The effects of varying protein and energy intakes on the growth and body composition of pigs

1. The effects of energy intake at constant, high protein intake

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The objective of the present experiment was to define the form of the relationship between varying levels of energy intake at constant, high protein intake and the performance of young pigs. By doing so it was expected that we could distinguish between four models that predict the pig's responses to its diet as rates of protein and lipid retention. Forty young pigs were assigned at 12 kg live weight either to an initial slaughter group (*n* 8) or to one of four allowances of starch intake at a constant intake of a high-protein feed (with 345 g crude protein (nitrogen × 6·25)/kg food). Half the pigs were killed after 4 weeks and half after 8 weeks on the treatments; at each slaughter point on each treatment half the pigs were entire males and half were females. Increasing the intake of starch (energy) resulted in significant increases in the rates of live weight, empty-body, protein and lipid gains of pigs slaughtered at both stages. There was no minimum positive lipid:protein ratio in the gain of the pigs. Male pigs deposited more protein and less lipid than females but this effect of sex on protein and lipid retention was seen only on the two highest allowances of starch intake. The calculated efficiency of protein utilization increased with increasing starch intake up to a maximum of 0·81, when probably the energy:protein in the diet became non-limiting. The results led to the rejection of two of the models that predict the rates of protein and lipid retention as responses to protein and energy intake, but the two remaining models could not be rejected, at least qualitatively.

Body composition: Protein utilization: Energy intake: Protein intake: Protein retention: Pigs

When an immature animal, such as a young pig, is given a feed at a controlled rate which is less than the rate of *ad lib.* intake, it can be seen as having a limiting supply of one or more resources. In such a case it is useful to see the animal as using some sets of rules to allocate the limited resource, or resources, between the functions that it is carrying out (Emmans & Fisher, 1986).

When an amino acid is the first-limiting nutrient in the feed, and the animal is given the feed at a controlled rate, it may be limited in its intake of energy, or protein, or both these resources. A problem is then to predict the responses of the animal to its diet as rates of protein and lipid retention. Models have been proposed as solutions to this problem. They are, briefly:

Model 1 (M1), the rate of protein retention depends only on the rate of supply of ideal protein, until some genetically determined maximum rate is reached, providing that the animal has some lipid reserves (Emmans, 1981; Emmans & Fisher, 1986); this assumption is also implicit in the equations (9 and 10) of the Agricultural Research Council (1981).

Model 2 (M2), the rate of protein retention depends only on the rate of protein supply providing only that the lipid:protein ratio of the gain exceeds some fixed value (Whittemore & Fawcett, 1976) which may be genetically determined (Whittemore, 1983).

Model 3 (M3), the rate of protein retention depends both on the rate of supply of protein and on the energy:protein ratio of the feed (Fuller & Crofts, 1977); the material efficiency with which protein is retained increases towards a maximum as the energy:protein ratio of the feed is increased.

Model 4 (M4), the rate of protein retention depends only on the ideal protein supply up to some, not clearly defined, level of supply; above this level of supply it depends only on the energy supply (Black *et al.* 1986).

All the models have some experimental support but also have problems, either in their formulation and quantitative predictions, or in their inconsistency with some experimental results. The experiment described here, the first in a short series, used a simple design to explore the effects of different levels of energy supply at a fixed nutrient supply on the performance of young pigs, to try to distinguish between the four models.

MATERIALS AND METHODS

Animals and Housing. Forty Cotswold F1 Hybrid Large White × Landrace pigs (twenty entire males and twenty females) from eight litters were moved immediately after weaning into the individual cages of the experimental unit. The weaned pigs had a mean live weight of 6·95 (SD 1·06) kg and were given free and continuous access to a high-quality commercial feed (Earlycare 404; BOCM Silcock).

The experimental unit consisted of two identical controlled-environmental rooms separated by a central working area. Each room had its own heating, lighting and ventilation system, with a water supply serving two opposing ranks of ten individual cages. Each cage contained one metal trough and a nipple drinker which gave free access to water. Underneath each trough a metal tray was placed where feed spillage was collected.

Feeds. A basal feed (P) with 12·91 MJ metabolizable energy (ME)/kg and 345 g crude protein (nitrogen × 6·25; CP)/kg fresh feed was formulated. The feed was over-abundant in minerals and vitamins in order to maintain the minerals:protein ratios similar to those of a standard commercial grower feed. Feed P was then diluted to varying extents with a mixture of starch, maize oil and wood fibre (feed S). The wood fibre was included in feed S to ensure the formation of normal faeces at high levels of inclusion of this feed. The compositions and chemical analyses of both feeds are given in Table 1. Comparison of the amino acid contents of the protein of feed P (Table 2) with that of the ideal protein proposed by the Agricultural Research Council (1981) suggested that lysine was the first-limiting amino acid.

Design. As each of the forty pigs used reached 12 kg live weight it was assigned either to an initial slaughter group (*n* 8) or to one of the four feeding treatments (*n* 8). The feeding treatments used the two feeds shown in Table 1; allowances were changed weekly as shown in Table 3. All pigs received the same quantities of feed P but different allowances of feed S, which supplied energy but no nutrients. The allowances of P were estimated to meet the nutrient requirements for the potential lipid-free growth of the pigs (Kyriazakis *et al.* 1990). The feeds were given as mash mixtures.

Half the pigs were killed after 4 weeks, and half after 8 weeks on the treatments. At each slaughter point on each treatment half the pigs were entire males and half females.

Management and slaughter procedures. Pigs were fed twice daily (at 09.00 and 17.00 hours) and weighed once weekly before feeding. Feed allowances were changed weekly. Any spillage and feed refusals were collected and weighed daily, and equivalent amounts refed to the animals later. The air temperature was gradually reduced from 28°, when the pigs were first moved, to 22° 2 weeks later, at which level it was held until the end of the experiment. This temperature was estimated to be within the thermoneutral range for

Table 1. *The composition and chemical analysis of the two feeds (g/kg fresh feed)*

Feed...	P	S
Ingredient (g/kg)		
Wheat	116·98	—
Wheat feed	298·51	—
Hipro soya bean	348·26	—
Fish meal	179·70	—
Maize oil	22·13	22·14
Limestone	11·45	—
Dicalcium phosphate	12·81	—
Salt	0·22	—
Vitamin and mineral supplement	7·46	—
Vitamin E supplement	2·49	—
Maize starch	—	942·86
Wood fibre	—	35·00
	1000·01	1000·00
Component (g/kg)		
Dry matter	888·00	875·00
Crude protein (nitrogen × 6·25)	345·00	nd
Crude fibre	42·00	nd
Diethyl ether extract	51·00	14·00
Ash	99·00	12·00
Calcium	20·00	nd
Phosphorus	13·00	nd
Starch	151·00	782·00
Metabolizable energy (MJ/kg)*	12·91	13·16

nd, not determined.
* Calculated by the European Association of Animal Production working group equation (Batterham, 1990).

Table 2. *The amino acid composition of the basal feed P (g/kg crude protein (nitrogen × 6·25 ; CP))*

Alanine	50·1
Arginine	69·1
Aspartic acid	103·4
Cystine	17·4
Glutamic acid	193·6
Glycine	60·9
Histidine	22·1
Isoleucine	41·7
Leucine	70·9
Lysine	56·4
Methionine	22·2
Methionine + cystine	39·6
Phenylalanine	43·3
Serine	47·0
Threonine	40·7
Tryptophan	16·2
Tyrosine	39·7
Valine	46·5

Table 3. *The allowances of feeds P and S on the four feeding treatments A, B, C and D*

| | | Treatment (feed S; g/d) | | | |
Week	All treatments (feed P; g/d)	A	B	C	D
1	400	0	100	200	300
2	500	0	125	250	375
3	600	0	150	300	450
4	700	0	175	350	525
5	800	0	200	400	600
6	900	0	225	450	675
7	1000	0	250	500	750
8	1100	0	275	550	825
1–8	750	0	187·5	375	562·5

individually caged pigs eating the lowest feed allowance (Agricultural Research Council, 1981).

On the twenty-eighth and fifty-sixth day of the experiment the pigs to be killed were fed normally, and on the following morning were weighed and killed by an injection of pentobarbitol sodium. The pigs were then dissected and the stomach, intestines and bladder were removed and weighed full, then stripped of their contents and weighed empty. Gut fill was calculated by difference. All the dissected fractions were then recombined and the whole minced, homogenized and, together with the blood, sub-sampled for chemical analyses (dry matter (DM) and the N, ash, lipid and gross energy (GE) contents of the DM).

DM was determined by freeze-drying to constant weight. The DM was analysed for: protein ($N \times 6.25$) by a micro-Kjeldhal procedure; lipid by Soxhlet extraction with light petroleum (b.p. 40–60°) for 8 h; ash by burning in a muffle furnace at 550°. The GE of the DM was determined by adiabatic bomb calorimetry. The summation of the protein, lipid and ash in the DM did not add up to unity and there were systematic deviations from unity due to treatment. However, when lipid was calculated from the GE and N values using the equation:

$$\text{lipid (g/g DM)} = (\text{GE (kJ/g DM)} - (23.8 \times 6.25 \times \text{N (g/g DM)}))/39.6, \qquad (1)$$

which assumes that the energy contents of protein and lipid are 23·8 and 39·6 MJ/kg respectively, these deviations were not evident. This suggested that the Soxhlet extraction did not retrieve all lipid from the samples. The lipid values derived from equation 1 were used for the analysis of the results.

Analysis of the results. The results were analysed by an analysis of variance as a randomized design with level of feeding, sex and time of slaughter as factors. One female pig on the highest feeding allowance became ill in the third week and it was removed from the experiment. It was treated as a missing value for the analyses of the results. Only on the highest level of intake (treatment D) was some small proportion of the offered feed refused at the later stages of the experiment by some pigs; the actual daily feed intakes were used in the analyses of the results.

RESULTS

The composition of the initial slaughter group at 12·04 kg live weight was 11·04 kg empty-body-weight, 1·661 kg protein and 0·904 kg lipid; there was no effect of sex. The compositions of the bodies of the pigs killed after 4 and 8 weeks are in Table 4. Increasing

the intake of feed S resulted in significant increases ($P < 0.001$) in the live weight and empty-body-weight, protein and lipid weights of pigs slaughtered at both stages. The effects of sex on these measurements were also highly significant ($P < 0.001$), with male pigs having heavier live weights and empty-body- and protein weights but lower lipid weights than females. It appeared that the effect of sex on protein weight was due to the heavier protein weights of males than females of the two highest allowances of the starch feed S (treatments C and D), but the interaction between level of intake and sex failed to be formally significant ($0.1 > P > 0.05$).

The relationship between ash and protein weights of the empty body of all pigs (including the initial slaughter group) was best expressed by the isometric equation:

$$\text{ash weight (kg)} = 0.192 \text{ protein weight} \quad \text{(residual SD (RSD) 0.059),} \tag{2}$$
$$\text{(SE 0.002)}$$

with no treatment or sex effects on the ash:protein ratio.

The relationship between water and protein weights of the empty body of all pigs was expressed by:

$$\ln \text{WA} = 1.617 + 0.0326\,s' + (0.855 - 0.0398\,s')\ln \text{P} \quad \text{(RSD 0.0279),} \tag{3}$$
$$\text{(SE 0.0168)} \quad \text{(SE 0.0248)} \quad \text{(SE 0.0106)} \quad \text{(SE 0.0161)}$$

where WA is the water weight (kg), P is the protein weight (kg) and s' is sex which equals zero for females and one for males. Thus, the allometric relationships between water and protein weights for the two sexes were:

$$\text{water (kg)} = 5.04 \text{ protein}^{0.855} \quad \text{for females,} \tag{4}$$
$$\text{water (kg)} = 5.21 \text{ protein}^{0.815} \quad \text{for males,} \tag{5}$$

with a significant ($P < 0.01$) difference in the values of the exponents.

The increase in the intake of S resulted in significant increases in both rates of protein and lipid deposition ($P < 0.001$; Table 5). The increase in the rate of protein deposition was evident up to the third level of intake (treatment C). Male animals deposited more protein and less lipid than female ones ($P < 0.001$) but this effect of sex on protein and lipid retention was seen only on the two highest allowances of S.

The daily rates of heat loss, and hence heat production, were calculated from the daily rates of ME intake and energy retention (Table 6). Both energy retention and heat loss were affected significantly ($P < 0.001$) by the increase in the allowance of S, suggesting that the animals were not cold at the lowest level of feeding. The effect of sex was significant on the rate of heat loss, with males losing slightly more heat than females.

DISCUSSION

The results show clearly that the rate of protein deposition was increased as energy intake was increased at a constant, non-limiting protein supply. The results thus reject the first model (M1) which suggests that the rate of protein retention depends only on the rate of supply of protein until some genetically determined maximum rate is reached (Emmans, 1981). The fact that above the third level of feeding (treatment C) there was no substantial increase in the rate of protein deposition suggests that at this level of feeding, pigs had reached their genetic potential, which differed between male and female pigs. A similar picture has been observed in other experiments where only the non-protein intake was varied and limited (e.g. Kita *et al.* 1989); above a certain level of feeding, protein retention did not increase any further and this was assumed to suggest the attainment of the genetic

Table 4. *The live weight, empty-body-weight, protein and lipid weights of male (M) and female (F) pigs given different amounts of a starch mixture† at 4 or 8 weeks from 12 kg live weight*

Age at slaughter (weeks)	Treatment‡	Live wt (kg) M	F	Empty body-wt (kg) M	F	Protein wt (kg) M	F	Lipid wt (kg) M	F
4	A	20·41	20·88	18·69	18·96	2·327	3·356	0·933	1·057
	B	24·42	23·31	22·83	22·19	3·987	4·024	1·302	1·378
	C	27·96	26·88	25·89	24·74	4·596	4·354	1·803	1·910
	D	28·07	27·48	26·24	25·51	4·502	4·413	2·029	2·528
8	A	36·24	33·32	33·20	30·49	6·168	5·595	1·500	1·846
	B	43·36	42·47	40·59	39·33	7·490	7·322	2·482	2·957
	C	48·84	44·16	45·79	41·51	8·628	7·427	3·093	5·225
	D	53·41	50·62	50·38	47·46	9·058	8·659	5·098	5·757
SED		1·326		1·270		0·223		0·287	
Statistical significance of:									
Treatment (T)		***		***		***		***	
Sex (S)		**		**		***		***	
Age (A)		***		***		***		***	
T×S		NS		NS		NS		*	
T×A		***		***		***		***	
S×A		*		**		**		**	
T×S×A		NS		NS		NS		*	

SED, standard error of difference; NS, not significant.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
† For details, see Tables 1 and 2.
‡ For details, see Table 3.

Table 5. *The rates of protein and lipid deposition of male (M) and female (F) pigs when given increasing amounts of a starch mixture† for 4 or 8 weeks from 12 kg live weight*

Age at slaughter (weeks)	Treatment‡	Protein gain (g/d)		Lipid gain (g/d)	
		M	F	M	F
4	A	60	60	3	4
	B	83	85	15	16
	C	104	97	33	35
	D	103	98	42	57
8	A	79	70	11	16
	B	104	101	29	37
	C	125	104	40	77
	D	132	123	76	84
SED		5·3		6·8	
Statistical significance of:					
Treatment (T)		***		***	
Sex (S)		**		**	
Age (A)		***		***	
T × S		NS		NS	
T × A		NS		NS	
S × A		NS		NS	
T × S × A		NS		NS	

SED, Standard error of difference; NS, not significant.
** $P < 0.01$, *** $P < 0.001$.
† For details, see Tables 1 and 2.
‡ For details, see Table 3.

potential. A Gompertz analysis for protein growth (Whittemore *et al.* 1988; Kyriazakis *et al.* 1990) suggested that the Gompertz protein-growth-rate parameter (B value) was about 0·0133/d for animals on the highest levels of feeding, which was similar to the value of 0·0135/d observed by Kyriazakis *et al.* (1990) for *ad lib.*-fed pigs assumed to be growing at their potential. When this B value is applied to like pigs of heavier weights it implies that they would be able to grow protein at an average daily maximum rate of 190 g/d in the live-weight range 30–90 kg. This high protein growth rate is comparable to the rates of 183 and 189 g/d deposited by pigs between 33 and 88 kg live weight and 45 and 90 kg live weight in the experiments by Rao & McCracken (1990) and Campbell & Taverner (1988) respectively, which are the highest rates of protein deposition for modern pig genotypes reported in the literature (not including the protein growth rates deposited by pigs administered with exogenous growth hormone, e.g. Campbell, 1988).

Not surprisingly the rate of lipid deposition was also increased by increasing the level of feeding, and hence, energy intake. Some animals on the lowest allowance (treatment A) lost small amounts of lipid but continued to deposit protein at appreciable rates. Thus, there was no minimum lipid:protein ratio in the gain (Ellis *et al.* 1983; Whittemore, 1983); rather it can be suggested that, even at very low levels of intake, protein can still be gained at the expense of energy drawn from the lipid reserves (Fowler *et al.* 1980). These results, in combination with the observed protein growth rates, reject the second model (M2) which suggested that the rate of protein retention depends only on the rate of protein supply, providing that the lipid:protein ratio of the gain exceeds some genetically determined fixed value (Whittemore, 1983).

Table 6. *The daily rates of metabolizable energy (ME) intake, gross energy (GE) retained and heat lost by male (M) and female (F) pigs given different amounts of a starch mixture† for 4 and 8 weeks from 12 kg live weight*

Age at slaughter (weeks)	Treatment‡	ME intake (MJ/d) M	ME intake (MJ/d) F	GE retained (MJ/d) M	GE retained (MJ/d) F	Heat lost§ (MJ/d) M	Heat lost§ (MJ/d) F
4	A	7·10	7·10	1·54	1·60	5·56	5·50
	B	8·93	8·93	2·58	2·64	6·35	6·29
	C	10·74	10·74	3·80	3·71	6·94	7·03
	D	12·52	12·53	4·11	4·58	8·41	7·95
8	A	9·68	9·68	2·31	2·31	7·38	7·37
	B	12·17	12·17	3·61	3·86	8·57	8·32
	C	14·50	14·64	4·54	5·53	9·96	9·11
	D	17·08	16·61	6·15	6·26	10·93	10·35
SED		0·052		0·308		0·308	
Statistical significance of:							
Treatment (T)				***		***	
Sex (S)				NS		*	
Age (A)				***		***	
T × S				NS		NS	
T × A				*		NS	
S × A				NS		NS	
T × S × A				NS		NS	

SED, Standard error of difference; NS, not significant.
* $P < 0.05$, *** $P < 0.001$.
† For details, see Tables 1 and 2.
‡ For details, see Table 3.
§ Calculated from the equation: heat lost = ME intake − GE retained (MJ/d).

Since the rate of protein deposition was not constant at a constant protein intake, the efficiency with which protein was utilized for protein deposition (e_p) was not constant but varied with the energy supply. The net efficiency of ideal protein utilization above maintenance can be calculated from the equation:

$$PR\ (kg/d) = e_p \times ((FI \times FCP \times v \times d_{cp}) - MP), \qquad (6)$$

where PR is the protein retained (kg/d), FI is feed intake (kg/d), FCP is the food CP content (kg/kg), v is the value of digested protein in relation to ideal protein (calculated to be 0·81 for feed P), d_{cp} is the digestibility of CP (assumed to be 0·85 for feed P) and MP is the ideal protein requirement for maintenance (kg/d). This equation is similar to that proposed by the Agricultural Research Council (1981), with the exception that the maintenance protein (MP) requirement is calculated on an ideal protein basis (Whittemore, 1983; Emmans & Fisher, 1986) rather than on a CP basis from the equation:

$$MP\ (kg/d) = 0.0040 \times P, \qquad (7)$$

where P is the protein weight of the pig.

The e_p values calculated from equation 6 for the four feeding treatments and the two sexes are shown in Table 7. These values reject the views that e_p is constant and independent of the energy supply (Stranks *et al.* 1988) and that e_p is a function of protein intake only (Agricultural Research Council, 1981), since the intake of protein in the present experiment was constant across the four treatments. An alternative idea (Fuller & Crofts, 1977) that

Table 7. *The efficiency of protein utilization* (e_p) *of male* (*M*) *and female* (*F*) *pigs when given increasing amount of a starch mixture†, at constant protein intake, for 4 or 8 weeks from 12 kg live weight*

Age at slaughter (weeks)	Treatment‡	e_p	
		M	F
4	A	0·495	0·498
	B	0·678	0·694
	C	0·843	0·782
	D	0·807	0·771
8	A	0·483	0·426
	B	0·632	0·618
	C	0·759	0·621
	D	0·781	0·745
SED		0·040	
Statistical significance of:			
Treatment (T)		***	
Sex (S)		*	
Age (A)		***	
T × S		NS	
T × A		NS	
S × A		NS	
T × S × A		NS	

SED, Standard error of difference; NS, not significant.
* $P < 0.05$, *** $P < 0.001$.
† For details, see Tables 1 and 2.
‡ For details, see Table 3.

e_p is a function of the supply of energy at constant protein intake is supported by these findings. Here it is proposed that e_p has a limiting value of slightly higher than 0·80 when protein intake is limiting and the energy supply is adequate (Fig. 1). When protein intake becomes non-limiting the value of e_p increases as protein retention increases with the increased energy supply.

The effect of sex on the e_p values of the animals (Table 7) was significant ($P < 0.05$), with male pigs using protein more efficiently than females. This effect could be explained in either of two ways. The first is that females have lower rates of maximum protein retention than males, so that protein intake becomes non-limiting at lower levels than for males; thus, the decline in the e_p values when protein intake is non-limiting is expected to be seen earlier in the females than in the males. The fact that the interaction between treatment and sex was not formally significant might reflect the small number of sex replicates per treatment. The second explanation is to accept that there is a true effect of sex on the efficiency of protein utilization, with e_p expected to vary with the sex and the genotype of the animal (Agricultural Research Council, 1981). The experimental support from the literature on the matter is contradictory and inconclusive. Ellis *et al.* (1983) and Campbell & Taverner (1988) have suggested that the sex and the genotype of the animal had an effect on e_p, whereas Campbell *et al.* (1983) have suggested that at lower levels of feeding both male and female pigs partitioned nutrients in an identical way. At higher levels of feeding females reached a plateau in their protein deposition earlier than males. The results of the experiment reported here could not distinguish between the two hypotheses.

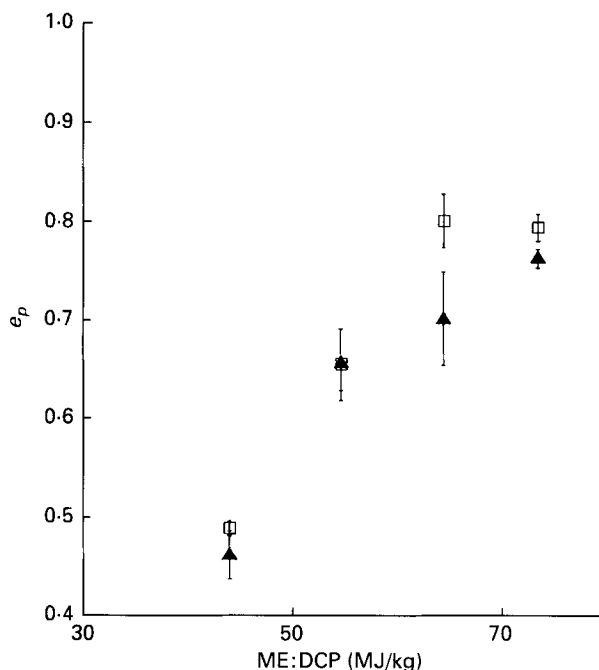When the actual ME intake was compared with the ME requirement predicted by the

Fig. 1. The efficiency of protein utilization (e_p) expressed as a function of the energy:protein ratio in the feed (MJ metabolizable energy (ME)/kg digestible crude protein (nitrogen $\times$ 6·25; DCP)), of male ($\square$) and female ($\blacktriangle$) pigs when given increasing amounts of a starch mixture. For details of feeds and treatments, see Tables 1–3 and p. 604.

Agricultural Research Council (1981) equation which uses protein retention (PR; kg/d), lipid retention (LR; kg/d) and scaled live weight ($LW^{0.63}$; kg) as terms:

$$ME_{INT} \text{ (MJ/d)} = 43 \cdot 9\ PR + 53 \cdot 5\ LR + 0 \cdot 719\ LW^{0.63}, \tag{8}$$

it was found that the predicted values were, on average, lower by 4 % than the actual values. This underestimation, consistent across the four treatments and the two sexes, could reflect either a shortcoming in the estimation of the feed spillage in the present experiment, since the Agricultural Research Council (1981) estimations are based on calorimetry experiments, or that the maintenance requirements for energy are underestimated by the Agricultural Research Council (1981) (Whittemore, 1983; Emmans & Fisher, 1986).

The results lead to the rejection of the first and second models (M1 and M2). Protein retention did depend on the rate of energy supply at constant high protein intake and there was no minimum positive lipid:protein ratio in the gain. This leaves the two other, less clearly stated models as not rejected, at least qualitatively. The results are in agreement with those of Campbell et al. (1985 a, b) at higher protein intakes where there was a response in protein retention to an increased supply of feed at equal protein intake. Further testing of these models, and an alternative, are described by Kyriazakis & Emmans (1992).

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