Nutrient supply and growth of cattle offered straw-based diets

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An experiment was conducted using steers cannulated at the rumen, duodenum and ileum to study the effects of increasing the levels of barley and fishmeal in straw-based diets. Diets A, B, C and D contained ammonia-treated straw, barley and fishmeal in the ratios, 67:33:0, 66:23:11, 53:47:0 and 52:36:12 (by weight) and were offered in daily amounts of 3·9, 3·9, 4·8 and 4·8 kg dry matter. The effects of barley were attributable to increased intakes of digestible organic matter and consequently to increased flows of microbial matter to the duodenum. There were no modifications in the balance of energy to nitrogen-yielding nutrients available for absorption. Introducing fishmeal into diets improved digestibility of cellulose and xylose by up to 6·7 and 4·7% respectively, and shifted digestion towards the large intestine. Second, it increased amino acid N supply to the small intestine which averaged 52·2, 63·2, 68·8 and 84·0 g/d with diets A, B, C and D. Some changes were also noted in the balance of amino acids absorbed. Consequently, the contribution of amino acids to metabolizable energy intake increased with the proportion of fishmeal in diets (0·17, 0·20, 0·18 and 0·21 for diets A, B, C and D).

Growth rates measured in heifers amounted to 259, 431, 522 and 615 g/d for diets A, B, C and D. They appeared to be related to intestinal amino acid supply.

Growth: Nutrient supply: Ruminant digestion: Cattle

In previous experiments, it has generally been found that, at a given intake of total digestible organic matter (DOMI), protein supplementation offered in excess relative to the metabolizable energy (ME) supply of the diets, according to Agricultural Research Council (1980), increased the live-weight gain of heifers to a larger extent with high-roughage diets than with high-concentrate diets (Smith *et al.* 1980*b*). Protein supplements that largely escape rumen degradation (e.g., white fishmeal) consistently supported higher weight gains than other, more degradable supplements (soya-bean meal, rapeseed meal or urea; Oldham & Smith, 1981). These results show that growth rate can be increased, at constant DOMI, by increasing the protein content of the diet and, by implication, that protein supplementation increased efficiency of nutrient use.

Straw diets are characterized by rumen fermentations with a high proportion of acetic acid in volatile fatty acids (VFA) (Oldham *et al.* 1977) and a limiting nitrogen supply. The use of dietary supplements with straw diets is, therefore, likely to alter the nutrient supply and balance to a greater extent than with high-concentrate diets. Increasing the level of either fishmeal or barley in a straw diet might alter the balance of nutrients towards a higher ratio of glucogenic precursors relative to acetate, by increasing either the undegradable dietary N or the propionate supply.

The objective of the work reported here was to measure the effects of altering the level of different concentrates (barley or fishmeal) in straw diets on the amounts and relative

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Table 1. *Ingredient composition of diets (g/kg dry matter (DM) offered) and average chemical composition (ash, nitrogen, acid-detergent fibre, indigestible acid-detergent fibre and carbohydrate fractions g/kg DM) of feedstuffs*

	Ammonia-treated straw	Barley	Fishmeal*
Ingredient composition of diets†			
A	670	330	—
B	660	230	110
C	530	470	—
D	520	360	120
Chemical composition of feedstuffs			
Ash	75·0	31·0	208·6
N	14·9	20·8	112·9
Acid-detergent fibre	484·0	75·6	24·3
Indigestible acid-detergent fibre	160·2	28·1	20·0
Fat	34·1	39·7	116·7
Cellulose-glucose	381·4	48·2	3·8
Starch-glucose	25·0	631·9	5·6
Arabinose	26·0	25·9	ND
Galactose	9·6	7·7	1·0
Xylose	135·8	52·5	ND

ND, not detected.

* Carbohydrate content of fishmeal being very low, it was not determined. Average values from fishmeal samples previously analysed by A. B. McAllan were used.

† In the digestion trial, calcium, phosphorus, magnesium, sodium and potassium intakes were equalized across diets. Sulphur was added as well as copper, zinc, manganese, iodine, iron, cobalt, vitamin A, cholecalciferol, and vitamin E. In the feeding trial, a commercial mineral supplement (40 g Super Mindif) was added to each ration daily.

proportions of the major end-products of digestion, and to test the proposition that changes in nutrient supply and balance could account for the different observed growth performances in heifers on these diets. A digestion experiment and a feeding trial were therefore conducted in parallel. Preliminary results have already been reported in Ortigues *et al.* (1986, 1989).

MATERIALS AND METHODS

Expt 1

Animals. Four Friesian steers (average initial weight 205 kg) were used in a 4 × 4 Latin Square design digestion experiment. They had previously been fitted with a rumen cannula and simple 'T' piece cannulas at the proximal duodenum (before the pancreatic duct) and distal ileum (Buttle *et al.* 1982).

Experimental plan. Each period of the experiment consisted of one week of transition to the new diets, 3 weeks of adaptation (days 1–20) and 2 weeks of measurements (days 21–35). During the adaptation period, sampling of marker-free faeces and digesta contents was carried out on days 15, 16 and 17. Total faecal collection was carried out from day 21 to 24 (collection period) and spot sampling of rumen fluid, duodenal and ileal contents concurrent with a total faecal collection were carried out on days 25–26 (sampling period). Further sampling of rumen fluid was carried out on day 30. Rates of dry matter (DM) and N disappearance from Dacron bags were obtained after rumen incubation of bags on days 33–35.

Diets and feeding. Four experimental diets were used (Table 1). Diets A and B were isoenergetic and contained ammonia-treated (35 g NH_3/kg fresh straw) winter barley straw and a concentrate portion in the ratio, 67:33 (w/w). The concentrate of diet A consisted of barley only, whereas that of diet B contained both barley and fishmeal (Provimi 66; British White Fishmeal Ltd). Each of these diets was then isoenergetically supplemented with barley; diets C and D respectively. In diet D, the level of fishmeal inclusion was adjusted relative to the estimated (Agricultural Research Council, 1980) ME intake so as to maintain the N:ME value similar to that of diet B. N:ME values were 1·77, 2·78, 1·77 and 2·81 for diets A, B, C and D respectively. This criterion was chosen to take account of the N–ME inter-relationships that are known to exist both in the rumen and in the animal tissues (Egan, 1974; Agricultural Research Council, 1980). These diets, formulated on isoenergetic and isonitrogenous (N:ME) bases, were arranged in a 2×2 factorial design, corresponding to the effects of dietary levels of barley or fishmeal.

Food was offered in two equal meals at 12 h intervals.

Administration of markers. Intestinal digesta flows were measured after infusing ruthenium-phenanthroline (Ru-Phe; MacRea & Evans, 1974; Evans *et al.* 1977), ytterbium acetate and Cr-EDTA (Binnerts *et al.* 1968) continuously into the rumen from day 18 to 27 at daily rates of 52 mg ruthenium, 281 mg ytterbium and 513 mg chromium. Microbial protein flows were measured by infusing ^{15}N-labelled ammonium sulphate (enriched at approximately 10 g atoms ^{15}N/100 g atoms N, Amersham International plc, Amersham, Bucks) continuously at a daily rate of 38 mg in each animal on days 24–26.

Sampling procedures and measurements. Bulked samples of straw, barley and fishmeal were taken during both the faecal collection and the digesta sampling periods.

Rumen fluid samples (days 25 and 26) were taken six times daily so as to represent every hour of a 12 h interval between meals. Further rumen fluid samples were obtained hourly on day 30 from 0 to 12 h postprandially. Subsamples were stored at −20° either as collected for VFA analysis or after acidification with a few drops of concentrated sulphuric acid for NH_3 determination. Rumen bacteria were harvested from rumen fluid samples on days 15, 16, 17 and 26 by differential centrifugation (Smith & McAllan, 1974).

Spot samples of intestinal digesta were collected 2 and 8 h postprandially on days 15, 16 and 17 and at the same time as rumen fluid samples on days 25–26. On collection, ileal samples were acidified with 3 M-hydrochloric acid (80 ml/kg). Samples of duodenal and ileal contents were subsequently bulked on an equal weight basis per period. Digesta was fractionated as whole contents subsamples and liquid and solid phases subsamples (centrifugation at 30000 ***g*** for 20 min). Particulate samples were freeze-dried and ground through a 1 mm screen, whereas liquid samples were stored at −20° for subsequent analyses. For the determination of microbial protein intestinal flows, fractions of samples from day 26 only were used.

Faecal grab samples were taken in the premarker period at 2 and 8 h postprandially. A total faecal collection was carried out in the collection and sampling periods using light webbing harnesses. Faecal DM was determined daily (drying at 105° for 48 h). Separate samples were either freeze-dried and ground (1 mm screen) to await chemical analysis or were acidified with 1·5 M-H_2SO_4 immediately on sampling for N determination.

Dacron bags (pore size 48 μm) were filled with all constituents of each respective diet, in the same proportions as in the diets offered to the steers in which the bags were going to be incubated. Incubation times were 0, 6, 12, 24, 48 and 72 h, with duplicate bags for each incubation time. Zero-time estimates were obtained after soaking bags in water at 39° for 5 min. All samples were freeze-dried, ball milled and analysed for their N content.

Chemical analysis. Rumen pH was determined immediately on sampling. Rumen VFA were analysed according to Sutton & Johnson (1969), using caproic acid as an internal

standard. Rumen NH_3 was measured by an automated procedure (Technicon Instruments Co., Basingstoke).

Digesta flows and estimated faecal outputs were obtained after analysis of dry samples for Ru and Yb and of liquid samples for Cr, using the corresponding marker-free samples as background matrices. Ru was analysed on pelleted samples by X-ray fluorescence spectrometry (Evans *et al.* 1977). Yb was analysed according to Siddons *et al.* (1985) after extraction of the Yb from the ashed material with 20 ml nitric acid (20 ml/l) containing 1 mg K as potassium chloride/ml.

Organic matter (OM) was obtained after 6 h ashing at 550°. Samples from periods of total faecal collection were analysed for their acid-detergent fibre (ADF; Goering & Van Soest, 1970) and N (Kjeldahl) contents. Digesta samples were analysed for total N (Kjeldahl), individual amino acids (Mason *et al.* 1980), individual carbohydrate fractions (cellulose-glucose, xylose, arabinose, galactose and starch-glucose; McAllan & Smith, 1974) and total fat (Sutton *et al.* 1970). NH_3-N was determined by an automated technique (Technicon Instruments Co., Basingstoke) on liquid phases of intestinal digesta.

^{15}N enrichment of freeze-dried bacterial or intestinal samples was measured by isotope-ratio mass spectrometry (VG isogas) after isolation of the non-NH_3-N (NAN) fraction as $(NH_4)_2SO_4$ by steam distillation.

Calculations. Intestinal DM flows were calculated according to a double-phase marker technique (Faichney, 1975), which corrects for lack of representativeness of the intestinal digesta samples. Cr and NH_3 concentrations in dry samples were estimated from their contents in liquid-phase samples and the DM contents of particulate samples. NAN in digesta was obtained by difference between total N and NH_3-N. Estimated faecal DM output was obtained from the amount of solid-phase marker (Ru or Yb) administered daily and the concentrations of each respective marker in the faeces.

The amounts of bacterial N flowing to the intestines were calculated from the ^{15}N enrichment in the NAN of the digesta samples reconstituted according to Faichney (1975) and the average ^{15}N enrichment in the rumen bacterial samples. A correction was applied for the natural enrichment in ^{15}N which was measured in the appropriate fractions of marker-free rumen bacteria and intestinal digesta samples taken on days 15–17.

Expt 2

Animals. Forty-eight winter-born, 9-month-old dairy heifers, of average starting weight 155 (SE 2·3) kg were used. This feeding trial was part of a larger experiment on compensatory growth (Smith *et al.* 1985) which required six treatment groups. Animals were balanced according to full initial live weights and randomly allocated to one of the six groups. Three groups of animals were offered the basal diet A (*n* 24), whereas each of the remaining groups received one of the other experimental diets. The feeding trial lasted 87 d, the first 20 d of which were considered as an adaptation period. Animals were wintered indoors.

Diets and feeding. The same four experimental diets and the same batches of feeds were used as described in Expt 1 (Table 1). At the start of the experiment, diets A and B supplied approximately 1·3 times the estimated (Agricultural Research Council, 1980) ME maintenance requirements (MEm), and diets C and D approximately 1·8 times MEm. Total amounts offered were kept unchanged over the whole experiment. Heifers were fed individually, twice daily with a 7 h interval between the morning and afternoon meals.

Measurements. Feeds were sampled once weekly for DM determination (drying at 105° for 48 h). Chemical characterization of feedstuffs was obtained from the digestion experiment.

Heifers were weighed twice weekly, 3·5 h after the morning meal. Body condition scores

(Mulvany, 1981) were taken once at the end of the experiment by five different people and averaged. An estimation of the energy content of the empty body-weight was made at the same time by ultrasonic transmission in the hind-limb (Anderson *et al.* 1982). Measurements could not be carried out on all animals so that out of the three groups that were receiving diet A only one was randomly chosen to undergo measurements (i.e. eight animals per experimental group were measured).

On days 60–62 of the experiment, blood was sampled by jugular puncture 4 h postprandially and rumen fluid was sampled with a tracheal tube 2·5 and 7 h postprandially. Heparinized blood was deproteinized immediately before glucose analysis by an automated colorimetric glucose oxidase (*EC* 1.1.3.4) method (Boehringer Mannheim GmbH). Serum was stored at −20° before determination of urea (Boehringer Mannheim GmbH) and non-esterifed fatty acids (NEFA, Brookes *et al.* 1984). Rumen pH, rumen VFA and rumen NH_3-N were determined as described previously.

Statistical analysis

Values were treated by analysis of variance using initial live weights as covariate (feeding trial) or according to a Latin Square design (digestion trial) with a 2×2 factorial arrangement of treatments (barley × fishmeal levels). Treatment means of the main effects were compared by the F ratio. If the interaction term was significant, individual means were compared using Student's t test. Results from rumen fermentation variables obtained both in the digesta sampling period and on day 30 were pooled and analysed according to a split-plot design. The subplot corresponded to a 'method' or 'day' effect: sampling of rumen fluid spread over 48 h (digesta sampling period) or over 12 h (day 30). All two- and three-way interactions were included in the model.

RESULTS

The chemical composition of the feed ingredients is presented in Tables 1 and 2.

Apparent whole tract digestibility of diets

DM intakes and apparent digestibility values of DM, OM, ADF and N measured during the faecal collection periods are reported in Table 3. The effects of increasing the level of barley in the diet were probably a result of the addition to the diet of a highly digestible feedstuff, whereas the enhancement of DM and OM digestibility with fishmeal appeared to stem from a significant increase in ADF digestibility.

Rumen fermentations

Values for all rumen variables have been averaged over time and day of sampling for each animal (Table 4), since there was no interaction between the diurnal pattern of rumen fermentation and dietary treatments.

Rumen NH_3-N concentrations were above 3·5 mM for all diets and at all times. The introduction of fishmeal into the diets significantly increased rumen NH_3-N concentrations at all times and raised the minimum value to 6·5 mM (Table 4).

Increasing the dietary level of barley did not greatly modify either total VFA concentrations or the pattern of rumen fermentation. Introducing fishmeal into the diet, on the other hand, significantly decreased total VFA concentrations with concurrent increases in rumen pH, mostly around meal times (Table 4). In general, the changes in VFA pattern were small and did not greatly modify the molar ratio of (acetate + *n*-butyrate):propionate.

Table 2. *Amino acid composition of feedstuffs (g nitrogen/kg dry matter)*

	Ammonia-treated straw	Barley	Fishmeal
Threonine	0·24	0·53	3·20
Methionine	0·06	0·19	1·76
Lysine	0·35	0·88	9·54
Valine	0·25	0·73	3·62
Isoleucine	0·17	0·46	2·67
Leucine	0·33	0·99	5·17
Histidine	0·26	0·82	5·66
Phenylalanine	0·18	0·58	2·14
Arginine	0·54	2·11	13·97
Aspartic acid	0·46	0·80	6·58
Serine	0·31	0·82	4·25
Glutamic acid	0·55	3·18	8·71
Glycine	0·47	0·99	10·49
Alanine	0·44	0·86	7·08
Cysteine	0·08	0·30	0·51
Tyrosine	0·11	0·34	1·67
Proline	0·29	1·89	4·24

Table 3. *Average dry matter intake (g/d) and apparent digestibility coefficient of dry matter, organic matter, acid-detergent fibre and nitrogen of straw-based diets*†

Diets...	A	B	C	D	SE of treatment means	Statistical significance of differences	
Dry matter intake	3904	3864	4783	4773	41·2	E***	
Digestibility							
Dry matter	0·633	0·660	0·667	0·689	0·0090	E*,	N*
Organic matter	0·649	0·677	0·680	0·701	0·0084	E*,	N*
Acid-detergent fibre	0·560	0·607	0·549	0·579	0·0116		N*
N	0·510	0·681	0·538	0·717	0·0122	E*,	N***

E, N, effects of energy and N supplementation respectively.
* $P < 0·05$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

Calculation of sites of digestion

As discussed elsewhere (Ortigues, 1987) digesta and nutrient flow values were not always the same when the Ru or the Yb marker systems were used. Insufficient information was available to justify relying preferentially on one of those two markers. Consequently, values for sites of digestion are given as estimated by both the Ru and Yb marker systems.

No correction was applied for the withdrawal of marker anterior to each sampling site, as any correction should necessarily take into consideration the rate of passage of digesta along the tract, and rate of passage was not measured in the present experiment. It was calculated, however, that digesta sampling resulted in an underestimation of faecal output by a maximum of 6%. Such a correction was similar across diets and should not invalidate comparisons among treatments.

Table 4. *Average rumen pH, ammonia-nitrogen concentrations (mM), volatile fatty acid (VFA) concentrations (mM) and molar proportions, and molar ratio of acetate+n-butyrate:propionate, measured in steers offered straw-based diets*†

Diets...	A	B	C	D	SE of treatment means	Statistical significance of differences
pH	6·86	6·91	6·71	6·98	0·048	N*
NH_3-N	6·15	11·94	5·74	11·89	0·786	N***
Total VFA concentrations	83·75	81·66	89·41	82·32	1·758	N*
VFA molar proportions						
Acetate	0·715	0·718	0·698	0·708	0·0057	
Propionate	0·172	0·170	0·181	0·166	0·0040	
n-Butyrate	0·091	0·087	0·094	0·094	0·0047	
Isobutyrate	0·005	0·006	0·005	0·007	0·0002	E*, N***, E × N*
Isovalerate	0·005	0·007	0·006	0·009	0·0006	N**
n-Valerate	0·009	0·010	0·012	0·012	0·0005	E**
n-Caproate	0·003	0·002	0·004	0·004	0·0003	E***
Acetate +*n*-butyrate:propionate	4·74	4·68	4·51	4·89	0·132	

E, N, effects of energy and N supplementation respectively.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

Table 5. *Organic matter intake (g/d), whole-tract digestibility and partial digestibilities in the stomachs relative to intake, in the small intestine relative to duodenal flow and in the large intestine relative to ileal flow; estimates were obtained with ytterbium and ruthenium as particulate-phase markers, in steers offered straw-based diets*†

Diets...	A	B	C	D	SE of treatment means	Statistical significance of differences
Intake	3521	3499	4406	4416	37·2	E***
Whole tract digestibility						
Yb	0·635	0·676	0·691	0·700	0·0075	E**, N*
Ru	0·690	0·729	0·726	0·764	0·0071	E**, N**
Partial digestibility						
In stomachs						
Yb	0·395	0·427	0·466	0·409	0·0322	
Ru	0·443	0·451	0·441	0·486	0·0120	
In small intestine						
Yb	0·325	0·265	0·361	0·383	0·0437	
Ru	0·214	0·226	0·333	0·282	0·0284	E*
In large intestine						
Yb	0·100	0·208	0·078	0·172	0·0557	
Ru	0·283	0·353	0·257	0·355	0·0205	N**

E, N, effects of energy and nitrogen supplementation respectively.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

Table 6. *Intake (g/d), whole-tract digestibility and partial digestibilities in the stomachs relative to intake and in the small or large intestine relative to duodenal or ileal flow of cellulose-glucose, xylose and starch-glucose; estimates were obtained with ytterbium and ruthenium as particulate-phase markers, in steers offered straw-based diets*†

Diets...		A	B	C	D	SE of treatment means	Statistical significance of differences
Glucose							
Intake		1004	990	1018	1031	17·1	
Digestibility:							
In whole tract	Yb	0·653	0·725	0·655	0·682	0·0114	N**
	Ru	0·706	0·769	0·695	0·749	0·0121	N**
In stomachs	Yb	0·652	0·633	0·659	0·592	0·0443	
	Ru	0·687	0·650	0·634	0·649	0·0357	
In large intestine	Yb	−0·021	0·183	−0·057	0·094	0·0624	N*
	Ru	0·188	0·323	0·157	0·302	0·0190	N***
Xylose							
Intake		400	382	441	427	5·9	E***, N*
Digestibility:							
In whole tract	Yb	0·657	0·707	0·694	0·677	0·0124	E × N*
	Ru	0·710	0·754	0·729	0·746	0·0151	
In stomachs	Yb	0·650	0·594	0·672	0·529	0·0728	
	Ru	0·695	0·615	0·642	0·597	0·0636	
In large intestine	Yb	−0·047	0·216	0·062	0·088	0·0687	
	Ru	0·188	0·359	0·238	0·311	0·0464	N*
Starch-glucose							
Intake		827	614	1462	1149	12·4	E***, N***, E × N**
Digestibility:							
In whole tract	Yb	0·948	0·940	0·963	0·957	0·0054	E*
	Ru	0·955	0·949	0·968	0·966	0·0047	E*
In stomachs	Yb	0·873	0·774	0·897	0·830	0·0409	
	Ru	0·887	0·780	0·891	0·857	0·0384	
In small intestine	Yb	0·42	0·63	0·44	0·73	0·194	
	Ru	−33·14	0·59	0·38	0·67	16·948	

E, N, effects of energy and N supplementation respectively.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

Partition of OM digestion in the digestive tract

Largely because of variations between marker systems in the estimation of OM flows, the partition of OM digestion along the gastrointestinal tract did not clearly identify the sites responsible for the previously mentioned increase in apparent OM digestibility (Table 5). For all diets, approximately 63% of the overall OM digestion occurred in the forestomachs.

Partition of carbohydrate digestion in the digestive tract

Cellulose–glucose. In general, whole tract digestibility of cellulose was similar for both diets A and C, at about 0·65–0·70 (Table 6). Virtually all this digestion occurred in the rumen, 99·8 and 86·6% (Yb) and 97·4 and 91·2% (Ru) for diets A and C respectively. Introducing fishmeal into the diets resulted in significant increases in the overall cellulose digestibility by 3–7% and this was mainly due to increased digestion in the large intestine with these diets. Absolute amounts of cellulose digested in the stomachs of animals receiving diets B and D were 622 and 602 g/d (Yb) and 641 and 664 g/d (Ru) respectively,

and were very similar to those in animals receiving diets A and C: 657 and 671 g/d (Yb) and 695 and 646 g/d (Ru) respectively. Nevertheless, the contribution of the stomachs to whole-gut digestibility fell significantly to 87·2 and 86·6% (Yb) and 84·4 and 86·7% (Ru) for diets B and D respectively. The increased digestibility in the large intestine accounted for up to 15% of the total digested with these two diets.

Hemicelluloses. The main component sugars of the hemicelluloses of the diets used were xylose, arabinose and galactose, which were present in approximate proportions of 0·75, 0·19 and 0·06 respectively. Whole-tract digestibility of xylose was about 0·70 on all diets and across both markers, and was only slightly and not consistently increased by raising the levels of either concentrate in the diets. However, as with the results for cellulose digestion, introduction of fishmeal into the diets shifted the site of xylose digestion towards the large intestine where its partial digestibility was significantly increased (Table 6).

Whole-tract apparent digestibilities of arabinose were also relatively high: 0·716, 0·739, 0·744 and 0·724 (SEM 0·0125; Yb) and 0·760, 0·781, 0·773 and 0·783 (SEM 0·0153; Ru) for diets A, B, C and D respectively. Arabinose intakes for these diets were 95·8, 87·0, 119·7 and 108·9 (SEM 1·12) g/d respectively. Raising the dietary level of barley increased, but raising that of fishmeal reduced ($P < 0·05$), the amounts of arabinose digested in the stomachs, reflecting intake differences. There were no changes in the partial digestibilities of arabinose with dietary treatments. Partition of galactose digestion along the tract did not yield any clear conclusions since the galactose content of the microbial population was not identified.

Starch. Starch was the major non-structural carbohydrate present in the diets used. It was almost completely digested in the whole tract. The major part of this digestion (from 82 to 94%) took place in the rumen (Table 6). Only small amounts of starch (from 10 to 20%) escaped rumen degradation and were digested in the small intestine with a partial digestibility of 0·40–0·70. Variability of the measurements was too large to detect any treatment effects. The aberrant value calculated for diet A with Ru (Table 6) stems from one animal for which estimated duodenal flow of starch was practically nil while ileal flow was 182 g/d.

Partition of N digestion along the digestive tract

Total N and NAN. Raising the dietary levels of both concentrates significantly increased the amounts of total N consumed daily by the animals (Table 7). Such differences in supply were not, however, consistently reflected throughout the digestive tract because of a large N gain between mouth and duodenum with diets devoid of fishmeal. Duodenal N flows corresponded to 156 and 134% (Yb) and 148 and 138% (Ru) of N intake for diets A and C compared with only 98 and 104% (Yb) and 95 and 93% (Ru) for diets B and D respectively (Table 7). Increase in barley, but not in fishmeal, significantly increased the amounts of N and NAN apparently absorbed from the small intestine of the steers (Table 8).

Effects of introducing fishmeal into the diets were detected in the large intestine only, with significantly higher N flows (Table 7) and digestion therein than with diets A and C. The quantities of N apparently digested in the large intestine were 3·9, 11·7, 2·5 and 12·6 (SEM 2·80; Yb) and 11·0, 16·4, 9·1 and 21·0 g/d (SEM 1·45; Ru) for diets A, B, C and D respectively.

Microbial protein synthesis. One animal receiving diet C showed an aberrant difference between the ^{15}N enrichment of the solid phase and that of the whole contents of duodenal digesta. Results for this animal of microbial protein synthesis were discarded and a missing value was estimated.

Amounts of microbial N flowing to the small intestine were significantly increased with the level of barley but reduced with the introduction of fishmeal into the diets (Table 7).

Table 7. *Intake and duodenal and ileal flows of total, non-ammonia-, microbial and amino acid-nitrogen (g N/d); estimates were obtained with ytterbium and ruthenium as particulate-phase markers in steers offered straw-based diets*†

Diets...		A	B	C	D	SE of treatment means	Statistical significance of differences
Intake							
Total N		62·7	103·3	82·0	137·3	1·93	E***, N***, E × N***
Total amino acid-N		32·6	65·1	47·7	92·4	0·71	E***, N***, E × N*
Duodenal flows							
Total N	Yb	97·9	101·2	110·1	142·5	4·46	E***, N**, E × N*
	Ru	92·6	97·9	113·5	128·1	1·70	E*, N**
Non-NH_3-N	Yb	93·6	93·8	105·4	134·3	4·26	E***, N*, E × N*
	Ru	88·3	90·5	108·9	119·8	1·83	E***, N*, E × N*
Microbial N	Yb	59·1	36·3	72·4	64·2	5·41	E*, N*
	Ru	55·6	35·2	73·4	57·5	5·53	E*, N*
Total amino acid-N	Yb	53·6	64·2	67·4	88·9	3·73	E*, N*
	Ru	50·8	62·1	70·1	79·1	1·40	E***, N***
Ileal flows							
Total N	Yb	36·2	44·4	39·8	49·8	3·09	N*
	Ru	38·6	43·8	42·2	50·3	1·70	E*, N**
Non-NH_3-N	Yb	32·9	39·6	36·3	44·2	2·70	N*
	Ru	35·2	39·0	38·8	44·7	1·50	E*, N*
Microbial N	Yb	14·4	15·7	20·0	18·0	1·45	E*
	Ru	16·0	15·5	22·0	18·2	2·07	
Total amino acid-N	Yb	16·8	21·5	20·6	25·3	1·92	N*
	Ru	17·9	21·0	21·8	25·5	1·35	E*, N*

E, N, effects of energy and N supplementation respectively.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

Table 8. *Apparent absorption in the small intestine of total, non-ammonia-, microbial and amino acid-nitrogen (g N/d) as well as efficiency of rumen microbial protein yield (g N/kg organic matter); estimates were obtained with ytterbium and ruthenium as particulate-phase markers in steers offered straw-based diets*†

Diets...		A	B	C	D	SE of treatment means	Statistical significance of differences	
Apparent absorption								
Total N	Yb	61·6	56·8	70·3	92·8	4·08	E**,	E × N*
	Ru	54·1	54·1	71·3	77·8	2·85	E***	
Non-NH_3-N	Yb	60·7	54·2	69·1	90·1	4·08	E**,	E × N*
	Ru	53·1	51·4	70·1	75·1	2·86	N***	
Microbial N	Yb	44·7	20·6	52·4	46·2	4·24	E*, N*	
	Ru	39·6	19·8	51·4	39·3	4·12	E*, N*	
Total amino acid-N	Yb	36·8	42·7	46·7	63·6	2·92	E**, N**	
	Ru	32·8	41·1	48·4	53·7	1·53	E***, N**	
Microbial yield								
	Yb	42·6	24·8	35·3	37·3	4·57		
	Ru	35·4	23·3	37·2	27·3	2·30	N**	

E, N, effects of energy and N supplementation respectively.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

These effects could be explained to a large extent by the amount of carbohydrates degraded in the rumen and also by a tendency for a lower efficiency of microbial yield in the presence of fishmeal (Table 8).

Amino acids. The proportions of total amino acid-N in duodenal NAN were significantly increased by fishmeal in diet B ($P < 0·01$). Values were 0·58, 0·69, 0·64 and 0·66 for diets A, B, C and D respectively. Consequently the responses to treatments in terms of total amino acid supply and apparent absorption were quite similar to those observed for the N values with the additional and significant effect arising from the introduction of fishmeal into the diets. Increasing the levels of barley or fishmeal augmented the amounts of total (Table 8) or individual (Table 9) amino acids apparently digested in the small intestine but not their partial digestibility therein. The balance among individual amino acids apparently absorbed from the small intestine was only slightly modified by treatments. Introducing fishmeal into the diets increased the proportions of methionine ($P < 0·01$), arginine ($P < 0·001$) and glycine ($P < 0·05$) apparently absorbed and decreased those of aspartic acid ($P < 0·01$), alanine ($P < 0·05$) and valine ($P < 0·05$); the effects on the last two amino acids were restricted to diet B. Raising the dietary level of barley on the other hand increased the proportions of glutamic acid ($P < 0·05$) and valine ($P < 0·05$) apparently absorbed and decreased those of alanine ($P < 0·01$), leucine ($P < 0·05$) and histidine ($P < 0·01$). These changes were however small, so that the ratio of essential:non-essential amino acids absorbed remained similar with all four diets used; this ratio averaged 0·87.

A notable effect of fishmeal was seen in the large intestine. Amounts of total amino acids apparently degraded in the large intestine of animals receiving diets B and D were significantly increased as a result of both a rise in the amounts of amino acids flowing past the ileum and in their partial digestibility therein. Total amino acids apparently degraded in the large intestine were 21, 50, 22 and 52 g/d (SEM 10·2; Yb) or 44, 64, 45 and 82 g/d (SEM 5·6; Ru) for diets A, B, C and D respectively. This effect was similar for all individual amino acids except histidine, cysteine and tyrosine.

Table 9. *Amounts of individual amino acids apparently absorbed (g N/d) from the small intestine; estimates were obtained with ytterbium and ruthenium as particulate-phase markers in steers offered straw-based diets*†

Diets...		A	B	C	D	SE of treatment means	Statistical significance of differences
Threonine	Yb	1·65	1·84	2·14	2·73	0·116	E***, N*
	Ru	1·48	1·76	2·21	2·28	0·105	E***
Methionine	Yb	0·51	0·64	0·59	1·01	0·057	E**, N**, E × N*
	Ru	0·45	0·60	0·62	0·84	0·033	E***, N***
Lysine	Yb	4·26	4·91	5·37	7·08	0·255	E***, N**
	Ru	3·91	4·74	5·54	6·14	0·132	E***, N**
Valine	Yb	1·77	2·06	2·49	3·10	0·121	E***, N*
	Ru	1·58	1·99	2·56	2·60	0·098	E***
Isoleucine	Yb	1·50	1·64	1·87	2·47	0·115	E**, N*
	Ru	1·34	1·57	1·92	2·09	0·094	E***
Leucine	Yb	2·35	2·78	2·96	3·98	0·190	E**, N**
	Ru	2·12	2·69	3·06	3·39	0·111	E***, N**
Histidine	Yb	1·79	1·95	1·87	2·33	0·184	
	Ru	1·52	1·84	1·95	1·68	0·084	
Phenylalanine	Yb	1·05	1·29	1·35	1·76	0·115	E*, N*
	Ru	0·92	1·24	1·39	1·48	0·094	E**
Arginine	Yb	4·44	6·11	6·02	9·08	0·463	E**, N**
	Ru	4·06	5·92	6·31	7·92	0·283	E***, N***
NEAA	Yb	17·50	19·50	22·05	30·08	1·366	E***, N**
	Ru	15·47	18·74	22·83	25·27	0·697	E***, N**

E, N, effects of energy and N supplementation respectively; NEAA, non-essential amino acids.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.

Partition of fat digestion along the digestive tract

Total fat did not appear to be well utilized with the diets offered. Although the amounts of fat consumed were significantly higher when the level of concentrates in the diets was increased (133, 168, 169 and 218 g/d, SEM 4·4, for diets A, B, C and D respectively), a large but differential gain of fat was noted between mouth and duodenum which cancelled most of the treatment differences in fat supply from the duodenum onwards. Amounts of fat apparently absorbed from the small intestine were small and variable: 17, 4, 40 and 52 g/d (SEM 19·8; Yb) and −21, −6, 38 and −9 g/d (SEM 23·6; Ru). Whole-tract digestibility of fat was −0·458, −0·102, −0·095 and 0·073 (SEM 0·0330; Yb) and −0·228, 0·076, 0·030 and 0·273 (SEM 0·0273; Ru) for diets A, B, C and D respectively.

In situ *feed characterization*

Degradation rate of the DM fraction of the whole diets was increased with the level of barley in the diets ($P < 0·001$) but decreased with the introduction of fishmeal ($P < 0·01$). Values were 0·0603, 0·0575, 0·0759 and 0·0661 (SEM 0·00168) for diets A, B, C and D respectively. Similarly, the degradation rate of the N fraction was reduced ($P < 0·001$) by fishmeal. Values were 0·0778, 0·0390, 0·0877 and 0·0380 (SEM 0·00359) in the same respective order.

Table 10. *Dry matter intake (kg/d), initial weights (kg), live-weight gains (g/d), body condition scores and energy content of empty body-weights (GJ or MJ/kg) of heifers offered straw-based diets; blood glucose, serum non-esterified fatty acids (NEFA) and urea concentrations (nM) are also shown*†

Diets...	A	B	C	D	SE of treatment means‡	Statistical significance of differences
Dry matter intake	3·23	3·26	4·15	4·15	—	
Initial wt	154	159	156	155	5·8	
Live-wt gain	259	431	522	615	23·1	E***, N***
Body scores	1·12	1·31	1·37	1·43	0·004	E***, N**
Energy content of final empty body-wt§						
GJ	1·56	1·63	1·71	1·77	0·025	E***, N*
MJ/kg	9·48	9·29	9·30	9·21	0·128	
Blood glucose	2·49	2·52	2·71	2·82	0·092	E**
Serum NEFA	96·5	134·4	58·0	118·2	22·36	N*
Serum urea	4·16	6·69	3·65	6·88	0·255	E*, N***

E, N, effects of energy and N supplementation repectively.
* $P < 0·05$; ** $P < 0·01$; *** $P < 0·001$.
† For details of diets, see p. 603 and Tables 1 and 2.
‡ For eight animals per treatment. With the basal diet, n 24, the standard error of treatment means should, therefore be divided by $\sqrt{3}$, except for the energy content of final empty body-weight.
§ Measured on thirty-two heifers only, eight from each group.

Growth performances

Increasing the dietary levels of concentrates significantly increased rates of live weight gain (calculated by regression of live weights *v.* period on trial (d)) and body condition. No changes were seen with treatments in the estimated energy content of the empty body (MJ/kg), indicating that the increase in total energy of the empty body, expressed as GJ, simply reflected the increased weights of the animals (Table 10).

The effects of treatments on rumen fermentation variables were similar to those noted in Expt 1 and are not reported. Concentrations of blood glucose (Table 10) were increased with dietary level of barley ($P < 0·01$); a similar trend existed with the introduction of fishmeal into the diets but did not reach statistical significance. Serum NEFA concentrations were markedly increased ($P < 0·05$) with diets B and D.

DISCUSSION

DM and OM digestion

Overall apparent digestibility values of DM and OM were within the range of 0·60–0·70 found by Smith *et al.* (1980*a*, *b*, 1983–4) with diets containing at least 500 g straw/kg and in similar experimental conditions. Increasing the levels of barley or fishmeal in straw-based diets enhanced the overall digestibility as expected from previous reports (Smith *et al.* 1980*a*, *b*; Amaning-Kwarteng *et al.* 1986). The partition of OM digestion along the tract did not really highlight any of the effects of supplementation. The addition of barley did not alter the sites of OM digestion, which can be explained by the small modifications in the forage:concentrate ratio and the fact that the amount of straw offered was kept

constant across diets (Sutton, 1980). Similarly, the introduction of fishmeal into diets did not change the partition of OM digestion, which confirms results of previous studies both in the rumen (McAllan & Smith, 1983) and in the small intestine (Oldham *et al.* 1977).

Carbohydrate digestion and rumen microbial growth

Within the range of marker error, the present results for carbohydrate digestion agree with those obtained by Ternrud & Neergaard (1986) using sheep fed on sodium hydroxide-treated straw, rolled barley, fishmeal and urea in the approximate proportions of 49:44:4:1·5 (by wt). Addition of barley (diets C and D) increased the supply of rapidly fermentable carbohydrates but resulted in only slight changes in digestibility. Straw digestibility, calculated by difference, remained unchanged by the addition of approximately 1 kg barley, as is often the case with cattle fed on diets containing at least 500 g straw/kg (Ørksov, 1986).

Introduction of fishmeal into diets increased the digestibility of plant structural carbohydrates (cellulose and xylose) and shifted their site of digestion from the rumen to the large intestine. These effects could be due in part to a reduction in rumen digestion through some increase in fat intake. The reduced rate of DM disappearance from Dacron bags and the reduction in rumen VFA concentrations around meal times measured in diets B and D were consistent with some impairment in rumen digestion (McAllan *et al.* 1983). Where fat supplements have been found to interfere with fibre digestion in the rumen, it has frequently been the case that there is a compensation with a noted shift in the site of digestion of DM, OM or fibre fractions (ADF, NDF, cellulose, hemicellulose) towards the large intestine (Ikwuegbu & Sutton, 1982; Jenkins & Palmquist, 1984).

Further improvement in intestinal digestibility of carbohydrates with diets B and D could also have originated from additional amino acid supply to the large intestine. Dixon & Nolan (1982) have shown that some increase in the flow of non-urea NAN to the large intestine was associated with a higher flow of VFA therein.

N digestion

Total N, NAN or amino acids as indices of N supply. When diets contain poor-quality roughages or a non-protein-N source, measurements of total N or NAN in the intestines can be poor indices of the 'useful' N supply to the animal (Spragg *et al.* 1986), particularly because of large variations in the endogenous N contribution to total NAN. In the present experiment, there was a substantial response to fishmeal in terms of amino acids apparently absorbed from the small intestine but not in terms of total N or NAN. The extent of N recycling into the stomachs of steers offered the diets devoid of fishmeal was considerable, and was probably the reason for the significantly lower proportions of amino acid-N in duodenal NAN with diet A. There is, however, a dearth of information relating to the composition of the endogenous protein (Toullec *et al.* 1983) and non-protein fractions (Buraczewski, 1986) and to their changes in composition with diets (Toullec *et al.* 1983). In the context of the Agricultural Research Council (1984) predictions of the N supply to the animal, total amino acid flows at the duodenum may not be sufficiently reliable. In the two diets devoid of fishmeal, a larger proportion of undegraded dietary N at the duodenum originated from straw, in which N is largely bound to the fibre fraction and is highly indigestible (Webster *et al.* 1984). Very wide dietary differences in the apparent intestinal absorption of NAN were measured by MacRae *et al.* (1985) and Redman *et al.* (1980), which could relate to the composition of undegraded dietary protein. In this context, it is pertinent that future schemes assessing the N utilization by ruminants should use true rather than apparent absorption coefficients. If variations in digestibility add to the differences in biological values (Rooke & Armstrong, 1987), responses to supplementation might be difficult to predict.

N degradability in feedstuffs. An attempt was made to estimate the N degradability in the non-protein-N of the supplements used in the present experiment. However, because of the non-protein-N supplied by the treated straw and because of different extents of N recycling across diets (Egan *et al.* 1986), we suggest that the amino acid-N degradability is nutritionally more meaningful. Microbial amino acid-N was assumed to amount to 81% of the total microbial N (Storm & Ørskov, 1983) and the duodenal non-microbial amino acid-N was assumed to correspond to the undegraded dietary proteins. Degradability values would, thereby, be underestimated; however, the error would not be larger than that which would be obtained after estimation of endogenous N at the duodenum because of the known dietary effects on endogenous N secretions (Bergner *et al.* 1983; Low & Rainbird, 1983; Toullec *et al.* 1983). In these conditions, 81% (Yb) or 69% (Ru) of barley amino acid-N seemed to be degraded in the rumen compared with 22 (Yb) or 23% (Ru) of fishmeal in diet B and 42 (Yb) or 52% (Ru) in diet D; fishmeal degradability values were obtained by difference. These values are similar to those reported by Amaning-Kwarteng *et al.* (1986) and Rooke & Armstrong (1987).

The lower amino acid degradability of fishmeal compared with that of barley was reflected in the reduced rate of total N disappearance from Dacron bags with diets B and D. The apparently higher degradability of fishmeal, when offered with larger amounts of barley, agrees with Cottrill *et al.* (1982) and the observations that the predominant proteolytic rumen bacteria are the saccharolytic ones (Cotta & Hespell, 1986).

Amino acid supply. Raising the level of barley in diets increased amino acid-N supply to the animal mostly through enhancing rumen microbial protein synthesis. Similar results were obtained by Amaning-Kwarteng *et al.* (1986) when a straw diet was supplemented with barley.

Introduction of fishmeal into diets increased amino acid-N supply to the animals largely through increasing the supply of undegraded dietary protein beyond the rumen, confirming previous results (Cottrill *et al.* 1982; Gill & Beever, 1982; Rooke & Armstrong, 1987). Fishmeal is claimed to modify the pattern of amino acids supplied to the intestines, although the picture is still confusing. Methionine seems to be most consistently reported as being increased by fishmeal supplementation (Mercer *et al.* 1980; Cottrill *et al.* 1982; Gill & Beever, 1982), although there are also reports indicating enhanced supplies of arginine (Gill & Beever, 1982; Rooke & Armstrong, 1987), aspartate (Mercer *et al.* 1980) and threonine (Cottrill *et al.* 1982).

A major effect of both forms of dietary supplement, though via different mechanisms was, therefore, an increase in total amino acid supplies to the animal, and this appeared to be a major factor in determining the effects of both dietary supplements on the growth of heifers offered the same diets in the associated feeding trial.

Balance among absorbed nutrients and growth performances

The responses to supplementation measured on growing heifers in the feeding trial confirmed results of previous experiments with comparable animals given similar diets (Smith *et al.* 1980*a*, *b*). With diets C and D, growth rates were elevated as predicted by Agricultural Research Council (1980) on the basis of elevated DOMI. The response to fishmeal, on the other hand, demonstrated the scope for additional growth at a given ME intake, when part of this ME originated from a low-degradability-protein supplement. Neither this effect nor the simultaneous enhancement in the efficiency of ME utilization for growth (Ortigues *et al.* 1989) was predicted by Agricultural Research Council (1980, 1984). A general underestimation of N requirements for tissue growth by Agricultural Research Council (1980) was already noted by Rohr *et al.* (1983) who calculated that the Institut National de la Recherche Agronomique (1978) would predict a 20–25% higher protein deposition in the heifers used by Smith *et al.* (1980*a*, *b*). Agricultural Research Council

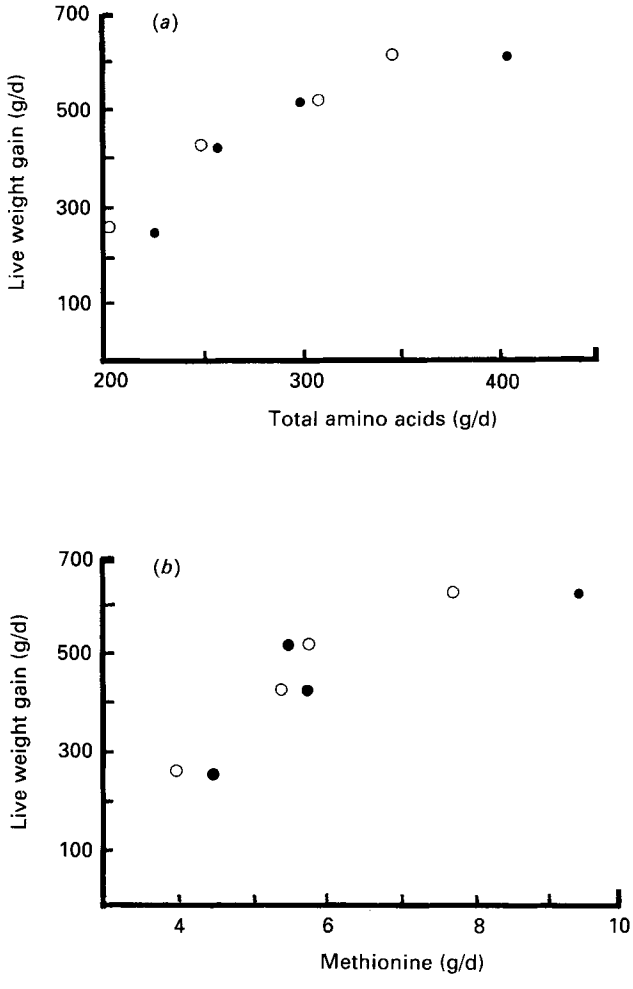

Fig. 1. Relations between amounts of total amino acids (*a*) or methionine (*b*) absorbed from the small intestine, obtained from measurements made in cannulated steers, using ytterbium (Yb, ●) or ruthenium (Ru, ○) as particulate-phase markers (Ortigues, 1987), and the live-weight gains of heifers measured in the present experiment. All animals were offered straw-based diets supplemented with barley or fishmeal (for details of diets, see p. 603 and Tables 1 and 2).

(1980) predicts a proportionally slower rate of protein deposition with increasing weight gains. Robelin & Daenicke (1980), however, questioned the validity of such a relationship for rates of gain lower than 500 g/d.

One aim of the present work was to use the knowledge of nutrient supply to interpret the patterns of growth achieved by heifers eating the same diets. In terms of nutrient supply, the major feature of the present results is that increasing the dietary levels of barley or fishmeal did not appear to modify greatly the rumen fermentation pattern and, therefore, the balance amongst absorbed VFA, nor did it modify the intestinal absorption of starch-glucose. On the other hand, the contribution of amino acids to total estimated ME intake increased with the proportion of fishmeal in diets and represented 0·171, 0·195, 0·178 and 0·211 of total ME intake for diets A, B, C and D respectively (Agricultural Research

Council, 1980). Thus, among the nutrient supply values obtained, only amino acids appeared to be related to growth rates measured (Fig. 1). The balance of individual essential amino acids was investigated and compared with the requirements estimated by Smith (1980) on the basis of the amino acid composition of the whole body of growing calves. Diets A and C appeared to be deficient in methionine but to provide excess of lysine and phenylalanine as often observed when comparing the composition of duodenal digesta with that of calf whole body (Buttery & Foulds, 1985). For all other essential amino acids, their relative supply by diets A and C was approximately adequate as defined by Smith (1980). Introduction of fishmeal into diets somewhat reduced the methionine deficiency but the estimated optimum balance of methionine was still not reached. However, it is unlikely that an increase in methionine absorption alone accounts to a large extent for the increased growth rates, even if the efficiency of methionine utilization is higher than that of other amino acids (MacRae & Lobley, 1986). Indeed, live-weight gains can essentially be explained in terms of total amino acids absorbed rather than in terms of individual amino acids absorbed such as methionine (Fig. 1). As the ratio of essential:non-essential amino acids absorbed from the small intestine was not modified by the dietary level of fishmeal, it can be concluded that the responses to fishmeal with straw-based diets were probably mediated by an increase in total amino acid supply. A similar conclusion was reached by MacRae & Ulyatt (1974) using sheep offered fresh herbages.

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