) \ T + 1.16 \ (\pm 0.05) \ T^2. \tag{1}$$

From equation no. 1 the rate of change in ME_m decreased with increase in T from 36·2 kJ/kg$^{0.75}$ per d per 1° at 10° to 24·6, 13·0, 1·4 and −10·2 at 15, 20, 25 and 30°, respectively.

k was determined at each value for T from the regression equation relating ER (kJ/kg$^{0.75}$ per d) to ME intake (kJ/kg$^{0.75}$ per d):

$$ER = k\,ME + c, \tag{2}$$

where ER was calculated as the difference between ME intake and H (Close *et al.* 1978). k decreased with increase in T from 0·79 at 10° to 0·63 at 30°, with 0·67 at the thermally-neutral temperature of 25° (Table 1). From the mean values of k and ME_m at 10 and 25°, that is, below and within the zone of thermal neutrality (Close & Mount, 1978) it was calculated that each 100 kJ/kg$^{0.75}$ per d decrease in ME_m was associated with a 0·04 reduction in k.

To determine whether the changes in k reflected change in the k_P and k_F, values of k_P and k_F at each value of T were calculated from the relation:

$$ME_p = aP + bF, \tag{3}$$

where ME_p is the energy available for production (kJ/kg$^{0.75}$ per d), calculated at each T–feeding level combination as the difference between ME and ME_m, and P and F are the quantities of protein and fat deposited (kJ/kg$^{0.75}$ per d) (Close *et al.* 1978). The values of a and b give the energy requirements for protein and fat synthesis expressed as kJ/kJ retained. The reciprocals of a and b are then the respective values for k_P and k_F. In calculating k_P and
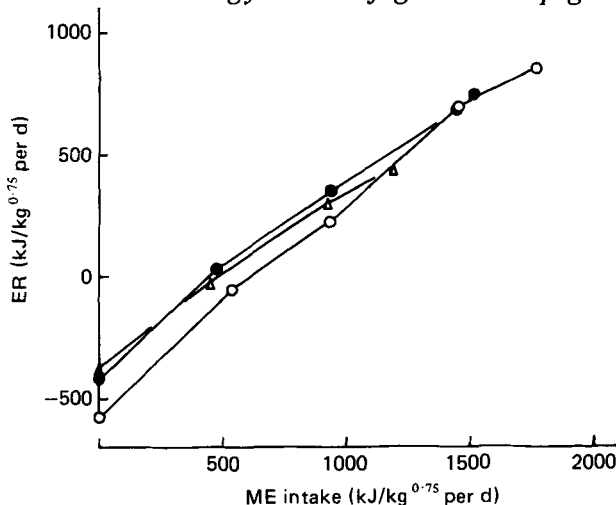
Fig. 1. The relation between energy retention (ER; kJ/kg$^{0.75}$ per d) and metabolizable energy (ME) intake (kJ/kg$^{0.75}$ per d) at environmental temperatures (deg) equivalent to 12·5 ($\bigcirc$—$\bigcirc$), 22·5 ($\bullet$—$\bullet$) and 30 ($\triangle$—$\triangle$).

k_F by this method it has been assumed that the ME$_m$ is independent of both level of feeding and body-weight within a narrow weight range when expressed per unit of metabolic body size (W$^{0.75}$).

Increasing T resulted in a decrease in both k_P and k_F from 0·78 at 10° to 0·63 at 30° with intermediate values of 0·75, 0·71 and 0·68 at 15, 20 and 25°, respectively (Table 1).

DISCUSSION

Below the critical temperature, part of the heat loss associated with protein and fat synthesis takes the place of some of the extra thermoregulatory heat production, and k is correspondingly higher. Under warmer conditions, where there is no extra thermoregulatory heat production, k would be expected to decrease because the heat production associated with synthesis then has to be dissipated as additional heat. This could account for the decrease in k from 0·79 at 10° to 0·63 at 30°, and suggests that k is dependent on the thermoregulatory demand of the environment. The mean value for k (partial efficiency of the utilization of energy for growth) of 0·67 agrees with the value of 0·665 found with groups of pigs at 20° (Verstegen *et al.* 1973), but the values of 0·79 and 0·75 at the subcritical temperatures of 10 and 15° are decidedly lower than the 0·99 that was found for the groups at 8°, although compatible with those of Fuller & Boyne (1972), who obtained values of 0·77 at 13° and 0·71 at 23° for pigs of 35 kg body-weight.

As feeding level is an important factor in determining the critical temperature (T_c), it follows that k should change if T_c changes as a result cf an increase in feeding level. The relation between ER and ME would then appear to be curvilinear. Analysis of the relation between ER and ME, at T equivalent to 12·5° (mean of results at 10 and 15°; Table 1, Close *et al.* 1978), 22·5° (mean of results at 20 and 25°) and 30°, that is mainly below, within and above the zone of thermal neutrality, suggests that the relation is curvilinear (Fig. 1). From Fig. 1 k at each value for T (Table 2) was calculated as (change in ER):(change in ME) for each 400 kJ/kg$^{0.75}$ per d increment in ME intake between 0 and 1600 kJ ME/kg$^{0.75}$ per d.

At 12·5° k was high relative to that at 22·5 and 30°, and the animals were always below their T_c. At 22·5°, an increase in ME intake resulted in a marked change in k from 0·95 below

Table 2. *The partial efficiency of energy retention* (k) *over several ranges of metabolizable energy* (ME) *intake at environmental temperatures equivalent to* 12·5, 22·5 *and* 30°

Environmental temperature (deg)	Ranges of ME intake (kJ/kg$^{0.75}$ per d)			
	0–400*	400–800	800–1200	1200–1600
12·5	0·96	0·80	0·82	0·75
22·5	0·95	0·75	0·65	0·68
30	0·77	0·68	0·60	—

* Values calculated on the basis that the fasting heat loss at 12·5, 22·5 and 30° was 573, 418 and 380 kJ/kg$^{0.75}$ per d, respectively. These were calculated on the basis that the fasting critical temperature is 25° and that fasting heat loss increases by 15·4 kJ/kg$^{0.75}$ per d per 1° below the critical temperature (see Table 4, Fig. 5 of Close & Mount, 1975).

Table 3. *Estimates of the energetic efficiencies of protein* (k$_P$) *and fat* (k$_F$) *synthesis in the pig, compiled from various sources*

Body-wt (kg)	k_P	k_F	Source
2–9	0·76	0·81	Kielanowski (1965)
20–90	0·35	0·73	Kotarbinska (1969)
20–90	0·43	0·77	Thorbek (1970)
25–110	0·52	0·70	Oslage, Gädeken & Fliegel (1970)
25–45	0·47	0·69	Close & Mount (1971)
5–25	0·76	0·78	Burlacu, Baia, Ionila, Moisa, Tascenco, Visan & Stoica (1973)
20–40	0·58	0·70	Close, Verstegen & Mount (1973)
30–110	0·52	0·70	Gädeken, Oslage & Fliegel (1974)
20–90	0·48	0·77	Thorbek (1975)
9–58	0·66	1·00	Burlacu, Illiescu & Stravi (1976)
20–50	0·71	0·71	Present results (mean values)

400 kJ/kg$^{0.75}$ per d, that is below the T_c, to 0·65–0·68 between 800 and 1600 kJ ME/kg$^{0.75}$ per d when the animals were above their effective T_c. T_c is equal to 22·5° at an ME intake between 400 and 800 kJ/kg$^{0.75}$ per d and the k value of 0·75 at this intake is similar to that below 400 kJ ME/kg$^{0.75}$ per d at 30°, which is very close to the T_c of the fasting animal (Close & Mount, 1975, 1978). From these results it may be concluded that below T_c, which depends upon the level of feeding, k varies between 1·0 and 0·8, decreasing to 0·8–0·7 at thermal neutrality and to 0·7–0·6 under warmer conditions. The relation between ME and ER derived from a series of observations on different planes of nutrition would consequently be curvilinear if the conditions used include those below and above T_c that ensue from the nutrition-environmental interactions.

k_P and k_F determined from the present investigation are within the range of estimates proposed from previous investigators (Table 3). Whereas with one exception k_F varies within the narrow range 0·69–0·82, estimates of k_P are more variable, ranging from 0·35 to 0·76. The energy cost of fat synthesis predicted from experimentation accords closely with that calculated on a theoretical basis (Schiemann, Hoffmann & Nehring, 1961; Blaxter, 1962; Armstrong, 1969). Schiemann *et al.* (1961) calculated that the energy from dietary fat is incorporated into accreted fat with an efficiency of 0·86, while that from dietary carbohydrate and protein are 0·76 and 0·66 respectively. On this basis, a conventional cereal-based ration containing 80 % of its energy as carbohydrate, 15 % as protein and 5 % as fat would be expected to have a k_F value of 0·75, indicating an energy requirement for fat synthesis of 53·1 kJ/g. The mean estimate from the present study (k_F 0·71) indicates a total energy cost of 56·1 kJ/g fat deposited.

The range of estimates of k_P proposed from various investigations are much lower than those of 0·75–0·94 calculated on theoretical grounds by Blaxter (1962), Schiemann (1963), Armstrong (1969) and Schiemann, Chudy & Herceg (1969). Kielanowski (1972, 1976) and Buttery & Boorman (1976) have discussed the energy cost of protein synthesis including the discrepancy between theoretical and predicted values. Theoretical calculations presuppose an ideal dietary supply for tissue synthesis where all amino acids are assumed in their correct proportions. However, no allowances have been made for the energy cost of synthesizing non-essential amino acids or for deaminating amino acids surplus to requirements as may occur under normal feeding practices. This may result in a lower than theoretical estimate of k_P.

Various hypotheses have been proposed for the wide range of predicted estimates of k_P. These include differences in technique, variation in body-weight with heavier animals having lower efficiencies, variations in dietary energy and protein concentrations and differences in the method of determination (Kielanowski, 1972; Pullar & Webster, 1974, 1977; Thorbek, 1975). However, it is possible that part of the variation could be attributed to differences in the level of feeding. Within the zone of thermal neutrality k decreases when the level of feeding increases, and this could represent a decrease in k_P, k_F or both. The range of estimates of k_F (Table 3) suggests that it is a less variable component in relation both to variations in body-weight and level of feeding. If k_F could be assumed constant, for a given body-weight and food type, it follows that the decrease in k with an increase in level of feeding could result from a reduction in k_P alone. From the mean values of ER, P and F at T equivalent to 22·5° (mean of results at 20 and 25°; Table 1 of Close *et al.* 1978) and if a k_F of 0·69 is similarly assumed (Table 1) it may be calculated from the relationship:

$$\frac{\text{ER}}{k} = \frac{P}{k_P} + \frac{F}{k_F}, \tag{4}$$

that the decrease in k from 0·75 to 0·65 with increase in level of feeding (Table 2) results from a change in k_P from 0·75 to 0·58. The estimates of ME_m corresponding to these estimates of k_P are 438 and 407 kJ/kg$^{0.75}$ per d, respectively, indicating an extent of interdependence between the variables (Pullar & Webster, 1974; Kielanowski, 1976). It is also possible that the decrease in k_P may be indicative of an increase in the mean rate of protein turnover associated with both a higher rate of synthesis and a greater body protein mass of the animals at the higher levels of food intake (Tschudy, Bacchus, Weissman, Watkin, Eubanks & White, 1959; Millward, Garlick, James, Sender & Waterlow, 1976; Steffee, Goldsmith, Pencharz, Schrimshaw & Young, 1976).

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