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Partition of portal-drained visceral net flux in beef steers

1. Blood flow and net flux of oxygen, glucose and nitrogenous compounds across stomach and post-stomach tissues*

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1. Blood from chronic indwelling catheters in the caudal aorta and anterior mesenteric, gastrosplenic and hepatic portal veins was used to measure blood flow and net flux of oxygen, glucose and nitrogenous compounds across hepatic portal-drained viscera (PDV), post-stomach (anterior mesenteric-drained viscera (MDV)) and stomach tissues of two beef steers (390 kg mean live weight).

2. Steers were fed in sequence on (1) chopped lucerne (*Medicago sativa*) hay (twelve meals/d), (2) chopped lucerne hay (two meals/d) and (3) a pelleted concentrate diet containing 780 g ground maize/kg (two meals/d). The lucerne hay and concentrate contained 26·5 and 16·8 g nitrogen/kg respectively.

3. Five measurements of net flux (blood flow multiplied by venous–arterial concentration differences (VA)) were obtained hourly on 2 d for each dietary regimen, beginning 0·5 h before feeding at 08.00 hours. Blood flow was measured by downstream dilution of *p*-aminohippurate (PAH).

4. Blood flow across MDV averaged 42% of PDV blood flow (665 litres/h).

5. Net use of O_2 across MDV accounted for 51% of net PDV use of O_2 (920 mmol/h). This disproportionate use of O_2 in relation to blood flow was due to greater VA for O_2 across MDV than across stomach tissues. Dietary regimen had no effect on the proportions of PDV blood flow and net O_2 consumption attributable to MDV or stomach tissues.

6. When lucerne was given, net glucose use across MDV represented 69% of PDV use (35 mmol/h). When concentrate was given, MDV glucose use switched to net absorption (29 mmol/h), reducing net PDV glucose use to 1 mmol/h.

7. When concentrate was given, net MDV absorption of α-amino-N (AAN) increased from 98 to 190 mmol/h, yet net PDV absorption (101 mmol/h) was not affected. Net stomach AAN flux increased from −7 to −69 mmol/h when concentrate was given, negating the increase in net MDV absorption.

8. Net absorption of ammonia-N across MDV represented 28 and 52% of net PDV absorption when lucerne and concentrate were given respectively. Net NH_3-N absorption across PDV was lower when lucerne was given than when concentrate was given (295 *v.* 154 mmol/h), reflecting lower dietary N intake (153 *v.* 83 g/d). Net MDV absorption of NH_3-N was not affected by diet. Net removal of blood urea-N (BUN) across PDV (101 mmol/h) was not affected by diet. Across MDV, BUN removal was lower when concentrate was given than when lucerne was given (32 *v.* 77 mmol/h). In beef steers, MDV tissues account for substantial portions of net flux of non-protein-N across PDV and are responsible for essentially all PDV absorption of AAN.

The unique development of the ruminant stomach allows extensive digestion, absorption and metabolism of dietary nutrients before they reach the gastric tissues and small intestine, where furthur digestion and absorption proceed much the same as in non-ruminants. In vivo measurements of the relative contribution of stomach or post-stomach tissues to absorption or metabolism by the total gastrointestinal tract have been limited to measurements of nutrient disappearance from digesta in cannulated animals (MacRae, 1974). These measurements do not account for the extensive metabolism of nutrients by gut tissue which determines their net appearance in the hepatic portal vein (Bergman & Wolff, 1971).

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The use of chronic indwelling catheters in appropriate blood vessels for obtaining in vivo measurements of net flux of metabolites across hepatic portal-drained viscera (PDV) tissues is a proven technique in sheep (Bergman & Wolff, 1971) and cattle (Huntington, 1984). By placing a catheter in the anterior mesenteric vein, just caudal to its junction with the gastrosplenic vein, blood flow and metabolite flux across the post-stomach tissues or mesenteric-drained viscera (MDV) can be measured. Janes *et al.* (1984, 1985) used this technique to measure MDV glucose and lactate metabolism in sheep. To our knowledge no one has reported measurements of net MDV flux of oxygen or nitrogenous compounds, or simultaneous measurements of PDV and MDV flux in ruminants. The first objective of the present study was to ascertain the contribution of post-stomach and stomach tissues to total PDV blood flow and net flux of O_2, glucose and nitrogenous compounds by comparing simultaneous measurements of PDV, MDV and stomach flux in beef steers. The second objective was to determine the effects of dietary regimen on these measurements.

MATERIALS AND METHODS

Preparation of animals and dietary protocol

Chronic catheters were surgically implanted into the hepatic portal, anterior mesenteric, gastrosplenic and mesenteric veins and caudal aorta of two Hereford steers (mean live weight 390 kg) using procedures described previously (Huntington, 1984) with the following modifications: steers were last fed 48 h and water was withheld for 12 h before surgery; the oesophagus was not intubated during surgery; a carotid artery was elevated (McDowell *et al.* 1966) in the event of iliac artery catheter failure; a double-catheter assembly similar to that of McGilliard & Thorp (1971) was inserted through a cranial branch of the common mesenteric vein and anchored such that one tip resided in the gastrosplenic vein and one tip resided in the anterior mesenteric vein, 30–50 mm caudal to its junction with the gastrosplenic vein. This double-catheter assembly consisted of two Teflon catheters (1·27 mm i.d., 2·29 mm o.d.) sheathed in silicone tubing (1·59 mm i.d., 3·18 mm o.d.). Approximately 200 mm of silicone tubing contained both Teflon catheters such that they could be inserted into the vein as one unit and the relative position of their tips would be fixed. The gastrosplenic vein catheter was anchored solidly to the wall of the portal vein and a loose suture was used at the insertion point so that the catheters could slip through the suture and reposition in the venous system during post-surgical recovery. Catheter lengths, design and implantation techniques were determined beforehand during necropsy of four Hereford steers (mean live weight 353·5 kg).

Steers were housed in individual pens with automatic water cups and allowed to exercise daily. At least 4 weeks before surgery and for 9 d after surgery steers were given 500 g chopped lucerne (*Medicago sativa*) hay (maximum stem length 40 mm; IRN-1-00-051) every 2 h and 50 g trace mineralized salt (TMS) at 08.00 hours using an automatic feeder. From day 9 to day 24, steers were fed on 3·0 kg chopped lucerne hay at 08.00 and 16.00 hours and received 50 g TMS at 08.00 hours. On day 24 steers were changed to a pelleted concentrate diet containing 780 g ground maize/kg (Table 1) over 12 d. This diet was provided (3·0 kg at 08.00 and 16.00 hours) for 15 d. Weekly composites of daily grab feed samples were analysed gravimetrically for dry matter (DM), and for nitrogen content by Kjeldahl procedures. The lucerne hay and pelleted concentrate averaged 962 and 946 g/kg DM respectively.

Blood sampling and blood flow measurements

Measurements of blood flow and net flux were obtained six times for each steer (twice on each of the three dietary regimens). Blood flow and net flux were measured 7 and 9 d after

Table 1. *Composition of concentrate diet*

Ingredient	g/kg dry matter
Ground maize	779·4
Ground lucerne* hay	100·0
Soyabean meal	50·0
Calcium chloride (88%)	8·8
Trace mineralized salt	5·0
Pellet binder†	56·8
Vitamins	
Retinol acetate	0·0344
Cholecalciferol	0·0025
E	0·0100

* *Medicago sativa.*
† Binder was lignin sulphonate. Pellet diameter was 15·9 mm.

surgery (timed-fed lucerne), 21 and 23 d or 22 and 24 d after surgery (meal-fed lucerne) and 49 and 51 d or 50 and 52 d after surgery (meal-fed concentrate). Blood flow in the portal and anterior mesenteric vein was determined by measuring dilution of *p*-aminohippurate (PAH, 90 g/l) infused continuously into the distal mesenteric vein catheter (Huntington, 1984). Infusion of PAH (1·2 ml/min) began immediately after a priming dose (15 ml) given at 07.00 hours, and continued through blood samplings at 07.30, 08.30, 09.30, 10.30 and 11.30 hours. Blood samples (30 ml) drawn into heparinized syringes were obtained simultaneously from the portal, gastrosplenic and anterior mesenteric vein and iliac artery catheters. Separate heparinized blood samples (3 ml) for O_2 analysis were obtained at each sampling time.

Sample analyses

Samples were kept on ice until analyses were completed, which usually was within 3 h of collection. Concentrations of blood urea-N (BUN), blood PAH, α-amino-N (AAN) and ammonia-N, and plasma PAH and glucose, were determined using the Technicon AutoAnalyzer System (Huntington, 1984). Enzymic methods were used for determining glutamate (Bernt & Bergmeyer, 1974) and glutamine (Lund, 1974) contents of whole blood samples deproteinized with 3·48 M-perchlorate and made basic (pH > 10) with 6 M-potassium hydroxide. Glutamate and glutamine analyses began immediately after all samples were collected and processed. Blood O_2 content was determined using an oximeter (Lexington Instruments, Watham, MA) as described by Huntington & Tyrrell (1985).

Calculations

Tissues of the PDV include the total digestive tract, pancreas, spleen and mesenteric fat. The three principal branches of the hepatic portal vein are the gastrosplenic vein (draining the rumen, reticulum, omasum, cranial abomasum, spleen and pancreas), the anterior mesenteric vein (draining the small intestine, caecum, large intestine, mesenteric fat and pancreas) and the gastroduodenal vein (draining the caudal abomasum, cranial duodenum and pancreas). Measurements of venous–arterial concentration differences (VA) obtained for the gastrosplenic and anterior mesenteric veins primarily represent VA for the stomach and post-stomach tissues respectively. Blood flows in the hepatic portal and anterior mesenteric veins were measured by dilution of PAH. Rates of net flux were calculated as the product of blood or plasma flow rate and blood or plasma VA for the total PDV and MDV. Estimates of net flux for stomach tisues were calculated as the difference between

PDV and MDV net flux or as the product of blood or plasma VA for the gastrosplenic vein multiplied by an estimate of gastrosplenic vein blood or plasma flow rate obtained by subtracting MDV from PDV flow rate. This estimate of stomach or gastrosplenic vein blood or plasma flow rate includes the relatively small contribution of the gastroduodenal vein to total hepatic portal vein blood or plasma flow.

Statistical analyses

Steers were sampled on 2 d on each dietary regimen to obtain better estimates of individual steer responses, not to test the effects of days. Therefore, mean arterial concentrations, VA and net flux values for each steer and diet were analysed using analysis of variance, testing the effects of steer and diet *v.* residual mean squares. Significant differences among dietary regimens were characterized using orthogonal contrasts testing differences between timed- and meal-fed lucerne and between lucerne and concentrate feeding. Dependent variable means were obtained for each sampling time by averaging the two measurements obtained within each steer and dietary regimen. These means were analysed using a model testing the effects of steer and time *v.* residual mean squares within each dietary regimen. Significant ($P < 0{\cdot}1$) responses over the time within each dietary regimen were evaluated using orthogonal polynomials testing linear, quadratic, cubic and quartic responses. Comparison of stomach flux rates obtained using the two methods of calculation were made using paired, two-tailed *t* tests. In view of the small numbers of degrees of freedom available, probability values have been given up to the 10%, rather than the more usual 5% level.

RESULTS

Recovery from surgery

Steers used for net flux measurements recovered from surgery rapidly and were consuming all feed offered within 3 d of surgery. The only feed refusals were by Rocky when he was given the high-grain diet. Catheters remained patent throughout the present study. In subsequent experiments, high PAH concentrations (greater than arterial PAH concentrations) were measured in blood sampled using the gastrosplenic vein catheters, indicating the suture anchoring the double catheter assembly had failed and the tip of the gastrosplenic vein catheter was within the portal or mesenteric vein. During necropsy of Rocky, conducted 5 months after surgery, little damage was found in the portal system. Some scar tissue developed in the area of the anchor suture for the double catheter and a section of the mesenteric vein branch through which the double catheter had been inserted had collapsed. Necropsy of Luigi, conducted 12 months after surgery, revealed that the double catheter assembly had pulled out of the venous system and that extensive scar tissue was present in the anterior mesenteric vein.

Blood flow

Rates of blood and plasma flow for PDV and MDV (Table 2) were not affected ($P > 0{\cdot}1$) by dietary regimen. Overall, MDV contributed 42% of blood and plasma flow across PDV. When steers were meal-fed lucerne, blood flow across PDV increased (linear $P < 0{\cdot}05$) following feeding (Table 3). Concomitant increases in MDV blood flow were not significant ($P > 0{\cdot}1$). When steers were meal-fed concentrate there were no significant changes ($P > 0{\cdot}1$) in blood flow (Table 4).

Net stomach flux calculation comparison

When compared statistically, net stomach flux of O_2 was similar ($P > 0{\cdot}1$) when calculated using stomach VA or using PDV minus MDV net flux (Table 5). Net stomach flux rates

Table 2. *Daily dry matter, nitrogen and energy intakes, body-weights and blood and plasma flow rates across mesenteric- and portal-drained viscera of two beef steers*

Diet...	Time-fed lucerne*	Meal-fed lucerne	Meal-fed concentrate	Mean	SEM
Body-wt (kg)	389·5	401·4	408·4	399·8	5·5
Daily intake					
Dry matter (kg)	5·780	5·780	4·95	5·500	0·280
N (kg)	0·153	0·153	0·083	0·130	0·023
ME (MJ)	48·325	48·325	60·066	52·237	3·935
Blood flow (l/h)					
Portal vein	588	657	752	665	55
Mesenteric vein	254	265	316	278	31
Plasma flow (l/h)					
Portal vein	453	466	520	480	22
Mesenteric vein	189	190	220	200	26

ME, metabolizable energy, calculated from dry matter intake.
* *Medicago sativa*.

obtained using the two methods of calculation were different ($P < 0·05$) for glucose and all the nitrogenous compounds measured, except glutamate (Table 5). Differences between methods for calculating stomach flux for some compounds may be due to variation associated with measurement of small VA differences. The tip of the gastrosplenic vein catheter was inserted against the flow and by necessity was positioned near the convergence of the three branches draining the stomach, pancreas and spleen. It is likely that VA differences measured at this point would be subject to variation and may not always represent the composite VA for all three branches. The contribution of the gastroduodenal vein to net PDV flux is not accounted for in our measurements of MDV flux or stomach VA, but would be included in stomach flux when calculated as the difference between PDV and MDV flux. For these reasons, the PDV minus MDV calculation of net stomach flux represents a more valid measurement for glucose and the nitrogenous compounds measured in the present study, and was used to calculate net stomach flux for the following results.

O_2

Concentration of O_2 in arterial blood (Table 6) was lower ($P < 0·05$) when lucerne was timed-fed than when meal-fed and greater ($P < 0·1$) when concentrate rather than lucerne was given. Net flux (Table 6) and VA of O_2 across MDV and PDV were unaffected by dietary regimen ($P > 0·1$), but VA across stomach tissues were lower ($P < 0·05$) when lucerne was time-fed than when lucerne was meal-fed. Overall, uptake of O_2 across MDV accounted for 51% of O_2 uptake across PDV. Increases in arterial O_2 (linear $P < 0·01$, quadratic $P < 0·01$, cubic $P < 0·1$) followed meal feeding of lucerne (Table 3). A simultaneous increase (linear $P < 0·05$, cubic $P < 0·05$) in VA for O_2 across MDV was associated with non-significant ($P > 0·1$) increases in O_2 consumption by MDV and PDV (Table 3).

Glucose

Arterial glucose concentrations (Table 6) were lower ($P < 0·05$) when steers were meal-fed lucerne than when time-fed lucerne and were lower ($P < 0·05$) when concentrate was given than when lucerne was given. Glucose VA and net flux (Table 6) were negative across PDV and MDV when lucerne was provided, indicating net use of glucose by both these tissue

Table 3. *Arterial concentration and metabolism of blood oxygen and nitrogenous compounds and plasma glucose across portal-drained viscera (PDV) of two beef steers meal-fed lucerne* (Medicago sativa)†

(Mean values for four determinations)

Sampling time (hours)...	07.30	08.30	09.30	10.30	11.30	SEM
Blood flow (l/h)						
MDV	196	322	285	282	242	26
PDV[a]	542	653	697	695	700	16
Plasma flow (l/h)						
MDV	143	220	202	207	179	18
PDV	396	447	495	499	493	14
Arterial concentration (mM)						
O_2[a, b, c]	5·52	6·53	5·84	5·54	5·42	0·05
Glucose[d]	4·42	4·26	4·15	4·17	4·26	0·07
α-Amino-N[a, b, c]	2·67	2·97	2·75	2·52	2·49	0·04
Glutamate[b, c]	0·141	0·161	0·156	0·146	0·148	0·002
Glutamine	0·185	0·242	0·263	0·243	0·250	0·020
Ammonia-N	0·29	0·34	0·30	0·28	0·26	0·02
Urea-N	10·84	11·39	11·84	11·84	11·66	0·28
MDV flux (mmol/h)						
O_2	−335	−593	−554	−483	−507	53
Glucose[b, d]	−20	−41	−24	−33	−16	3
α-Amino N	103	122	101	105	90	9
Glutamate	−0·52	−0·70	−1·98	−0·07	0·61	0·60
Glutamine	−2·78	−1·82	−3·83	−3·76	−1·03	2·11
Ammonia-N	58	136	106	93	80	22
Urea-N	−70	−143	−103	−131	−64	47
PDV flux (mmol/h)						
O_2	−762	−994	−1032	−948	−1035	59
Glucose	−37	−41	−29	−29	−26	12
α-Amino-N	107	114	86	88	90	20
Glutamate	−3·47	−4·96	−6·08	−3·10	−3·63	0·86
Glutamine	−2·78	−1·82	−3·83	−6·27	−2·43	3·49
Ammonia-N[b]	258	397	401	348	336	28
Urea-N	−109	−67	−29	−124	−139	78
Stomach flux (mmol/h)						
O_2	−427	−401	−478	−465	−528	85
Glucose	−14	−1	−5	4	−11	11
α-Amino-N	5	−8	−15	−17	0	20
Glutamate	−2·95	−4·26	−4·10	−3·03	−4·24	0·92
Glutamine	−0·44	4·53	3·52	−2·50	−1·40	2·89
Ammonia-N	200	261	295	256	256	46
Urea-N	−39	76	74	7	−74	44

MDV, mesenteric-drained viscera.
[a, b, c, d] Linear, quadratic, cubic and quartic response repectively: $P < 0·05$.
† 3·0 kg chopped lucerne hay at 08.00 and 16.00 hours.

beds. On a net basis, tissues of MDV accounted for 69% of the glucose used by the total PDV when lucerne was given. When concentrate was given, glucose VA and net flux increased ($P < 0·05$), approaching zero across PDV and becoming positive across MDV. Glucose VA for stomach tissues were comparably small and stomach net flux of glucose (Table 6) was not affected by diet ($P > 0·1$). When lucerne was time-fed, arterial glucose concentration fluctuated (linear $P < 0·05$, quadratic $P < 0·05$) slightly (values not shown). Following meal feeding of lucerne, MDV glucose use (Table 3) increased (quadratic $P < 0·05$, quartic $P < 0·05$).

Table 4. *Arterial concentration and metabolism of blood oxygen and nitrogenous compounds and plasma glucose across portal-drained viscera (PDV) of two beef steers meal-fed concentrate*†

(Mean values for four determinations)

Sampling time (hours)...	07.30	08.30	09.30	10.30	11.30	SEM
Blood flow (l/h)						
MDV	333	340	373	235	234	57
PDV	808	762	756	710	692	41
Plasma flow (l/h)						
MDV	232	232	265	158	167	41
PDV	541	510	527	506	516	33
Arterial concentration (mM)						
O_2[a,b,c]	5·86	6·05	5·74	5·76	5·54	0·11
Glucose[d]	4·18	4·00	4·00	4·12	3·92	0·16
α-Amino-N	3·17	3·28	3·12	3·10	3·18	0·06
Glutamate	0·144	0·142	0·143	0·143	0·156	0·008
Glutamine	0·202	0·201	0·198	0·187	0·189	0·012
Ammonia-N	0·40	0·37	0·33	0·34	0·35	0·04
Urea-N	5·44	5·69	5·60	5·51	5·32	0·26
MDV flux (mmol/h)						
O_2	−475	−530	−597	−366	−382	110
Glucose[b,d]	13	17	50	33	29	9
α-Amino-N	149	248	240	121	145	42
Glutamate	−1·26	2·54	0·70	0·14	−4·24	2·62
Glutamine	5·39	11·52	11·85	3·95	10·15	4·15
Ammonia-N	72	93	99	65	57	16
Urea-N	−36	−57	−20	−31	−16	8
PDV flux (mmol/h)						
O_2	−1017	−1064	−980	−992	−919	85
Glucose	−11	−12	8	8	3	16
α-Amino-N	109	140	116	106	138	22
Glutamate	−3·72	1·63	−4·16	−4·93	−17·54	9·06
Glutamine	−1·38	9·45	−0·26	8·64	11·48	11·05
Ammonia-N[b]	138	171	159	148	166	22
Urea-N	−113	−148	−69	−119	−51	29
Stomach flux (mmol/h)						
O_2	−542	−534	−383	−626	−537	114
Glucose	−24	−29	−43	−25	−28	12
α-Amino-N	−40	−108	−124	−15	−7	42
Glutamate	−2·46	−0·91	−4·87	−5·07	−13·31	6·59
Glutamine	−6·77	−2·06	−12·11	4·68	1·33	7·23
Ammonia-N	66	78	60	83	109	31
Urea-N	−77	−91	−49	−88	−35	28

MDV, mesenteric-drained viscera.

[a,b,c,d] Linear, quadratic, cubic and quartic response respectively: $P < 0·05$.

† 3·0 kg concentrate at 08.00 and 16.00 hours.

AAN

Arterial AAN concentrations (Table 6) were greater ($P < 0·1$) when concentrate was given than when lucerne was given. Net AAN appearance across MDV (Table 6) was greater ($P < 0·05$) when the concentrate diet was given, yet increases in AAN flux were not significant across PDV tissues (Table 6). Overall, MDV flux of AAN was 27% greater than PDV flux, indicating that essentially all AAN absorption or appearance across PDV is attributable to MDV. Stomach use of AAN (Table 6) increased ($P < 0·05$) when

Table 5. *Comparison of methods for calculating net stomach flux (mmol/h) of two beef steers*

	n	Method A†	Difference‡	SEM	Statistical significance: *P* <
Oxygen	58	−464	−11	12	0·33
Glucose	58	−2	14	5	0·01
Ammonia-nitrogen	58	223	52·9	7·0	0·01
Urea-N	57	−58	−26	9·3	0·01
α-Amino-N	58	7	32·8	7·0	0·01
Glutamate	58	−4·76	−0·56	0·4	0·18
Glutamine	57	2·26	2·92	1·4	0·04

† Gastrosplenic venous–arterial difference times portal–mesenteric vein blood flow.
‡ Method A minus method B (portal-drained viscera flux minus mesenteric-drained viscera flux).

concentrate was given. Following meal-feeding of lucerne, arterial AAN (Table 3) increased slightly (linear $P < 0·01$, qaudratic $P < 0·05$, cubic $P < 0·01$). With the concentrate diet, VA for AAN across PDV were elevated (cubic $P < 0·05$) 0·5 and 3·5 h after steers were fed (Table 4).

Glutamate and glutamine

Glutamate net flux and VA across MDV, PDV and stomach tissues (Table 6) were negative, indicating net utilization by these tissues, and were not affected by dietary treatment ($P > 0·1$). Tissues of MDV accounted for only 13% of net PDV utilization of glutamate. Glutamine VA across PDV and MDV changed ($P < 0·1$) from negative to positive values when steers were changed from lucerne to the concentrate diet. Changes in glutamine flux across MDV and PDV (Table 6) were only significant ($P < 0·1$) for MDV. Stomach flux of glutamate and glutamine (Table 6) was not affected by diet ($P > 0·1$). Following meal-feeding of lucerne, arterial glutamate (Table 3) increased (quadratic $P < 0·01$, cubic $P < 0·01$) 0·5 h after feeding and then declined gradually. When lucerne was time-fed (values not shown), glutamine net flux across MDV fluctuated between negative (utilization) and positive (absorption) values (quartic $P < 0·05$). There were no significant time effects ($P > 0·1$) when concentrate was given (Table 4).

NH_3-N

When lucerne was time-fed, VA across PDV and stomach tissues were lower ($P < 0·05$) than when lucerne was meal-fed. When concentrate was given, VA for NH_3-N across PDV and stomach tissues were lower ($P < 0·01$) than when lucerne was given. Net PDV absorption of NH_3-N (Table 6) was greater ($P < 0·05$) for meal- than time-fed lucerne and lower ($P < 0·1$) when concentrate was given than when lucerne was given. Net flux of NH_3-N across MDV (Table 6) was unaffected by dietary regimen ($P > 0·1$). When averaged across dietary regimens, MDV flux was 33% of NH_3-N absorption across PDV. Stomach absorption of NH_3-N (Table 6) was not affected by dietary treatment ($P > 0·1$) There were some fluctuations in VA for stomach tissues (quadratic $P < 0·05$) with timed-fed lucerne (values not shown). Both VA (quadratic $P < 0·05$) and net flux (quadratic $P < 0·05$) of NH_3-N across PDV increased following meal-feeding of lucerne (Table 3). This increase in net appearance was due to greater VA in initial samplings and due to elevated blood flow for later samplings.

Table 6. *Arterial concentration and metabolism of blood oxygen and nitrogenous compounds and plasma glucose across portal-drained viscera of two beef steers*

Diet...	Time-fed lucerne (*Medicago sativa*)	Meal-fed lucerne	Meal-fed concentrate	Mean	SEM
Arterial concentration (mM)					
O_2	4·73‡	5·76	5·80†	5·45	0·13
Glucose	4·57‡	4·25	4·04*	4·29	0·05
α-Amino-N	2·41	2·68	3·17†	2·75	0·15
Glutamate	0·174	0·150	0·146	0·157	0·014
Glutamine	0·206	0·237	0·195	0·212	0·016
Ammonia-N	0·25	0·29	0·36	0·30	0·03
Urea-N	10·17	11·57	5·51*	9·08	0·53
Mesenteric-drained viscera flux (mmol/h)					
O_2	−424	−496	−487	−469	18
Glucose	−22	−26	29*	−7	7
α-Amino-N	92	104	190*	128	14
Glutamate	−0·81	−0·53	−0·46	−0·60	0·88
Glutamine	−1·85	−2·65	9·37†	1·63	2·37
Ammonia-N	69	95	80	81	20
Urea-N	−48‡	−106	−32*	−62	7
Portal-drained viscera flux (mmol/h)					
O_2	−804	−955	−996	−920	103
Glucose	−38	−32	−1*	−24	5
α-Amino-N	85	97	121	101	19
Glutamate	−3·91	−4·25	−5·95	−4·70	3·28
Glutamine	−2·16	−1·90	6·32	0·75	3·36
Ammonia-N	242‡	348	154†	248	24
Urea-N	−89	−96	−101	−96	17
Stomach flux (mmol/h)					
O_2	−379	−460	−509	−446	112
Glucose	−16	−5	−31	−17	9
α-Amino-N	−7	−7	−69*	−28	7
Glutamate	−3·10	−3·72	−5·49	−4·10	2·44
Glutamine	−0·31	0·74	−3·05	−0·87	1·06
Ammonia-N	173	253	73	166	42
Urea-N	−38	9	−68	−33	23

Significantly different from time-fed or meal-fed lucerne: † $P < 0·10$, * $P < 0·05$.
Significantly different from meal-fed lucerne: ‡ $P < 0·05$.

BUN

Arterial BUN concentrations (Table 6) were 49% lower ($P < 0·05$) when steers were fed on concentrate than when they were fed on lucerne. Across PDV, VA and net flux of BUN (Table 6) were similar among treatments. Across MDV, VA and net flux of BUN (Table 6) were greater ($P < 0·1$) when lucerne was given than when concentrate was given, and when lucerne was meal-fed than when lucerne was time-fed. Net removal of BUN across MDV (Table 6) was also greater ($P < 0·05$) when lucerne was meal-fed than when time-fed and lower ($P < 0·05$) when concentrate was given than when lucerne was given. When lucerne was given, MDV accounted for 83% of PDV removal of arterial BUN. The concentrate diet resulted in less net MDV removal of BUN, such that only 32% of PDV flux was accounted for by MDV. When lucerne was meal-fed, MDV removal of BUN was

greater than PDV removal and stomach flux was slightly positive. In contrast to effects of diet on BUN across MDV, VA across stomach tissue were less negative ($P < 0.05$) when lucerne was meal-fed than when lucerne was time-fed, and were more negative ($P < 0.05$) when concentrate was given than when lucerne was given. Stomach removal of BUN (Table 6) was not affected by dietary treatment. There were slight changes in arterial BUN concentrations (linear $P < 0.01$) and VA for BUN across PDV (cubic $P < 0.05$) when lucerne was time-fed (values not shown).

DISCUSSION

Blood flow

An initial concern with the use of PAH dilution for measuring MDV blood flow was that inadequate mixing of blood and PAH might result in PAH streaming because sampling occurs caudal to the turbulence created by the convergence of the gastrosplenic and mesenteric veins (Schambye, 1955). Streaming of PAH would be evidenced by extremely high, low or variable blood flow measurements. Although variation as a percentage of average flow was greater for MDV than PDV, actual variation (l/h) was less for MDV than PDV (Table 2). The presence of catheters in the anterior mesenteric vein may enhance mixing of PAH with blood, thereby reducing variation in both MDV and PDV blood flow measurements.

In sheep, estimates of proportional blood flow across splanchnic tissues obtained using labelled microspheres have suggested that MDV contributes from 42 to 57% of blood flow across PDV (Hales, 1973; Schaefer & Young, 1980). The percentage contribution of MDV to PDV blood flow in our study averaged 42%, ranging from 21 to 82% for the fifty-eight measurements obtained. Conrad *et al.* (1958) used ^{32}P-labelled erythrocytes to estimate gastrosplenic vein blood flow in anesthetized calves. Their estimate of gastrosplenic blood flow (16·8 ml/min per kg body-weight) is similar to the difference between blood flow for PDV and MDV in the present study (16·6 ml/min per kg body-weight).

Postprandial increases in portal vein blood flow have been reported in meal-fed sheep (Bensadoun & Reid, 1962) and cattle (Carr & Jacobson, 1968). Steers ate all lucerne hay offered within 1 h. Luigi ate all the concentrate offered within 30 min, but Rocky had consumed only 1·58 kg of the 3 kg of concentrate given by the end of the sampling period, which could explain the absence of significant postprandial blood flow changes when concentrate was given.

O_2

Uptake of O_2 is a measure of metabolic activity and can be used to estimate heat production attributable to respiratory metabolism (Huntington & Tyrrell, 1985). Tissues of MDV accounted for 51% of PDV uptake of O_2 and 41% of PDV blood flow. This disproportionate use of O_2 by MDV was due to greater VA for O_2 across MDV. Differences in VA for stomach tissue and MDV are probably the result of differences in composition or metabolic activity between tissues drained by the anterior mesenteric and gastrosplenic veins. Estimates of the distribution of PDV organ weights of beef steers (56% stomach, 44% MDV; Jones *et al.* 1985) reflect proportions for blood flow more closely than proportions for O_2 consumption.

Glucose

Net use of glucose by PDV of forage-fed ruminants has been demonstrated in other studies (Huntington, 1984). Janes *et al.* (1984) also reported net use of glucose by MDV of sheep fed on forage and net MDV glucose absorption in sheep fed on a concentrate diet containing 780 g ground maize/kg, a source of starch which is less degradable in the

reticulo-rumen than other cereal starches. Measurements of [^{14}C]glucose metabolism by MDV of the same sheep (Janes *et al.* 1985) found that MDV use of arterial glucose was similar for forage and concentrate diets. When steers in the present study were fed on the concentrate diet (which contained 780 g ground maize/kg), net absorption of glucose across MDV did not result in net glucose absorption by PDV, but was reflected by a significant reduction in net PDV glucose use (Table 6).

Increased stomach glucose utilization for maize *v.* lucerne diets was suggested by Janes *et al.* (1985). Trends in the present study (Table 6) agree with, but do not definitively substantiate, their hypothesis. Further work using multicatheterized ruminants is needed to define changes in glucose metabolism across PDV tissues induced by dietary manipulations.

AAN

Net flux of AAN across MDV was always higher than that for PDV (Table 6), indicating a net loss of AAN across stomach tissues. Increases in MDV absorption of AAN when concentrate was given did not result in significant increases in PDV absorption due to the increase in AAN use by stomach tissues (Table 6). Reasons for the increase in net arterial AAN use by stomach tissue when steers were changed from lucerne to concentrate are not clear. Harmon (1986) found that when incubated in vitro, rumen tissue from steers fed on 900 g concentrate/kg diet utilized more glucose and glutamine than rumen tissue from steers fed on lucerne.

Increased MDV absorption of AAN when concentrate was given is of interest, since dietary N intake was lower for the concentrate than for the lucerne diet (153 *v.* 83 g/d). Possible explanations for this increase in MDV absorption of AAN include greater duodenal appearance of dietary protein, since maize-gluten has been shown to be less degradable in the rumen than lucerne protein (National Research Council, 1985), or that rumen or post-rumen microbial fermentation, or both, was improved by the increased energy and rumen undegradable starch content of the diet. Improved rumen fermentation might increase the flow of microbial protein to the small intestine resulting in greater AAN absorption.

Glutamine and glutamate

Prior *et al.* (1981) reported negative net PDV flux of glutamate in steers fed on lucerne and negative net PDV flux of both glutamate and glutamine when concentrate was given. In the present work, glutamate was utilized on a net basis across PDV for both lucerne and concentrate and glutamine was utilized across PDV when lucerne was given (Table 6). There was net absorption of glutamine across MDV and PDV when concentrate was given (Table 4).

NH_3-N

Dietary effects on PDV absorption of NH_3-N appeared to be due to effects on stomach flux, because MDV flux was unaffected (Table 6; $P > 0{\cdot}1$). However, changes in net stomach NH_3-N flux were not significant, in spite of significant differences in stomach VA. Increased PDV absorption of NH_3-N when lucerne was meal-fed *v.* time-fed could be due to a meal effect. Lewis *et al.* (1957) reported that in sheep, portal vein concentrations of NH_3-N increased after feeding and followed an increase in rumen NH_3-N concentration. Decreased NH_3-N absorption across PDV when concentrate was given in the present study (Table 6) could be attributed to decreases in dietary N intake (153 *v.* 83 g/d), decreased rumen degradation of dietary protein or increased microbial-N incorporation in the rumen. The percentage of NH_3-N absorption across PDV resulting from MDV absorption was higher when concentrate was given, since MDV absorption was unaffected. If more dietary protein did escape rumen fermentation when concentrate was given, it did not result in an increase in NH_3-N absorption across MDV (Table 2).

Models of N metabolism for lactating dairy cows fed on a mixed ration (Danfaer, 1979) and for sheep fed on lucerne (Nolan, 1975), estimate that 34–43% of dietary N absorbed as NH_3-N is attributable to absorption across post-stomach tissues. In the present study, MDV absorption of NH_3-N when lucerne or concentrate was given was 28 and 52% of PDV absorption respectively. In sheep fed on lucerne (Wolff *et al.* 1972), NH_3-N absorption across PDV represented 65% of total N absorption and was 48% of dietary N intake. In the present study, net NH_3-N absorption across PDV represented 57% of dietary N intake and was 2·8 times greater than PDV absorption of AAN when lucerne was time-fed. As indicated by Nolan (1975), a substantial portion of NH_3-N absorbed across PDV may be derived from degradation of BUN transferred into the gut lumen.

BUN

Our measurements of MDV removal of BUN averaged 54% of PDV removal of BUN when lucerne was time-fed, which is slightly lower than the estimates of Danfaer (1979) and Nolan (1975). When lucerne was meal-fed, MDV removal of BUN was greater than that for PDV, indicating that removal across stomach tissues was negligible (Table 6). Across all dietary regimens in the present study, MDV removal of BUN accounted for 65% of PDV removal. Studies in sheep fed on various grass diets have shown that from 76 to 91% of urea degradation in the digestive tract occurs post-ruminally (Norton *et al.* 1978, 1982*a*, *b*). The models of Nolan (1975) and Danfaer (1979) predict that BUN recycling into the gut lumen is 30% of dietary N intake. In our study, PDV removal of arterial BUN was 20% of dietary N intake when lucerne was given and 41% of dietary N intake for concentrate. The predictions of Danfaer (1979) and Nolan (1975) include urea cycling via the saliva, which varies with diet.

In conclusion, measurements of blood flow and net flux of glucose across stomach, post-stomach and total PDV tissues of two beef steers agree well with previous measurements obtained using various techniques in the ovine (e.g. Hales, 1973; Janes *et al.* 1985) and bovine (Conrad *et al.* 1958). Measurements of net flux of nitrogenous compounds compare favourably with models for sheep (Nolan, 1975) and cattle (Danfaer, 1979) which attribute substantial portions of PDV N flux to MDV tissues. Dietary regimen had no effect on the percentage contribution of MDV to PDV blood flow (42%) and O_2 consumption (51%). When lucerne was given, the MDV accounted for 70% of glucose use across the total PDV. Net absorption of glucose occurred across the MDV when concentrate was given, reducing net PDV glucose use. Increased stomach use of AAN suggests substrate metabolism by ruminant stomach tissues differ when concentrate *v.* lucerne is given. These shifts in net flux across stomach and post-stomach tissues may relate to differences in dietary nutrient utilization and deserve further investigation.

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