Energy and nitrogen intake, expenditure and retention at 32° 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 in growing broiler fowl kept at 32° and given diets with metabolizable energy contents from 8 to 15 MJ/kg and crude protein ($N \times 6.25$; CP) contents of 130 and 210 g/kg. The temperature of 32° was chosen for comparison with earlier measurements at 20° to minimize heat produced for the maintenance of body temperature. The effects of diet composition were observed when the same birds were taken from 20 to 32°. The tendency for energy intake to increase with dietary energy concentration was less at 32 than at 20°. The lower heat increments measured for the high-fat diets did not, therefore, confer an increased ability to sustain higher energy intake at 32°. HP was about 17% lower at 32 than at 20°; the change in HP between 20 and 32° was not significantly influenced by diet composition. The absence of significant effects of diet composition on HP, combined with the significant trend in energy intake, produced significant differences (related both to dietary energy and dietary protein concentrations) in total energy retention and in the partition of retained energy between protein and fat. As at 20°, variation in energy retention and in the composition of retained energy were the main responses to variation in dietary CP concentration and energy intake; a significantly higher energy cost of unit protein accretion on the low-CP diets was insufficient to produce an elevation in total HP because the higher unit energy cost was balanced by a lower absolute rate of protein accretion.

Energy metabolism: Nitrogen metabolism: Environmental temperature: Fowl

The metabolic rate and energy intake of the growing fowl decrease almost linearly over a wide range as ambient temperature increases, without firm evidence of a zone of minimal metabolic rate below 35°. This is true of both acclimated and unacclimated birds, whether fed or fasted (Farrell & Swain, 1977*a*, *b*). In a previous experiment (MacLeod, 1990), the energy metabolism responses of chickens, kept at 20°, to a wide range of dietary energy concentrations coupled with two widely differing dietary protein concentrations to produce an extreme range of protein:energy ratios were investigated. Because of the effects of ambient temperature on energy expenditure and requirements, however, it is predictable that responses of heat production (HP) and body composition to dietary protein:energy ratio will also be sensitive to temperature. The birds previously kept at 20° were, therefore, studied also at 32° on the same diets. Direct statistical comparisons of 20 and 32° means must, therefore, be viewed with caution, since the birds were slightly older when exposed to 32° and had been exposed to the diets and experimental conditions for a longer period. A formal statistical comparison of the effects of diet is possible, however, between the within-bird changes produced by the increase in temperature from 20 to 32°.

The three main questions to be investigated by study at 32° were: (1) do the lower heat increments found at 20° for the high-fat diets alleviate the reduction of food intake

produced by temperature increase? The basis of this hypothesis is that there should be less metabolic heat for the bird to dissipate per unit food energy consumed; (2) if relative hyperphagia occurs, as at 20°, is there any evidence for the existence of regulatory diet-induced thermogenesis? It is probable that the expression of such a response would be modified by ambient temperature; (3) how is the partition of body energy deposition between fat and protein affected by environmentally-induced changes in food intake and HP?

MATERIALS AND METHODS

The experiment immediately followed that of MacLeod (1990), using the same birds and diets. Many of the procedures were unchanged.

Three target metabolizable energy (ME) concentrations (8, 13 and 15 MJ/kg) were formulated at each of two crude protein (nitrogen × 6·25; CP) concentrations (130 and 210 g/kg) (see Tables 1 and 2 of MacLeod, 1990). 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/kg to the base mix.

Temperature treatments

One hundred female broiler chicks from a commercial line were fed *ad lib.* from 21 d old on one of the ten diets described previously. They were maintained, in pairs, at 20° until 36 d of age (MacLeod, 1990), when ambient temperature was acutely increased to 32°. Energy and N intakes and losses were measured in paired birds from day 4 to day 6 at 32°. Fasting heat production (HP_b) and endogenous faecal and urinary energy and N losses were measured on day 8 after an initial day of fasting. The lighting pattern was 23 h light–1 h dark, giving an approximation to a commercial lighting cycle.

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. The total of 100 birds gave ten (as five pairs) on each diet. The main between-diet comparison was of the within-bird changes produced by the increase in temperature from 20 to 32°. The 32° means were also compared. Both analyses were by two-way analysis of variance.

Energy and N metabolism measurements

HP was measured by means of indirect calorimetry. Daily excreta collections were made over 3 d during feeding and over the second day of fasting. Freeze-dried food and excreta samples were analysed for energy and N. Details of methods and of calculation of true metabolizable energy (TME), total energy retention (R_E), N retention (R_N), energy retained as CP ($R_{E,P}$), energy retained as fat ($R_{E,F}$) and fat retention were given by MacLeod (1990).

RESULTS AND DISCUSSION

Intakes

As at 20° (MacLeod, 1990) there was a significant effect of dietary energy concentration on TME intake (I_{TME}) ($P < 0.001$), although there was less of a tendency at 32° for I_{TME} to increase with energy concentration (Table 1) (the gradient of the relationship between

daily energy intake and dietary TME concentration at 32° was about 50 kJ per bird for every MJ/kg increase in TME compared with 80 kJ per bird for every MJ/kg at 20°). This led to a significant ($P < 0.001$) effect of dietary energy concentration on the decrease in intake between 20 and 32°. There were strong correlations between decrease in intake (I_{TME}, 20° − I_{TME}, 32°) and both I_{TME}, 20° (r 0.769; df 34; $P < 0.001$) and dietary energy metabolizability (I_{TME}/I_E, where I_E is gross energy intake) measured at 20° (r 0.575; df 34; $P < 0.001$). An increase in metabolizability of L1 and H1 (the two highest-fibre diets) at 32° contributed to this effect. The cause of the increased metabolizability is not known. Contrary to the hypothesis (see p. 195) that the lower heat increment of a high-fat diet would permit greater intake at high temperatures, the tendency for high fat content to increase energy intake was, therefore, less at 32 than at 20°. There was no indication of higher energy intake on added-fat diets L4 and H4 than on the iso-energetic added-carbohydrate diets L3 and H3. The high energetic efficiency of fat deposition indicated by a low heat increment (Tasaki & Kushima, 1979) did not, therefore, give the hypothesized benefits at 32°. Perception by the bird of the absolute intake of energy, therefore, seems to have been more important, in terms of control, than the heat increment associated with its metabolism. There was a significant effect of protein concentration on food intake at 32° which did not occur at 20°, but this was not associated with a difference in efficiency of utilization (k) or the complementary heat increment.

As at 20°, control of energy intake took priority over control of N intake. In relative terms, therefore N intake decreased on both dietary CP levels by about the same amount (25%) as the decrease in energy intake between temperatures. N intake (Table 6), therefore, decreased by a significantly greater ($P < 0.001$) absolute amount on the high-protein diets.

The food intake results give support to experiments which have failed to show significant advantages of a high-fat diet in terms of enhanced heat tolerance or have shown that a high-fat diet fed at high ambient temperatures confers no food intake advantage beyond that found in cooler conditions (Persons et al. 1967; Kubena et al. 1972, 1973; Dale & Fuller, 1979).

Energy expenditure

There was no significant effect of diet treatment on HP when the effect of the greater body-weight of the birds on the high-protein diets was removed by scaling on kg body-weight$^{0.75}$ (Table 2). HP was 17% lower at 32 than at 20°; the difference between 20 and 32° measurements was not significantly affected by either dietary energy or dietary protein (Table 2). HP_b and the differences between HP_b at 20 and 32° were also unaffected by diet, but HP_b decreased proportionally more (30%) than fed HP. This indicated a greater heat increment at 32°, which led to a significant ($P < 0.05$) decrease in k for maintenance and growth ($k_{m,g}$) at 32° (Table 3). Unlike the case at 20°, maintenance energy requirement was significantly ($P < 0.001$) affected by dietary protein content, being about 8% greater on the higher-protein diets. Despite this, there was no significant dietary effect on the 20–32° change in maintenance requirement (Table 3).

The range of I_{TME} at 32° was 1.4–2.4 times I_{TME} at maintenance (a 1.7-fold increase, as at 20°; MacLeod, 1990). As at 20°, however, neither the large range of intakes as functions of maintenance energy requirement nor the large differences in dietary CP, stimulated a response in HP which could be interpreted as regulatory. Even when the possible masking effect of cold-induced thermogenesis was reduced by elevating ambient temperature from 20 to 32°, there was, therefore, no indication of regulatory diet-induced thermogenesis.

Table 1. *Effects of diet on body-weight, dry matter intake, energy intake and on the differences between measurements in the same birds at 32 and 20°*

(The difference was calculated for each bird-pair as (measurement at 32°) – (measurement at 20°))

Diet*	Body-wt (g)	Dry matter intake			TME intake		
		g/bird per d	g/kg W^{0.75} per d	32–20° difference (g/kg W^{0.75} per d)	kJ/bird per d	kJ/kg W^{0.75} per d	32–20° difference (kJ/kg W^{0.75} per d)
L1	777	111	144	−32	1021	1316	−296
L2	829	108	127	−49	819	1008	−470
L3	870	82	95	−38	1122	1344	−378
L4	846	90	106	−19	1187	1402	−127
L5	990	79	85	−34	1255	1257	−762
H1	891	103	120	−30	1007	1151	−262
H2	1022	121	125	−39	894	917	−400
H3	969	76	82	−49	970	1035	−786
H4	873	85	97	−48	1086	1247	−737
H5	979	79	86	−26	1291	1312	−396
SEM (individual treatments *n* 5)	53·5	4·2	6·8	6·3	57·8	58·0	69·5
Least significant difference (df 8; *P* < 0·05)	123·1	9·7	15·7	14·7	133·3	133·8	162·0
L diets mean	862	94	111	−34	1081	1266	−407
H diets mean	947	93	102	−38	1050	1133	−516
Statistical significance of:							
Protein level effect H *v*. L: *P*	< 0·05	NS	< 0·05	NS	NS	< 0·01	< 0·05
Energy concentration/source: *P*	NS	< 0·001	< 0·001	NS	< 0·001	< 0·001	< 0·001
Interaction: *P*	NS	NS	NS	< 0·05	NS	NS	< 0·001

L1–L5, low-protein diets; H1–H5, high-protein diets; TME, true metabolizable energy; NS, not significant; W^{0.75}, metabolic body size (body-weight^{0.75}).
* For details of composition, see MacLeod (1990).

Table 2. *Effects of diet on fed and fasting heat production and respiratory quotient (RQ) of growing fowl and on the differences between these measurements at 32 and 20°*

Diet*	Fed heat production			Fasting heat production			Fed RQ	Fasted RQ
	kJ/bird per d	kJ/kg W^0.75 per d	32–20° difference (kJ/kg W^0.75 per d)	kJ/bird per d	kJ/kg W^0.75 per d	32–20° difference (kJ/kg W^0.75 per d)		
L1	556	718	−113	319	389	−179	1·02	0·71
L2	576	678	−185	345	412	−149	0·98	0·71
L3	619	706	−183	371	422	−213	1·06	0·71
L4	581	687	−79	341	405	−143	0·94	0·72
L5	608	633	−165	398	415	−183	0·92	0·70
H1	642	732	−113	358	402	−165	0·93	0·72
H2	667	685	−126	378	388	−217	0·87	0·71
H3	677	719	−202	419	449	−175	0·95	0·70
H4	626	712	−160	383	425	−189	0·86	0·72
H5	664	702	−128	412	421	−208	0·85	0·72
SEM (individual treatment; n 5)	25·8	23·0	30·9	18·9	16·1	25·9	0·024	0·010
LSD (df 8; $P < 0.05$)	59·5	53·0	72·0	43·6	37·1	60·3	0·056	0·023
L diets mean	588	684	−145	355	409	−173	0·98	0·71
H diets mean	655	710	−146	390	417	−191	0·89	0·71
Statistical significance of:								
Protein level effect H v. L: P	< 0·001	NS	NS	< 0·01	NS	NS	< 0·001	NS
Energy concentration/source: P	NS	NS	NS	< 0·01	NS	NS	< 0·001	NS
Interaction: P	NS	NS	NS	NS	NS	NS	NS	NS

L1–L5, low-protein diets; H1–H5, high-protein diets; NS, not significant; LSD, least significant difference; W^0.75, metabolic body size (body-weight^0.75).

* For details of composition, see MacLeod (1990).

Table 3. *Effects of diet on efficiency of energy utilization, maintenance energy requirements and net energy intake of growing fowl and on the differences between these measurements at 32 and 20°*

Diet*	$k_{m,g}$ 32°	$(k_{m,g})-(k_{m,g})$ (32°) (20°)	Maintenance TME			Net energy intake		
			kJ/bird per d	kJ/kg $W^{0.75}$ per d	32–20° difference (kJ/kg $W^{0.75}$ per d)	kJ/bird per d	kJ/kg $W^{0.75}$ per d	32–20° difference (kJ/kg $W^{0.75}$ per d)
L1	0·78	−0·02	452	583	−98	796	1023	−270
L2	0·70	−0·04	528	642	−58	576	718	−368
L3	0·79	−0·02	467	564	−188	887	1078	−328
L4	0·78	−0·03	482	576	−89	935	1120	−136
L5	0·82	−0·03	537	545	−126	1039	1048	−671
H1	0·73	−0·01	534	620	−102	736	861	−190
H2	0·66	−0·12	637	658	−68	602	622	−409
H3	0·73	−0·04	648	691	−60	706	759	−648
H4	0·77	−0·05	526	611	−77	839	975	−671
H5	0·82	−0·03	535	533	−105	1052	1080	−364
SEM (individual treatment; n 5)	0·017	−0·023	32·3	34·4	32·6	54·6	57·2	71·0
LSD (df 8; P < 0·05)	0·039	−0·054	74·5	79·3	76·0	125·9	131·9	165·4
L diets mean	0·77	−0·03	493	582	−112	847	997	−355
H diets mean	0·74	−0·05	576	627	−82	787	859	−456
Statistical significance of:								
Protein level effect H v. L : P	< 0·01	NS	< 0·001	< 0·05	NS	NS	< 0·001	< 0·05
Energy concentration/source : P	< 0·001	NS	NS	NS	NS	< 0·001	< 0·001	< 0·001
Interaction : P	NS	NS	NS	NS	NS	NS	NS	< 0·001

L1–L5, low-protein diets; H1–H5, high-protein diets; TME, true metabolizable energy; $k_{m,g}$, efficiency of energy utilization for maintenance and growth; NS, not significant; LSD, least significant difference; $W^{0.75}$, metabolic body size (body-weight$^{0.75}$).

* For details of composition, see MacLeod (1990).

$$R_E$$

The absence of significant diet composition effects on HP, combined with significant effects on I_{TME}, resulted in significant differences in R_E related both to dietary energy and CP ($P < 0.001$) (Table 4). Changes in retention between 32 and 20° were also significantly influenced by both dietary energy ($P < 0.01$) and CP ($P < 0.05$); R_E from L diets decreased by 32% and R_E from H diets by 46%. There was also a significant interaction between energy and CP. The greater part of the reduction in R_E was in the form of fat. Fat deposition decreased by 37% on the L diets and 60% on the H diets between 20 and 32°. The mean proportion of total energy retained as fat was 0.53 at 32° compared with 0.61 at 20°. Protein energy retention decreased by 19 and 28% on L and H diets respectively between 20 and 32°. These decreases were of similar magnitude to those measured in TME and N intakes. The larger decreases in R_E as fat occurred because HP at 32° decreased less than I_E, while protein deposition rate decreased in proportion to I_E. HP was, therefore, sustained at the expense of fat deposition. (If HP and I_E had decreased at the same rate while protein deposition as a fraction of CP intake had remained constant, no change in composition of body energy gain would have resulted. If HP had decreased more rapidly than I_E while protein deposition had been maintained, the birds would have become fatter at 32°. Any change in gross efficiency of N retention as temperature increased would also influence composition of gain.)

Gross TME retention efficiencies at 32° and the 20–32° differences were significantly affected by both CP and energy characteristics of the diet; retention was about 20% lower on the H diets than on the L diets ($P < 0.05$).

Multiple regression analysis was used, as in MacLeod (1990), to compare the partial energetic efficiencies and costs of protein (k_p and $1/k_p$ respectively) and fat (k_F and $1/k_F$ respectively) synthesis. Regressions were calculated for all five L diets, all five H diets and for all ten diets combined. The equations are shown, with coefficients equal to $1/k_p$ and $1/k_F$ respectively. Standard errors of coefficients and constants are in parentheses next to the corresponding mean. The proportion of variation accounted for by the regression (r^2) appears in parentheses after each equation:

L diets (df 24): $I_{TME} = 410$ (SE 16.5) $+ 2.47$ $R_{E.P}$ (SE 0.24) $+ 0.91$ $R_{E.F}$ (SE 0.007) (r^2 0.99),

H diets (df 24): $I_{TME} = 417$ (SE 18.5) $+ 1.99$ $R_{E.P}$ (SE 0.12) $+ 0.92$ $R_{E.F}$ (SE 0.07) (r^2 0.99),

all diets (df 49): $I_{TME} = 453$ (SE 11.4) $+ 2.06$ $R_{E.P}$ (SE 0.02) $+ 0.96$ $R_{E.F}$ (SE 0.04) (r^2 0.99).

k_p was, therefore, 0.40 (i.e. $1/2.47$) on low-protein diets and 0.50 on high-protein diets; combining both sets of diets gave 0.49. k_F was greater than 1 in all cases, possibly for the reasons given by Roux et al. (1976) and mentioned by MacLeod (1990). The energy cost of protein deposition was significantly higher on the low-protein diets, reinforcing the statistically insignificant trend at 20° (MacLeod, 1990) and agreeing with the results of Coyer et al. (1987). The higher energy cost of unit protein accretion on the L diets, although insufficient to produce a rise in total HP, would help to account for the similarity between $k_{m.g}$ values on the L and H diets at both 20 and 32°. It is difficult to explain why lower dietary CP should be associated with an increase in cost of unit protein accretion. A higher rate of protein degradation and resynthesis (turnover) would be a possible mechanism, but it seems likely that protein turnover would be increased rather than decreased by the H diet (Millward et al. 1975). On the L diets, there may be a greater need for the interconversion of amino acids to maximize deposition of body protein, but interconversions of amino acids are more often exergonic than endergonic (Schulz, 1978), so this effect is unlikely to lead to a net increase in energy cost. As Coyer et al. (1987) suggested, there may be an increase in a component of HP which is statistically but not mechanistically linked to rate of protein accretion; in the case of rats, Coyer et al. (1987) proposed that the component may have been catecholamine-mediated diet-induced thermogenesis. Any such effect in the present

Table 4. *Effects of diet on energy retention, gross energetic efficiency of growing fowl and on the differences between these measurements at 32 and 20°*

Diet*	Energy retention			Gross TME efficiency	
	kJ/bird per d	kJ/kg $W^{0.75}$ per d	32–20° difference (kJ/kg $W^{0.75}$ per d)	32°	32–20° difference
L1	440	565	−184	0·43	−0·02
L2	218	278	−295	0·25	−0·14
L3	478	554	−238	0·46	−0·01
L4	578	683	−30	0·46	0·00
L5	612	615	−533	0·46	−0·12
H1	351	405	−112	0·35	−0·01
H2	187	194	−268	0·18	−0·18
H3	278	298	−529	0·24	−0·21
H4	429	494	−584	0·40	−0·14
H5	618	627	−261	0·48	−0·03
SEM (individual treatment; n 5)	52·4	57·7	67·5	0·042	0·037
LSD (df 8; $P < 0.05$)	120·8	133·1	157·3	0·097	0·086
L diets mean	465	539	−256	0·41	−0·06
H diets mean	373	404	−351	0·33	−0·12
Statistical significance of:					
Protein level effect H *v.* L: P	< 0·01	< 0·001	< 0·05	< 0·01	< 0·05
Energy concentration/source: P	< 0·001	< 0·001	< 0·01	< 0·001	< 0·05
Interaction: P	NS	NS	< 0·001	NS	< 0·01

L1–L5, low-protein diets; H1–H5, high-protein diets; TME, true metabolizable energy; NS, not significant; LSD, least significant difference; $W^{0.75}$, metabolic body size (body-weight$^{0.75}$).
* For details of composition, see MacLeod (1990).

experiment was insufficient to cause a significant increase in total HP or a significant decrease in $k_{m,g}$, since the higher unit cost of protein accretion on the L diets was balanced by the lower absolute quantity of protein retained. This resulted in the mean total energy cost of protein accretion (including the chemical energy of retained protein) being higher on the H diets (490 *v.* 454 kJ/kg body-weight$^{0.75}$ per d). Changes in fat deposition (Table 5) rather than energy expenditure, therefore, constituted the major sink for 'excess' energy intake.

R_N

Gross (R_N/I_N, where I_N is N intake) and partial ($\Delta R_N/\Delta I_N$) efficiencies of N retention, and N maintenance requirement (Table 6), were all significantly influenced ($P < 0.001$) by dietary energy characteristics, but only N maintenance requirement was significantly affected by dietary CP ($P < 0.001$). N maintenance requirement was also significantly correlated with CP:TME ratio (r 0·749; df 34; $P < 0.001$). Gross N retention efficiency was, predictably, negatively correlated with N maintenance requirement (r −0·548; df 34; $P < 0.001$) and positively correlated with partial efficiency of N retention (r 0·940; df 34; $P < 0.001$). N maintenance requirement per unit metabolic body size (body-weight$^{0.75}$) decreased between 20 and 32° by 39 % on L diets and 19 % on H diets, but this did not lead to a significant increase in gross efficiency because of the decrease in total N intake.

Losses of fat and protein during fasting

Total endogenous energy loss (Table 7) consists mainly of HP_b; both its absolute magnitude and decrease with temperature rise, therefore, corresponded closely with the HP_b results and were not significantly affected by either dietary energy or N when adjusted

Table 5. *Effects of diet on energy retention as fat and protein by growing fowl and on the differences between these measurements at 32 and 20°*

Diet*	Energy retained as fat			Energy retained as protein		
	kJ/bird per d	kJ/kg $W^{0.75}$ per d	32–20° difference (kJ/kg $W^{0.75}$ per d)	kJ/bird per d	kJ/kg $W^{0.75}$ per d	32–20° difference (kJ/kg $W^{0.75}$ per d)
L1	278	357	−189	162	208	6
L2	69	96	−206	150	185	−86
L3	332	393	−176	146	169	−55
L4	423	505	−30	155	185	7
L5	435	445	−446	176	174	−83
H1	351	138	−71	241	277	−32
H2	187	−25	−203	210	220	−65
H3	278	95	−377	188	203	−151
H4	429	264	−412	203	236	−167
H5	618	339	−194	286	294	−61
SEM (individual treatment; n 5)	52·4	54·4	58·5	19·6	20·2	27·1
LSD (df 8; $P < 0.05$)	120·8	125·4	136·3	45·2	46·6	11·6
L diets mean	465	359	−210	158	184	−42
H diets mean	373	162	−251	225	246	−95
Statistical significance of:						
Protein level effect H *v.* L:*P*	< 0·01	< 0·001	NS	< 0·001	< 0·001	< 0·01
Energy concentration/source:*P*	< 0·001	< 0·001	< 0·05	< 0·05	NS	< 0·05
Interaction:*P*	NS	NS	< 0·001	NS	NS	< 0·01

L1–L5, low-protein diets; H1–H5, high-protein diets; NS, not significant; LSD, least significant difference; $W^{0.75}$, metabolic body size (body-weight$^{0.75}$).
* For details of composition, see MacLeod (1990).

Table 6. *Effects of diet on nitrogen intake, N maintenance requirement, efficiencies of N retention of growing fowl and on the differences between these measurements at 32 and 20°*

Diet*	N intake			N maintenance requirement			Gross efficiency of N retention		Partial efficiency of N retention	
	g/bird per d	g/kg $W^{0.75}$ per d	32–20° (g/kg $W^{0.75}$ per d)	g/bird per d	g/kg $W^{0.75}$ per d	32–20° difference (g/kg $W^{0.75}$ per d)	32°	32–20° difference	32°	32–20° difference
L1	2·46	3·19	−0·72	0·65	0·84	−0·63	0·44	0·10	0·59	0·09
L2	2·39	2·84	−1·09	0·57	0·69	−0·23	0·44	−0·03	0·58	−0·04
L3	1·92	2·21	−0·88	0·33	0·39	−0·32	0·52	0·01	0·63	−0·04
L4	2·02	2·38	−0·44	0·39	0·46	−0·37	0·52	0·09	0·64	0·04
L5	2·09	2·24	−0·87	0·35	0·37	−0·21	0·59	0·04	0·74	0·06
H1	3·72	4·32	−1·08	0·92	1·09	−0·35	0·48	0·08	0·63	0·08
H2	4·21	4·34	−1·36	1·00	1·07	−0·41	0·33	−0·00	0·44	−0·02
H3	2·77	2·96	−1·78	0·79	0·84	−0·04	0·45	−0·04	0·63	0·04
H4	3·08	3·51	−1·74	0·64	0·74	−0·05	0·45	−0·07	0·56	−0·04
H5	3·60	3·98	−1·14	0·57	0·58	−0·14	0·61	0·07	0·74	0·09
SEM (individual treatment; *n* 5)	0·170	0·266	0·204	0·086	0·104	0·123	0·038	0·043	0·039	0·046
LSD (df 8; *P* < 0·05)	0·392	0·613	0·475	0·198	0·239	0·287	0·088	0·100	0·090	0·107
L diets mean	2·18	2·57	−0·799	0·46	0·55	−0·35	0·50	0·04	0·64	0·02
H diets mean	3·48	3·82	−0·421	0·79	0·86	−0·20	0·46	0·01	0·60	0·03
Statistical significance of:										
Protein level effect H *v.* L: *P*	< 0·001	< 0·001	< 0·001	< 0·001	< 0·001	NS	NS	NS	NS	NS
Energy concentration/source: *P*	< 0·001	< 0·001	NS	< 0·001	< 0·001	NS	< 0·001	NS	< 0·001	NS
Interaction: *P*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

L1–L5, low-protein diets; H1–H5, high-protein diets; NS, not significant; LSD, least significant difference; $W^{0.75}$, metabolic body size (body-weight$^{0.75}$).

* For details of composition, see MacLeod (1990).

Table 7. *Effects of previous diet on endogenous energy loss, on its partition between fat and protein in growing fowl and on the differences between these measurements at 32 and 20°*

Diet*	Total endogenous energy loss			Energy lost as fat		Energy lost as protein		Proportion lost as fat	
	kJ/bird per d	kJ/kg $W^{0.75}$ per d	32–20° difference (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	32°	32–20° difference
L1	347	424	−194	298	363	48	60	0·86	0·04
L2	372	445	−162	322	385	50	60	0·87	0·02
L3	379	447	−249	345	407	32	38	0·91	0·02
L4	374	446	−155	336	401	37	43	0·90	0·04
L5	435	455	−189	394	411	41	44	0·91	0·00
H1	396	445	−178	311	348	85	97	0·78	0·02
H2	414	425	−231	345	352	69	74	0·83	0·01
H3	457	491	−183	383	411	71	76	0·84	−0·03
H4	416	461	−201	370	410	45	51	0·89	0·01
H5	451	462	−221	395	404	57	57	0·88	−0·01
SEM (individual treatment; n 5)	18·8	17·8	27·8	19·8	17·3	7·6	8·6	0·019	0·016
LSD (df 8; P < 0·05)	43·4	41·3	64·8	45·7	39·9	17·5	19·8	0·044	0·037
L diets mean	381	443	−190	339	393	42	49	0·89	0·02
H diets mean	427	457	−203	361	385	65	71	0·84	0·00
Statistical significance of:									
Protein effect H *v.* L: *P*	< 0·001	NS	NS	NS	NS	< 0·001	< 0·001	< 0·001	< 0·05
Energy concentration/source: *P*	< 0·01	NS	NS	NS	< 0·01	< 0·05	< 0·01	< 0·01	NS
Interaction: *P*	NS	NS	NS	NS	NS	NS	NS	NS	NS

L1–L5, low-protein diets; H1–H5, high-protein diets; NS, not significant; LSD, least significant difference; $W^{0.75}$, metabolic body size (body-weight$^{0.75}$).

* For details of composition, see MacLeod (1990).

for body-weight. Absolute energy loss as fat increased significantly with dietary energy concentration. CP concentration had significant effects on energy lost as protein ($P <$ 0.001) and on proportion of energy lost as fat ($P < 0.001$). The influence of previous diet on losses during fasting may be due either to the preferential catabolism of nutrients which are most available during feeding or to the differences in body composition resulting from diet.

Conclusions

Contrary to the initial hypothesis, the lower heat increment associated with high-fat diets conferred relatively less of an advantage of higher intake at 32 than at 20°. Although there was a wide range of energy intakes as multiples of maintenance energy requirement, there was no indication that variation in HP was used as a mechanism for control of energy retention; as at 20°, variations in energy retention and body composition remained the main responses to variations in dietary CP concentration and CP:ME ratio. A higher energy cost per unit protein accretion ($1/k_p$) on the low-CP diets was insufficient to produce an elevation of total HP; the higher unit energy cost was balanced by the lower absolute rate of protein accretion. A smaller proportion of energy was retained as fat at 32 than at 20° because, while protein accretion rate decreased in proportion to I_E, HP decreased less than I_E, leaving HP to be sustained at the expense of fat deposition.

REFERENCES

Coyer, P. A., Rivers, J. P. W. & Millward, D. J. (1987). The effect of dietary protein and energy restriction on heat production and growth costs in the young rat. *British Journal of Nutrition* **58**, 73–85.

Dale, N. M. & Fuller, H. L. (1979). Effect of low temperature, diet density, and pelleting on the preference of broilers for high fat rations. *Poultry Science* **58**, 1337–1339.

Farrell, D. J. & Swain, S. (1977a). Effects of temperature treatments on the heat production of starving chickens. *British Poultry Science* **18**, 725–734.

Farrell, D. J. & Swain, S. (1977b). Effect of temperature treatments on the energy and nitrogen metabolism of fed chickens. *British Poultry Science* **18**, 735–748.

Kubena, L. F., Reece, F. W., Deaton, J. W. & May, J. D. (1972). Heat prostration of broilers as influenced by dietary energy source. *Poultry Science* **51**, 1744–1747.

Kubena, L. F., Reece, F. W., Deaton, J. W. & May, J. D. (1973). The effect of dietary fat level on heat prostration of broilers. *Poultry Science* **52**, 1691–1693.

MacLeod, M. G. (1990). Energy and nitrogen intake, expenditure and retention at 20° in growing fowl given diets with a wide range of energy and protein contents. *British Journal of Nutrition* **64**, 625–637.

Millward, D. J., Garlick, P. J., Stewart, R. J. C., Nnanyelugo, D. O. & Waterlow, J. C. (1975). Skeletal-muscle growth and protein turnover. *Biochemical Journal* **150**, 235–243.

Persons, J. N., Wilson, H. R. & Harms, R. H. (1967). Relationship of diet composition to survival time of chicks when subjected to high temperature. *Proceedings of the Society for Experimental Biology and Medicine* **126**, 604–606.

Roux, C. Z., Hofmeyr, H. S. & Meissner, M. M. (1976). The prediction and description of growth from the partitioning of energy for heat production and the synthesis of protein and fat. In *Energy Metabolism of Farm Animals. Proceedings of the 7th European Association of Animal Production Symposium*, pp. 157–160 [M. Vermorel, editor]. Clermont-Ferrand: G. de Bussac.

Schulz, A. R. (1978). Simulation of energy metabolism in the simple-stomached animal. *British Journal of Nutrition* **39**, 235–254.

Tasaki, I. & Kushima, M. (1979). Heat production when single nutrients are given to fasted cockerels. In *Energy Metabolism. Proceedings of the 8th European Association of Animal Production Symposium*, pp. 253–256 [L. E. Mount, editor]. London: Butterworths.

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