*British Journal of Nutrition* (1986), **56**, 595–605



# Effect of previous nutrition on body composition and maintenance energy costs of growing lambs

BY C. L. FERRELL, L. J. KOONG AND J. A. NIENABER

*USDA, ARS, Roman L. Hruska US Meat Animal Research Center, Clay Center, NE 68933, USA*

(*Received 3 September 1985 – Accepted 27 May 1986*)

1. Forty-eight intact male lambs (30 kg) were fed to gain 16 (H), 5 (M) or −6 (L) kg during a 42 d interval (period 1). Lambs from each of the H and M groups were fed to gain either 16 (HH, MH), 5 (HM, MM) or −6 (HL, ML) kg and lambs from the L group were fed to gain 27 (LS), 16 (LH) or 5 (LM) kg during the ensuing 42 d (period 2).

2. Fasting heat production (FHP) of four lambs from each treatment was determined at the end of period 2.

3. Weights and compositions of the carcass, offal and digesta-free body as well as weights of major internal organs were determined for four lambs of each treatment at the end of periods 1 and 2.

4. Within groups of lambs of similar weight at the end of period 2, body composition was, in general, similar, but FHP was greater in lambs that had been on higher planes of nutrition during period 2.

5. Within groups of lambs of similar weight, lambs that were fed at higher planes of nutrition during period 2 had greater weights or proportions of liver, small intestine, large intestine and stomach.

6. Neither weight of the liver, kidney, stomach, small intestine, large intestine nor daily fasting heat production were constant functions of body-weight. Relations of these traits to body-weight changed with rate of gain.

7. Regression analysis indicated that the feeding of lambs at higher planes of nutrition during period 1 resulted in higher maintenance requirements of those lambs during period 2.

The phenomenon of compensatory gain, in which a faster or more efficient rate of gain, or both, has been observed following a period of nutritional or environmental stress, has been studied for a number of years (for review, see Wilson & Osbourn, 1960). Webster (1979) reviewed some of the current literature and concluded that the compensatory-gain response was primarily a result of differences in the composition of body tissue gained during the period of realimentation. Information available in this area, however, is not consistent. Information is available, for example, to show that at similar body-weights, body fat is increased (Searle *et al.* 1972), not changed (Burton & Reid, 1969) or decreased after a period of realimentation. Several reports (Marston, 1948; Walker & Garrett, 1970; Graham & Searle, 1972; Graham *et al.* 1974; Foot & Tulloh, 1977; Ledger & Sayers, 1977; Gray & McCracken, 1979; Andersen, 1980) have shown that fasting heat production (FHP) or maintenance requirements decrease in response to low levels of feed intake. Other reports (Flatt & Coppock, 1963; Drew & Reid, 1975; Webster *et al.* 1982) indicate FHP or maintenance requirements were not influenced by nutritional level. In many of these studies, however, the influences of nutritional level, duration of nutritional treatment, age or body weight have been confounded. Therefore, the objectives of the present study were to evaluate the influence of nutritional manipulation on body composition of lambs at the same age and weight and to ascertain the effects of previous nutritional manipulation on food utilization by lambs.

## EXPERIMENTAL

### *Animals and diets*

Forty-eight intact male crossbred (1/2 Suffolk, 1/4 or 3/8 Rambouillet, 1/8 or 1/4 Finnish Landrace) lambs were obtained shortly after weaning and weighed about 30 kg. Lambs were

confined in individual pens (1·3 × 1·3 m) and fed on a pelleted diet comprising (g/kg) 450 lucerne (*Medicago sativa*), 450 maize, 50 soya-bean meal, 5 limestone, 5 sodium chloride, 5 ammonium chloride, 25 lignin sulphate, 10 bone meal, 0·5 vitamins A, D and E supplement (2·64 mg vitamin A, 22 $\mu$g vitamin D and 0·44 mg vitamin E per g) and 0·0825 monensin at assigned levels once daily throughout the study. The diet contained 10·6 MJ metabolizable energy and 150 g crude protein (nitrogen × 6·25)/kg. The room in which the lambs were housed was maintained at 21° and lighting was controlled (12 h light–12 h dark).

*Experimental procedure*

Sixteen lambs were assigned to each of three treatments during period 1 (Fig. 1, p. 599). Lambs assigned to the high (H) level of nutrition were fed to gain 16 kg during the 42 d period (period 1). Lambs assigned to the medium (M) and low (L) treatments were fed to gain 5 and −6 kg respectively during this period. At the end of period 1, four lambs from each group were killed. The remaining twelve lambs from the H group were randomly assigned to three groups and fed to gain 16 (HH), 5 (HM) or −6 (HL) kg during the ensuing 42 d period (period 2). Similarly, four lambs from the M treatment were fed to gain 16 (MH), 5 (MM) or −6 (ML) kg and four lambs from the L treatment were fed to gain 27 (LS), 16 (LH) or 5 (LM) kg during period 2. At the end of the 84 d study, target weights were: 62 kg for lambs assigned to treatment HH, 51 kg for lambs assigned to treatments HM, MH and LS, 40 kg for lambs assigned to treatments HL, MM and LH and 29 kg for lambs assigned to treatments ML and LM. Live weights were obtained twice weekly; minor adjustments (usually 50 or 100 g/d) in individual feed allowances were made at those times to achieve the target weight changes.

At the end of period 2, lambs were fasted for 48 h and then moved to open-circuit indirect calorimetry chambers. Beginning 8 h later, oxygen consumption, carbon dioxide production and methane production were determined during a 16 h period. The equipment and procedures used for these determinations have been described previously (Nienaber & Maddy, 1985). Because $CH_4$ was not produced in measurable quantities, FHP of each lamb was calculated from consumption of $O_2$ and production of $CO_2$. The resulting values were adjusted to 24 h. Lambs were killed immediately after the conclusion of these determinations.

*Sampling and chemical methods*

At the end of periods 1 and 2, lambs were stunned with a captive bolt gun and exsanguinated. Blood was collected and the pelt, head and shanks were removed. Lambs were eviscerated and digesta were removed from the gastrointestinal tract. Weights of blood, pelt-head-shanks, warm carcass, liver, heart, kidney, spleen, stomach complex, small intestine, large intestine and the remaining tissues were recorded. All non-carcass body components were then combined and will be subsequently referred to as offal. The carcass and offal were frozen (−2°) and stored pending further processing. Weight loss during storage was assumed to be water loss.

The carcass of each lamb was subsequently ground by use of a large meat grinder and then mixed. This procedure was repeated three times. Three samples (100–150 g) were taken at random from the aggregate, wrapped in cheesecloth (weighed previously) and the sample plus cheesecloth weight was recorded. The offal was processed similarly. Samples were stored at −2° until analysed. Dry matter content of the samples was determined by freeze-drying to a constant weight and water content was calculated as the difference between weights of the wet and dry sample. Fat content of the samples was determined as the difference in dry weight before and after extraction with diethyl ether in a large Soxhlet apparatus for 7 d. The dry diethyl-ether-extracted samples were ground by use of a Wiley

mill (1 mm screen). N content of the fat-free dry sample was determined by macro-Kjeldahl and crude protein was calculated as N × 6·25. Ash content was determined after 24 h at 575°. Carcass and offal compositions were calculated from weights of those tissues and percentage composition. Weights of empty-body chemical components were calculated as the sum of carcass and offal components.

### *Statistical methods*

Values were analysed by analysis of variance and regression techniques using procedures provided by the Statistical Analysis System (Barr *et al.* 1979). If the analysis of variance test indicated significant treatment effects, means within groups of animals of similar weight (i.e. HM, MH, LS; HL, MM, LH; or ML, LM) or within groups of animals that gained weight at similar rates during period 2 (HH, MH, LH; HM, MM, LM; or HL, ML) were compared by Student's *t* test.

## RESULTS

Mean initial weights of animals assigned to each of the final treatment groups were similar (Table 1). Mean weights (kg) of lambs killed at the end of period 1 were 44·9 (H), 35·5 (M) and 25·4 (L; residual SD 0·96) kg compared with mean weights of 45·1, 35·0 and 24·5 kg for lambs not killed at 42 d but assigned to H, M and L treatments during period 1 (Table 1). Lambs assigned to the HH, LS and LH groups did not attain target weights during period 2 (Fig. 1, Table 1). Weights of lambs assigned to the other treatment groups were similar to the target weights during and at the end of the 42 d period. Daily food intake required to achieve the target weights decreased from the high to the low treatment within each 42 d period (Table 1). Also, within a final weight group (e.g. HL, MM, LH), daily food intake over the entire 84 d test was lower for lambs that had been assigned to gain at lower rates during period 1 ($P < 0·05$).

Weights of the empty (digesta-free) body, empty-body chemical components and organ weights (except spleen) differed ($P < 0·05$) among treatment groups at the end of period 1 (Table 2). That weights of these body constituents differed in response to altered levels of feed intake during period 1 was consistent with experimental protocol. It should be noted, however, that weights of empty-body water (553 *v.* 555 *v.* 577 g/kg) and protein (182 *v.* 195 *v.* 212 g/kg) increased ($P < 0·025$), and weight of fat (218 *v.* 200 *v.* 160 g/kg) decreased in proportion to empty-body-weight as plane of nutrition decreased from H to L. Weights of liver and small intestine decreased ($P < 0·01$), weight of heart increased ($P < 0·05$) and weights of other organs remained constant ($P > 0·10$) in proportion to empty-body-weight as plane of nutrition decreased. Similar findings were observed when weights of organs were expressed relative to empty-body protein.

Lambs fed to attain heavier body-weights had greater weights of empty-body (Table 3) and weights of empty-body chemical components at the end of period 2. Within groups of lambs that had the same targeted final weight, empty-body-weight differed (i.e. HM = MH > LS and HL = MM > LH). Thus amounts of empty-body chemical components relative to empty-body-weight are reported. The LS lambs had a greater proportion of water and a lower proportion of fat than HM or MH lambs. Few other patterns of significance were observed when comparisons were made within groups of lambs that had similar final weights. Within those groups, however, FHP (kJ/kg body-weight$^{0·75}$ per d) increased ($P < 0·05$) as plane of nutrition during period 2 increased. For example, FHP of HM, MH and LS lambs was 321, 365 and 412 kJ/kg body-weight$^{0·75}$ per d respectively and FHP of LM, LH and LS lambs was 290, 347 and 412 kJ/kg body-weight$^{0·75}$ per d respectively. Conversely, FHP did not differ among groups of lambs that had similar rates

Table 1. *Live weight and feed intake of lambs assigned to different nutritional treatments*
(Mean values for four lambs)

| Days of treatment... Treatment | Live weight (kg) | | | Daily dry feed intake (g) | | |
|---|---|---|---|---|---|---|
| | 0 | 42 | 84 | 0–42 | 43–84 | 0–84 |
| HH | 29·8 | 44·5 | 55·8 | 1556 | 1820 | 1688 |
| HM | 29·9 | 45·5 | 50·6 | 1557 | 1231 | 1403 |
| MH | 29·3 | 35·5 | 49·0 | 1014 | 1453 | 1234 |
| LS | 29·7 | 24·7 | 44·0 | 410 | 1531 | 970 |
| HL | 29·6 | 45·2 | 39·8 | 1545 | 622 | 1083 |
| MM | 30·0 | 35·5 | 39·8 | 951 | 882 | 917 |
| LH | 28·9 | 24·3 | 36·9 | 411 | 1057 | 734 |
| ML | 28·1 | 34·0 | 29·1 | 992 | 343 | 667 |
| LM | 29·1 | 24·4 | 28·7 | 426 | 645 | 535 |
| Residual SD | 1·57 | 0·87 | 1·33 | 48 | 66 | 49 |

Treatments are described by a two-letter code such that the first letter indicates lambs which were fed to attain weight gains of 16 (H), 5 (M) or −6 (L) kg during the period from 0 to 42 d. The second letter indicates lambs which were fed to attain weight gains of 27 (S), 16 (H), 5 (M) or −6 (L) kg during the period from 43 to 84 d.

of gain during period 2 (e.g. FHP for HM, MM and LM lambs was 321, 299 and 290 respectively ($P > 0{\cdot}10$)) even though the weight, composition, and composition of gain differed substantially among those groups of lambs.

Lambs that were heavier at slaughter, in general, had greater organ weights (Table 4) than those that were lighter. When comparisons were made among groups of lambs of similar weight, lambs that had been on a higher plane of nutrition during period 2 had greater ($P < 0{\cdot}05$) weights (or proportions) of liver, kidney, large intestine, small intestine and stomach, with no difference ($P > 0{\cdot}10$) in weight of spleen and a lower ($P < 0{\cdot}05$) weight of heart than lambs fed at lower planes of nutrition. For example, weights of livers of HM, MH and LS lambs were 537, 628 and 668 g respectively ($P < 0{\cdot}05$). Conversely, when lambs that had similar rates of gain during period 2 were compared, proportions of liver, heart, kidney and spleen were similar among groups (e.g. liver weights were 13·7, 13·6 and 14·6 g/kg body-weight for HM, MM and LM lambs ($P > 0{\cdot}10$)) but components of the gut were greatest in lambs that had been fed to gain at the lower level during period 1.

The response of FHP to nutritional manipulation appeared to be most closely paralleled by that of the liver, kidney, small intestine and stomach. Simple correlations between weights of these organs and FHP were 0·69, 0·68, 0·82 and 0·68 respectively. Similar correlations were observed between average daily gain (0·67) or daily food intake (0·69) and FHP during period 2, whereas lower correlations were observed between offal (0·48), carcass (0·37) or empty-body-weight (0·42) and FHP.

The relation between weight of a specific organ and body-weight is usually represented by a power function. An exponent greater than, less than or equal to 1·0 indicates that rate of growth of an organ is greater than, less than or equal to that of the whole animal. However, findings reported in Table 4 indicated that lambs of similar weight but different rates of gain had different weights of certain organs. Results of regression analyses (Table 5) indicate that at the end of period 2, weights of the liver, kidney, stomach, small intestine and large intestine each varied in proportion to a power of body-weight but that for each

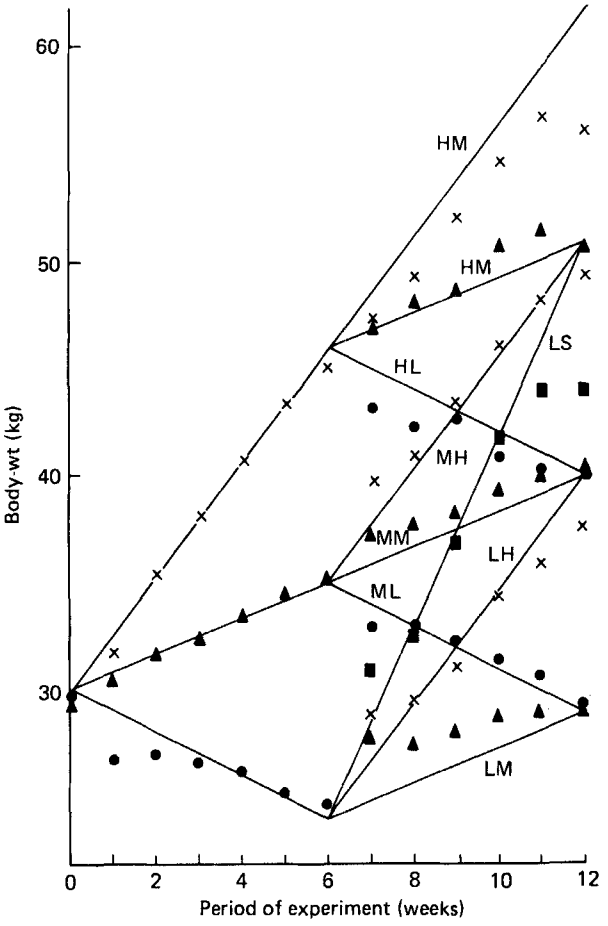


Fig. 1. Live body-weight of lambs assigned to various treatment groups with respect to period on test. Lambs assigned to gain 16 (H), 5 (M) or −6 (L) kg during period 1 (0 to 42 d) are indicated by ×, ▲ and ● respectively. Similarly, lambs fed to gain 16 (HH, MH, LH), 5 (HM, MM, LM) and −6 (HL, ML) kg during period 2 (43–84 d) are also indicated by ×, ▲ and ● respectively. Those fed to gain 27 (LS) kg are indicated by ■. Solid lines indicate target weights with respect to period on test.

of these organs, the power increased with rate of body-weight-gain during period 2. Analysis of the relation of daily heat production (DHP, kJ/d) to empty-body-weight (EBW, kg) and average daily gain (ADG, kg/d) during period 2 resulted in similar findings. The resulting equation was:

$$\text{DHP} = 361\ \text{EBW}^{0{\cdot}668+0{\cdot}238\ \text{ADG}}\ R^2\ 0{\cdot}81.$$

Both regression coefficients were highly significant ($P < 0{\cdot}001$). This result suggested that DHP was a function of EBW raised to a power which increased with increased rate of gain during period 2.

Regressions of rate of gain on body size and food intake for lambs during period 2 that had been assigned to different planes of nutrition during period 1 (Table 6) suggest that efficiency of live-weight gain was higher and the amount of food required to maintain body-weight was lower during period 2 for lambs that had been fed to gain at lower rates during period 1.

Table 2. *Weights of the empty body, empty-body chemical components and various organs of lambs killed at the end of the first 42 d feeding period (period 1)*

(Mean values for four lambs)

| Empty-body component | Treatment | | | Residual SD |
|---|---|---|---|---|
| | H | M | L | |
| Wt (kg) | 34·0 | 26·8 | 18·4 | 1·37 |
| Water (kg) | 18·8 | 14·9 | 10·6 | 0·84 |
| Fat (kg) | 7·4 | 5·4 | 2·9 | 0·68 |
| Protein (kg) | 6·2 | 5·2 | 3·9 | 0·18 |
| Ash (kg) | 1·34 | 1.17 | 0·88 | 0·076 |
| Liver (g) | 887 | 494 | 335 | 68·0 |
| Heart (g) | 171 | 149 | 130 | 17·3 |
| Kidney (g) | 149 | 104 | 74 | 12·9 |
| Spleen (g) | 65 | 60 | 50 | 9·7 |
| Large intestine (g) | 406 | 385 | 255 | 47·8 |
| Small intestine (g) | 753 | 561 | 305 | 48·6 |
| Stomach (g) | 1131 | 839 | 493 | 95·6 |

H, M and L lambs were fed to gain 16, 5 and −6 kg during the first 42 d feeding period respectively.

Residual SD estimates are based on 9 error degrees of freedom. SE may be calculated as residual SD/$\sqrt{n_i}$ where $n_i = 4$.

Table 3. *The effect of nutritional treatment on weight of empty body, relative amounts of empty-body chemical components and fasting heat production of lambs at the end of the second 42 d feeding period (period 2)*

(Mean values for four lambs)

| Treatment | Empty body-wt (kg) | Empty-body components (g/kg empty-body-weight) | | | | Fasting heat production (kJ/kg body-wt$^{0·75}$ per d) |
|---|---|---|---|---|---|---|
| | | Water | Fat | Protein | Ash | |
| HH | 44·9 | 516 | 262 | 179 | 38·0 | 373 |
| HM | 40·6[a] | 521[a] | 249[a] | 182[a] | 40·0[a] | 321[a] |
| MH | 38·8[a] | 529[a] | 250[a] | 175[a] | 37·2[a] | 365[a, b] |
| LS | 34·5[b] | 593[b] | 185[b] | 176[a] | 36·9[a] | 412[b] |
| HL | 30·5[a] | 557[a] | 199[a] | 196[a] | 46·4[a] | 290[a] |
| MM | 31·2[a] | 545[a] | 226[a] | 180[b] | 42·2[a, b] | 295[a, b] |
| LH | 28·3[b] | 573[a] | 203[a] | 181[b] | 38·1[b] | 347[b] |
| ML | 22·0[a] | 587[a] | 171[a] | 190[a] | 46·3[a] | 286[a] |
| LM | 21·8[a] | 573[a] | 185[a] | 189[a] | 41·9[a] | 290[a] |
| Residual SD | 1·54 | 24 | 22 | 11 | 4·0 | 42·2 |

Treatments are described by a two-letter code such that the first letter indicates lambs which were fed to attain weight gains of 16 (H), 5 (M) or −6 (L) kg during the period from 0 to 42 d. The second letter indicates lambs which were fed to attain weight gains of 27 (S), 16 (H), 5 (M) or −6 (L) kg during the period from 43 to 84 d.

Residual SD estimates are based on 27 error degrees of freedom. SE may be calculated as residual SD/$\sqrt{n_i}$, where $n_i = 4$.

[a,b] For each column, means within an end-point weight group (i.e. HH; HM, MH, LS; HL, MM, LH; or ML, LM) with different superscript letters were significantly different ($P < 0·05$).

Table 4. *Organ weights of lambs assigned to different levels of nutrition*

(Mean values for four lambs)

| Treatment | Liver (g) | Heart (g) | Kidney (g) | Large intestine (g) | Small intestine (g) | Stomach (g) | Spleen (g) |
|---|---|---|---|---|---|---|---|
| HH | 788 | 173 | 138 | 337 | 495 | 992 | 79 |
| HM | 537[a] | 165[b] | 108[a] | 323[a] | 407[a] | 882[a] | 70[a] |
| MH | 628[b] | 140[a] | 112[a] | 303[a] | 411[a] | 922[a] | 68[a] |
| LS | 668[c] | 155[a,b] | 121[b] | 385[b] | 532[b] | 972[b] | 70[a] |
| HL | 409[a] | 141[a] | 92[a] | 289[a,b] | 310[a] | 680[a] | 63[a] |
| MM | 433[a] | 121[b] | 94[a] | 256[a] | 330[a] | 684[a] | 67[a] |
| LH | 458[b] | 116[b] | 93[a] | 310[b] | 432[b] | 759[b] | 56[a] |
| ML | 291[a] | 120[a] | 74[a] | 233[a] | 291[a] | 521[a] | 48[a] |
| LM | 313[a] | 92[b] | 77[a] | 223[a] | 287[a] | 521[a] | 39[a] |
| Residual SD | 45 | 13 | 12 | 49 | 43 | 79 | 12 |

Treatments are described by a two-letter code such that the first letter indicates lambs which were fed to attain weight gains of 16 (H), 5 (M) or −6 (L) kg during the period from 0 to 42 d. The second letter indicates lambs which were fed to attain weight gains of 27 (S), 16 (H), 5 (M) or −6 (L) kg during the period from 43 to 84 d.

Residual SD estimates are based on 27 error degrees of freedom. SE may be calculated as residual SD/$\sqrt{n_i}$, where $n_i = 4$.

[a,b,c] For each organ, means within an end-point weight group (i.e. HH; HM, MH, LS; HL, MM, LH; or ML, LM) with different superscript letters were significantly different ($P < 0{\cdot}05$).

Table 5. *Regressions of organ weights on empty-body-weight and average daily gain of lambs*

(Model is log (organ weight) = $b_0 + b_1 \times (\log \text{EBW}) + b_2 \times \text{ADG} \times (\log \text{EBW})$ or, if transformed, organ weight (g) = $b_0\ \text{EBW}^{b_1 + b_2 \times \text{ADG}}$, where EBW is empty-body-weight (kg), ADG is average daily gain (g/d) and $b_0$, $b_1$ and $b_2$ are constants. Thirty-six observations are included in each regression)

| | Regression coefficients | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Organ | $b_0$ | SE | $b_1$ | SE | $b_2$ | SE | Residual SD | $R^2$ |
| Liver | 2·95 | 0·29 | 0·90 | 0·09 | 0·190 | 0·033 | 0·11 | 0·90 |
| Heart | 2·53 | 0·32 | 0·69 | 0·08 | — | — | 0·13 | 0·66 |
| Kidney | 2·54 | 0·28 | 0·58 | 0·08 | 0·095 | 0·032 | 0·11 | 0·77 |
| Stomach | 4·23 | 0·27 | 0·67 | 0·08 | 0·136 | 0·031 | 0·10 | 0·84 |
| Small intestine | 4·66 | 0·37 | 0·34 | 0·11 | 0·212 | 0·042 | 0·14 | 0·69 |
| Large intestine | 4·30 | 0·44 | 0·38 | 0·13 | 0·095 | 0·049 | 0·16 | 0·44 |
| Spleen | 1·49 | 0·46 | 0·76 | 0·12 | — | — | 0·17 | 0·56 |

Table 6. *Food utilization of lambs following a period of nutritional manipulation*

(Model 1 is $Y = b_1 X_1 + b_2 X_2$, where $Y$ is average daily gain (g/d), $X_1$ is metabolic body size (kg body-weight$^{0.75}$), $X_2$, is daily dry matter intake (g/d), and $b_1$ and $b_2$ are constants. Model 2 is $Y = b_1 + b_2 X$ where $Y$ is average daily gain (g/kg body-weight$^{0.75}$ per d) and $X$ is daily dry matter intake (g/kg body-weight$^{0.75}$ per d). Twelve observations were included in each regression)

| Treatments | Model | Regression coefficients | | | | $R^2$ | Residual SD | Maintenance requirement (g/kg body-wt$^{0.75}$ per d) |
|---|---|---|---|---|---|---|---|---|
| | | $b_1$ | SE | $b_2$ | SE | | | |
| HH+HM+HL | 1 | −19·6 | 2·4 | 0·359 | 0·033 | 0·94 | 49 | 54·6 |
| | 2 | −20·0 | 2·3 | 0·364 | 0·032 | 0·93 | 2·7 | 55·1 |
| MH+MM+ML | 1 | −19·7 | 1·8 | 0·446 | 0·026 | 0·98 | 35 | 44·1 |
| | 2 | −19·8 | 1·8 | 0·447 | 0·028 | 0·96 | 2·5 | 44·3 |
| LS+LH+LM | 1 | −12·9 | 3·6 | 0·423 | 0·041 | 0·99 | 40 | 30·5 |
| | 2 | −13·3 | 3·7 | 0·427 | 0·044 | 0·91 | 3·3 | 31·2 |

Treatments are described by a two-letter code such that the first letter indicates lambs which were fed to attain gains of 16 (H), 5 (M) or −6 (L) kg during the period from 0 to 42 d. The second letter indicates lambs which were fed to attain weight gains of 27 (S), 16 (H), 5 (M) or −6 (L) kg during the period from 43 to 84 d.

## DISCUSSION

The findings presented demonstrate that efficiency of food utilization and the amount of food required to maintain body-weight may be influenced by previous plane of nutrition. This observation is supported by several reports including those of Walker & Garrett (1970), Graham *et al.* (1974), Foot & Tulloh (1977), and Ledger & Sayers (1977). These findings suggest that food required to maintain body-weight is not a constant function of body-weight but may be altered by plane of nutrition. This result is not surprising since maintenance requirements have been shown to vary due to several other factors including sex (Ferrell *et al.* 1979; Webster *et al.* 1982), season (Blaxter & Boyne, 1982), temperature (Close, 1978) and age (Blaxter *et al.* 1966).

Many of the differences in efficiency of utilization of food for growth or maintenance of body-weight have been attributed to differences in body composition or proportions of water, protein and fat in body-weight gain (e.g. Garrett, 1971; Webster, 1979). Some of the results observed in the present study may be attributed to these factors. Lambs assigned to lower planes of nutrition during period 1 weighed less (by design) and contained less fat and protein than lambs assigned to the higher planes of nutrition. Gains by those lambs during period 2 generally contained a higher proportion of water and lower proportions of fat and protein.

Other results reported in the present paper, however, tend to conflict with the view that body composition and proportions of water, fat and protein have a major influence on energy expenditure. At the end of period 2, higher FHP values were observed in association with higher planes of nutrition during period 2. For example, FHP values for HL, MM and LH lambs were 290, 295 and 347 and for HM, MH and LS lambs were 321, 365 and 412 kJ/kg body-weight$^{0.75}$ per d respectively. Thus, differences in FHP were observed in lambs of similar age, weight and composition. Furthermore, lambs that had higher FHP values tended to contain (usually not significant) lower masses of protein and fat, and the weight gained tended to contain a lower proportion of fat, a similar proportion of protein and a higher proportion of water than lambs of similar weight that had lower FHP values. Thus, any trends observed were in the opposite direction of those which would be expected based on the results of Graham *et al.* (1974), Koong (1977), Pullar & Webster (1977) and

Ferrell *et al.* (1979). The present results suggest that fasting energy expenditure was altered by previous nutritional treatment and that the differences observed were not attributable to measurable differences in body composition or to differences in proportions of water, fat and protein in the gain.

An alternative suggestion is that fasting energy expenditure is related to the rate of body-weight gain or rate of gain of fat, protein, or both fat and protein. When groups of lambs that had similar rates of body-weight gain during period 2 were compared (e.g. HM *v.* MM *v.* LM), estimates of FHP were not significantly different ($P > 0{\cdot}10$). However, as noted above, FHP at the end of period 2 increased with rate of gain during period 2. This was observed in animals of the same age and weight (e.g. HM *v.* MH *v.* LS) as well as in animals that differed in weight (e.g. LM *v.* LH *v.* LS). Thus, fasting energy expenditure, scaled by metabolic body size (body-weight$^{0{\cdot}75}$), appeared to be related to rate of body-weight gain, even though body-weight and body composition were very dissimilar. When comparisons were made among animals that had similar rates of body-weight gain during period 2, rate of gain of fat or protein mass differed substantially. These findings suggest that an increase in fasting energy expenditure associated with increased rate of body-weight gain was not directly related to the rate of accretion of body fat or protein. These results support the suggestion of Millward *et al.* (1976) that heat production commonly attributed to body protein accretion (by mathematical techniques to partition energy among maintenance, protein and fat accretion; Kielanowski, 1976; Koong, 1977; Pullar & Webster, 1977; Ferrell *et al.* 1979) may actually be a result of a general increase in heat production that is usually correlated with, but not necessarily directly related to, components of protein accretion.

In contrast to components of body composition or composition of gain, variation in FHP associated with nutritional manipulation tended to be paralleled by the weights of certain visceral organs. Further, weights of several organs, as well as daily heat production, were each found to be related to body-weight raised to a power which increased with rate of body-weight gain. These results suggest that neither visceral organ weights nor daily heat production were constant functions of body-weight. Relation of these traits to body-weight changed with rate of gain.

Considerable evidence has accumulated which suggests that emphasis on economically important animal characteristics (e.g. body composition) has perhaps distracted from other biologically important considerations. Smith (1970) suggested that energy expenditures of visceral organs were a major proportion of basal energy expenditures. Smith (1970) estimated that about 30% of basal energy expenditures resulted from the metabolism of the gastrointestinal tract, liver and heart and that an additional 22% was contributed by the kidney, skin and brain. Smith & Baldwin (1974) observed that weights of the liver, heart, mammary gland, lungs, rumen, abomasum, intestines, spleen and adrenals were larger in lactating than in non-lactating cows. Smith & Baldwin (1974) suggested that changes in tissue weights may be related to differences in maintenance energy expenditures for lactating *v.* non-lactating cows. Canas *et al.* (1982) further showed that weight and metabolic activities of the liver, heart and gastrointestinal tract of rats increased during lactation and with increased feed intake. They suggested that a 24% increase in maintenance energy expenditures during lactation could be explained on the basis of changes in relative weight of the liver, heart and kidney. Consistent with these observations, Ferrell *et al.* (1976) estimated that about 37% of fasting energy expenditures of pregnant and non-pregnant Hereford Heifers were attributable to energy expenditures of the liver, kidney and heart. They also provided information to suggest that the weight and energy expenditures of the liver and kidney increased with increased feed intake. High energy expenditures of visceral organs such as the liver and gastrointestinal tract have been further documented on the basis

of blood flow and $O_2$ consumption (Webster & White, 1973; Thompson & Bell, 1976; Edelstone & Holzman, 1981; Lomax & Baird, 1983).

That visceral organs have a high rate of energy expenditure does not preclude protein synthesis having a large direct or indirect impact on basal energy expenditures. Results reported by Webster *et al.* (1978), for example, suggest a strong relation between total body protein synthesis and heat loss in congenitally obese and lean rats. Numerous other studies, such as those reported by Lobley *et al.* (1980) and Simon *et al.* (1982), demonstrate the high fractional protein synthesis rate of liver and gastrointestinal tract tissues. The findings of Lobley *et al.* (1980) and Simon *et al.* (1982) suggest that total protein synthesis in the liver and gastrointestinal tract tissues is greater than that in skeletal muscle in both cattle and pigs.

Various metabolic processes were likely altered by the nutritional treatments imposed in this study. The findings reported suggested that a portion of the variation in energy expenditure resulting from nutritional manipulation was associated with variation in weights of highly metabolically active visceral organs. Furthermore, an approach has been suggested whereby variations in basal energy expenditures associated with rate of gain, or other sources of variation, may be incorporated into the relation between energy expenditure and body size. An understanding of the underlying causes of variation in energy expenditures is required.

## REFERENCES


Andersen, B. B. (1980). *Annals Zootechnie* **29**, 85–92.

Barr, A. J., Goodnight, J. H., Sall, J. P. & Helwig, J. T. (1979). *SAS User's Guide*. NC: Statistical Analysis System Institute.

Blaxter, K. L. & Boyne, A. W. (1982). *Journal of Agricultural Science, Cambridge* **99**, 611–620.

Blaxter, K. L., Clapperton, J. L. & Wainman, F. W. (1966). *Journal of Agricultural Science, Cambridge* **67**, 67–75.

Burton, J. H. & Reid, J. T. (1969). *Journal of Nutrition* **97**, 517–524.

Canas, R., Romero, J. J. & Baldwin, R. L. (1982). *Journal of Nutrition* **112**, 1876–1880.

Close, W. H. (1978). *British Journal of Nutrition* **40**, 433–438.

Drew, K. R. & Reid, J. T. (1975). *Journal of Agricultural Science, Cambridge* **85**, 215–220.

Edelstone, D. I. & Holzman, I. R. (1981). *American Journal of Physiology* **240**, G297–G304.

Ferrell, C. L., Crouse, J. D., Field, R. A. & Chant, J. L. (1979). *Journal of Animal Science* **49**, 790–801.

Ferrell, C. L., Garrett, W. N., Hinman, N. & Gritching, G. (1976). *Journal of Animal Science* **42**, 937–950.

Flatt, W. P. & Coppock, C. E. (1963). *Journal of Dairy Science* **46**, 638 Abstr.

Foot, J. Z. & Tulloh, N. M. (1977). *Journal of Agricultural Science, Cambridge* **88**, 135–142.

Garrett, W. N. (1971). *Journal of Animal Science* **32**, 451–456.

Graham, N. McC. & Searle, T. W. (1972). *Australian Journal of Agricultural Research* **23**, 97–108.

Graham, N. McC., Searle, T. W. & Griffiths, D. A. (1974). *Australian Journal of Agricultural Research* **25**, 957–971.

Gray, R. & McCracken, K. J. (1979). In *Energy Metabolism, European Association for Animal Production Publication* no. 26, pp. 163–167 [L. E. Mount, editor]. London: Butterworths.

Kielanowski, J. (1976). In *Protein Metabolism and Nutrition, European Association for Animal Production Publication* no. 16, pp. 207–215 [D. J. A. Cole, K. N. Boorman, P. J. Buttery, D. Lewis, R. J. Neale and H. Swan, editors]. London: Butterworths.

Koong, L. J. (1977). *Journal of Nutrition* **107**, 1724–1728.

Ledger, H. P. & Sayers, A. R. (1977). *Journal of Agricultural Science, Cambridge* **88**, 11–26.

Lobley, G. E., Milne, V., Lovie, J. M., Reeds, P. J. & Pennie, K. (1980). *British Journal of Nutrition* **43**, 491–502.

Lomax, M. A. & Baird, G. D. (1983). *British Journal of Nutrition* **49**, 481–496.

Marston, H. R. (1948). *Australian Journal of Science and Research* **B1**, 93–129.

Millward, D. J., Garlick, P. J., James, W. P. T., Sender, P. & Waterlow, J. C. (1976). In *Protein Metabolism and Nutrition*, pp. 49–69 [D. J. A. Cole, K. N. Boorman, P. J. Buttery, D. Lewis, R. J. Neale and H. Swan, editors]. London: Butterworths.

Nienaber, J. A. & Maddy, A. L. (1985). *Transactions of the American Society of Agricultural Engineers* **28**, 555–560.

Pullar, J. D. & Webster, A. J. F. (1977). *British Journal of Nutrition* **37**, 355–363.

Searle, T. W., Graham, N. McC. & O'Callaghan, M. (1972). *Journal of Agricultural Science, Cambridge* **79**, 371–382.

Simon, O., Bergner, H. & Muchmeyer, R. (1982). *British Journal of Nutrition* **48**, 571–582.
Smith, N. E. (1970). Quantitative simulation analyses of ruminant metabolic functions: basal; lactation; milk fat depression. PhD Thesis, University of California.
Smith, N. E. & Baldwin, R. L. (1974). *Journal of Dairy Science* **57**, 1055–1060.
Thompson, G. E. & Bell, A. W. (1976). In *Energy Metabolism of Farm Animals*, *European Association for Animal Production Publication* no. 19, pp. 37–40 [M. Vermorel, editor]. Clermont-Ferrand: G. de Bussac.
Walker, J. J. & Garrett, W. N. (1970). In *Energy Metabolism of Farm Animals*, *European Association for Animal Production Publication* no. 13, pp. 193–196 [A. Schurch and C. Wenk, editors]. Zurich: Juris Druck & Verlag.
Webster, A. J. F. (1979). In *Energy Metabolism*, *European Association for Animal Production Publication* no. 26, pp. 461–466 [L. E. Mount, editor]. London: Butterworths.
Webster, A. J. F., Lobley, G., Reeds, P. J. & Pullar, J. D. (1978). *Proceedings of the Nutrition Society* **37**, 21A.
Webster, A. J. F., Smith, J. S. & Mollison, G. S. (1982). In *Energy Metabolism of Farm Animals*, *European Association for Animal Production Publication* no. 29, pp. 237–240 [A. Ekern and F. Sundstol, editors]. Lillehammer: Agricultural University of Norway.
Webster, A. J. F. & White, F. (1973). *British Journal of Nutrition* **29**, 279–292.
Wilson, P. N. & Osbourn, D. F. (1960). *Biological Reviews* **35**, 324–363.

*Printed in Great Britain*