Energy metabolism and body composition of young pigs given low-protein diets

BY K. J. McCRACKEN[1,2] AND A. McALLISTER[1]

[1]*Agricultural and Food Chemistry Research Division, Department of Agriculture, Northern Ireland and* [2]*The Queen's University of Belfast, Newforge Lane, Belfast BT9 5PX*

1. The energy metabolism of young pigs offered low-protein diets to appetite or a normal starter (diet 1, 225 g crude protein (nitrogen × 6·25; CP)/kg dry matter (DM)) to maintain zero energy balance was studied using indirect calorimetry and slaughter. The treatments were: T1, diet 1; T2, 46 g CP/kg DM; T3, 21 g CP/kg DM; T4, 17 g CP/kg DM; T5, 21 g CP/kg DM and no supplemental thiamin.

2. Daily heat production (kJ/d per kg body-weight $(W)^{0.75}$) declined on all treatments from a pre-experimental value of 613. The greatest decline was observed in T1 pigs where the final value was 375.

3. There was a progressive reduction in energy intake from 5·4 MJ/d for T2 pigs to 3·0 MJ/d for T4 and T5 pigs ($P < 0.001$). The mean intake of T1 pigs was 2·3 MJ/d.

4. There were highly significant treatment differences ($P < 0.001$) in gain of live-weight and in the gain of carcass DM, CP, fat and energy.

5. There were marked treatment effects on body composition. T1 pigs showed a decrease in the proportion of carcass fat and an increase in the proportion of carcass CP during the experiment while the other four treatments caused large increases ($P < 0.001$) in carcass DM and fat content and no change in CP content. These changes resulted in large differences in the energy content of the gain, the mean values (MJ/kg) being 0·6, 35·5 and 88 for T1, T2 and T3 pigs respectively. T4 and T5 caused energy gain coupled with weight loss.

6. A linear regression of energy retention (ER; MJ/d per kg $W^{0.75}$) on metabolizable energy (ME) intake yielded the equation

$$ER = 0.78\ ME - 0.365, \quad r\ 0.96.$$

7. These results indicate that heat production declines when the growth rate of young pigs is reduced either by restriction of energy or of protein intake. They do not support the suggestion that low-protein diets give rise to increased 'diet-induced' thermogenesis.

Despite the accumulated evidence from farm and laboratory non-ruminant animals (Breirem & Homb, 1972; Webster, 1981) that the efficiency of energy utilization for protein deposition is lower than for fat deposition, the belief is still held by some that very low-protein diets increase heat production and reduce energetic efficiency (Gurr *et al.* 1980; Lunn & Austin, 1983). This belief originated in the USA as a result of pair-feeding studies on rats (Hogan & Pilcher, 1933; Forbes *et al.* 1935; Hamilton, 1939a, b; Black *et al.* 1955) and was supported by the experiments of Miller & Payne (1962) on rats and pigs.

McCracken (1968, 1975) demonstrated that the results obtained in the rat were due to an experimental artefact produced by the pair-feeding technique. The efficiency of energy utilization was unaffected by dietary protein content when the pattern of food intake was controlled.

Conflicting results have been obtained using young pigs. Calculations based on the results of Lowrey *et al.* (1963) show that pigs consuming a diet containing 50 g crude protein (nitrogen × 6·25; CP)/kg utilized energy at least as efficiently as those consuming a diet containing 180 g CP/kg (McCracken, 1968). Fuller (1983) used diets containing 25, 80 or 250 g CP/kg and concluded that his results did not support the suggestion that 'low-protein diets evoke rates of heat production greatly in excess of those expected from calorimetric observations of animals given a range of conventional diets'. However, Gurr *et al.* (1980) concluded that low-protein diets result in elevated energy expenditure (so-called 'diet-induced

Table 1. *Experimental treatments*

Treatment	Diet*	Feeding level	No. of replicates
T1	1	Restricted (140 g/d)	5
T2	2	*ad lib.*	5
T3	3	*ad lib.*	4
T4	4	*ad lib.*	4
T5	5	*ad lib.*	3

* For details of diets, see Table 2.

thermogenesis'). In attempting to explain these contradictions it seemed that, in those experiments where a positive N balance had occurred (Lowrey *et al.* 1963; Fuller, 1983), efficiency of energy utilization was unimpaired whereas poor efficiency of energy utilization was associated with negative N balance (Gurr *et al.* 1980). On further examination of their paper it became apparent that the low-protein pigs of Gurr *et al.* (1980) may also have suffered from thiamin deficiency. Thiamin deficiency has been found to reduce feed efficiency in young pigs even under conditions of controlled intake (Heineman *et al.* 1946; Miller *et al.* 1955).

The present experiment was initially designed to study the effects of mild or severe restriction of dietary protein intake, leading to positive or negative N balance, on the energy utilization and growth of piglets. After two replicates had been completed a further treatment was included to examine the effect of combining thiamin deficiency with a low dietary protein intake. The initial results have been reported (McCracken, 1983).

EXPERIMENTAL

Animals and management

Male pigs (Large White × Landrace cross) were obtained from the Agricultural Research Institute, Hillsborough, Co. Down. They were weaned at approximately 14 d and given a pelleted starter diet until approximately 28 d of age to ensure that appetite was well-established. When 24 d old they were transferred to individual metabolism cages in a controlled-environment room. The temperature was $29 \pm 1°$ and relative humidity $50 \pm 5\%$. Continuous low-intensity light was provided. Water was available in a metal trough and was replenished frequently. The water troughs were cleaned daily. The diets were pelleted and food was offered three times daily at 09.00, 15.00 and 22.00 hours to minimize food spillage.

Experimental design

Five replicates were conducted, each with pigs from one litter. The experimental treatments are shown in Table 1. In addition one pig from each litter was killed for initial carcass analysis. The composition and analysis of each diet is given in Table 2. Diet 1 was a typical starter diet for early-weaned pigs. Prior to the introduction of the experimental treatments the pigs were given diet 1 (300 g/d) and one 24 h measurement of heat production was made on each pig in a closed-circuit respiration chamber (Jordan, 1971).

The pigs were introduced to the experimental diets in a randomized sequence based on body-weight so that measurements of heat production could be made at equivalent times after the start of the experiment. In replicates 1 and 2, heat production was measured every 3rd day (replicate 1, treatments 1, 2, 3; replicate 2, treatments 1, 2, 4) and, in replicates 3–5, heat production was measured every 4th day (treatments 1, 2, 4, 5). Replicate 1 was

Table 2. *Compositions (g/kg) and analyses* of the experimental diets*

Diet...	1		2	3, 5†	4
Ground flaked maize	317	Diet 1	200	80	60
Dried skim milk	280	Starch	390	475	482
Fatted skim milk (400 g fat/kg)	140	Tallow	90	100	100
Fish meal (650 g crude protein/kg)	120	Lactose	180	200	210
Sucrose	100	Sucrose	100	100	100
Groundnut oil	40	Dicalcium phosphate	37	42	45
Trace minerals–vitamins‡	3	Trace minerals–vitamins	3	3	3
Crude protein (g/kg)	225		46	21	17
Metabolizable energy (MJ/kg)	18·2		17·6	17·3	17·2
Calcium (g/kg)	11·1		15·2	15·0	16·3
Phosphorus (g/kg)	7·3		9·9	9·4	9·8

Crude protein, $N \times 6.25$.

* Dry matter basis.

† Thaimin omitted from the trace mineral–vitamin supplement for diet 5.

‡ The trace mineral–vitamin supplement supplied (mg/kg): iron 140, zinc 80, copper 40, manganese 30, iodine 2·5, cobalt 1·2, selenium 0·1, choline chloride 150, nicotinic acid 12, calcium pantothenate 10, riboflavin 5, menadione 5, pyridoxine hydrochloride 3·5, thiamin hydrochloride 1·2, cyanocobalamin 0·001, retinol 14, chlolecalciferol 0·04, α-tocopherol acetate 5.

discontinued after 15 d when the T2 pig developed a high temperature and stopped eating. In subsequent replicates the experiment lasted 25 d.

Measurements of energy and protein intake and retention

Feed was weighed daily and, except for treatment 1, was offered in sufficient quantity to ensure that food was always available. To reduce contamination of the excreta a piece of plastic sheet was placed under the cage floor in front of the feed trough. Food refusals and spilt food were collected daily and dried to constant weight in a force-draught oven at 100°.

Faeces, urine and any spilt food escaping the plastic sheet were collected into a plastic receptacle containing 0·1 l sulphuric acid (0·2 M). Each morning the excreta were filtered through linen cloth. The liquid and solid fractions were stored separately at +4 and −20° respectively for subsequent analysis.

At the end of the experiment the pigs were killed by injection of sodium pentobarbitone, certain organs were removed and weighed, undigested food residues were removed from the digestive tract and the carcasses prepared for analysis as described by McCracken *et al.* (1980). The CP contents of the diets, excreta and carcasses were determined by the macro-Kjeldahl method and carcass fat by the Soxhlet method (40–60° b.p. petroleum ether). Crude ash contents of the diets and carcasses were determined after combustion at 500° in a muffle furnace. The gross energy contents of the diets and freeze-dried excreta were determined in an adiabatic bomb calorimeter. Carcass energy content was calculated from the carcass CP and fat using the factors 23·8 and 39·3 MJ/kg respectively. The initial carcass protein, fat and energy of the pigs in each replicate were estimated from the composition of the slaughtered littermate.

Table 3. *Metabolizable energy (ME) intake (MJ/d), weight gain (g/d) and weights (g/kg carcass) of liver, kidney, small intestine and large intestine of pigs given a restricted amount of diet 1 (T1) or given ad lib. diet 2 (T2), diet 3 (T3), diet 4 (T4) or diet 5 (T5)†*

(Mean values and standard error of the difference; no. of animals per treatment in parentheses)

	T1 (5)	T2 (5)	T3 (4)	T4 (4)	T5 (3)	SED	Statistical significance (12 df)
Initial weight (kg)	7·48	7·80	7·70	7·64	7·83	0·135	NS
ME intake	2·27	5·43	4·48	3·04	2·96	0·449	***
Weight gain	58	77	18	−23	−13	19·5	***
Liver	23·5	33·6	31·5	34·5	42·1	3·31	**
Kidney	3·8	4·0	3·9	5·2	4·7	0·28	**
Small intestine	29·1	35·4	31·9	39·6	40·9	1·79	***
Large intestine	15·6	15·1	14·4	15·5	14·0	1·21	NS

NS, not significant. ** $P < 0.01$, *** $P < 0.001$.
† For details of diets, see Table 2.

Statistical analysis

The results were subjected to analysis of variance using an iterative procedure to adjust for missing values.

RESULTS

The mean initial weight of the replicate 1 pigs was 6·56 kg (range 6·3–6·8 kg). In replicates 2–5 the mean initial weight was 7·97 kg (range 7·66–8·76 kg). The mean weight gains (g/d; Table 3) were significantly different ($P < 0.001$). There was a progressive reduction in energy intake from 5·4 MJ/d on diet 2 to 3·0 MJ/d on diets 4 and 5 ($P < 0.001$).

Liver weight (g/kg carcass) was significantly ($P < 0.01$) higher in the animals given low-protein diets than in T1 animals (Table 3). Kidney weight (g/kg carcass) was higher ($P < 0.01$) in T4 and T5 animals and a similar pattern ($P < 0.001$) was observed in the weight of the small intestine. In contrast, the weight of the large intestine was unaffected by treatment.

Daily heat production during the pre-experimental period averaged 613 (SEM 8·0) kJ/d per kg $W^{0.75}$ (seventeen observations) and was not significantly different between treatments. Heat production declined during the experiment on all treatments, particularly during the first few days (Fig. 1). The decline was greatest on treatment T1, the value on day 25 being 375 kJ/d per kg $W^{0.75}$. The values obtained with T4 and T5 animals were only slightly higher, averaging 410 and 398 kJ/d per kg $W^{0.75}$ respectively on day 25. Heat production of T2 pigs was approximately 25% higher throughout the experiment.

There were marked treatment effects on body composition. The mean (with SEM) dry matter (DM), CP and fat levels of the starting controls (five observations) were 275 (6·8), 144 (3·8) and 92 (8·5) g/kg. The mean carcass energy content was 7·07 (0·289) MJ/kg and the mean total energy was 52·9 (2·76) MJ. T1 pigs showed a decrease in the proportion of carcass fat and an increase in the proportion of carcass CP during the experiment while the other four treatments caused large increases in carcass DM and fat content ($P < 0.001$) and no change in CP content (Table 4). There were highly significant differences ($P < 0.001$) in the gains of DM, CP and fat due to treatment. The highest values for DM and fat gains were obtained with T2 pigs and the lowest with T1 pigs. CP gain was highest with T1 pigs and declined with decreasing dietary CP content. The CP gain calculated from continuous
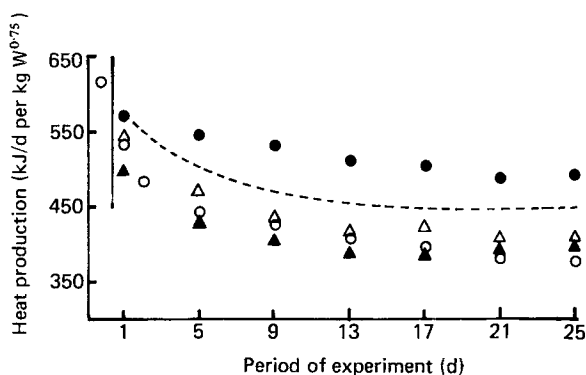
Fig. 1. Daily heat production (kJ/d per kg body-weight $(W)^{0.75}$) of young pigs given a normal or low-protein diet for 25 d. (○) T1, (●) T2, (△) T4, (▲) T5. (For details of treatments see Tables 1 and 2.) Each point represents the mean of three or four observations (replicates 2 to 5). (‐‐‐‐‐), Corrected heat production of T4 and T5 pigs based on the slaughter results. The pre-experimental value (613 kJ/d per kg $W^{0.75}$, mean of seventeen observations on pigs given 300 g/d of diet 1) is included for comparison.

Table 4. *Content of dry matter (DM), fat, and crude protein (nitrogen × 6·25; CP) in the carcass (g/kg) and gains of DM, fat, CP and energy from slaughter or CP by balance of pigs given a restricted amount of diet 1 (T1), or given* ad lib. *diet 2 (T2), diet 3 (T3), diet 4 (T4) or diet 5 (T5)†*

(Mean values and standard error of the difference; no. of animals per treatment in parentheses)

	T1 (5)	T2 (5)	T3 (4)	T4 (4)	T5 (3)	SED	Statistical significance (12 df)
DM	267	408	408	371	350	12·1	***
CP	168	149	148	143	147	9·2	*
Fat	57	216	212	184	151	12·6	***
DM gain (g/d)	12·3	71·8	49·6	19·8	17·6	9·58	***
Fat gain (g/d)	−7·6	56·9	43·4	23·9	15·7	8·67	***
CP gain (g/d)	16·4	7·8	2·2	−4·6	−1·5	2·34	***
CP balance (g/d)	17·4	5·9	−1·3	−4·9	−2·5	0·92	***
Energy gain (MJ/d)	0·10	2·48	1·78	0·83	0·59	0·342	***

* $P < 0.05$, *** $P < 0.001$.
† For details of diets, see Table 2.

N balance was in good agreement with the slaughter results except for T3 animals in which the slaughter method indicated a small gain and the balance method a small loss. This discrepancy was entirely due to one pig which appeared to gain 0·19 kg CP whilst only gaining 0·21 kg live weight. There were highly significant differences in energy retention ($P < 0.001$), mirroring the differences in energy intake. T1 pigs were almost in energy equilibrium whereas T2 pigs gained 2·5 MJ/d, 46% of their metabolizable energy (ME) intake.

When expressed in relation to metabolic body-weight (kg $W^{0.75}$) the ME intake of T2 pigs was approximately 2·2 times greater than that of T1 pigs (Table 5) whereas the intakes of T4 and T5 pigs were only 40% higher than the mean T1 intake. Heat production calculated from the slaughter results was highest for T2 pigs ($P < 0.01$) and lowest for T1 pigs. The mean heat production values obtained in the respiration chamber were lower than

8

Table 5. *Metabolizable energy (ME) intake and energy retention (ER) and heat production (HP) calculated from slaughter or determined in a closed-circuit respiration chamber (kJ/d per kg body-weight$^{0.75}$) and calculated energy requirement (ME$_m$) for zero energy balance of pigs given a restricted amount of diet 1 (T1) or given ad lib. diet 2 (T2), diet 3 (T3), diet 4 (T4) or diet 5 (T5)†*

(Mean values and standard error of the difference; no. of animals per treatment in parentheses)

	T1 (5)	T2 (5)	T3 (4)	T4 (4)	T5 (3)	SED	Statistical significance (12 df)
ME intake	484	1067	949	694	673	70·7	***
ER	24	479	378	191	139	60·7	***
HP slaughter	460	589	570	503	534	34·4	**
HP chamber	420	522	ND	441	429	36·3	**
ME$_m$‡	453	453	464	450	495	48·5	NS

NS, not significant.   ** $P < 0.01$,   *** $P < 0.001$.
† For details of diets, see Table 2.
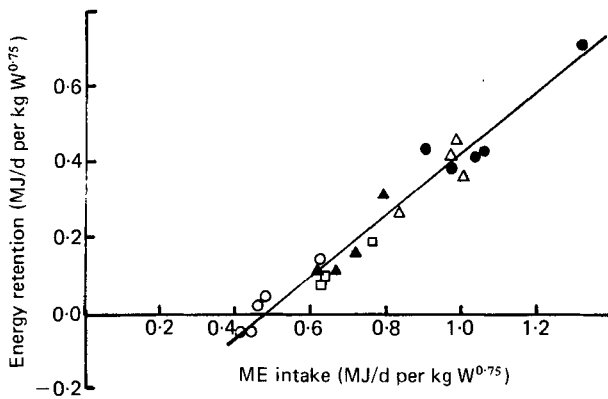‡ Assuming efficiency of utilization of energy for production, 0·78.

Fig. 2. Energy retention (ER) (from slaughter results) *v.* metabolizable energy (ME) intake (MJ/d per kg body-weight (W)$^{0.75}$; standard errors in parentheses) of young pigs given a normal or low-protein diet for 25 d. (○), T1, (●) T2, (△) T3, (▲) T4, (□) T5. For details of treatments, see Tables 1 and 2.

$$ER = 0.78 \, (0.049) \, ME - 0.365 \, (0.040), \quad r \, 0.96$$

those obtained by slaughter. The difference was least with T1 pigs and greatest with T5 pigs where the slaughter value was almost 25% higher than the chamber value. A linear regression of ER (MJ/d per kg W$^{0.75}$; standard errors in parentheses), determined by slaughter, on ME intake (Fig. 2) yielded the equation:

$$ER = 0.78 \, (0.049) \, ME - 0.365 \, (0.040), \quad r \, 0.96.$$

Applying the mean efficiency of utilization of energy (k) of 0·78 to the individual treatments yielded estimates of the ME required for energy equilibrium of 453, 453, 464, 450 and 495 kJ/d per kg W$^{0.75}$ for T1 to T5 respectively; these values were not significantly different.

DISCUSSION

The low-protein diets (diets 2 and 3) used in the first replicate were chosen to provide a small positive N balance (diet 2) and a negative N balance (diet 3). When the first replicate was completed it seemed that pigs on diet 3 were still maintaining N equilibrium. Diet 4 was introduced to ensure a negative N balance in the subsequent replicates. Diet 5 was introduced in the third replicate because of the possibility that the low-protein diet of Gurr *et al.* (1980) had not been supplemented with thiamin.

In each replicate, littermate pigs were used in order to minimize errors due to differences in body composition and variations in metabolic rate. The start of the experiment was staggered so that measurements of heat production in the respiration chamber could be made at the same chronological stages in the experiment. This also permitted the opportunity of starting all the animals in one replicate at approximately the same weight. These measures were considered necessary in view of the relatively small changes in carcass protein and energy which could be expected to occur in relation to the initial carcass contents. Despite these precautions some anomalies arose presumably due to within-litter variation in initial carcass composition. The most striking example was the T3 pig in replicate 3 which appeared to gain 0·19 kg CP whilst only gaining 0·21 kg live weight. In view of the considerable fat gain which occurred and taking account of the CP gain of the other T3 pigs it seems unlikely that this pig gained any CP. To account for the apparent gain in terms of initial composition the CP content would have been 167 g/kg compared with the value of 143 g/kg for the slaughtered littermate. Similar within-litter variation has been observed on occasions in this laboratory (K. J. McCracken, unpublished results).

One of the most notable trends was the reduction in food intake from diet 2 to diets 4 and 5 (Table 3). Although the protein content of diet 2 was only 46 g/kg and protein deposition was extremely limited, energy intake was not much less than that of pigs on normal diets. During the 25 d period one pig consumed 7·2 MJ/d, corresponding to 1·3 MJ/d per kg $W^{0·75}$, and gained 4 kg live weight of which 2·3 kg was fat. The intakes of T3 pigs were similar to those of the low-protein pigs of Gurr *et al.* (1980) but about 10% lower when expressed in relation to metabolic body-weight. This small difference may have been due to the higher environmental temperature in the present experiment. The intakes of pigs on diets 4 and 5 were little more than half that of T2 pigs, and food spillage was very large. However, with the collection system employed, food spillage did not result in any error in the measurement of ME intake. Reductions in food intake have been reported previously in cases of thiamin deficiency (Heineman *et al.* 1946; Miller *et al.* 1955). There is no obvious explanation for the large difference in intake of T3 and T4 pigs although it is interesting to speculate that this may have been related to the extent of N deficiency.

The poor agreement between the measurements of heat production by slaughter and indirect calorimetry (Table 5) was disturbing, although the differences were not as large as some of those reported by Gurr *et al.* (1980). They could not be attributed to errors in estimating food intake nor to systematic errors in carcass energy retention. Hence, it would appear that carcass results were more correct than indirect calorimetry. Two factors appear to have been mainly responsible for the discrepancy. It was noticed that the pigs appeared to be less active in the respiration chamber than in the metabolism room. This may have been due to removal of visual and audible stimuli and presumably affected all pigs to some extent. This view is supported by the higher heat production of pigs of similar weight and food intake (McCracken & Caldwell, 1980), but kept in groups of three, which averaged 695 kJ/d per kg $W^{0·75}$ compared with 613 for our pigs during the pre-experimental period. In addition it was noted that the low-protein pigs tended to eat less in the respiration chamber and this would have caused some reduction in heat production. A curve of

Table 6. *Estimates of energy required for energy equilibrium (ME_m; kJ/d per kg body-weight$^{0.75}$) of young pigs given normal diets*

Source	Method of determination	ME_m
McCance & Mount (1960)†	Indirect calorimetry	240
Kielanowski (1965)	Slaughter, regression	573
Burlacu *et al.* (1973)	Indirect calorimetry, regression	601
Kirschgessner & Muller (1974)	Slaughter, regression	513
Close & Stanier (1980)	Slaughter, regression	544
McCracken *et al.* (1980)	Slaughter, regression	644
Gray & McCracken (1980)	Indirect calorimetry	579, 667
Dunkin & Campbell (1982)	Slaughter, regression	445

† Amount of feed offered was just sufficient to maintain body-weight.

corrected daily heat production for T4 and T5 pigs is shown in Fig. 1. This was obtained, first of all, by correcting the daily values (assuming extra heat production = 0·22 extra ME intake) to the mean intake on the day prior to and following a chamber measurement and then applying a standard percentage correction to the chamber values so that the difference between slaughter and chamber results was made similar to that observed for T1 pigs (Table 5). This still indicates that heat production declined throughout the experiment and particularly during the first few days.

The differences in carcass composition and in the gains of weight, CP, fat and energy emphasize the dangers in making assumptions about energy retention from body-weight change. Whereas the energy content of the gain of T1 pigs averaged 0·6 MJ/kg, that of T2 pigs averaged 35·5 MJ/kg. T3 pigs gained more DM than live weight and the energy content of the gain averaged 88 MJ/kg. T4 and T5 pigs showed increases in DM coupled with weight loss representing infinite increases in the energy content of gains. The phenomenon of weight increase associated with low-energy gain or even energy deficit has been reported in growing animals on intakes close to the maintenance energy requirements (McCracken, 1975). This experiment proves conclusively that the opposite phenomenon, namely, energy gain coupled with weight loss, can also occur if the supply of dietary protein is insufficient to meet maintenance requirements.

The range of ME intakes achieved by the treatments yielded an opportunity to apply a linear regression model to the data. It is recognized that this regression is a compound of within- and between-diet effects and that the error of the regression coefficient is quite large. However, a single line provided as good a fit as separate slopes or intercepts and the mean efficiency of utilization of energy (k), 0·78 is identical to the figure obtained by calorimetry (McCracken & Caldwell, 1980) for young pigs given a normal diet and higher than the k value obtained by slaughter (McCracken *et al.* 1980). The estimate of the energy required for zero energy balance (maintenance, ME_m) of 468 kJ/d per kg $W^{0.75}$ is at the low end of the spectrum of estimates of ME_m in young pigs given normal diets (Table 6). It is generally accepted that restriction of energy intake causes a reduction in basal metabolic rate. The most striking example of this is the severely undernourished pigs of McCance & Mount (1960) where ME_m was reduced to 240 kJ/d per kg $W^{0.75}$ (Table 6). It appears from the present results that the maintenance requirement is reduced whether the reduction in growth rate is due to restriction of energy or of protein. It is not possible to state that level of energy intake has no effect on the maintenance requirement when protein intake is restricted because it is not possible to take account of the contribution of directly

incorporated dietary fat to the net efficiency of energy utilitization for fattening. Furthermore, as discussed by McCracken (1975), it is difficult to choose an acceptable basis for relating maintenance energy requirement to body-weight when gross differences in body composition exist.

The results have failed to confirm a reduction in the efficiency of energy utilization when negative N balance occurs either as a result of insufficient dietary protein alone or in combination with thiamin deficiency, although the energy retention of the thiamin-deficient group (T5) was slightly reduced compared with T4 pigs at similar ME intakes. Whilst it may be argued that the intakes of T4 and T5 pigs were too low to have caused increased heat production this argument cannot be applied to the T3 pigs whose intakes were similar to those of the low-protein pigs of Gurr *et al.* (1980). If we accept that the CP retention by the balance method is unlikely to be underestimated then the T3 pigs were in negative N balance albeit to a lesser extent than the T4 or T5 pigs.

It is therefore necessary to look for some other factor or factors which may have contributed to the discrepancy between this and previous studies. The results of Miller & Payne (1962) are probably due to a combination of four factors: (1) carcass energy loss by the energy-restricted pigs which apparently received only 250 kJ ME/d per kg $W^{0.75}$, (2) consequent depression of the metabolic rate to levels similar to those observed by McCance & Mount (1960), (3) errors in measurement of food intake due to spillage of the low-protein diets, (4) energy retention on the low-protein diet with little change in body-weight. If we accept the surprisingly high intake reported by Miller & Payne (1962) and apply the values for ME_m and k obtained in the present experiment, the energy retention of Miller & Payne's (1962) low-protein pigs would have been 2·3 MJ/d, a value little different from that of the T3 animals whose mean live-weight gain was only 18 g/d.

The results of Gurr *et al.* (1980) are not entirely consistent. In their Expt 2, energy expenditure calculated from slaughter was almost twice that determined by indirect calorimetry. In Expt 3 it appears that the group 1 pigs dissipated almost all the extra energy consumed, as heat. Groups 2 and 3 remained in the respiration chamber throughout the period of measurement and it would seem that, in this case, heat production measured by indirect calorimetry would be more accurate than the slaughter results. In these groups the calculated ER for low- and high-protein pigs lies on the regression line shown in Fig. 2 of the present paper.

Taking account of the above comments and of the results of Lowrey *et al.* (1963), Fuller (1983) and those reported in this paper, it is concluded that low-protein diets do not increase thermogenesis in the young pig even under conditions which result in small N deficits.

REFERENCES

Black, A., Maddy, K. H. & Swift, R. W. (1955). *Journal of Nutrition* 42, 415–422.
Breirem, K. & Homb, T. (1972). *Handbuch der Tierernahrung*, vol. 2, pp. 547–584. [W. Lenkeit, K. Breirem and E. Craseman, editors]. Hamburg: Paul Parey.
Burlacu, G., Baia, G., Ionila, D., Moisa, D., Tascenco, V., Visan, I. & Stoica, I. (1973). *Journal of Agricultural Science, Cambridge* 81, 295–302.
Close, W. H. & Stanier, M. W. (1980). *European Association for Animal Production* Publ. no. 26, 399–402.
Dunkin, A. C. & Campbell, R. G. (1982). *European Association for Animal Production* Publ. no. 29, 198–201.
Forbes, E. B., Swift, R. W., Black, A. & Kahlenberg, O. J. (1935). *Journal of Nutrition* 10, 461–479.
Fuller, M. F. (1983). *Journal of Nutrition* 113, 15–20.
Gray, R. & McCracken, K. J. (1980). *European Association for Animal Production* Publ. no. 26, 163–167.
Gurr, M. I., Mawson, R., Rothwell, N. J. & Stock, M. J. (1980). *Journal of Nutrition* 110, 532–542.
Hamilton, T. S. (1939*a*). *Journal of Nutrition* 17, 565–582.
Hamilton, T. S. (1939*b*). *Journal of Nutrition* 17, 583–599.
Heineman, W. W., Ensminger, M. E., Cunha, T. J. & McCullough, E. L. (1946). *Journal of Nutrition* 31, 107–125.
Hogan, A. G. & Pilcher, R. W. (1933). *Missouri Agricultural Experimental Station Research Bulletin* no. 195.
Jordan, J. W. (1971). *Agricultural Progress* 46, 9–25.

Kielanowski, J. (1965). *European Association for Animal Production* Publ. no. 11, 13–20.
Kirschgessner, M. & Muller, H. L. (1974). *Archiv fur Tierenahrung* **24**, 215–225.
Lowrey, R. S., Pond, W. G., Loosli, J. K. & Barnes, R. H. (1963). *Journal of Animal Science* **22**, 109–114.
Lunn, R. G. & Austin, S. (1983). *British Journal of Nutrition* **49**, 9–16.
McCance, R. A. & Mount, L. E. (1960). *British Journal of Nutrition* **14**, 509–518.
McCracken, K. J. (1968). Energy metabolism of young rats subjected to a deficiency of calories or of protein. PhD thesis, University of Cambridge.
McCracken, K. J. (1975). *British Journal of Nutrition* **33**, 277–289.
McCracken, K. J. (1983). *Proceedings of the Nutrition Society* **42**, 4A.
McCracken, K. J. & Caldwell, B. J. (1980). *European Association for Animal Production* Publ no. 26, 445–448.
McCracken, K. J., Eddie, S. M. & Stevenson, W. G. (1980). *British Journal of Nutrition* **43**, 305–320.
Miller, D. S. & Payne, P. R. (1962). *Journal of Nutrition* **78**, 255–262.
Miller, E. R., Schmidt, D. A., Hoefer, J. A. & Luecke, R. W. (1955). *Journal of Nutrition* **56**, 423–430.
Webster, A. J. F. (1981). *Proceedings of the Nutrition Society* **40**, 121–128.