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Energy and nitrogen intake, expenditure and retention at 20° in growing fowl given diets with a wide range of energy and protein contents

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Heat production (HP) and the intake and retention of energy and nitrogen were measured at 20° in growing female broiler fowl given diets with metabolizable energy (ME) contents ranging from 8 to 15 MJ/kg at each of two crude protein (nitrogen × 6·25; CP) contents (130 and 210 g/kg). ME intake was partially controlled by the birds, but increased by 30 % over the range of dietary ME concentration. CP intake varied directly with dietary CP:ME ratio, indicating that control of energy intake took priority and that food intake did not increase in order to enhance amino acid intake on low-CP diets. Maintenance energy requirement and fasting HP were not affected by diet. Although the HP of fed birds was significantly affected by dietary energy source, there was no evidence for regulatory diet-induced thermogenesis as energy intake increased. Total energy retention doubled on the higher-energy diets as a result of increased intake and retention efficiency in the absence of any compensation by diet-induced thermogenesis. The proportion of energy retained as fat was negatively correlated with dietary CP:ME ratio. It was concluded that the growing female broiler fowl responded to large differences in energy intake and dietary CP concentration not by changes in rate of energy dissipation as heat but by changes in the quantity of energy retained and in the partition of retained energy between body protein and body fat.

Energy intake: Nitrogen metabolism: Thermogenesis: Broiler fowl

The domestic fowl (*Gallus domesticus*) controls its energy intake over a range of dietary crude protein (nitrogen × 6·25; CP):metabolizable energy (ME) ratios (Hill & Dansky, 1954). There is a tendency, however, for energy intake to increase with ME concentration, even when the CP:ME ratio is held constant (Fisher & Wilson, 1974). This tendency has been accentuated by reducing the CP:ME ratio (Davidson *et al.* 1961, 1964, 1968). Davidson *et al.* (1964) described an increase in calculated heat production (HP) in response to increased ME intake on a low CP:ME diet, although they were later unable to confirm this result by direct measurement of heat loss (Davidson *et al.* 1968). This diet-related and possibly regulatory increase in HP is comparable with observations in mammals (Miller & Payne, 1962; Rothwell & Stock, 1979, 1982; Gurr *et al.* 1980; Coyer *et al.* 1987). The observations in mammals have also not proved universally repeatable (Hervey & Tobin, 1982; Barr & McCracken, 1984). In both avian and mammalian species, changes in dietary CP:ME ratio have more commonly been shown to be accommodated by changes in body composition (Bartov *et al.* 1974; McCracken & McAllister, 1984). In the context of regulatory thermogenesis, it may be pertinent that an effector of diet-induced thermogenesis analogous to the brown adipose tissue of some mammals has yet to be identified in the fowl (Johnston, 1971); the tropical origin of *Gallus domesticus* may have offered no selective advantage in evolving such a tissue for a thermoregulatory role.

The experiment reported in the present paper was designed to measure the extent to which any changes in energy and protein intake produced by a wide range of CP:ME ratios

Table 1. *Compositions of base formulations used in producing the experimental diets*

Composition (g/kg)	High protein (H)	Low protein (L)
Maize	410	660
Soya-bean meal	423	231
Fish meal	70	38
Meat-and-bone meal	70	38
Limestone flour	7	8
Choline chloride	4	5
Dicalcium phosphate	4	5
Sodium chloride	4	5
Vitamin supplement*	4	5
Mineral supplement*	4	5

* Composition of supplements (mg/g supplement): vitamins: retinol 720 μg, cholecalciferol 8 μg, tocopherol 10·0, menaphthone 0·52, riboflavin 1·6, nicotinic acid 11·2, pantothenic acid 4·0; minerals: copper 1·40, iodine 0·16, iron 32, magnesium 120, manganese 40, zinc 20.

Table 2. *Composition of experimental diets*

Diet	Base H* (g/kg)	Base L* (g/kg)	Starch (g/kg)	Maize oil (g/kg)	Cellulose (g/kg)	Sand (g/kg)	CP† (g/kg)	TME† (MJ/kg)	CP:TME (g:MJ)
L1	0	650	0	0	350	0	13·0	7·6	1·7
L2	0	650	0	0	177	173	13·2	7·9	1·7
L3	0	650	290	0	60	0	13·5	12·4	1·1
L4	0	650	0	115	235	0	13·3	11·5	1·2
L5	0	650	90	200	60	0	15·5	14·7	1·1
H1	710	0	0	0	290	0	20·9	8·9	2·3
H2	710	0	0	0	117	173	20·4	7·5	2·7
H3	710	0	290	0	0	0	21·0	12·1	1·7
H4	710	0	0	115	175	0	21·1	13·4	1·6
H5	710	0	90	200	0	0	26·5	14·5	1·8

CP, crude protein (nitrogen × 6·25; TME, true metabolizable energy; H, high protein; L, low protein.

* For details of composition, see Table 1.

† Measured by the techniques described on pp. 626–627.

were accommodated by changes in HP, in energy retention or in body composition. The experiment therefore incorporated two factors previously cited as stimuli of diet-induced thermogenesis: high energy intake and low dietary protein content.

MATERIALS AND METHODS

Formulation of diets

Three target ME concentrations (8, 13 and 15 MJ/kg) were formulated at each of two CP concentrations (130 and 210 g/kg) (Tables 1 and 2). For each CP concentration there were two diets at 8 MJ/kg, which differed in that one had only cellulose (of wood origin; CEPO, Sweden) as a diluent, while the other had a mixture of cellulose with mineral sand; this comparison was to test for limitation of intake by volume. At each CP concentration, there were also two diets at 13 MJ/kg, which differed in whether the energy was added to the base diet as starch or as maize oil. The remaining diet at each CP concentration (15 MJ/kg) was formulated by adding 200 g maize oil to each kg base mix.

The lysine contents of the low- and high-CP diets were 6·7 and 12·0 g/kg respectively;

methionine + cystine contents were 4·5 and 6·8 g/kg. The high-CP diets therefore supplied amino acid:ME ratios ranging from the requirement for maximum growth rate (Agricultural Research Council, 1975) on the 15 MJ/kg diet to 2 × requirement on the 7·5 MJ/kg diets. The low-CP diets had sub-optimal amino acid:ME ratios in all but the 8 MJ/kg diets.

Experimental design and statistical analysis

The experiment was performed as a randomized block design with five time blocks. The ten diets were assigned randomly within each block. There were, therefore, five replicates of each diet. A total of 100 birds was used, giving ten (as five pairs) on each diet. Analysis of results was by two-way analysis of variance.

Birds and initial treatment

Female broiler chicks (1 d old) from a commercial line (D. B. Marshall, Newbridge, Ltd) were obtained in batches at 14 d intervals (so that they were of identical age in each time block) and reared to 21 d of age on a common diet. At 21 d of age they were randomly allocated (in pairs) to cages in a poultry house kept at 20°. The lighting pattern was 23 h light–1 h dark, giving an approximation to a commercial lighting cycle. At 21 d of age they were also given one of the ten experimental diets *ad lib.* At 28 d old, the birds were moved (still in pairs) to randomly allocated calorimetry chambers for energy and N metabolism measurements, which took place when the birds were between 29 and 36 d of age.

Experimental protocol

HP was measured by means of the indirect calorimetry apparatus and methods described by Lundy *et al.* (1978) with improvements to the gas analysis system (MacLeod *et al.* 1985). The birds were fasted for their first 48 h in the calorimeter chambers. The first 24 h allowed the birds to reach a basal level of metabolism; fasting HP (HP_b) and endogenous faecal and urinary energy and N losses were measured for the second 24 h. A day of *ad lib.* feeding was then allowed before energy and N balances were measured in the fed state during days 4, 5 and 6. Stability of results between days 4 and 6 was taken to indicate that 1 d of recovery was sufficient after fasting.

Excreta collection and calculation of ME

Excreta were collected in polymethacrylate (Perspex) trays placed on the floors of the calorimetric chambers. Daily collections were made over 3 d during feeding and over the second day of fasting. The samples were stored at −20° in sealed aluminium dishes until they were freeze-dried and ground for analysis. True ME (TME) intake (I_{TME}) (Sibbald, 1976) was calculated as

$$I_{TME} = I_E - ((\text{faecal} + \text{urinary})\ \text{energy}) + (\text{endogenous}\ (\text{faecal} + \text{urinary})\ \text{energy}),$$

where I_E is gross energy intake.

Chemical analysis of food and droppings

N contents were measured by the Kjeldahl method, using Buchi digestion and distillation. Fat contents were measured by petroleum ether extraction following hydrolysis in 3 M-hydrochloric acid. Energy contents were measured by adiabatic bomb calorimetry.

Calculation of energy retention and partition

Total energy retention (R_E) was calculated as

$$R_E = I_E - ((\text{faecal} + \text{urinary})\ \text{energy}) - \text{HP},$$

Table 3. *Effects of dietary protein and energy on intakes of dry matter, energy and nitrogen of growing fowl and mean body-weight during the measurement period*

Diet*	TME (MJ/kg)	CP (g/kg)	Body-wt (g)	Dry matter intake (g/bird per d)	Dry matter intake (g/kg $W^{0·75}$ per d)	TME intake (kJ/bird per d)	TME intake (kJ/kg $W^{0·75}$ per d)	N intake (g/bird per d)	N intake (g/kg $W^{0·75}$ per d)	Net energy intake (kJ/bird per d)	Net energy intake (kJ/kg $W^{0·75}$ per d)
L1	7·6	13·0	560	111	176	902	1440	2·45	3·91	699	1117
L2	7·9	13·2	669	126	177	1044	1469	2·79	3·93	773	1088
L3	12·4	13·5	692	96	132	1274	1759	2·24	3·09	1045	1443
L4	11·5	13·3	642	86	125	1049	1520	1·95	2·81	858	1243
L5	14·7	15·5	781	94	118	1509	1875	2·51	3·11	1304	1620
H1	8·9	20·9	692	107	150	1018	1411	3.85	5.40	763	1058
H2	7·5	20·4	814	135	164	1074	1318	4·67	5·71	840	1031
H3	12·1	21·0	801	104	131	1361	1710	3·78	4·74	1066	1337
H4	13·4	21·1	682	103	145	1474	2081	3·70	5·25	1240	1749
H5	14·5	26·5	763	87	112	1343	1730	3·91	5·12	1139	1469
SEM (individual treatments, *n* 5)			55·1	6·0	6·4	982	103.9	0·208	0·246	88·7	100·6
LSD (df 8, $P < 0·05$)			127·1	13·9	14·8	226·4	239·6	0·480	0·567	204·5	232·0
L diets mean			669	103	146	1155	1612	2·39	3·37	936	1302
H diets mean			749	107	140	1254	1650	3·98	5·24	1010	1329
Protein level effect, high *v.* low			$P < 0·05$	NS	NS	NS	NS	$P < 0·001$	$P < 0·001$	NS	NS
Energy concentration/source			$P < 0·05$	$P < 0·001$	$P < 0·001$	$P < 0·001$	$P < 0·001$	$P < 0·01$	$P < 0·01$	$P < 0·001$	$P < 0·001$
Interaction			NS	NS	$P < 0·05$	NS	$P < 0·01$	NS	NS	NS	$P < 0·05$

L1–L5, low protein; H1–H5, high protein; TME, true metabolizable energy; CP, crude protein (N × 6·25); $W^{0·75}$, metabolic body size; SEM, standard error of the mean; LSD, least significant difference; NS, not significant.

* For details of composition, see Tables 1 and 2.

N retention (R_N) was determined as

$$R_N = I_N - ((\text{faecal} + \text{urinary})\ \text{N}),$$

where I_N is N intake, and CP retention as 6·25 R_N. Energy retained as CP was given by 23·7 × 6·25 R_N. Energy retained as fat could, therefore, be calculated by subtracting energy retained as CP from R_E. Retention of fat by weight was then calculated by dividing fat energy by 39·2. The values of 23·7 and 39·2 kJ/g used for the energy contents of protein and fat are those quoted by Znaniecka (1967).

RESULTS

Food intake

Control of energy intake was indicated by a decrease of about 30% in dry matter intake (Table 3) as TME concentration increased (r –0·756; df 47; $P < 0·001$). Control was not exact, however, and this reduction in food consumption still permitted an increase of about 30% in TME intake (r 0·768; df 47; $P < 0·001$). Because of the tendency for net efficiency of energy utilization for maintenance and growth ($k_{m,g}$; Table 4) to increase with dietary fat content, the intake of net energy between lowest and highest TME concentrations increased by about 40%.

There was no effect of CP concentration on food intake apart from an interaction ($P < 0·05$) with the effect of dietary TME concentration when intakes were expressed in terms of metabolic body size (kg body-weight $(W)^{0·75}$).

N intake (Table 3) was significantly affected by dietary CP concentration ($P < 0·001$). The absence of significant control of N intake was indicated by the similarity in the ratios of N intakes (0·64) and dietary N concentrations (0·62) on the L and H diets. Further confirmation came from the close correlation (r 0·767, df 47, $P < 0·001$) between N intake and CP:ME ratio.

Energy expenditure

HP per bird (but not per kg $W^{0·75}$) was significantly affected ($P < 0·05$) by dietary concentrations of both energy and protein (Table 4). HP was maximal with the intermediate-energy high-carbohydrate diets L3 and H3 rather than those in which energy intake was highest. For the latter diets (L4, L5, H4, H5) net utilization efficiencies ($k_{m,g}$ calculated for each bird-pair as $\Delta R_E/\Delta I_{TME}$; Table 4) were significantly higher than those for the other diets, except L3. Therefore, although $k_{m,g}$ was significantly ($P < 0·001$) affected by the carbohydrate and fat contents of the diet, it was not influenced by dietary CP concentration.

Significant dietary effects on HP_b per bird (Table 4) resulted from differences in body-weight and were absent when the measurements were expressed in terms of $W^{0·75}$. Maintenance TME requirement per kg $W^{0·75}$ (Table 4), calculated as the I_{TME} required to give zero retained energy (i.e. $HP_b/k_{m,g}$), was similarly unaffected by either dietary CP or dietary energy concentrations.

Respiratory quotient (RQ: Table 4) was significantly ($P < 0·001$) affected by dietary carbohydrate, fat and CP contents. The effect of added fat was particularly noticeable. Birds in all treatments had a mean RQ of about 0·72 during fasting.

R_E

R_E and gross efficiency of energy retention were significantly affected by dietary energy ($P < 0·001$) but not by CP concentration (Table 5). There was a very strong correlation between R_E and TME concentration (r 0·782; df 47; $P < 0·001$).

The amount of energy retained as fat (Table 5) was strongly associated with dietary

Table 4. *Effects of dietary protein and energy on heat production (HP), net efficiency of energy utilization for maintenance and growth ($k_{m,g}$), maintenance energy requirement and respiratory quotient (RQ) of growing fowl*

			Fed HP		Fasting HP			Maintenance TME requirement			
Diet*	TME (MJ/kg)	CP (g/kg)	(kJ/bird per d)	(kJ/kg $W^{0.75}$ per d)	(kJ/bird per d)	(kJ/kg $W^{0.75}$ per d)	$k_{m,g}$	(kJ/bird per d)	(kJ/kg $W^{0.75}$ per d)	Fed RQ	Fasting RQ
L1	7·6	13·0	524	830	322	568	0·76	470	742	1·01	0·72
L2	7·9	13·2	615	863	344	561	0·74	504	705	1·00	0·71
L3	12·4	13·5	642	889	413	634	0·82	543	753	1·05	0·71
L4	11·5	13·3	530	766	339	548	0·81	450	653	0·98	0·73
L5	14·7	15·5	633	798	428	597	0·87	532	673	0·97	0·72
H1	8·9	20·9	610	845	356	567	0·75	522	724	0·94	0·72
H2	7·5	20·4	662	811	428	604	0·78	592	726	0·89	0·71
H3	12·1	21·0	732	921	436	623	0·78	598	754	0·95	0·72
H4	13·4	21·1	616	871	382	614	0·84	491	695	0·88	0·71
H5	14·5	26·5	641	830	437	629	0·85	559	728	0·88	0·72
SEM			37·5	26·7	24·7	23·1	0·023	32·9	30·4	0·020	0·008
LSD			86·5	61·6	57·0	53·3	0·053	75·9	70·1	0·046	0·018
L diets mean			589	829	369	582	0·80	500	705	1·00	0·72
H diets mean			652	855	408	608	0·80	552	725	0·91	0·72
Protein level effect, high *v.* low			$P < 0.05$	NS	$P < 0.05$	NS	NS	$P < 0.05$	NS	$P < 0.001$	NS
Energy concentration/source			$P < 0.05$	$P < 0.05$	$P < 0.01$	NS	$P < 0.001$	$P < 0.05$	NS	$P < 0.001$	NS
Interaction			NS	NS	NS	NS	NS	NS	NS	NS	NS

L1–L5, low protein; H1–H5, high protein; TME, true metabolizable energy; CP, crude protein (N × 6·25); $W^{0.75}$, metabolic body size; SEM, standard error of the mean; LSD, least significant difference; NS, not significant.

* For details of composition, see Tables 1 and 2.

Table 5. *Energy retention, partition of retained energy between fat and protein and gross efficiency of true metabolizable energy (TME) retention of growing fowl*

			Energy retention							
			Total		As fat		As protein			
Diet*	TME (MJ/kg)	CP (g/kg)	(kJ/bird per d)	(kJ/kg $W^{0\cdot75}$ per d)	(kJ/bird per d)	(kJ/kg $W^{0\cdot75}$ per d)	(kJ/bird per d)	(kJ/kg $W^{0\cdot75}$ per d)	Fraction of energy retained as fat	Gross efficiency of TME retention
L1	7·6	13·0	349	565	229	367	121	197	0·65	0·34
L2	7·9	13·2	401	567	211	299	190	268	0·53	0·38
L3	12·4	13·5	599	824	431	591	168	232	0·72	0·47
L4	11·5	13·3	491	713	368	535	123	178	0·75	0·46
L5	14·7	15·5	843	1036	638	784	206	252	0·76	0·55
H1	8·9	20·9	373	517	172	239	201	279	0·46	0·36
H2	7·5	20·4	377	462	145	177	232	285	0·38	0·35
H3	12·1	21·0	598	749	338	423	260	326	0·56	0·43
H4	13·4	21·1	828	1168	520	733	308	435	0·63	0·56
H5	14·5	26·5	666	852	333	411	333	441	0·48	0·49
SEM			80·1	102·7	68·8	91·3	24·8	33·7	0·046	0·047
LSD			184·7	236·8	158·7	210·5	57·2	77·7	0·106	0·108
L diets mean			537	741	375	515	162	225	0·68	0·44
H diets mean			568	750	302	397	267	353	0·49	0·44
Protein level effect, high *v*. low			NS	NS	NS	$P < 0\cdot05$	$P < 0\cdot001$	$P < 0\cdot001$	$P < 0\cdot001$	NS
Energy concentration/source			$P < 0\cdot001$	$P < 0\cdot001$	$P < 0\cdot001$	$P < 0\cdot001$	$P < 0\cdot01$	$P < 0\cdot05$	$P < 0\cdot001$	$P < 0\cdot001$
Interaction			$P < 0\cdot05$	$P < 0\cdot05$	$P < 0\cdot05$	NS	NS	$P < 0\cdot01$	NS	NS

L1–L5, low protein; H1–H5, high protein; CP, crude protein (N × 6·25); $W^{0\cdot75}$, metabolic body size; SEM, standard error of the mean; LSD, least significant difference; NS, not significant.

* For details of composition, see Tables 1 and 2.

energy ($P < 0{\cdot}001$). The effect of CP concentration was less distinct and attained significance ($P < 0{\cdot}05$) only when results were adjusted for $W^{0{\cdot}75}$. There were strong negative correlations between CP:TME ratio and both rate of fat retention (r 0·755; df 47; $P < 0{\cdot}001$) and proportion of energy retained as fat (r 0·806; df 47; $P < 0{\cdot}001$). The rate of energy retention in the form of protein was significantly affected both by dietary CP ($P < 0{\cdot}001$) and by dietary energy characteristics ($P < 0{\cdot}05$). There was also a significant interaction ($P < 0{\cdot}01$) between the latter two factors.

A comparison of the partial energetic efficiencies (k_P and k_F) and costs ($1/k_P$ and $1/k_F$) of protein and fat deposition on the grouped low-protein (L) and high-protein (H) diets was made by multiple regression analysis. The equations are shown below, the coefficients for R_E being equal to $1/k_P$ and $1/k_F$ respectively. Standard errors of coefficients and constants are shown in parentheses next to the corresponding mean. The proportion of variation accounted for by the regression is in parentheses after each equation.

L diets (df 24): $I_{TME} = 455$ (SE 16·8) + 2·13 $R_{E,P}$ (SE 0·24) + 0·98 $R_{E,F}$ (SE 0·07) (0·99)
H diets (df 24): $I_{TME} = 488$ (SE 22·5) + 1·75 $R_{E,P}$ (SE 0·17) + 0·97 $R_{E,F}$ (SE 0·08) (0·99)
all diets (df 49): $I_{TME} = 475$ (SE 12·3) + 1·78 $R_{E,P}$ (SE 0·11) + 1·01 $R_{E,F}$ (SE 0·04) (0·98)

Partial energetic efficiency of protein deposition, k_P was, therefore, 0·47 (i.e. 1/2·13) on L diets and 0·57 on H diets. Combining both sets of diets gave 0·56. Although there was a tendency for the energy cost of protein deposition to be higher (and k_P lower) on the L diets, this tendency was not statistically significant. The values for k_F were close to unity in all cases.

R_N

Gross efficiency of R_N, partial efficiency of R_N (calculated as $\Delta R_N/\Delta I_N$) and N maintenance requirement (calculated as I_N where $R_N = 0$) were all significantly ($P < 0{\cdot}001$) affected by dietary energy concentration (Table 6). Both indices of efficiency tended to increase with dietary energy, while maintenance requirement tended to decrease. Only maintenance requirement, however, was significantly influenced by dietary CP ($P < 0{\cdot}05$), being positively correlated with CP concentration (r 0·736, df 47, $P < 0{\cdot}001$) and with CP:TME ratio (r 0·576; df 47; $P < 0{\cdot}001$). Gross efficiency of R_N was negatively correlated with N maintenance requirement (r −0·797; df 47; $P < 0{\cdot}001$) and positively with partial efficiency of R_N retention (r 0·938; df 47; $P < 0{\cdot}001$).

Losses of fat and protein during fasting

When measurements were expressed on a kg $W^{0{\cdot}75}$ basis, there was no significant effect of either dietary CP or dietary energy on total losses of body energy reserves during fasting (Table 7). However, dietary energy had highly significant effects ($P < 0{\cdot}001$) on partition of energy loss between fat and protein, a greater proportion being lost as fat on the higher-energy diets. Dietary CP concentration had a significant effect ($P < 0{\cdot}01$) only on the absolute quantity of energy lost as protein.

DISCUSSION

Intakes

The variation in I_{TME} and net energy intake indicated imperfect control of voluntary intake. I_{TME}, at 1·8–3 times maintenance energy requirement, ranged from just below to well above typical intakes for birds of this type and age. There was, therefore, a range of response from slight energy restriction on diets L1, L2, H1 and H2 to energy hyperphagia on diets L4, L5, H4 and H5. The gradient of the relationship between energy intake and dietary TME

Table 6. *Efficiencies of nitrogen retention and N maintenance requirement of growing fowl*

					N maintenance requirement	
Diet*	TME (MJ/kg)	CP (g/kg)	Gross efficiency of N retention	Partial efficiency of N retention	(g/bird per d)	(g/kg $W^{0·75}$ per d)
L1	7·6	13·0	0·34	0·51	0·93	1·44
L2	7·9	13·2	0·46	0·60	0·64	0·89
L3	12·4	13·5	0·51	0·66	0·52	0·72
L4	11·5	13·3	0·43	0·60	0·57	0·83
L5	14·7	15·5	0·54	0·67	0·45	0·59
H1	8·9	20·9	0·36	0·51	1·23	1·75
H2	7·5	20·4	0·34	0·46	1·16	1·48
H3	12·1	21·0	0·46	0·57	0·71	0·90
H4	13·4	21·1	0·56	0·65	0·52	0·74
H5	14·5	26·5	0·57	0·66	0·56	0·72
SEM			0·036	0·035	0·111	0·161
LSD			0·083	0·081	0·254	0·371
L diets mean			0·45	0·61	0·62	0·90
H diets mean			0·46	0·57	0·84	1·11
Protein level effect			NS	NS	$P < 0·01$	$P < 0·05$
Energy concentration/source			$P < 0·001$	$P < 0·001$	$P < 0·001$	$P < 0·001$
Interaction			$P < 0·05$	NS	NS	NS

L1–L5, low protein; H1–H5, high protein; TME, true metabolizable energy; CP, crude protein (N × 6·25); $W^{0·75}$, metabolic body size; SEM, standard error of the mean; LSD, least significant difference; NS, not significant.

* For details of composition, see Tables 1 and 2.

concentration (calculated from the results in Table 3) was 66 kJ/bird for every MJ/kg increase in TME intake. This gradient is close to the upper end of the range of those reviewed by Fisher & Wilson (1974). Its steepness may have resulted partly from a combination of a negative effect of cellulose and sand diluents on palatability and a positive effect of added fat (Cherry, 1982). The range of energy intakes was still controlled to well below the 2-fold range of dietary TME concentration. Measured TME concentrations of the high-cellulose diets L1, L2, H1 and H2 were similar to those calculated on the basis of a value of 0 MJ/kg for added cellulose, indicating that there was no appreciable contribution of cellulolysis to TME. A different source of cellulose, bird age or dietary history might have produced a different result (Duke *et al.* 1984). Control of energy intake took priority over any control of CP intake, allowing CP intake to vary in direct proportion to dietary CP:TME ratio. Energy overconsumption was therefore not used by the birds as a means of increasing amino acid intake. A similar result over a 12-fold range of CP concentrations was described by Harris *et al.* (1988) in the Zucker rat.

HP

Despite the wide range of energy and CP intakes produced by the experimental design, there was no evidence of a regulatory change in HP in response either to high-energy or low-CP diets and intakes. HP reached a peak on the high-carbohydrate diets (L3 and H3) and tended to be lowest on the high-fat diets, on which energy intakes were maximal. The HP of fasting birds varied even less with diet. These results were consistent with a low heat increment from fat and inconsistent with regulatory diet-induced thermogenesis. This was confirmed by the results for $k_{m,g}$ (efficiency of utilization of total ME for maintenance and growth). On the other hand, the similarity of $k_{m,g}$ for the two levels of CP is difficult to

Table 7. *Energy losses and partition of energy losses during fasting*

			Total endogenous energy loss		Energy lost as fat		Energy lost as protein		
Diet*	TME (MJ/kg)	CP (g/kg)	(kJ/bird per d)	(kJ/kg $W^{0.75}$ per d)	(kJ/bird per d)	(kJ/kg $W^{0.75}$ per d)	(kJ/bird per d)	(kJ/kg $W^{0.75}$ per d)	Fraction of energy lost as fat
L1	7·6	13·0	349	617	288	507	61	109	0·82
L2	7·9	13·2	371	606	315	514	56	92	0·85
L3	12·4	13·5	445	686	395	607	50	78	0·88
L4	11·5	13·3	366	593	316	511	50	81	0·86
L5	14·7	15·5	460	643	417	580	43	63	0·90
H1	8·9	20·9	390	623	301	477	89	145	0·76
H2	7·5	20·4	463	656	383	536	80	119	0·82
H3	12·1	21·0	467	669	408	582	59	86	0·87
H4	13·4	21·1	411	661	362	582	48	78	0·88
H5	14·5	26·5	473	681	418	603	54	78	0·88
SEM			25·1	24·1	25·9	24·8	5·8	9·9	0·016
LSD			57·9	55·6	59·8	57·3	13·4	22·8	0·037
L diets mean			398	629	346	544	52	85	0·86
H diets mean			441	658	374	556	67	102	0·84
Protein level effect			$P < 0.05$	NS	NS	NS	$P < 0.001$	$P < 0.01$	NS
Energy concentration/source			$P < 0.01$	NS	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Interaction			NS	NS	NS	NS	NS	NS	NS

L1–L5, low protein; H1–H5, high protein; TME, true metabolizable energy; CP, crude protein (N × 6·25); $W^{0.75}$, metabolic body size; SEM, standard error of mean; LSD, least significant difference; NS, not significant.

* For details of composition, see Tables 1 and 2.

reconcile with classical ideas of the cost of protein synthesis (Millward *et al.* 1976) but agrees with the results of Close *et al.* (1983) with pigs and Coyer *et al.* (1987) with rats; it does not fit simple models for estimating the net energy of feedstuffs, in which protein is given a k value of 0·20 lower than that of carbohydrate (de Groote, 1974). Although there was a large range of protein accretion rates, especially between the high and low CP concentrations, there was no indication of the relationship between fasting HP and protein accretion which might have been predicted from the results of Keller (1980), who described a correlation between fasting HP and growth rate in the chicken.

R_E

The 2-fold range of R_E at each CP concentration resulted from the combination of increased intake and increased $k_{m,g}$ in the absence of regulatory diet-induced thermogenesis. Most of the variation in retention was in the form of fat, but protein retention also increased with TME concentration, presumably because less protein was required as a source of energy. The strong correlation between proportion of energy gained as fat and CP:TME ratio confirmed the susceptibility of the growing fowl's body composition to dietary influences. The equality of gross efficiencies of TME retention between protein levels was unexpected in the light of the differing compositions of R_E and the different theoretical energetic efficiencies of protein and fat deposition.

As the HP results suggested, there was no significant change in the energy cost of protein accretion between high-CP and low-CP diets. This result contrasts with the doubling of energy costs of protein deposition in rats fed on diets containing between 166 and 68 g CP/kg (Coyer *et al.* 1987) but agrees with results from pigs fed between 258 and 153 g CP/kg (Close *et al.* 1983). The mean level of k_P was similar to that of 0·51 found by Petersen (1970) in growing chickens. As in the last three papers quoted, the calculated energy cost of protein synthesis (about 2 kJ/kJ protein) was considerably higher than stoichiometric calculation would predict (1·15 kJ/kJ; Millward *et al.* 1976). Only part of this discrepancy is likely to be due to resynthesis associated with protein turnover and, as Coyer *et al.* (1987) suggest, much of it may be attributable to parallel but causally unrelated increases in HP. The high k_F on all diets is probably a result of the collinearity between protein and fat deposition, which is known to limit the reliability of the multiple-regression technique for estimating k_P and k_F (Roux *et al.* 1976).

Female broilers were used for the present study. The influence of this choice on the result may be important but can only be determined by further experiment.

R_N

The catabolism of amino acids as an energy source was indicated by the high N maintenance requirement and low gross and partial efficiencies of R_N observed as CP:TME ratio increased. A wide range of protein intake inevitably resulted from the precedence given to control of energy intake; the contribution of protein to energy intake therefore increased greatly as the energy concentration of the diet decreased. Conversely, the proportion of non-protein energy decreased, leaving amino acids to function increasingly as energy substrates through either oxidation, gluconeogenesis or lipogenesis. Evans & Scholz (1971) demonstrated that chicks have a well-developed ability to increase the rate of gluconeogenesis from protein when fed on a high-protein, carbohydrate-limited diet. The differences in rate of amino acid deamination persisted even during fasting in the present experiment and contributed to the higher maintenance requirement for N on the high-protein diets.

CONCLUSIONS

Growing female fowl responded to large differences in voluntary energy intake and dietary protein concentration by changes in the quantity and chemical form of retained energy but not in the rate of energy dissipation as heat.

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