Effect of food intake on protein and energy metabolism in finishing beef steers

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1. The effects of progressive reduction in food intake from 1·6 × maintenance (1·6 M) to approximately maintenance (M′) and then to zero (fasting) on energy expenditure and leucine kinetics were examined in Hereford × Friesian finishing beef steers.

2. Estimates of whole body protein synthesis and protein oxidation were obtained from the specific radioactivity of free leucine in blood and of exhaled carbon dioxide during continuous infusions of $[1-{}^{14}C]$leucine. Protein synthesis contributed a minimum of 0·19 to total heat production across all three intakes.

3. The apparent efficiencies with which synthesized protein was retained were 0·28 between 1·6 M and M′ and 1·04 between M′ and fasting. The greater efficiency below M′ reflected probable use of amino acids as energy sources during fasting, which would be spared as soon as feed was available.

4. Nitrogen derived from protein oxidation made a minor contribution to urine N at both 1·6 M (0·45) and M′ (0·36) but provided a significant proportion to the increment in urine N between intakes (0·68).

5. Amino acid absorption, estimated indirectly as the sum of protein oxidation and protein retention, represented only 0·28 of N intake at M′ and 0·38 at 1·6 M but the contribution to the increment in N intake between these two diet levels was greater (0·56).

6. The estimated efficiency of utilization of absorbed amino acids between M′ and 1·6 M was 0·45.

Rates of gain, and hence commercial productivity, for farm livestock are directly linked to protein deposition, itself the resultant of the opposing processes of protein synthesis (PS) and protein degradation. Over the past 20 years attention has focused on protein metabolism through an interest in both the energetic efficiency of the deposition process (e.g. Kielanowski, 1976; Garlick, 1980) and the factors which influence, either separately or in concert, synthesis and degradation. Limited observations have been made for most commercial species both for whole body PS and for individual tissues, e.g. pigs (Garlick *et al.* 1976; Simon *et al.* 1978), sheep (Buttery *et al.* 1975; Combe *et al.* 1979; Davis *et al.* 1981) and cattle (Lobley *et al.* 1980), but systematic studies on endocrinological, physiological and nutritional influences have been few, especially when compared with the range of investigations made on laboratory animals. Thus the effects of food intake on protein dynamics have been rigorously examined in only two of the larger species, man and pig. While the findings from man cover a wide range of conditions, from the recovering malnourished child to the obese adult (e.g. Young *et al.* 1975; Golden *et al.* 1977; Clugston & Garlick, 1982*b*), many of these studies are restricted to clinical situations and are often hampered by ethical considerations. The studies on the pig (Reeds *et al.* 1980) dealt with young growing animals and derived values for the efficiencies of various components of protein metabolism. It is important to know whether the kinetics exhibited by the young, fast-growing, simple-stomach animals can be extended to other species and alternative physiological ages. The present study describes the rates of whole body PS and energy expenditure in growing beef steers in the fattening phase when food intake was progressively reduced from 1·6 × maintenance, through maintenance to zero (fasting). Preliminary analyses from the results have been incorporated in earlier reviews (Lobley, 1986; MacRae & Lobley, 1986).

METHODS

Animals and diet

The eight Hereford × Friesian steers (420–520 kg live weight (LW); 24–30 months of age) were those used in Expt A of the report by Lobley *et al.* (1985) on the effects of an anabolic steroid preparation on the energy and protein metabolism of growing steers. Four animals (nos 2, 5, 6 and 7) had a previous history of treatment with a combined preparation of trenbolone acetate and oestradiol-17β. Two treatments had been given, the second of which was at least 3 months before the present series of measurements and had been shown to have no significant effect on the variables determined (see Lobley *et al.* 1985). The diet was ruminant diet AA6 (ABRO, Edinburgh; 17·5 MJ gross energy/kg dry matter (DM), 9·7 MJ metabolizable energy (ME)/kg DM, 25·2 g nitrogen/kg DM), supplied from continuous belt feeders (see Lobley *et al.* 1985).

Measurements were made on all steers at each of three intakes. The first were made at the initial intake offered as the production ration during the growth study (Lobley *et al.* 1985) and approximated to 1·6 × energy maintenance (M). Animal no. 1 did not consume the full ration during the first chamber measurement and its intake was reduced to 1·4 M (Table 1). The intake for each steer was then reduced to approximately M (M', assessed as 533 kJ ME/kg LW$^{0.75}$ per d). For three steers (nos. 2, 6 and 7), because of management difficulties, the decrease was delayed for 3 weeks after the first measurements were made. The second set of measurements were started after each animal had received the M' intake for 14 d, i.e. energy and N balance determinations were made between days 15 and 19 and leucine kinetics measured on either day 19 or 20. Immediately after this the animals were fasted for 4 d. Collections of excreta were made for each individual day of the fast, and leucine kinetics were measured between 96 and 108 h after the last feed was offered.

Measurements

Apparatus and procedures were as described previously (Lobley *et al.* 1985). Measurements (4 d) of energy expenditure and N retention were made on harnessed animals accommodated in automated confinement respiration chambers. For animals at 1·6 M and M' intakes, excreta were pooled for the 4 d of collection. Values for the fasted animals relate to excretions during the last day of fast. Irreversible loss rate (flux; ILR) of leucine was determined from blood free-leucine specific radioactivity (SR) and fractional oxidation rate (FO) from the amount of radioactivity which appeared as carbon dioxide; both determinations were made during the last 4 h of 10-h continuous infusions of [1-^{14}C]leucine.

Calculations. Leucine and protein kinetics were calculated as follows:

$$\text{ILR (mmol/h)} = \frac{\text{infusion rate } (\mu\text{Ci/h})}{\text{SR blood free-leucine } (\mu\text{Ci/mmol})},$$

$$\text{FO} = \frac{\text{SR }^{14}\text{CO}_2 \ (\mu\text{Ci/mmol}) \times \text{CO}_2 \text{ produced (mmol/h)}}{\text{infusion rate } (\mu\text{Ci/h})},$$

$$\text{protein oxidized (PO; g N/d)} = \text{FO} \times \text{ILR} \times 8\cdot24,$$
$$\text{PS (g N/d)} = (1 - \text{FO}) \times \text{ILR} \times 8\cdot24.$$

The factor 8·24 used to convert leucine kinetics (mmol/h) to equivalent g protein N/d follows the general procedure used by Lobley *et al.* (1980) based on a mean leucine content in body protein of cattle of 0·38 g leucine/g protein N.

Experimental design and statistical procedures

The design adopted for this experiment was constrained by the known effect that previous nutrition has on measurements of heat production at maintenance intake or fasting. Presumably these differences in energy expenditure also reflect carry-over effects on metabolism. In order to minimize the problems of interpretation, a procedure similar to that used in rigorous calorimetric studies was adopted where fasting heat production is measured after an extended period (usually 14–21 d) at maintenance intake, measurements at maintenance having been made during the later part of this period. Under these conditions it was decided that a simple uni-directional, decremental design would be adequate although it is recognized that some limitations are introduced with this approach.

The data were analysed using a two-way analysis of variance. Where appropriate, treatment means were compared using the *t* statistic. Unless stated otherwise, standard error of difference (SED) comparisons are based on residual degrees of freedom of 14. The relations between PS and ME intake and between heat production and PS were tested further by regression analysis. Differences in slopes between animals were found not significant and a common slope was therefore applied.

In all analyses differences in body-weight were not taken into account. Intake, an important determinant of metabolic rate, was set as a function of body-weight so differences between animals would be partly compensated. Within animals considerable differences in live weight existed between 1·6 M and fasting (range 18–67 kg) but the majority of this would represent changes in gut-fill and body water and not accurately indicate changes in the metabolic mass of each animal.

Derived calculations based on incremental differences between 1·6 M and M′ or between M′ and fasting are presented as means with SE where *n* 8.

RESULTS

Mean intakes of N and gross energy plus energy losses in excreta are given in Table 1. Other values for individual animals are given in Tables 2 to 4. Statistical analyses of all measurements showed that no significant effects could be attributed to whether or not the steers had previously been implanted with the preparations of anabolic steroids.

For the 6 weeks before the first measurement, mean weight gain was 1·1 (range 0·5 to 1·4) kg/d. At this growth rate, expected N retention would be 22 g N/d (predicted from Table 1.23, Agricultural Research Council, 1980). During the 4 d balance procedure at 1·6 M, mean N retention was measured at 26 g N/d (Table 1). The average efficiencies of utilization of ME (Δenergy retention/ΔME intake, calculated for each animal) were 0·76 (SE 0·02) between M′ and fasting and 0·56 (SE 0·03) between 1·6 M and M′.

The average M requirement for all animals was estimated as 517 (SE 11) kJ ME/kg $LW^{0·75}$ per d based on interpolation of the data between M′ and fasting. This was slightly less than the value used for the ration setting and, in consequence, most animals were in positive energy and N retention at M′ intake (Table 2). Mean fasting metabolic rate was 396 (SE 17) kJ/kg fasted $weight^{0·75}$ per d.

At each decrement of intake there were significant ($P < 0·001$) decreases in heat production (HP), energy retention, protein deposition (N retention $\times$ 6·25), urine N elimination and PS.

Linear regressions were applied to the following relations:
between PS (g N/d) and ME intake (MJ/d)

$$PS = 271 + 1·65 \text{ (SE 0·18) ME} \quad \text{residual SD 32·3, } r^2 \text{ 0·79, df 22}$$

Table 1. *Daily intakes of nitrogen and gross energy (GE) with losses of energy as faeces, urine and methane for steers fed to* $1 \cdot 6 \times$ *maintenance* $(1 \cdot 6 \, M)$, *maintenance* (M') *and fasted*

(Mean values with standard errors, n 8)

	1·6 M*		M'		Fasted	
	Mean	SE	Mean	SE	Mean	SE
Intake:						
N (g)	229	8	141	3	—	—
GE (MJ)	163·9	4·3	98·6	5·2	—	—
Energy losses (MJ):						
Faeces	59·4	1·6	35·9	1·1	8·1	3·0
Urine	4·9	0·2	3·5	0·2	1·6	0·3
CH$_4$	10·0	0·3	7·3	0·3	0·3	0·1

* *n* 7, steer no. 1 fed 1·4 × maintenance.

Table 2. *Metabolizable energy (ME) intake, heat production (HP), protein synthesis (PS), nitrogen retention (NR), leucine fractional oxidation (FO), protein oxidation (PO) and urine N losses (UN) for steers fed to* $1 \cdot 6 \times$ *maintenance*

Animal no.	Live wt (kg)	ME intake (MJ/d)	HP (MJ/d)	PS* (g N/d)	NR (g N/d)	FO	PO† (g N/d)	UN (g N/d)
1‡	423	67·9	57·5	423	26·3	0·075	31·7	87
2§	461	80·0	61·8	428	19·6	0·101	48·3	123
3	465	89·3	63·3	422	14·9	0·162	81·2	143
4	507	96·9	69·5	412	25·6	0·131	62·0	124
5§	521	92·6	73·6	468	44·1	0·114	60·5	122
6§	501	89·1	69·6	368	22·9	0·093	37·8	124
7§	448	83·2	65·2	429	23·0	0·115	55·6	112
8	501	95·8	66·8	485	28·9	0·127	70·8	138
Mean	478	86·9	65·9	429	25·7	0·115	56·0	122
SEM	12	3·4	1·8	13	3·0	0·026	16·4	6

* Calculated from leucine irreversible loss rate (mmol/h) × (1 − leucine FO) × 8·24.
† Calculated from leucine irreversible loss rate (mmol/h) × leucine FO × 8·24.
‡ 1·4 × maintenance.
§ Previous history of treatment with anabolic steroids.

and between HP (MJ/d) and PS (g N/d)

$$HP = -0 \cdot 507 + 0 \cdot 151 \, (\text{SE} \; 0 \cdot 017) \, PS \quad \text{residual SD } 5 \cdot 7, \; r^2 \; 0 \cdot 78, \; \text{df } 22.$$

Based on an energy cost for polypeptide formation of 28 kJ/g N (Millward *et al.* 1976), PS accounted for 0·19 of total HP. At predicted zero energy retention (M) PS was calculated as 368 g N/d (3·68 g N/kg $LW^{0 \cdot 75}$ per d). At zero intake (fasting) PS was determined as 278 (SE 10) g N/d (2·86 g N/kg fasted weight$^{0 \cdot 75}$ per d). The apparent efficiency of protein deposition: PS differed below and above M'; between M' and fasting it was 1·04 (SE 0·16) compared with 0·24 (SE 0·03) between 1·6 M and M'.

At 1·6 M, FO was variable between animals (range 0·16–0·08, Table 1) but decreased consistently when intake was reduced to M' (mean difference 0·036, SED 0·011, $P < 0·001$). When intake was decreased from M' to fasting, FO increased (mean difference 0·043, SED

Table 3. *Metabolizable energy (ME) intake, heat production (HP), protein synthesis (PS), nitrogen retention (NR), leucine fractional oxidation (FO), protein oxidation (PO) and urine N losses (UN) for steers fed to maintenance (M')*

Animal no.	Live wt (kg)	ME intake (MJ/d)	HP (MJ/d)	PS* (g N/d)	NR (g N/d)	FO	PO† (g N/d)	UN (g N/d)
1	392	42·5	44·4	345	−1·4	0·058	21·2	66
2‡	456	57·8	49·8	341	2·4	0·078	29·0	88
3	465	54·7	51·4	353	4·2	0·101	39·7	87
4	471	57·1	55·6	340	6·8	0·075	27·7	77
5‡	491	57·4	55·5	313	9·3	0·073	24·7	92
6‡	505	55·8	55·9	332	9·5	0·080	29·0	86
7‡	460	50·6	55·3	356	9·2	0·057	21·4	78
8	478	59·2	50·9	343	2·2	0·104	40·0	78
Mean	465	54·4	52·4	340	5·3	0·078	29·1	82
SEM	12	1·9	1·4	13	1·4	0·006	2·6	3

* Calculated from leucine irreversible loss rate (mmol/h) × (1-leucine FO) × 8·24.
† Calculated from leucine irreversible loss rate (mmol/h) × leucine FO × 8·24.
‡ Previous history of treatment with anabolic steroids.

Table 4. *Heat production (HP), protein synthesis (PS), nitrogen retention (NR), leucine fractional oxidation (FO), protein oxidation (PO) and urine N loss (UN) for fasted steers*

Animal no.*	Live wt (kg)	HP (MJ/d)	PS† (g N/d)	NR (g N/d)	FO	PO‡ (g N/d)	UN (g N/d)
1[12]	368	32·4	255	−58·2	0·150	44·9	58·2
2[12]§	443	33·8	262	−46·6	0·151	46·7	46·6
3[9]	428	37·6	288	−60·2	0·151	51·1	60·2
4[8]	440	40·0	222	−46·3	0·094	23·0	46·3
5[7]§	463	41·4	285	−34·4	0·120	38·7	34·4
6[7]§	466	43·9	293	−46·9	0·085	27·4	46·9
7[7]§	429	46·2	304	−47·1	0·127	44·1	47·1
8[8]	456	41·3	312	−47·2	0·094	32·5	47·2
Mean	437	39·6	278	−48·4	0·122	38·6	48·4
SEM	11	1·7	10	2·8	0·010	3·5	2·8

* Superscript numbers refer to month number during which fast measurements were made.
† Calculated from leucine irreversible loss rate (mmol/h) × (1 − leucine FO) × 8·24.
‡ Calculated from leucine irreversible loss rate (mmol/h) × leucine FO × 8·24.
§ Previous history of treatment with anabolic steroids.

0·011, $P \simeq 0·01$). PO was greatest at 1·6 M but variable (range 32–81 g N/d, Table 1), declined significantly as intake was reduced to M' (mean difference 26, SED 5, $P < 0·001$) and increased slightly as intake reduced to zero (mean difference 9, SED 5, $P < 0·10$).

DISCUSSION
Limitation of the ILR procedure
Measurement of the ILR (flux) of an amino acid through the blood pool provides a simple, non-destructive method from which the minimum rate of whole body PS and PO can be estimated and which is ideally suited for studies on large farm animals and man. The

procedure does have limitations and uncertainties and these have been extensively detailed elsewhere (e.g. Waterlow *et al.* 1978; Reeds & Lobley, 1980). Briefly the most serious problem involves the assumptions that the SR of the blood free-amino acid chosen can be related to the SRs of the precursors for PS (the amino acyl-*t*-RNAs) and amino acid oxidation (the intracellular oxo-acid), and that these relations do not alter significantly at different treatments. Only in specific circumstances (e.g. see p. 463) can these assumptions be tested. In consequence the absolute quantitative significance of the data and any calculations further derived must be treated with appropriate caution. The method will tend to underestimate the true rate of PS and probably also PO. The procedural and economic problems associated with studies of protein metabolism in cattle does make recourse to this procedure necessary however. Analysis of the information gained does allow potential areas of interest to be identified which can then be examined further where alternative techniques are available.

PS and energy expenditure

The response of whole body PS to changes in intake for cattle follows the pattern already observed for man (e.g. Golden *et al.* 1977; Clugston & Garlick, 1982*a*) and pigs (Reeds *et al.* 1980). These measurements were all made with the ILR procedure and in consequence suffer from the limitations described above but increases in PS in response to extra intake have been observed also for specific tissues (Garlick *et al.* 1973; Stein *et al.* 1976).

The energy costs of peptide-bond formation contribute to total energy expenditure and, across a wide range of species, for adults fed at maintenance a minimum of approximately 0·15 of heat production is associated with PS (Garlick, 1980). This relation may also hold apparently at non-maintenance intakes; 0·21 in young pigs between M and 3 M (Reeds *et al.* 1980), 0·25 in fed and fasted humans (from Clugston & Garlick, 1982*a*), and 0·19 for cattle between 1·6 M and fasting (present study; see also MacRae & Lobley, 1986). Other cellular processes related to metabolic rate are known to increase as food intake is elevated, e.g. Na^+–K^+ ion pumping (McBride & Milligan, 1985), while above maintenance, fat synthesis and deposition are also raised. In consequence such general stimulation of metabolic processes may maintain in gross terms the apparent relation between any single process and total energy expenditure without necessarily requiring intimate links between processes or indeed common responses between individual tissues.

N retention and PS

The apparent efficiency of N retention:PS between 1·6 M and M′ was, at 0·24, lower than that reported for the recovering malnourished child (0·73; Golden *et al.* 1977) and the young growing pig (0·46; Reeds *et al.* 1980). A value of 0·42 can be derived from the data of Davis *et al.* (1981) based on the changes in PS and N retention associated with exogenous casein administration to young growing lambs (see Lobley, 1986). The lower efficiency observed for the steers in the present study may be related to their age and physiological condition. While the human, pig and sheep determinations were made on young animals with high rates of protein gain, the cattle were in the finishing stage with a protein energy deposition:total energy deposition of 0·18 (SE 0·04; range 0·06–0·33). A few months earlier this ratio had been 0·26 (Lobley *et al.* 1985) which indicates the progress of the fattening condition. Clearly the relation between N retention and protein synthesis is not a constant either between or within species as marked improvements in N retention can be achieved by administration of anabolic steroids without a concomitant change in protein synthesis (Lobley *et al.* 1985).

Between M′ and fasting, increments of synthesized protein were retained at an efficiency apparently greater than 1·0, but this is misleading as the negative N retention for fasted

animals includes a proportion of amino acids used as an energy source which can be spared as soon as additional energy becomes available from dietary intake (Hovell *et al.* 1983). As food intake is increased, therefore, the reduced requirement to mobilize amino acids from tissue protein for energy sources results in improved N retention without the necessity for significant changes in protein synthesis. The difference between endogenous N loss reported for infusion-maintained cattle at energy M intake but zero N intake (320–325 mg N/kg $LW^{0.75}$ per d; Ørskov & MacLeod, 1982) and fasted steers (510 mg N/kg $LW^{0.75}$ per d; present study) suggest that approximately 18 g N of the 48 g urine N in the fasting steers might have been spared if adequate food energy had been available. Even when such a correction is applied, however, the apparent efficiency of N retention: PS between M′ and fasting is, at 0·68, still greater than that between M′ and 1·6 M.

Indirect estimation of amino acid supply

Amino acid absorption cannot be easily determined in ruminants, even with use of present-day surgical preparations (see Lobley, 1986), but an estimate of available N can be obtained from the sum of protein deposition (from N retention) and PO (from isotope measurements). This indirect procedure is unproven but partial validation can be shown in the fasted animal. At zero intake urine N in the form of urea and ammonia should result predominantly from tissue amino acid catabolism; in practice the estimate of PO was 0·94 (SE 0·07) of urine N present as urea plus ammonia, which together comprised 0·86 of total urine N. The close agreement here agrees well with the value near to unity observed for fed pigs (Reeds *et al.* 1980) when a similar comparison was made.

This type of validation cannot be extended to the fed ruminant. First, amino acids absorbed come from a mixture of feed, bacterial and endogenous proteins in unknown proportions and probably dissimilar in composition to the 'average' protein of animal tissue (see MacRae & Reeds, 1980; MacRae & Lobley, 1986). Leucine in ruminant digesta is usually in slight excess (up to 0·2) relative to other amino acids and consequently PO would be overestimated proportionally. Second, and more serious, in the fed situation a substantial fraction of the urine N will comprise urea and NH_3 derived from protein degraded to NH_3 in the rumen and large intestine and this will not be traced by leucine kinetics.

In the fed situation, therefore, the method can be used to assess the proportion of urine N derived from tissue amino acid catabolism and, by difference, that from fermentation. The PO: urine N values at M′ and 1·6 M were 0·36 (SE 0·03) and 0·45 (SE 0·03) respectively. Apparent N digestibility at both intakes was 0·67–0·70 but at least half the urine N is derived from microbial by-products, with a greater proportion at the lower intake. These values are compatible with those observed using detailed ^{15}N tracer techniques to follow digestive processes at single intakes (e.g. Siddons *et al.* 1985). The large contribution of fermentation-derived N in urine, however, obscures significant changes in the amount of available N as intake is altered. Analysis of the difference in urine N between 1·6 M and M′ shows that 0·68 (SE 0·11) is attributable to PO. This is compatible with increased intake leading to greater rates of passage of digesta, a lower proportion of rumen NH_3 production and increased available amino acid. This highlights the need to employ response or incremental approaches when unravelling the complexity of ruminant N kinetics.

Amino acid absorption and efficiency of protein metabolism

The response in PS to estimated amino acid N absorption was 1·80 (SE 0·15) g N synthesized/g N absorbed between 1·6 M and fasting, and 1·87 (SE 0·17) g N synthesized/g N absorbed between 1·6 M and M′. These values are similar to the PS: digestible N of 1·55 reported for pigs (Reeds *et al.* 1980) and this suggests that amino acid supply was not

limiting PS and the overall efficiency of utilization. In both experiments, however, increases in N availability were associated with increases in energy intake, so responses to either variable cannot be assessed independently.

Absorbed amino acid-N was calculated to represent only 0·28 (SE 0·02) and 0·38 (SE 0·02) of N intake at M′ and 1·6 M respectively. Again these individual values conceal the marked changes in the nature of the N supply as between these intakes the absorbed amino acid, N was calculated as 0·56 (SE 0·07) of intake N.

The calculated efficiency with which absorbed amino acid N was retained above M′ was 0·45 (SE 0·06). This estimate can be compared with values obtained by the more traditional procedures for the determination of efficiency of utilization of absorbed amino acids which are based on comparison at different intakes between N retention and amino acid absorption measured, for infusion-maintained ruminants, between abomasal input and either ileum or faeces, or, for conventionally fed animals, between duodenum and ileum. For young (25–40 kg) infusion-maintained lambs, values of efficiency between 0·63 and 1·11 have been observed or can be calculated (Storm *et al.* 1983; Lobley, 1986). Agricultural Research Council (1980) has adopted a value of 0·75 derived from studies with young (100 kg) calves fed on basal rations supplemented with various protein sources. From the studies of MacRae and colleagues with more mature (50–70 kg) sheep offered fresh and dried grasses, values of 0·5–0·66 can be computed (see Lobley, 1986) which are closer to the value derived from the kinetic analysis in the present study. These calculations encompass a range of measurement techniques all of which have disadvantages but again the trend is towards lower efficiencies with the older animals where rates of protein gain are less and fat accretion is augmented.

While the limitations of the techniques used must be borne in mind and suitable caution exercised in application of the absolute values, the dynamic relations between food intake, PS and energy expenditure are clearly seen. Previous observations on protein metabolism in ruminants have usually been restricted to single intakes or feeding *ad lib.* (for review see Mathers & Miller, 1979). The incremental nature of the present experiment has allowed responses to be analysed, and this is particularly important for N availability because of the penalties on N supply which can result from rumen fermentation. Alterations in efficiency of N retention do not appear to be directly related to PS, although this must play a significant role, but rather indicate that other controls of amino acid fates must be involved. Clearly further investigations, in which additional techniques are employed, need to be conducted on animals at younger ages and in different physiological states to determine those processes which have the major influence on protein anabolism in the ruminant.

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