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Nitrogen metabolism, rumen fermentation, and water absorption in red deer, goats, and sheep

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Abstract Comparisons between species and seasons in nitrogen (N) retention, rumen ammonia concentration, rumen volatile fatty acid (VFA) proportions, and water flows along the digestive tract were measured with red deer, goats, and sheep fed a chaffed lucerne hay diet ad libitum. Measurements were made in summer (S) and winter (W). Rumen ammonia kinetics were measured in the three species during W only using continuous infusions of ^{15}N. Red deer showed greater N retention in S than in W ($P < 0.05$), whereas goats showed no seasonal trends ($P > 0.05$) in N retention, with sheep being intermediate. Sheep and goats showed no ($P > 0.05$) seasonal differences in rumen ammonia (NH_3-N) concentration (158–181 mg N/litre), whereas deer showed an increase from W to S (110 versus 172 mg N/litre; $P < 0.01$). The irreversible loss rate (IRL) of NH_3-N from the rumen (mg N/g N intake) during W was in the order goats > sheep > deer. Sheep showed no seasonal differences in rumen VFA patterns, whereas both deer ($P < 0.05$) and goats ($P < 0.05$) showed greater acetate/propionate (Ac/Pr) ratios in S than in W. In S, the Ac/Pr ratio was in the order deer > sheep > goats whereas there were no species differences ($P > 0.05$) in W. There were no ($P > 0.05$) seasonal differences in drinking water or in total water intakes (g/g DMI or g/kg$W^{1.0}$ per day) in deer, goats, and sheep. Sheep showed no significant seasonal differences ($P > 0.05$) in rumen water outflow or rumen net water balance (g/kg$W^{1.0}$ per day). In contrast, deer and goats showed greater ($P < 0.01$) rumen water outflow, net rumen water balance (including saliva flow), and intestinal water absorption in S compared to W. It was calculated that both recycling of N to the rumen and rumen NH_3 absorption during W were in the order goats > sheep > deer. It was concluded that the high rumen NH_3 IRL in goats may be a factor in their superior rumen fibre digestion, especially when consuming low-quality roughage diets, and that high Ac/Pr ratios in deer may be a contributing cause of their increased metabolic heat production during S.

Keywords rumen fermentation; nitrogen metabolism; water absorption; deer; goats; sheep

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INTRODUCTION

Comparative studies have shown that, relative to sheep, temperate species of deer have a more pronounced cycle of voluntary feed intake (VFI), with a maximum in summer (S) and a minimum in winter (W; Milne et al. 1978). Red deer show a similar cycle in rumen pool size (Milne 1980; Domingue et al. 1991a). Despite the summer increase in VFI, there is no reduction in apparent DM digestibility in red deer during S (Milne et al. 1978), whereas goats show a reduction in DM digestibility in S compared with W (Domingue et al. 1991a). Goats have also been shown to digest fibre more efficiently than sheep, particularly when fed low-quality roughage diets (Watson & Norton 1982; Doyle et al. 1984; Howe et al. 1988; Domingue et al. 1991a,b).

Objectives of the present experiment were to investigate species and seasonal differences in nitrogen (N) retention, rumen ammonia (NH_3) concentration,

rumen volatile fatty acid (VFA) proportions, and the flow of water along the digestive tract in deer, goats, and sheep fed a medium-quality forage ad libitum during W and S. The three species were also compared during W for rates of rumen ammonia production (here defined as the irreversible loss rate; IRL).

EXPERIMENTAL

Diet

The animals were fed on the same batch of a lucerne (*Medicago sativa*) hay both in S and in W. This contained (g/kg DM), 28.4 g N, 216 g cellulose, 76 g hemicellulose, and 104 g lignin. The hay was chaffed into 50-80 mm lengths and placed upon belt feeders which delivered the day's ration in 24 feeds, at 1 h intervals.

Animals

Five castrated hand-reared red deer (94.8 ± 5.46 (SD) kg), seven castrated Angora × New Zealand feral goats (42.5 ± 4.83 kg), and eight Border Leicester × Romney wether sheep (57.5 ± 6.58) were used in S and in W. All animals were fistulated in the rumen and fitted with permanent rubber cannulae (63 mm i.d. for goats and sheep; 83 mm i.d. for deer). The animals were housed individually in metabolic crates. All were aged 2.5 years when the experiment commenced, with further details being given by Domingue et al. (1991a).

Experimental design

The W (Southern hemisphere) experiment was conducted in May–June and the S experiment in November–December, using the following protocol in both instances. After an adaptation period of 12 days, N balance was measured over Days 13–20 with the animals fed at ad libitum, feed offered being 1.15 of that consumed. Rumen fluid samples were taken during that period for NH_3-N, VFA, and pH determinations. Feed offered was then restricted to 1.035 of ad libitum intake. To determine the IRL of NH_3-N from the rumen, ^{15}N-ammonium chloride was infused into the rumen during Days 27–29, added to a solution of indigestible markers. The animals had their rumen contents emptied by "bailing" on Day 29.

Marker infusion procedures

The two inert markers, chromium (Cr) complex of ethylene diamine tetraacetic acid (Cr-EDTA; Binnerts et al. 1968), and ruthenium tris (1,10- phenanthroline)-ruthenium (II) chloride (Ru-phen; Tan et al. 1971), were prepared and administered into the rumen over Day 24–29 in the S and W experiments. Cr-EDTA marks the liquid phase, whereas Ru-phen is a particular phase marker; both were infused in order to measure rumen fractional outflow rate (Domingue et al. 1991a). ^{15}N-ammonium chloride salt (95.55 atoms % excess; Amersham International plc, Amersham (UK)), was added to the dual-marker solution (589.3 mg $^{15}NH_4Cl$/kg solution; pH = 6.7), during the last 42 h of marker infusion into the rumen in W only. ^{15}N infusion commenced at 1800 h on Day 27 and concluded at 1200 h on Day 29. The infusion rate was 63.25 mg ^{15}N/day for deer, 41.93 mg ^{15}N/day for goats, and 51.62 mg ^{15}N/day for sheep.

Sample collection procedures

Samples of feed offered, feed refusals, faeces, and urine were collected daily from each animal during the N balance trial, and all samples were pooled at –20°C. Urine was collected daily into buckets containing 100 ml H_2SO_4 to keep the pH below 3. Samples of feed, feed refusals, rumen digesta, and faeces were freeze-dried, ground (1 mm mesh), and used for laboratory analysis. Rumen digesta for Cr and Ru samples were ground to pass a 0.5 mm mesh size.

Rumen fluid samples for NH_3-N, pH, and VFA were taken on Days 14, 17, and 20, at 1000 h and 1500 h. The rumen fluid samples for NH_3-N and VFA were deproteinised and centrifuged immediately after sampling, using procedures described by Domingue et al. (1991b). The supernatant fluid was stored at –20 °C.

Rumen fluid samples were taken for th determination of enrichment (atoms % excess) or rumen NH_3-N with ^{15}N before the start of ^{15}N infusion (background sample) and after 24, 30, 37, and 42 h of ^{15}N infusion. At "bailing" on Day 29, representative samples of rumen fluid, rumen digesta NAN, and rumen bacterial N were obtained from the whole rumen digesta and the enrichment of NH_3-N with ^{15}N determined. The rumen fluid samples containing ^{15}N were processed as described by Nolan & Stachiw (1979). Rumen bacterial samples were obtained from the rumen digesta using the procedures described by Nolan & Leng (1972).

Laboratory methods

Samples of feed offered, feed refusals, faeces, and urine were analysed for total N by the Kjeldahl

method. VFA were determined by gas chromatography (Shimadzu Gas Chromatograph, GC 81) and NH_3-N (in rumen fluid samples without ^{15}N) was analysed by the procedures described by Domingue et al. (1991b). The pH of rumen fluid was determined on a PHM 61, Laboratory pH meter (Radiometer (Copenhagen) Ltd.) immediately after sampling. Cr and Ru in freeze-dried rumen contents were determined by X-ray fluorescence spectrometry (Domingue et al. 1991a)

Rumen fluid samples, rumen digesta NAN, and rumen bacterial samples containing ^{15}N were processed for mass spectroscopy, using the procedures described by Domingue et al. (1991b). ^{15}N enrichment was then determined using a mass spectrometer (Model MS10; GEC AEI Electronics (Ltd.), England), using the precautions and methods described by Nolan & Leng (1972).

Calculations

The IRL of NH_3-N (gN/day) was expressed as the rate (mass/unit time) that NH_3-N leaves the rumen pool and does not return during the experimental period (Nolan & Leng, 1974) (Equation 1). Enrichment of rumen NH_3-N with ^{15}N in the sample taken at bailing, after 42 h of ^{15}N infusion, was used in the calculation of IRL.

$$\text{IRL (gN/day)} = \frac{\text{Infusion rate of } ^{15}\text{N (g/day)}}{\text{Enrichment at plateau of rumen } NH_3\text{-N with } ^{15}\text{N}} \quad (1)$$

The proportion of bacterial N arising from the rumen NH_3-N pool was calculated from Equation 2.

$$\frac{\text{Enrichment at plateau of bacterial-N with } ^{15}\text{N} \times 100}{\text{Enrichment at plateau of rumen } NH_3\text{-N with } ^{15}\text{N}} \quad (2)$$

The proportion of rumen digesta NAN that comprised bacterial N in the rumen was calculated from Equation 3.

$$\frac{\text{Enrichment at plateau of rumen digesta NAN with } ^{15}\text{N} \times 100}{\text{Enrichment at plateau of rumen bacterial N with } ^{15}\text{N}} \quad (3)$$

Both rumen liquid pool size and fractional outflow rate (FOR) of Cr-EDTA were determined by Domingue et al. (1991a) in the same experiment as used here. Hence the same deer, goats, and sheep were fed the same diet at the same intakes as were used here during both W and S. The water outflow from the rumen was then calculated as:

$$\text{Rumen liquid pool (g)} \times \text{FOR of Cr-EDTA (per day)} \quad (4)$$

Rumen water balance was calculated as the difference between rumen water outflow and total water intake (g/day); it represents the combined total of salivary secretion and net inflow of water across the rumen wall. Apparent absorption of water from the intestines was calculated as the difference between rumen water outflow and faeces water output.

Statistical methods

Analysis of variance procedures were used to determine differences between animal species and seasons. Mean values with the standard error of the means (SEM) are presented.

The values presented for NH_3-N, VFA, and pH are the means of seven observations per animal, comprising samples taken at 1000 and 1500 h on Days 14, 17, and 20 and at bailing on Day 29. Since there were no significant differences ($P>0.05$) between day and/or time of the day at which sampling occurred, the mean values were used in all calculations.

RESULTS

Nitrogen retention

Seasonal effects

Deer showed a seasonal trend in N balance, with an increase in S compared to W (278 versus 107 mg N/kg $W^{0.75}$ per day; SED 77.0; $P < 0.05$), principally because of a significant reduction in urinary N excreted (% of N digested; $P < 0.05$; Table 1). Goats showed no seasonal trends in N retention (mg N/100g DMI per day; $P > 0.05$), whereas sheep tended to occupy an intermediate position between deer and goats. N retention was low in sheep and deer in W.

Rumen ammonia concentration

Seasonal effects

Both sheep and goats showed no differences ($P > 0.05$) in rumen NH_3-N concentration (mg N/litre), rumen NH_3-N pool size (mg N/g N intake), or NH_3-N outflow (mg N/g N intake per day) from the rumen, between S and W (Table 2). In contrast, deer showed an increase from W to S in rumen NH_3-N concentration (100 versus 172 mg N/litre; SED 16.1; $P < 0.01$), rumen NH_3-N pool size (10.4 versus 22.7 mg N/g NI; SED 2.86; $P < 0.001$) and in NH_3-N outflow from the rumen (40.9 versus 86.4 mg N/g NI; SED 9.68; $P < 0.001$). There were no seasonal differences ($P > 0.05$) in rumen pH between the three species.

Species effects

In W, deer had a lower concentration of rumen NH_3-N ($P < 0.01$), lower rumen NH_3-N pool size ($P < 0.01$), and a lower outflow of NH_3-N in the water leaving

Table 1 Nitrogen (N) intake, excretion, and balance in deer, goats, and sheep fed on lucerne hay at ad libitum intake, in summer and in winter.

		Deer	Goats	Sheep	SEM
Intake (mg/kg $W^{0.75}$ per day)	S[a]	1715	1883	1556	84.0
	W	1450	1749	1710	92.9
Faecal excretion (mg/kg $W^{0.75}$ per day)	S	549	573	480	24.1
	W	532	490	572	34.8
Urinary excretion (mg/kg $W^{0.75}$ per day)	S	889	956	852	82.3
	W	833	888	1002	46.9
Nitrogen balance					
mg N/kg $W^{0.75}$ per day	S	278	351	225	36.6
	W	107	371	139	20.6
mg N/100 g DMI	S	426	514	437	59.9
	W	213	638	232	30.6
Apparent digestibility (%)	S	67.9	70.0	69.2	0.35
	W	63.0	72.3	67.0	0.72
Urine N (percentage digested)	S	76.8	81.2	80.0	3.43
	W	91.3	70.0	88.8	1.75

[a]S = summer; W = winter.

Table 2 Kinetics of ammonia (NH_3-N) production in the rumen of deer, goats, and sheep fed on lucerne hay at ad libitum intake in winter, together with the rumen NH_3-N concentration, rumen NH_3-N pool size, and NH_3-N outflow from the rumen, in summer and in winter.

		Deer	Goats	Sheep	SEM
Total N intake (NI)	S[a]	1.90	1.95	1.43	0.076
(g/kg $W^{0.75}$ per day)	W	1.63	1.63	1.61	0.087
Rumen NH_3-N kinetics					
NH_3-N concentration (mg N/litre)	S	172	158	181	5.5
	W	110	165	172	6.3
NH_3-N pool size (mg N/g NI)	S	22.7	24.0	29.9	1.61
	W	10.4	22.2	29.1	1.38
NH_3-N outflow in winter (mg N/g NI)	S	86.4	56.5	69.4	4.64
	W	40.9	53.2	70.5	2.58
Irreversible loss rate (IRL) of NH_3-N (mg N/g NI)	W	535	692	607	35.9
IRL - NH_3-N outflow in water (mg N/g NI)	W	494	639	536	35.7
Bacterial N from NH_3-N (%)	W	36.6	48.0	40.0	1.99
Bacterial N (% digesta NAN)	W	63.4	52.0	60.0	1.99
Total N in rumen digesta (% DM)	W	2.39	2.69	2.44	0.03
Total N in isolated rumen bacterial cells (% DM)	W	6.62	6.25	6.17	0.14
Rumen pH	S	6.57	6.54	6.42	0.046
	W	6.61	6.59	6.45	0.042

[a]S = summer; W = winter.

the rumen ($P < 0.01$) than did sheep. In S, however, there were no differences ($P > 0.05$) between deer and sheep in these measurements.

Goats, compared to sheep, showed no differences in rumen NH_3-N concentration during W ($P > 0.05$), but had a lower concentration in S ($P < 0.05$). The NH_3-N outflow from the rumen (mg N/g N intake per day) and rumen NH_3-N pool size (mg N/g N intake) were not different ($P > 0.05$) from sheep in S. In W, however, both the NH_3-N pool size and the outflow of NH_3-N in the water leaving the rumen were lower in goats ($P < 0.05$) than in sheep.

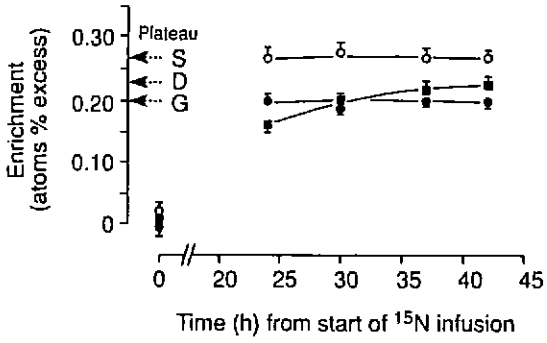

Fig. 1 Enrichment with ^{15}N (atoms % excess) of rumen fluid NH_3-N during intra-ruminal infusions of ^{15}N ammonium chloride in deer (■), goats (●), and sheep (○) SEM).

Ammonia production rate in the rumen

Figure 1 shows the enrichment of rumen NH_3-N with ^{15}N (atoms % excess) over time, during the continuous intraruminal infusion of $^{15}NH_4Cl$. Plateau enrichment of rumen NH_3-N was reached after 24 h infusion in both goats and sheep and after 36 h in deer. It is assumed that the higher rumen FOR of liquid from the rumen of deer (Domingue et al. 1991a) might have delayed the attainment of plateau enrichment.

Both IRL of NH_3-N (mg N/g N intake) and IRL minus the rumen NH_3-N outflow rate (mg N/g N intake), which represents the combined values for NH_3-N incorporated into microbial N and total NH_3-N absorbed through the rumen epithelium, was in the order goats > sheep > deer, with the difference between goats versus sheep and goats versus deer being significant ($P < 0.05$).

The proportion of bacterial N derived from rumen NH_3-N tended to be greater in goats than in sheep ($P = 0.12$) and deer ($P < 0.10$), but there was no difference ($P > 0.05$) between sheep and deer.

Rumen fermentation patterns

Seasonal effects

Both deer (4.20 versus 3.62; SED 0.210; $P < 0.05$) and goats (3.76 versus 3.37; SED 0.177; $P < 0.05$) showed a greater Ac/Pr ratio in S compared to W, whereas sheep showed no evidence of a seasonal trend ($P > 0.05$; Table 3). Goats also showed an increase in S in the molar proportions of acetate ($P < 0.05$), whereas deer showed a S decrease in the molar proportions of propionate ($P < 0.01$).

Species effects

In S, the Ac/Pr ratio was in the order deer > sheep > goats, with the difference between deer and goats attaining significance at $P < 0.01$, and between goats and sheep at $P < 0.05$. In W, there were no differences ($P > 0.05$) in the Ac/Pr ratio between the three species.

Water transactions

Seasonal effects

There were no seasonal differences ($P > 0.05$) in the intakes of drinking water or total water (g/g DMI or g/kg $W^{1.0}$ per day) in all three species (Table 4).

Sheep did not show a seasonal trend ($P > 0.05$) in the rumen water outflow or net rumen water balance (g/kg $W^{1.0}$ per day). Rumen water outflow (g/kg $W^{1.0}$ per day); Table 4) showed an increase in S compared to W both in deer (293 versus 194; SED 20.8; $P < 0.001$) and in goats (288 versus 220; SED

Table 3 Total VFA concentration and the molar proportions of acetate, propionate, and *n*-butyrate in the rumen of deer, goats, and sheep fed on lucerne hay at ad libitum intake, in summer and in winter.

		Deer	Goats	Sheep	SEM
Total VFA (mmol/litre)	S[a]	151	151	194	3.9
	W	138	119	167	3.0
Molar concentration (moles %)					
Acetate	S	72.7	70.7	71.7	0.41
	W	70.8	69.0	69.9	0.42
Propionate	S	17.4	18.8	18.0	0.28
	W	19.5	20.2	19.1	0.26
n-butyrate	S	5.48	5.97	5.96	0.169
	W	5.34	5.69	6.43	0.177
Acetate/propionate ratio	S	4.20	3.76	4.01	0.085
	W	3.62	3.37	3.76	0.061

[a]S = summer; W = winter.

17.6; $P < 0.01$). Deer (235 versus 135; SED 24.5; $P < 0.001$) and goats (219 versus 154; SED 20.7; $P < 0.01$) also showed an increase in the net rumen water balance (g/kg $W^{1.0}$ per day) in S compared to W, with the magnitude of the increase being greater in deer (+74%), than in goats (+42%). Intestinal water absorption (g/kg $W^{1.0}$ per day) was greater in S compared to W (Table 5), both in deer (279 versus 188; SED 17.8; $P < 0.001$) and in goats (275 versus 206; SED 15.0; $P < 0.001$). When expressed as g/g DMI, the increases in S of the net rumen water balance and rumen water outflow in deer and goats were of smaller magnitude than when expressed as g/kg $W^{1.0}$ per day, but were in the same direction. It appears that both deer and goats have a greater recycling of water into the rumen in S compared to W, that this is not a result of seasonal differences in total water intakes (g/kg $W^{1.0}$ per day), and that they also have greater absorption of water from the intestine at this time. Faeces DM proportion increased from W to S in sheep (0.38 versus 0.47; SED 0.024; $P < 0.01$) and in goats (0.42 versus 0.49; SED 0.026; $P < 0.05$) but not in deer ($P > 0.05$).

Species effects

When compared to sheep on a g/kg $W^{1.0}$ basis, deer showed lower net rumen water balance ($P < 0.05$) during W, and a trend towards a higher rumen net water balance in S, which just failed to attain significance ($P = 0.06$). Goats, compared to sheep, also tended to have a greater rumen net water balance during S ($P = 0.07$), but in W there were no significant ($P > 0.05$) differences between the two species. Faeces DM proportion during S was lower for deer than for sheep and goats ($P < 0.01$), with there being no other significant between-species differences.

DISCUSSION

The domestic sheep used in this study, crossbreds of two temperate breeds, showed no evidence of seasonal differences in N retention, internal recycling of water to the rumen, or in rumen fermentation patterns. In contrast, the red deer, which are also a temperate species, showed marked seasonal differences in N retention, rumen fermentation patterns, internal

Table 4 Drinking water and total water intakes, water outflow from the rumen, and net rumen water balance in deer, goats, and sheep, fed on lucerne hay at ad libitum intake, in summer (S) and in winter (W).

		Deer	Goats	Sheep	SEM
Drinking water					
g/kg $W^{1.0}$ per day	S	55.7	64.7	52.7	3.15
	W	55.2	60.9	54.1	3.89
g/g DMI	S	2.56	2.63	3.06	0.201
	W	3.25	2.42	2.62	0.126
Total water intake[1]					
g/kg $W^{1.0}$ per day	S	58.9	68.7	55.3	3.1
	W	58.7	66.1	58.1	4.2
g/g DMI	S	2.70	2.78	3.21	0.202
	W	3.46	2.63	3.83	0.125
Rumen water outflow[2]					
g/kg $W^{1.0}$ per day	S	293	288	204	16.9
	W	194	220	237	9.8
g/g DMI	S	13.7	11.4	11.5	0.94
	W	11.4	9.0	11.7	0.40
Rumen net water balance[3]					
g/kg $W^{1.0}$ per day	S	235	219	149	15.7
	W	135	154	179	7.6
g/g DMI	S	11.0	8.7	8.3	0.83
	W	8.0	6.3	8.9	0.36

[1]Drinking water + water in feed.
[2]Rumen liquid pool × FOR (per day) of Cr-EDTA.
[3]Rumen outflow – total water intake = salivary secretion + net inflow of water across rumen wall.

recycling of water to the rumen, and rumen NH_3-N concentration. The goats appeared to occupy an intermediary position, showing similar seasonal differences to those observed in deer, but of smaller amplitude.

Nitrogen retention

The increased N retention observed in deer during S can be explained as part of the increase in growth which is known to occur in spring/summer in red deer (Drew 1976; Mitchell et al. 1976; Hamilton & Blaxter 1981). In view of its association with long daylength, high food intake, and rapid weight gain, prolactin may be a hormone involved in the increase in N retention in deer in S (Suttie & Kay 1985); prolactin injections have increased growth in reindeer during winter (Ryg & Jacobsen 1982) and have increased N retention in lambs (Brinklow & Forbes 1982).

Rumen digestive efficiency

As VFI of deer increases from W to S (Milne et al. 1978), there is an accompanying increase in rumen digesta load (Milne 1980; Domingue et al. 1991a), with there being no reduction in apparent DM digestibility. Results of the present experiment show that there are also increases in the internal recycling of water to the rumen (including saliva) and in rumen NH_3-N concentration in ad libitum-fed deer from W to S. These two factors combined might have contributed to apparent DM digestibility remaining high when VFI and rumen size increase during S.

Although the W rumen NH_3-N concentration in deer was above the threshold of 50 mg of NH_3-N/litre, below which microbial crude protein production is suppressed (Satter & Slyter 1974), the low concentration (110 mg N/litre) could have limited the rate of rumen carbohydrate fermentation (Mehrez et al. 1977; Krebs & Leng 1984; Perdok & Leng 1989). This could potentially be a contributing factor to the low seasonal VFI of red deer during W. Internal recycling of water to the rumen (including saliva) did not increase as markedly during S in goats as in deer, and may be a factor contributing to the decrease in apparent DM digestibility of goats in S compared to W (Domingue et al. 1991a).

Rumen ammonia kinetics

The interpretation of isotope kinetic data requires that the N pools and N transactions in the pools be under steady-state conditions (Nolan & Leng 1972; Nolan 1975). This was achieved during the present experiment by feeding at hourly intervals, with the animals fed at 1.035 ad libitum intake. Fig. 1 indicates that enrichment of rumen NH_3-N with ^{15}N had attained plateau values several hours before the sample was taken for the calculation of IRL (bailing, after 42 h continuous infusion).

A model of N flows into and out of the rumen of deer, goats, and sheep during W has been constructed (Fig. 2), based upon a number of assumptions. These are that rumen microbes would leave the rumen with the same FOR as Ru-phen (Faichney 1980), that undegraded plant NAN would leave the rumen on the

Table 5 Apparent water absorption from the intestines, faeces water output, and faeces dry matter proportion in deer, goats, and sheep fed lucerne hay at ad libitum intake, in summer and in winter.

		Deer	Goats	Sheep	SEM
Intestinal water absorption					
g/kg $W^{1.0}$ per day	S[a]	279	275	194	16.2
	W	188	206	220	9.1
g/g DMI	S	13.1	10.9	10.9	0.90
	W	10.7	8.4	11.0	0.38
Faeces water output					
g/kg $W^{1.0}$ per day	S	13.3	12.1	9.9	0.77
	W	11.4	13.6	16.9	0.63
g/g DMI	S	0.62	0.46	0.56	0.042
	W	0.68	0.60	0.78	0.028
Faeces DM proportion					
	S	0.37	0.49	0.47	0.031
	W	0.40	0.42	0.38	0.030

[a]S = summer; W = winter.

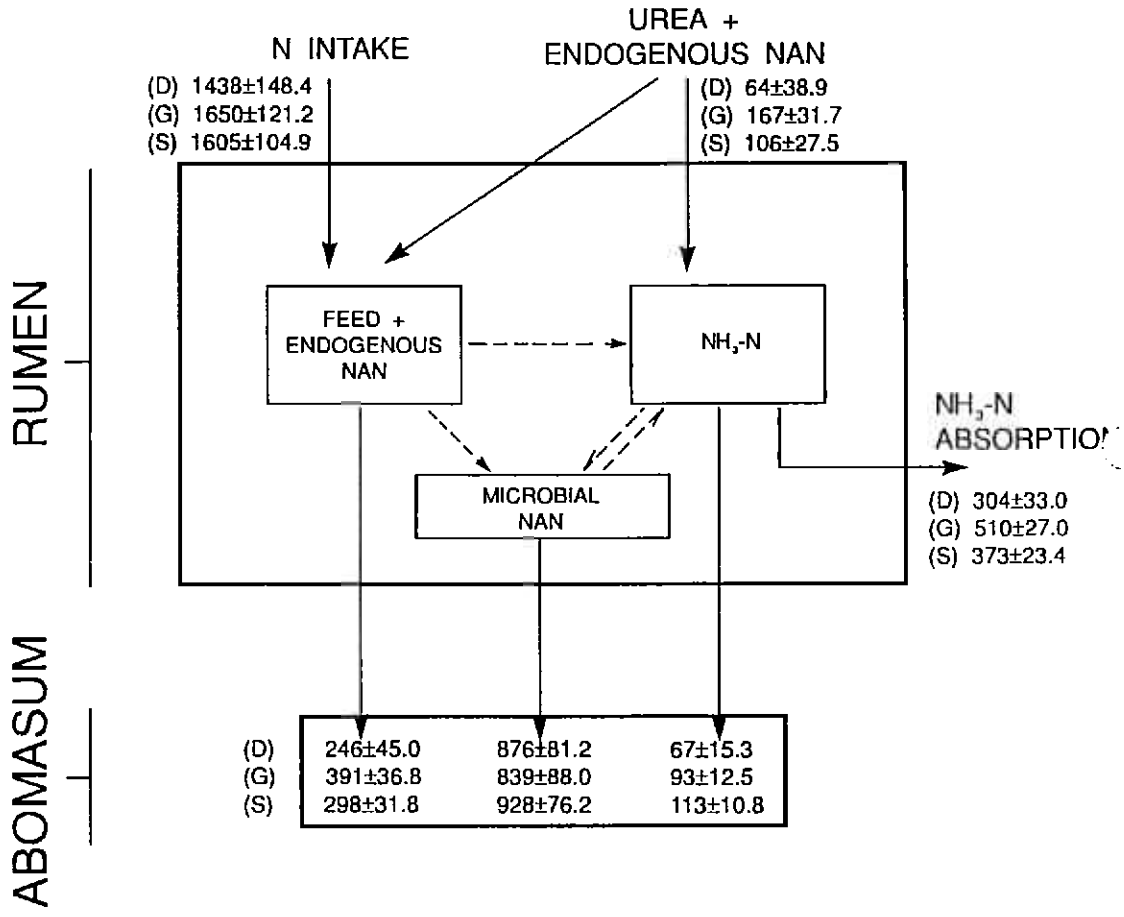

Fig. 2 Schematic representation of N kinetics (mg N/kg $W^{0.75}$ per day) in the rumen of deer (D), goats (G), and sheep (S), fed on lucerne chaff ad libitum during winter.

same particle as undegraded lignin and therefore have the same FOR, that apparent absorption of NH_3 from the rumen could be calculated as per Equation 5 (Siddons et al. 1985), and that urea + endogenous NAN input to the rumen could be calculated as the difference between the predicted N outflows and total N intake of the diet.

$$\text{Apparent rumen NH3 absorption} = \frac{\text{Infused } ^{15}\text{N (/day)} - ^{15}\text{N calculated to have flowed from the rumen (/day)}}{\text{Rumen NH}_3\text{-N } ^{15}\text{N enrichment}} \quad (5)$$

These assumptions seem valid for the sheep, as the value for duodenal NAN flow/total N intake calculated from Fig. 2 (0.76) is close to that predicted from the equation of Hogan et al. (1970) (0.79), using the N concentration and organic matter digestibility of the diet fed in the present study. As the same measurements and assumptions were used for goats and deer, it seems probable that values for these species in Fig. 2 have been predicted with a similar degree of accuracy. The model shows that during W both recycling of urea and endogenous NAN to the rumen and apparent rumen ammonia absorption were greatest for goats, least for deer, and intermediate for sheep. The greater predicted rate of urea + endogenous NAN recycling to the rumen supports the measured greater rates of salivary N secretion during eating in goats than in sheep (Seth et al. 1976; Domingue et al. 1991c). Increased recycling of N to the rumen is a possible factor in the superior apparent digestibility of fibre by goats than sheep, especially when consuming low-quality diets (Watson & Norton 1982;

Doyle et al. 1984; Howe et al. 1988), where it is associated with increased ammonia concentration (Domingue et al. 1991b). Rumen NH_3 kinetics were not studied in S. However, as rumen NH_3 concentration in deer was much higher in S than in W, it is possible that rumen NH_3 IRL in this species may increase markedly from W to S and this needs to be investigated in future experiments.

Rumen VFA proportions

Previous ruminant work has indicated that as the dilution rate of water (i.e. FOR) from the rumen increases, there are associated increases in the molar proportion of acetate and decreases in the molar proportion of propionate (Harrison et al. 1975), and increases in the rates of microbial protein outflow to the abomasum (Isaacson et al. 1975; Thomson et al. 1975).

In the present study, changes in rumen Ac/Pr ratio were best related to the ratio FOR Cr EDTA/FOR lignin (Domingue et al. 1991a), these being (W, S) for deer (4.8:1.0, 6.0:1.0), goats (2.8:1.0, 3.1:1.0), and sheep (3.1:1.0, 3.2:1.0). This indicates that first, changes in rumen outflow rate of water relative to particulate matter may be a contributing cause to changes in rumen VFA patterns in the three species fed this diet, and second, that there could be a substantial increase in the efficiency of rumen microbial protein output from W to S in species such as the red deer.

In mathematical modelling studies, Black et al. (1987) have shown that the efficiency of utilisation of metabolisable energy (ME) above maintenance is very low in ruminants fed forage diets producing high Ac/Pr ratios, because of insufficient NADPH being generated from glucose metabolism to allow all the acetate to be incorporated into body lipid. The result is a high oxidation rate of acetate, and hence a high heat production by the animal. In the present studies, it seems that the considerable increase in Ac/Pr ratio of rumen VFA that occurred in deer from W to S may be a contributing factor to the increased metabolic heat production that occurs in this species during S (Silver et al. 1969).

In conclusion, the present studies have shown seasonal differences in red deer of N retention, rumen ammonia concentration, rumen Ac/Pr ratio, and water recycled into the rumen. Seasonal changes in the latter two were also evident in the goat, but of smaller amplitude. The rumen ammonia kinetic data help to explain the superior fibre digestion of the goat, especially when consuming low-quality roughage diets. Changes in rumen VFA proportions may be one contributing factor to the increased metabolic heat production of deer during S. Further research is needed into seasonal changes in digestive function in deer, to obtain a more fundamental understanding of these changes and their underlying causes.

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