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A COMPARATIVE STUDY OF VOLUNTARY INTAKE AND RUMEN DIGESTION BY DEER, GOATS AND SHEEP

A thesis presented in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy in Animal Science
at Massey University, Palmerston North,
New Zealand

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DEDICATION

To my mother and father, to whom I am thankful for everything.

ABSTRACT

The following experiments were carried out to study the voluntary feed intake and rumen digestion of Red Deer and Angora-NZ feral goats, compared to Border-Leicester/Romney cross sheep, namely: (1) Intake and utilisation of a low quality threshed prairie grass straw (13.7 g N/Kg DM) by goats and sheep; (2) chewing behaviour per 24 h during eating and ruminating by goats and sheep fed on lucerne hay, and the efficiencies of chewing during eating and ruminating upon the breakdown of feed particles; (3) seasonality in nutrient supply by deer, goats and sheep fed on a medium quality lucerne hay diet (28.3 g N/Kg DM) in summer and in winter, and (4) the role of melatonin (Me) in the control of seasonal VFI in Red Deer.

1. Goats showed a superior utilisation of the low quality forage diet, with a greater voluntary intake (g/Kg $W^{0.75}$/d) of DM (55.6 g vs 33.8 g) and DDMI (17.4 g vs 8.2 g), apparent digestibilities of DM (31.2% vs 24.3%) and total fibre (36.8% vs 32.6%), especially that of lignin (11.3% vs 5.3%), when compared to sheep. The greater VFI (g/Kg $W^{0.75}$/d) by goats was associated with a larger rumen pool size (g/Kg $W^{0.75}$ of (DM + liquid) by goats than sheep (334.7 g vs 213.5 g). The superior fibre digestibility by goats was associated with a greater rumen NH_3-N concentration (mg N/L: 115 mg vs 80 mg), greater production rates of NH_3-N in the rumen (IRL: g N/Kg $W^{0.75}$/d of 0.84 for goats and 0.49 for sheep). A mechanism for increasing rumen NH_3-N concentration in goats was apparent through slower rates of inflow and outflow of water from the rumen (g/g DMI/d). Goats also showed greater rumen molar proportions of valerate and butyrate, and a tendency for a longer rumen MRT (h) of particulate DM (lignin and Ru-Phen), compared to sheep. Goats had smaller proportions (5.1% vs 9.6%) of large particles (>4.0 mm), and greater proportions (19.4% vs 16.1%) of small particles (<1.0 mm) in the rumen contents than sheep. The factors listed above would all favour the potential growth and attachment to feed particles of fibre-digesting bacteria in the rumen of goats, compared to sheep.

2. Goats spent more time chewing during eating (+3.1 h/24 h) and less time chewing during ruminating (-2.2 h/24 h) than sheep when fed on lucerne hay. Goats had a greater number of chews/min spent eating (154 vs 128) than sheep, and a smaller number of chews during ruminating (79 vs 100) than sheep. The efficiency of chewing during eating in breaking down feed particles to <1.0 mm (<C.EAT>) was greater by goats than by sheep (85% vs 48%) and <C.RUM> was smaller by goats than sheep (48% vs 59%). When corrected for the number of chews spent chewing during eating and ruminating, the differences in <C.EAT> and <C.RUM> between goats and sheep disappeared (for <C.EAT>, 2.1% vs 2.4%; for <C.RUM>, 0.6% vs 0.6%).

3. Sheep showed no evidence of seasonal cycles of VFI when fed on lucerne hay. In contrast to sheep, deer showed marked seasonal cycles of an increase in summer of voluntary DMI (+33.8%), DDMI (+29.9%), MEI (+25%), apparent fibre digestibility (+11.2%), MRT of lignin (+26%), rumen pool of DM + liquid (51.3%), internal recycling of water to the rumen (+74.1%), rumen NH_3-N concentration (+56.4%) and Ac/Pr ratio (+16%). All the cycles showed a trough in winter and a marked increase in summer. The expansion in the rumen pool size, a longer rumen MRT of digesta and a greater recycling of water into the rumen, allowed for an increase in VFI (without depressing apparent DMD), and for an increase in apparent fibre digestibility in summer.

Goats also showed an increase in voluntary DMI in summer (+19.7%), associated with increases in a number of rumen digestive functions, which were all not as marked as for deer. Unlike deer, the increased VFI in summer occurred at the expense of a reduced apparent DMD (-9.8%) and fibre digestibility (-5.8%).

Deer showed a faster rumen FOR of liquid (15.6%/h) than goats (10.0%/h) and sheep (10.4%/h) both in summer and in winter. Goats digested lignin, the least digestible component of fibre, more efficiently than sheep, both in summer (18.9% vs 14.6%) and in winter (21.9% vs 9.4%). The greater fibre digestibility by goats than sheep in winter was associated with a greater rate of NH_3-N production in the rumen (IRL of 1.13 g vs 0.98 g (g N/Kg $W^{0.75}$/d)). The threshold to passage of particles through the reticulo-omasal orifice was 1.0 mm

for deer, goats and sheep, with more than 98% of the particles in the faeces being <1.0 mm.

4. Exogenous subcutaneous implants of melatonin (Me) in spring in castrated male Red Deer caused reductions in VFI, water-filled rumen capacity, rumen digesta load, and heart rate (beats/min), to occur in both early and in late summer. Melatonin possibly entrains the seasonal cycles of VFI in Red Deer to photoperiod, and controls the seasonality of VFI. Methods are suggested for reducing the magnitude of the winter depression in VFI in Red Deer stags, using immunisation against Me.

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ABBREVIATIONS USED IN THIS THESIS

Cr-EDTA	Chromium complex of ethylenediamine tetraacetic acid
DDMI	Digestible dry matter intake
DM	Dry matter
DMD	Apparent dry matter digestibility
DMI	Dry matter intake
DOMI	Digestible organic matter intake
FDPR	Fractional disappearance rate
FDR	Fractional degradation rate
FOR	Fractional outflow rate
GH	Growth hormone
HCl	Hydrochloric acid
H_2SO_4	Sulphuric acid
ID	Internal diameter
IGF-I	Insulin-like growth factor I
IM	Intramuscular
IRL	Irreversible loss rate
IU	International units
K_2SO_4	Potassium sulphate
LH	Luteinising hormone
LHRH	Luteinising hormone releasing hormone
LWT	Liveweight
M	Metabolisable energy for maintenance
MCF	Malignant catarrhal fever
ME	Metabolisable energy
Me	Melatonin
MRT	Mean retention time
N	Nitrogen
^{15}N	Stable isotope of nitrogen
NaOH	Sodium hydroxide
NH_4Cl	Ammonium chloride
NH_3-N	Ammonia
$(NH_4)_2SO_4$	Ammonium sulphate
OD	Outer diameter
OM	Organic matter
OMD	Apparent organic matter digestibility
OMI	Organic matter intake
P	Prolactin

ABBREVIATIONS (continued)

RF	Rumen fluid
Ru-Phen	Ruthenium tris (1,10-phenanthroline)-ruthenium (II) chloride
s.c.	Subcutaneous
T	Testosterone
TH	Thyroid hormone
VFA	Volatile fatty acid
VFI	Voluntary feed intake
v/v	volume by volume
$W^{0.75}$	Metabolic liveweight

INTRODUCTION

During the last 140 years, New Zealand (NZ) has developed an efficient pastoral grazing system for the farming of sheep and cattle. At present, the total population of sheep in New Zealand is 62,244,000, and the total population of dairy cattle and beef cattle estimated at 3,195,000 and 4,804,000 respectively (NZ Meat and Wool Board's Economic Service,1988).

In very recent times, there have been major developments in the deer and goat industries in New Zealand, and these are now seen as alternative farmed species in a diversified pastoral industry.The New Zealand Game Industry Board (GIB) has made statistical projections of a deer population of 883,262 in 1989, and increasing to a predicted population of 2,550,752 heads by 1995 (or a 3-fold increase in the next 6 years). Although deer farming originated in New Zealand, it is now being practised on a worldwide basis.

New Zealand has a population of 1,054,000 goats at present (including the feral, the Angora and Cashmere breeds) (Drew and Bigham, 1987). The Cashmere Producers of New Zealand (CAPRONZ) have predicted that by 1990, 660,000 Cashmere goats will be farmed in New Zealand, reaching 4 million in 1995 (or a 6-fold increase in the next 5 years). Goat production is important worldwide and a recent survey by the F.A.O (1987) estimated the world population of goats at 492 million, with 94% of the world goat population being reared in the developing countries.

Research in the nutrition of deer and goats is limited, despite the increasing trends in production in New Zealand and worldwide. There are likely to be limitations in the use of the sheep as a model for nutritional studies with goats or deer (Van Soest, 1982).

The objectives of the present study were to define the processes of voluntary feed intake (VFI), nutrient digestion and nutrient utilisation in goats and deer, particularly how these might differ from sheep, and to identify any particular advantages or disadvantages these species might have over sheep. Particular attention was paid to the following:

1. Seasonality in VFI, nutrient digestion and formation of the end-products of rumen digestion in deer and goats, compared to sheep.

2. Comparisons of digestive efficiency between sheep, deer and goats in both summer and in winter, and an examination of the reasons for any differences found, when fed on a medium quality diet.

3. Comparisons of digestive efficiency between goats and sheep when fed on a low quality diet.

4. Examination of reasons for the seasonality of nutrient utilisation in deer, and suggest methods for the control of feed intake.

5. Aspects of methodology have been evaluated, and improvements made during the course of the study.

The unit of comparison in the present interspecies comparison study has been the body-weight raised to the three-quarter power ($W^{0.75}$), i.e the metabolic weight. All the measured productive functions of sheep, deer and goats, have been commonly expressed per Kg $W^{0.75}$ (unless otherwise stated), and compared on that basis. This was based on the assumption that the metabolic requirements of all animals are related to their metabolic weight, and that is constant ($W^{0.75}$) for all animal species (Brody, 1945; Kleiber, 1961; Blaxter, 1962).

CHAPTER ONE. A REVIEW OF THE LITERATURE.

1.1. INTRODUCTION

In this chapter the nutritional work which has been published on goats and deer will be reviewed, and related to comparable studies with sheep, where extensive data have accumulated over the past thirty years. The sheep can be regarded here as the control animal, which has been domesticated, fed and genetically selected by man for approximately 6000 years. In comparison, deer have been recently farmed and fed (last decades), with goats occupying an intermediate position. Reference will also be made to the cattle and to lesser known ruminants like the bedouin goat, reindeer and chamois.

A review of the literature on the goat vs sheep, and to a lesser extent on deer vs sheep comparison studies, calls for some reservations in the interpretation of the data. The trial procedures have to be examined, especially in comparison studies with goats and sheep fed on low quality forages. The control of intake and feeding management adopted, magnitude of the refusals and chemical composition of the refusals have not always been reported. If the composition of the refusals is unknown, it is difficult to assess the composition of the true intake. This may result in an overestimation of the apparent digestibility of dry matter and fibre, and of nitrogen (N) balance (Van Soest, 1982).

The time of the year at which goat vs sheep comparisons have been carried out is not always stated. At this time, it is not known whether goats show any seasonal trends in voluntary feed intake. On the other hand, data on the deer vs sheep studies always make reference to the season, (e.g. Milne, MacRae, Spence and Wilson, 1978), or to the exact imposed photoperiod conditions, mimicking seasonal variations (e.g. Suttie and Simpson, 1985).

Several goat vs sheep and deer vs sheep comparisons reported in the literature have been made using three animals per group; to obtain valid conclusions it is essential that larger numbers of animals per group be used.

Other aspects of importance are the age, breed and production class of the experimental animals. If animals of different age groups and in different physiological states are compared, this may bias the results of inter-species comparisons.

1.2 VOLUNTARY FEED INTAKE AND DIGESTIBILITY IN DEER, GOATS AND SHEEP

1.2.1 Goats vs Sheep

1.2.1.1 Voluntary Feed Intake

Table 1.1 shows that a wide variety of feeds have been used in goat/sheep comparison studies, namely:

1. High/medium quality forages (37.0-15.0 g N/Kg DM),
2. Low quality forages (15.0-5.1 g N/Kg DM), and
3. Browse (29.0-15.0 g N/Kg DM).

Data in Table 1.1 show that, when fed on high/medium quality forages, both goats and sheep have a similar intake (g/Kg $W^{0.75}$/d). When fed on low quality forages, goats generally achieve a significantly higher intake (g/Kg $W^{0.75}$/d), than sheep.

Compared to sheep, goats consume more (g/Kg $W^{0.75}$/d) of a browse diet. A 50% difference in intake has been reported (Howe, Barry and Popay, 1988; McCabe and Barry, 1988).

Table 1.2 shows the voluntary intake of forage diets by two breeds of goats. The desert breed is superior on a low quality forage, and the temperate breed is superior on a high quality forage. These results show differences in intake between breeds within the same species (Choshniak, Arnon and Shkolnik, 1984; Silanikove, 1986).

It can be concluded that goats, unlike sheep, do not show a depression in VFI, when fed on low quality forages and browse diets.

1.2.1.2 Selection of Feed by Goats and Sheep

Goats are considered to be more selective feeders than sheep when grazing and browsing (Devendra and Burns, 1970; French, 1970). The

Table 1.1. Voluntary feed intake (organic matter intake (OMI) or dry matter intake (DMI)) of forage and browse diets by goats and sheep (g/Kg $W^{0.75}$/d).

Feed offered	Dietary N (g/Kg DM)	Intake parameter	Goats	Sheep	Sig	Author
1. High/medium quality forages						
Lucerne hay	37.0	OMI	47.4	47.4	NS	Wilson (1977)
Clover hay	28.0	OMI	67.6	60.7	NS	Doyle & Egan (1980)
Lucerne hay/ oaten chaff	21.0	DMI	37.8	38.4	NS	Gamble & Mackintosh (1982)
Pangola grass	19.5	OMI	49.5	47.8	NS	Watson & Norton (1982)
Clover hay	30.8	OMI	67.6	60.7	NS	Doyle *et al.* (1984)
Lucerne hay	37.3	DMI	67.8	67.0	NS	Antoniou *et al.* (1985)
Lucerne hay	28.0	DMI	82.7	76.4	*	Wahed & Owen (1986)
Lucerne hay	31.2	DMI	73.0	69.4	NS	McCabe *et al.* (1988)
MEAN	29.1		61.7	58.5		
2. Low quality forages						
Hyparrhenia grass hay	10.5	DMI	40.5	35.0	*	Gihad (1976)
Zambian natural grass	10.6	DMI	40.5	35.0	*	Gihad *et al.* (1980)
Rice straw	5.4	DMI	50.0	46.9	*	Gihad *et al.* (1980)
Pangola grass	8.2	OMI	32.6	31.9	NS	Watson & Norton (1982)
Dry Hummra grass	5.1	DMI	42.1	53.5	*	Mousa *et al.* (1983)
L. rigidum hay	7.7	OMI	45.5	48.0	NS	Doyle *et al.* (1984)
L. rigidum hay + clover hay	11.4	OMI	34.6	34.1	NS	Doyle *et al.* (1984)
Barley straw	8.2	DMI	24.9	21.7	*	Antoniou *et al.* (1985)
NaOH-treated straw	5.9	DMI	53.7	35.0	*	Alrahmoun *et al.* (1986)
NaOH-treated straw	5.6	DMI	30.0	22.9	*	Masson *et al.* (1986)
MEAN	7.9		39.4	36.4		
3. Browse diets						
C. cristata leaves	15.0	OMI	48.4	50.8	NS	Wilson (1977)
Willow (*S. viminalis*)	24.3	DMI	88.6	46.6	***	McCabe *et al.* (1988)
Gorse	29.0	DMI	61.2	34.7	*	Howe *et al.* (1988)
MEAN	22.8		66.1	44.0		

DMI = Dry matter intake

OMI = Organic matter intake

*** $P<0.001$; * $P<0.05$; NS Non-significant.

Table 1.2. Voluntary dry matter intake (DMI, g/Kg $W^{0.75}$/d) of forage diets by the Desert and Temperate breeds of goat.

Feed offered	N (g/Kg DM)	Breed	Voluntary DMI (g/Kg $W^{0.75}$/d)	Sig
Alfalfa hay	26.0	D	63.9	*
		T	95.0	
Rhodes grass + alfalfa hay	17.9	D	72.7	NS
		T	72.5	
Wheat straw	5.8	D	31.6	NS
		T	29.6	

(from Silanikove, 1986.)

D = Desert breed; T = Temperate breed.

* $P<0.05$; NS Non-significant.

grazing behaviour of cattle, goats and sheep has been compared on a ryegrass/white clover pasture (Collins and Nicol, 1986, 1987). Cattle selected for a higher proportion of green leaf, goats consumed more stem and sheep selected preferentially for clover. Similarly, it was found that goats rejected clover in a mixed sward and consumed more gorse (Clark, Lambert, Rolston and Dymock, 1982).

Van Soest (1982), implied that the results obtained from grazing tend to suggest that under stall-feeding conditions, selective intake by goats and/or sheep might result in overestimating the intake and digestibility of one species over another. Limited data, reported in Table 1.3, suggest that goats are less selective than sheep when fed "ad-lib" under stall-feeding conditions. Goats, in contrast to sheep, appear to select for fibre (Brown and Johnson, 1985; Wahed and Owen, 1986).

1.2.1.3 Digestible Organic Matter Intake

The data in Table 1.4, show that when fed on high/medium quality forages, the digestible organic matter intake (DOMI) of goats is similar to sheep (g/Kg $W^{0.75}$/d). However, when fed on low quality forages and on browse diets, goats are slightly superior to sheep. It appears that on both diets, goats achieve a higher DOMI by, (i) a higher organic matter intake (OMI), and (ii) a higher apparent organic matter digestibility (OMD).

Alam, Poppi and Sykes (1985), calculated the relationship (Equation 1) between DOMI (g/Kg $W^{0.75}$/d) of goats and sheep fed on 8 forage diets (26.8-6.6 gN/Kg DM). The equation (1) derived was:

$$\text{DOMI (goats)} = 0.74\ \text{DOMI (sheep)} + 10.6 \quad (r = 0.94) \qquad (1)$$

Alam et al. (1985), concluded from the ratio of DOMI goats/sheep that, as the OMD of the forage offered fell below 0.60, goats showed a superior DOMI than sheep. These findings are supported by Howe et al. (1988), who calculated that goats had a superior digestible dry matter intake (DDMI) than sheep as the apparent dry matter digestibility (DMD) of forages declined below 0.65.

Table 1.3. Chemical composition of feed offered and refusals (g/Kg DM) by goats and sheep, when fed at "ad-lib" intake, under stall-feeding conditions.

Feed	Chemical composition (g/Kg DM)			Author
	Feed offered	Feed refusals		
		Goats	Sheep	
Lucerne hay:	28	23	16	Wahed & Owen
Nitrogen				(1986)
ADF	391	449	466	
Ammonia-treated barley straw:				
Nitrogen	17	12.2	11.6	Wahed & Owen
ADF	567	600	612	(1986)
Wheat straw:				
Nitrogen	20	10.6	6.9	Brown & Johnson
NDF	410	610	720	(1985)
Wheat straw:				
Nitrogen	19.5	7.0	6.6	Brown & Johnson
NDF	520	720	760	(1985)
Wheat straw:				
Nitrogen	18.4	5.9	6.4	Brown & Johnson
NDF	620	780	790	(1985)

ADF = acid detergent fibre

NDF = neutral detergent fibre.

Table 1.4. Apparent digestibility (%) of organic matter (OMD) and dry matter (DMD), digestible organic matter intake (DOMI) and digestible dry matter intake (DDMI) by goats and sheep fed on forage and browse diets (g/Kg $W^{0.75}$/d).

Table 1.4.1. OMD and DMD (%) by goats and sheep.

Feed offered	Dietary N (g/Kg DM)	Digestibility	Goats	Sheep	Author
1. *High/medium quality forages*					
Lucerne hay	37.0	OMD	63.2	63.1	Wilson (1977)
Lucerne hay/ oaten chaff	21.0	DMD	64.6	63.5	Gamble & Mackintosh (1982)
Pangola grass	19.5	OMD	63.0	61.4	Watson & Norton (1982)
Lucerne hay	23.8	DMD	59.0	60.0	Alam *et al.* (1983)
Clover hay	30.8	OMD	72.1	71.3	Doyle *et al.* (1984)
Lucerne hay	37.0	DMD	66.2	67.4	Antoniou *et al.* (1985)
MEAN	28.2		64.7	64.5	
2. *Low quality forages*					
Hyparrhenia grass hay	10.5	DMD	53.9	53.6	Gihad (1976)
Pangola grass	8.2	OMD	58.3	53.3	Watson & Norton (1982)
Meadow hay	7.1	DMD	62.0	61.0	Alam *et al.* (1983)
Dry hummra grass	5.1	DMD	54.4	51.7	Mousa *et al.* (1983)
L. rigidum hay	7.7	OMD	64.9	57.3	Doyle *et al.* (1984)
Clover hay + *L. rigidum*	11.4	OMD	49.5	45.6	Doyle *et al.* (1984)
Ryegrass straw	8.4	OMD	53.0	54.0	Alam *et al.* (1985)
Barley straw	6.6	OMD	50.0	51.0	Alam *et al.* (1985)
Barley straw	8.2	DMD	48.0	44.1	Antoniou *et al.* (1985)
NaOH-treated straw	5.6	DMD	63.6	41.8	Masson *et al.* (1986)
Ryegrass hay	13.3	DMD	64.3	63.2	Masson *et al.* (1986)
Barley straw	6.8	OMD	36.0	37.5	Tan *et al.* (1987)
MEAN	8.2		54.8	51.2	
3. *Browse diets*					
C. cristata leaves	15.0	OMD	35.0	29.3	Wilson (1977)
A. pendula leaves	27.0	OMD	46.7	43.4	Wilson (1977)
H. oleifolium leaves	20.0	OMD	43.1	40.2	Wilson (1977)
Willow (*S. viminalis*)	24.3	DMD	62.0	60.0	McCabe *et al.* (1988)
Gorse	29.0	DMD	65.3	64.6	Howe *et al.* (1988)
MEAN	23.1		50.4	47.5	

Table 1.4.2. DDMI and DOMI by goats and sheep (g/Kg $W^{0.75}$/d).

Feed offered	Dietary N (g/Kg DM)	Intake Parameter	Goats	Sheep	Author
1. High/medium quality forages					
Lucerne hay	37.0	DOMI	30.2	29.9	Wilson (1977)
Lucerne hay	29.4	DDMI	55.8	55.2	Boer et al. (1982)
Lucerne hay/ oaten chaff	21.0	DDMI	24.4	24.4	Gamble & Mackintosh (1982)
Pangola grass	19.5	DOMI	31.2	29.3	Watson & Norton (1982)
Lucerne hay	23.8	DDMI	43.1	50.4	Alam et al. (1983)
Clover hay	30.8	DOMI	48.7	43.3	Doyle et al. (1984)
Lucerne hay	37.0	DDMI	44.9	45.2	Antoniou et al. (1985)
MEAN	28.4		39.7	39.7	
2. Low quality forages					
Hyparrhenia grass hay	10.5	DDMI	21.8	18.8	Gihad (1976)
Barley straw	6.3	DDMI	26.7	22.1	Boer et al. (1982)
Pangola grass	8.2	DOMI	19.0	17.0	Watson & Norton (1982)
Meadow hay	7.1	DDMI	31.0	30.6	Alam et al. (1983)
Dry hummra grass	5.1	DDMI	22.9	27.7	Mousa et al. (1983)
L. rigidum hay	7.7	DOMI	29.5	27.5	Doyle et al. (1984)
Ryegrass straw	8.4	DOMI	23.6	20.7	Alam et al. (1985)
Barley straw	6.6	DOMI	19.8	16.5	Alam et al. (1985)
Barley straw	8.2	DDMI	12.0	9.6	Antoniou et al. (1985)
NaOH-treated straw	5.6	DDMI	14.6	12.5	Masson et al. (1986)
Ryegrass hay	13.3	DDMI	39.1	35.9	Masson et al. (1986)
Barley straw	6.8	DOMI	7.5	5.9	Tan et al. (1987)
MEAN	10.5		22.3	20.4	
3. Browse diets					
C. cristata leaves	15.0	DOMI	17.0	14.9	Wilson (1977)
Willow	24.3	DDMI	53.8	27.1	McCabe et al. (1988)
Gorse	29.0	DDMI	40.0	22.4	Howe et al. (1988)
MEAN	22.8		36.9	21.5	

When fed on browse diets, it appears that goats show an increasing superiority in DDMI over sheep, as the lignin content of the forage (g/Kg DM) increases above 120 g/Kg DM (Howe et al., 1988). A regression relationship (Equation 2) was derived by Howe et al. (1988), and was based on 6 browse diets fed to goats/sheep in comparison studies reported in the literature.

$$\text{DDMI (goats/sheep)} = -0.67 + 0.014 \text{ lignin} \quad (r = 0.98;\ P<0.01) \qquad (2)$$

Four factors might contribute to the higher DOMI and OMD by goats when fed on low quality forages and on browse diets, namely:

1. A higher digestion rate in the reticulo-rumen (hereafter referred to as the rumen) of goats, possibly influenced by a more efficient chewing of the feed during eating by goats, compared to sheep.

2. A longer mean retention time of digesta (MRT, h) in the rumen of goats, and therefore a longer exposure of the digesta to microbial attack.

3. A larger rumen volume in goats (g/Kg $W^{0.75}$), to conciliate the observations of a higher voluntary OMI with higher OMD in goats.

Limited data in Table 1.5 show that the MRT of particulate matter (labeled with ^{103}Ru-Phen) is longer in the rumen of goats, both on low and high quality forages, with the difference reaching significance on the low quality forages. Data in Table 1.5 also indicate that goats have a longer rumen MRT of water (labeled with Cr-EDTA), and hence a lower dilution rate of water in the rumen, compared to sheep. These findings are consistent both on low and high quality forages.

Data in Table 1.6 indicate that goats have a seemingly larger rumen volume than sheep (as a proportion of $W^{0.75}$), when fed on both high and low quality forages.

Table 1.5. Mean retention time of particulate phase (Ru-Phen) and liquid phase (Cr-EDTA) of digesta in the rumen of goats and sheep fed on forages (MRT, h).

Table 1.5.1. MRT (h) of Ru-Phen in the rumen.

Feed Offered	Dietary N (g/Kg DM)	Goats	Sheep	Sig	Author
Subterranean clover hay	28.0	17	14	*	Doyle et al. (1980)
Wimmera ryegrass hay	7.0	29	21	*	Doyle et al. (1980)
Grass-clover hay	11.0	26	20	*	Doyle et al. (1980)
MEAN	15.3	24.0	18.3		

Table 1.5.2. MRT (h) of Cr-EDTA in the rumen.

Feed Offered	Dietary N (g/Kg DM)	Goats	Sheep	Sig	Author
Pangola grass	19.5	12.1	9.4	*	Watson & Norton (1982)
Lucerne hay/ oaten chaff	21.0	12.2	9.5	*	Gamble et al. (1982)
Pangola grass	8.2	13.1	10.7	*	Watson & Norton (1982)
MEAN	16.2	12.5	9.9		

* $P<0.05$

Table 1.6. Volume of rumen contents (litres, L) of goats and sheep fed on forage diets (as a proportion of $W^{0.75}$).

Feed Offered	Dietary N (g/Kg DM)	Goats	Sheep	Sig	Author
Lucerne hay/ oaten hay	21.0	0.29	0.35	NS	Gamble & Mackintosh (1982)
Pangola grass	19.5	0.31	0.22	*	Watson & Norton (1982)
Pangola grass	8.2	0.30	0.25	*	Watson & Norton (1982)
Meadow hay	14.7	0.53	0.46	NS	Alrahmoun *et al.* (1985)
MEAN	15.9	0.36	0.32		

* $P<0.05$; NS Non-significant.

There is no data on an integrated study comparing the associated effects of voluntary OMI with (i) OMD, (ii) MRT of digesta, (iii) dilution rate of water in the rumen and (iv) rumen volume, between goats and sheep when fed on high or low quality forages, during summer and/or winter.

1.2.1.4 Apparent Fibre Digestibility

Table 1.7 shows that three analytical systems have been used for the determination of apparent fibre digestibility in goat vs sheep comparison studies, namely:

1. The Detergent System (Van Soest and Wine, 1967),
2. The Comprehensive Carbohydrate Fractionation (Bailey, 1967), and
3. The Proximate Analysis.

When fed on high/medium quality forages, the mean values calculated in Table 1.7 indicate that goats generally digest all the components of fibre slightly better than sheep, although the differences do not always attain significance.

When fed on low quality forages, goats show a greater superiority in digesting fibre than sheep. The superiority increases with an increase in the content of dietary fibre (El Hag, 1976; Gihad, 1976; Doyle, Egan and Thalen, 1984). Limited data in Table 1.8 indicate that the apparent digestibility of lignin is significantly higher in goats compared to sheep (Jones, Larsen, Javed, Donefer and Gaudreau 1972).

When fed on browse, data in Tables 1.7 and 1.8 indicate that goats compared to sheep, have a consistently higher apparent fibre digestibility. The superiority between the two species is greater for the least digestible fraction of the diet (lignin), intermediate for hemicellulose, and least for cellulose (Howe et al., 1988).

Data in Table 1.9 show that the Desert breed of goat digested lignin more efficiently than the Temperate breed, when fed both on high/medium and low quality forages, and digested cellulose and hemi-

Table 1.7. Apparent digestibility of fibre (%) by goats and sheep fed on forage and browse diets.

Feed offered	Dietary fibre Method	g/Kg DM	Digestibility (%) Goats	Sheep	Sig	Author
1. High/medium quality forages						
Berseem hay	CF	235	64.3	65.8	NS	El Hag (1976)
Lucerne hay	NDF	490	46.9	47.2	NS	Wilson (1977)
Pangola grass	NDF	798	75.3	73.4	NS	Watson & Norton (1982)
Clover hay	CF	372	68.8	67.4	NS	Doyle et al. (1984)
Meadow hay	NDF	514	80.0	78.0	NS	Alam et al. (1985)
Prairie grass hay	NDF	603	70.0	67.0	NS	Alam et al. (1985)
Lucerne hay	CF	241	51.3	56.2	NS	Antoniou et al. (1985)
MEAN		465	65.2	65.0		
2. Low quality forages						
Lokh grass	CF	342	74.4	71.6	NS	El Hag (1976)
Hummra grass	CF	364	59.6	54.2	**	El Hag (1976)
Zambian grass hay	CF	379	60.3	56.5	*	Gihad (1976)
Pangola grass	NDF	773	71.3	63.5	*	Watson & Norton (1982)
L. rigidum	CF	717	67.3	58.9	*	Doyle et al. (1984)
L. rigidum + clover hay	CF	758	54.0	51.1	NS	Doyle et al. (1984)
Barley straw	NDF	802	56.0	59.0	NS	Alam et al. (1985)
Ryegrass straw	NDF	687	52.0	54.0	NS	Alam et al. (1985)
Barley straw	CF	404	56.7	52.8	NS	Antoniou et al. (1985)
MEAN			61.3	57.9		
3. Browse diets						
Gorse	C	503	60.2	57.2	*	Howe et al. (1988)

CF = Crude Fibre by Proximate Analysis.
NDF = Detergent System (Van Soest & Wine, 1967).
C = Comprehensive Carbohydrate Fractionation (Bailey, 1967).
** $P<0.01$; * $P<0.05$; NS Non-significant.

Table 1.8. Apparent digestibility of lignin (%) by goats and sheep.

Feed offered	Dietary lignin (g/Kg DM)	Goats	Sheep	Sig	Author
Wilted alfalfa	80	18.5	13.7	NS	Jones et al. (1972)
Low DM corn silage	55	22.9	15.3	*	Jones et al. (1972)
Gorse	171	31.5	25.5	**	Howe et al. (1988)
MEAN	102	24.3	18.2		

** P<0.01; * P<0.05; NS Non-significant.

Table 1.9. Apparent digestibility of fibre (%) by the Desert and Temperate breeds of goat.

Feed offered	Dietary fibre (g/Kg DM)			Breed	Digestibility (%)		
	Cellulose	Hemicellulose	Lignin		Cellulose	Hemicellulose	Lignin
Alfalfa hay	345	87	76	D	72.4^{NS}	70.5^{NS}	17.4*
				T	72.1	68.1	- 0.5
Rhodes grass + alfalfa hay	300	258	67	D	68.1*	65.2*	14.7*
				T	61.3	57.3	7.2
Wheat straw	401	309	142	D	60.1*	57.3*	15.3*
				T	47.2	42.1	3.7

(from Silanikove, 1986)

D = Desert breed; T = Temperate breed.

* $P<0.05$; NS Non-significant.

cellulose more efficiently when fed on the low quality forages (Silanikove, 1986).

More work is required in goat vs sheep comparison studies to determine why goats are superior to sheep in degrading fibrous substrates.It is known that microbial attachment to the fibrous substrates in the rumen is a pre-requisite to the degradation of fibre (Cheng, Akin and Costerton, 1977; Forsberg and Lam, 1977; Cheng, Stewart, Dinsdale and Costerton, 1983). Chewing, during eating and rumination, contribute to particle size reduction and offer the rumen with small particles (<1.0 mm) of larger surface area (Akin, 1979, 1983; Cheng et al., 1983).

There are no studies at present on the comparative efficiencies in particle size reduction between goats and sheep, during eating and ruminating.

1.2.1.5 Nitrogen Balance

Data in Table 1.10 show that, when fed on high/medium quality forages, there is no difference in nitrogen (N) retention between goats and sheep. When fed on low quality forages, limited data in Table 1.10 suggest that both goats and sheep are in negative N balance, but the N lost by sheep is greater than in goats. The apparent greater N retention by goats, when fed on low quality forages, compared to sheep, might be influenced by two factors, namely:

1. A greater capacity of goats to recycle and conserve N. One limited study by Seth, Rai, Yadav and Pandey (1976), showed that goats had a higher rate of salivary secretion than sheep, but the actual recycling of N to the rumen in goats, compared to sheep is unknown.

2. A lower water intake (ml/Kg DMI) by goats, (as observed by Gihad, El-Bedawy and Mehrez, 1980; Alam, Poppi and Sykes, 1983; Howe et al., 1988), and predisposing them to a greater N conservation. Mousa, Ali and Hume (1983) observed a greater N retention in both goats and sheep, under conditions of water deprivation.

Table 1.10. Nitrogen (N) retention by goats and sheep (mg/100 g DMI) fed on forage diets.

Feed offered	Dietary N (g/Kg DM)	N intake (g/d)		N retained (mg/100 g DMI)		Sig	Author
		Goats	Sheep	Goats	Sheep		
1. High/medium quality feeds							
Lucerne hay/ oaten chaff	21.0	9.6	10.3	160	260	NS	Gamble & Mackintosh (1982)
Pangola grass	19.5	14.2	16.2	593	498	NS	Watson & Norton (1982)
Clover hay	30.8	41.9	33.1	485	566	*	Doyle *et al.* (1984)
MEAN	23.8	21.9	19.9	413	441		
2. Low quality feeds							
Zambian grass	10.5	4.8	8.0	-263	-273	NS	Gihad (1976)
Pangola grass	8.2	3.9	4.5	52	- 96	NS	Watson & Norton (1982)
L. rigidum	7.4	7.1	6.1	- 56	-115	*	Doyle *et al.* (1984)
L. rigidum + clover hay	11.4	7.8	6.5	-122	-371	NS	Doyle *et al.* (1984)
MEAN	9.4	5.9	6.3	-97.3	-214		

* $P<0.05$; NS Non-significant.

There is no data on the comparative efficiency of N recycling, and N conservation by the two species, when fed on high/medium and low quality forages.

1.2.1.6 Rumen Ammonia Concentration

Data in Table 1.11 indicate that the rumen ammonia (NH_3-N) concentration of goats and sheep (mg N/L), is similar when both species are fed on high/medium quality forages. When fed on low quality forages, however, goats sustain a consistently higher rumen NH_3-N concentration (78.0 mg N/L), than sheep. The mean rumen NH_3-N concentration for sheep is 41 mg N/L, which is below the critical level (50 mg N/L), at which microbial activity is claimed to be suppressed (Satter and Slyter, 1974).

Determinations of NH_3-N concentrations in the rumen fluid alone are difficult to interpret in quantitative terms, without any measurements of the (i) recycling of N into the rumen, (ii) recycling within the rumen, and (iii) rates of microbial synthesis in the rumen. There are no studies to date on the N transactions in the rumen of goats, using ^{15}N kinetics, with animals in steady state. On the other hand, quantitative data of rumen N transactions are well documented for sheep fed both on low and high quality forages (Nolan, Norton and Leng, 1976; Nolan and Stachiw, 1979; Dixon and Nolan, 1986; McNabb, Barry, Dellow and Nolan, 1989).

1.2.1.7 Maintenance Energy Requirements

Limited data of goat vs sheep studies indicate that the metabolisable energy (ME) required for maintenance (M) is higher in goats, compared to sheep.

Mohammed and Owen (1980), reported M values for 2-year old goats (Equation 3), and 3-year old sheep (Equation 4).

$$M\ (\text{goats}) = 0.434 + 0.01\ W^{0.75} \qquad (3)$$

$$M\ (\text{sheep}) = 0.301 + 0.01\ W^{0.75} \qquad (4)$$

Table 1.11. Rumen ammonia concentration (NH_3-N, mg N/L) in goats and sheep fed on forage and browse diets.

Feed offered	Dietary N (g/Kg DM)	Rumen NH_3-N (mg N/L) Goats	Sheep	Author
1. High/medium quality feeds				
Pangola grass hay	19.0	145	141	Watson et al. (1982)
Lucerne/wheat straw	-	265	226	Cabrera et al. (1983)
Lucerne hay	-	483	479	Cabrera et al. (1983)
Lucerne hay	37.3	273	281	Hadjipanayiotou et al. (1983)
Meadow hay	23.9	191	161	Alam et al. (1985)
Prairie grass hay	26.8	234	151	Alam et al. (1985)
Ryegrass hay	17.5	106	91	Alam et al. (1985)
Lucerne hay	37.3	268	350	Antoniou et al. (1985)
MEAN	27.0	246	235	
2. Low quality feeds				
Pangola grass hay	8.2	106	43	Watson et al. (1982)
Wheat straw	-	53	29	Cabrera et al. (1983)
Barley straw	9.4	74	45	Hadjipanayiotou et al. (1983)
Barley straw	8.2	108	90	Antoniou et al. (1985)
Ryegrass straw	8.4	60	41	Alam et al. (1985)
Cockfoot straw	10.3	78	65	Alam et al. (1985)
Barley straw	6.6	43	37	Alam et al. (1985)
Meadow hay	7.1	54	15	Alam et al. (1985)
Soda-treated barley straw	5.9	128	8	Alrahmoun et al. (1986)
MEAN	8.0	78	41	
3. Browse feeds				
Acacia	23.0	94	54	Antoniou et al. (1985)
Acacia	23.0	65	69	Hadjipanayiotou et al. (1983)
MEAN	23.0	80	62	

where ME = 0.81 x digestible energy,
M = ME required in MJ/d.

The calculation estimated that the ME requirements of goats was higher (+ 44%) than sheep (Mohammed and Owen, 1980). On the other hand, Alam et al. (1983), estimated the ME (MJ/Kg $W^{0.75}$/d) requirements of kids and lambs to be 0.393 and 0.379, respectively. Holmes and Moore (1981), reported that the ME required for M in New Zealand feral goats was 0.39 MJ/Kg $W^{0.75}$/d, compared to a calculated value of 0.32 for an adult sheep.

The recommendations for ME requirements vary for different breeds of goats. The National Research Council (NRC) data (M=0.409 MJ/Kg $W^{0.75}$/d), are based on tropical and desert breeds of goats (NRC, 1981), and the French data (M=0.641 MJ/Kg $W^{0.75}$/d) are based exclusively on temperate breeds (Sauvant, 1981). The apparent differences in the American and French recommendations for ME reflect the lower energy requirements typical of the desert goats (Silanikove, 1986).

It can be concluded that goats require more energy per unit of Kg $W^{0.75}$ than sheep, for the achievement of maintenance of energy equilibrium. It is not known if ME requirements of goats change with season.

1.2.2 Deer vs Sheep

1.2.2.1 Voluntary Feed Intake

The VFI of deer is markedly seasonal. The VFI of deer falls sharply in late autumn/early winter, then increases in spring/summer (Pollock, 1975; Drew, 1976; Milne et al., 1978; Fennessy, 1981; Suttie and Simpson, 1985).

Figure 1.1 (Kay, 1979), shows the effects of castration and sex on the seasonal VFI of deer. Both castrates and intact stags, and hinds show a similar trend in seasonal appetite cycle. However, the VFI of intact stags shows a drastic decline in winter, and a marked increase in spring. In contrast, the castrates and hinds show a

gradual loss of appetite in winter, and a less pronounced increase in VFI in spring.

Similar seasonal changes in VFI have been noted in other Cervids, like the reindeer, caribou, moose and white-tailed deer (McEwan and Whitehead, 1970; Holter, Urban and Hayes, 1977; Ryg and Jacobsen, 1982a).

The domestic sheep also shows a seasonal variation in intake, with a small reduction in VFI in winter (Kay, 1979; Blaxter and Boyne, 1982). On the other hand, the feral sheep like the Soay breed, shows a pronounced seasonal appetite cycle, similar to the deer (Kay, 1979; Kay and Suttie, 1981; Argo and Smith, 1983). It is possible that the magnitude of seasonal VFI cycle in the domestic sheep has been greatly attenuated, because of the longer amount of time they have been subjected to selection, breeding and controlled feeding.

There is now compelling evidence to suggest that changing daylength is the stimulus to the seasonal appetite cycle in deer, and in domestic sheep (Kay, 1979; Simpson, Suttie and Kay, 1984; Suttie and Simpson, 1985). Figure 1.2 (Kay, 1979), shows the VFI of intact stags and domestic sheep, when subjected to an artificial six-month photoperiod. It can be concluded that both the deer and domestic sheep respond to increases in daylength, by increasing their VFI. The deer respond differently to the domestic sheep, by showing peaks and troughs in the appetite cycles as the daylength changes. On the other hand, the domestic sheep shows an attenuated seasonal appetite cycle (Kay, 1979).

Data in Table 1.12 of deer vs sheep (castrates) comparison studies confirm the seasonal appetite cycle in sheep and deer. The following conclusions can be drawn from data in Table 1.12, namely:

1. When fed on high/medium and low quality forages, and on browse diets, both sheep and deer show a higher VFI (g/Kg $W^{0.75}$/d) in summer, compared to winter. The increase in intake from winter to summer is greater in deer, compared to sheep, confirming the difference in response to photoperiod changes by the two species.

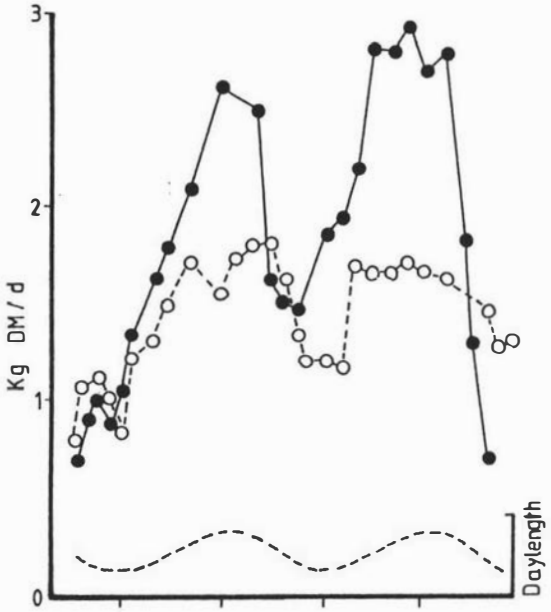


Figure 1.1a. Seasonal voluntary feed intake of a pelleted diet by intact (•) and castrate (o) stags (from Kay, 1979).

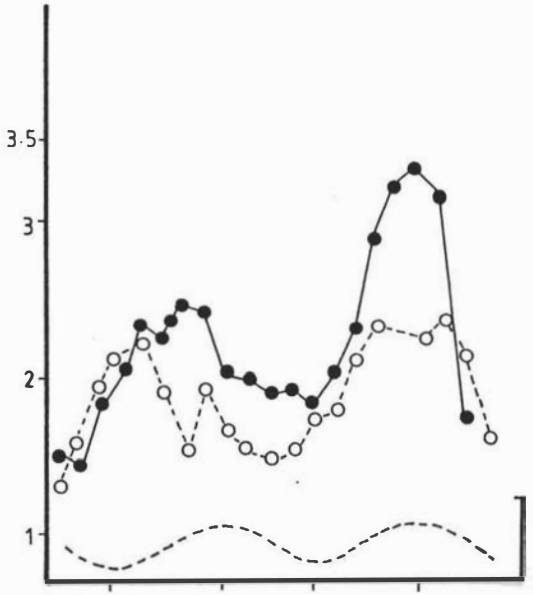


Figure 1.1b. Seasonal voluntary feed intake of a pelleted diet by (•) intact stags and (o) hinds (from Suttie et al., 1987).

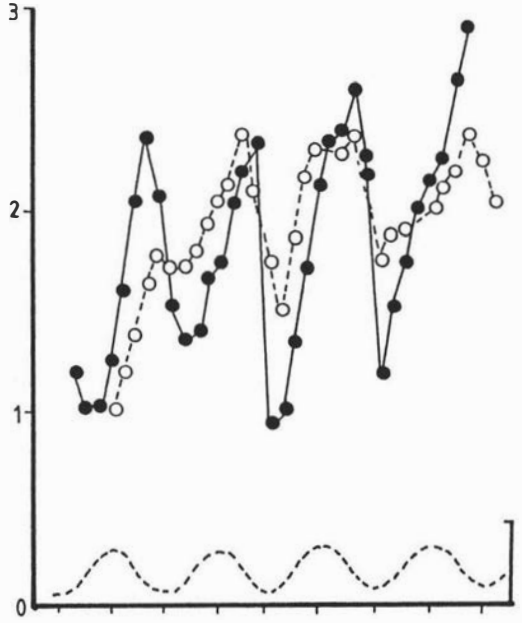


Figure 1.2. Voluntary feed intake of a pelleted concentrate diet by intact Red Deer stags (•) and intact domestic Suffolk cross rams (o), subjected to an artificial six-month photoperiod (from Kay, 1979).

Table 1.12. Seasonal voluntary feed intake of forage and browse diets by castrated deer and sheep (g/Kg $W^{0.75}$/d).

Feed offered	Dietary N (g/Kg DM)	Intake Parameter	Season	Deer	Sheep	Sig	Author
1. Forage diets							
Dried grass pellets	28.3	OMI	S	82.3	88.2	NS	Milne et al. (1978)
Dried grass pellets	28.3	OMI	W	57.3	71.3	*	Milne et al. (1978)
Pelleted diet	22.5	DMI	W	65.3	80.4	*	Fennessy et al. (1980)
Lucerne hay	31.2	DMI	S	75.4	69.4	NS	McCabe et al. (1988)
Agrostis-festuca hay	13.2	OMI	S	70.0	24.6	*	Milne et al. (1978)
Agrostis-festuca hay	13.2	OMI	W	38.3	20.2	*	Milne et al. (1978)
Meadow hay	9.7	DMI	W	53.7	54.8	NS	Fennessy et al. (1980)
MEAN			S W	75.9 53.7	60.7 56.7		
2. Browse diets							
Heather hay	10.3	OMI	S	54.9	23.8	*	Milne et al. (1978)
Heather hay	10.3	OMI	W	34.1	17.0	*	Milne et al. (1978)
Willow (S. viminalis)	24.3	DMI	S	68.6	46.6	*	McCabe et al. (1988)
MEAN			(S + W)	52.5	29.1		

OMI = organic matter intake.

DMI = dry matter intake.

S = summer; W = winter.

* $P<0.05$; NS Non-significant.

2. When fed on high/medium quality forages, there are no differences in VFI (g/Kg $W^{0.75}$/d) between deer and sheep in summer. In winter, the sheep achieve a higher VFI than deer, with a mean difference of 24% between the two species.

3. When fed on low quality forages, deer appear to have a higher VFI (g/Kg $W^{0.75}$/d) than sheep, both in summer and in winter (Milne et al., 1978, Scottish data). In contrast, the New Zealand data (Fennessy, Greer and Forss, 1980), on deer/ sheep winter intake of a low quality forage diet showed no significant differences between the two species.

4. When fed on browse diets, the deer show a superior VFI (g/Kg $W^{0.75}$/d) to sheep, both in summer and winter.

1.2.2.2. Selection of Feed by Deer and Sheep

There is no published data known to the author on a grazing trial comparing deer and sheep. It is known, however, that deer do feed selectively at pasture, and this is expressed mostly in summer with an increase in the quality and availability of forage (Kay and Staines, 1981; Hofmann, 1983, 1985; Lavers, Lee, Wilson and Mills, 1985).

Under controlled feeding conditions indoors, Fennessy et al. (1980), reported that there were no differences between sheep and deer in the composition of feed residues, when fed on meadow hay. Both species showed selection of the feed under offer, with the residues containing a higher proportion of cellulose and a lower proportion of N.

1.2.2.3. Digestibility

The following conclusions can be made from limited data of digestibility studies and rumen MRT of digesta in deer vs sheep comparison studies, and summarised in Table 1.13. The conclusions are based on the mean values of the high/medium and low quality forage diets which were under offer.

Table 1.13. Digestibility of forage diets (%) and mean retention time (MRT, h) of Ru-Phen in the rumen of deer and sheep, in summer and in winter.

Table 1.13.1. Apparent digestibility of organic matter (OMD, %) and rumen MRT (h) of Ru-Phen.

Feed offered	Season	OMD (%)		Rumen MRT (h) of Ru-Phen		Author
		Deer	Sheep	Deer	Sheep	
Dried grass pellets	S	58	61	12	13	Milne et al. (1978)
Dried grass pellets	W	61	67	13	19	Milne et al. (1978)
Pelleted diet	W	77	71	ND	ND	Fennessy et al. (1980)
Agrostis-festuca	S	46	52	23	28	Milne et al. (1978)
Agrostis-festuca	W	41	48	17	25	Milne et al. (1978)
Meadow hay	W	51	47	ND	ND	Fennessy et al. (1980)
MEAN	S	52.0	56.5	17.5	20.5	
	W	57.5	58.3	15.0	22.0	

Table 1.13.2. Apparent digestibility of fibre (NDF), cellulose (C), hemi-cellulose (H)).

Feed offered	Season	Fibre Component	Deer	Sheep	Author
Dried grass pellets	S	NDF	57	60	Milne et al. (1978)
Dried grass pellets	W	NDF	52	63	Milne et al. (1978)
Pelleted diet	W	C	38	33	Fennessy et al. (1980)
Pelleted diet	W	H	52	43	Fennessy et al. (1980)
Agrostis-festuca	S	NDF	42	49	Milne et al. (1978)
Agrostis-festuca	W	NDF	36	43	Milne et al. (1978)
Meadow hay	W	C	48	42	Fennessy et al. (1980)
Meadow hay	W	H	56	50	Fenessy et al. (1980)
MEAN	S		49.5	54.5	
	W		47.0	45.7	

NDF = neutral-detergent fibre

S = summer; W = winter.

ND = not determined.

1. The mean values of OMD indicate that both deer and sheep digest the OM component of the feed as efficiently in summer as in winter, despite the greater OMI in summer in both species (Table 1.12).

2. The mean values of apparent fibre digestibility indicate that sheep show a small increase in the apparent fibre digestibility (+ 1.5 %) in summer compared to winter. Deer digest the fibre component of the feed better in summer (+ 5.5%) than in winter.

3. The increase in OMD and apparent fibre digestibility from winter to summer, are associated with an increase in OMI (Table 1.12), in both sheep (+ 15.5%) and deer (+ 53.0%).

4. The increase in apparent fibre digestibility from winter to summer, is associated with a decrease in the rumen MRT of Ru-Phen in sheep (- 1.7 h), and an increase (+ 2.7 h) in deer.

5. The Scottish data (Milne et al. 1978), indicate that sheep digest fibre and OM more efficiently than deer, both in summer and in winter, and are associated with longer rumen MRT of Ru-Phen in sheep. The Scottish data appear to conflict with the NZ data (Fennessy et al., 1980), where deer appear to digest fibre and OM better than sheep.The rumen MRT of digesta was not measured by Fennessy et al. (1980).

The conclusions drawn from Table 1.13 lead to the postulate, made by Milne et al. (1978) and Hofmann (1985), that deer can achieve a higher OMI and DOMI in summer, together with an increase in the rumen MRT of digesta, possibly by a compensatory enlargement of the rumen volume in summer. This has not been measured experimentally yet in the deer, by using repetitive measurements of rumen capacity and rumen digesta load in summer and in winter.

1.2.2.4 Fasting Metabolism and Maintenance Energy Requirements in Deer

The deer shows a marked seasonal rhythm of fasting metabolic rate (Silver, Colovos, Holter and Hayes, 1969), heart rate and activity

(Moen, 1978), which are greatest in summer and reduced in winter (Table 1.14).The domestic sheep (Blaxter and Boyne, 1982), also shows an attenuated annual rhythm of metabolism, with greater ME requirements in summer than in winter.Comparative studies between sheep and deer indicate that the sheep have lower (- 40%) ME requirements (MJ/Kg $W^{0.75}$/d) than deer (Simpson, Webster, Smith and Simpson, 1978).

The annual rhythms of metabolism shown in deer have been associated with their seasonal cycles of growth and VFI (Barry, Suttie and Milne, 1989).

1.3 PHYSIOLOGICAL CONTROL OF SEASONAL FEED INTAKE IN DEER: A HORMONAL BASIS

There is strong evidence that the seasonal cycle of VFI in deer is under the control of changing daylength (Simpson et al., 1984; Suttie and Simpson, 1985). It has been postulated that the hormone melatonin (Me), entrains the seasonal cycles of VFI, growth and metabolism in deer to changes in photoperiod (Barry et al., 1989). Melatonin is secreted by the pineal gland during hours of darkness (Plotka, Seal, Letellier, Verme and Ozaga, 1981; Bubenik, 1983; Lincoln, 1983, 1985). Hence long periods of short daylength (autumn/winter) lead to high concentrations of plasma Me (Lincoln and Almeida, 1981; Bittman, Dempsey and Karsch, 1983; Bubenik, 1983).

The seasonal hormonal status of deer has been studied extensively (Table 1.15), and the seasonal patterns of hormonal secretions have been associated with seasonal cycles in (i) body growth, (ii) VFI, (iii) metabolic rate, (iv) reproductive activity and breeding season and (v)antler development. The hormones that underlie these seasonal cycles, namely prolactin (P), growth hormone (GH), the insulin-like growth factor I (IGF-I), gonadal and thyroid hormones, all show a seasonal pattern in their release and plasma concentrations. The seasonal hormonal status for testosterone (T), P, GH and IGF-I in the deer are shown diagrammatically in Figure 1.3, with the seasonal cycle of VFI superimposed.

Table 1.14. Estimation of seasonal metabolisable energy requirements (ME) for maintenance, and fasting metabolism (FMR) for deer.

Species	Technique	FMR or ME	Season	MJ/Kg $W^{0.75}$/d	Author
White-tailed deer	Indirect calorimetry	FMR	S	0.60	Silver et al., (1969)
			W	0.41	
Reindeer	Calorimetry	ME	W	0.84	McEwan & Whitehead (1970)
White-tailed deer	Regression analysis	ME	S	0.70	Holter et al. (1977)
			W	0.50	
Red Deer	Calorimetry	ME	S	0.50	Simpson et al. (1978)
			W	0.45	
Red Deer	Regression analysis	ME	S	0.57	Fennessy et al. (1981)
			W	0.57	

S = summer; W = winter.

Table 1.15. Studies of seasonal hormonal status and associated seasonal physiology in deer.

Hormone	Associated seasonal physiology	Author
MELATONIN	- Onset of breeding season - Initiation of growth cycles - Initiation of antler development	Bubenik (1983); Bubenik & Smith (1985); Fennessy & Suttie (1985); Fennessy et al. (1985); Asher et al. (1988); Fisher et al. (1988); Barry et al. (1989).
PROLACTIN	- Rate of body growth - Voluntary feed intake - Antler development	Suttie (1980); Ryg & Jacobsen (1982b); Barrell et al. (1985); Suttie & Kay (1985); Loudon et al. (1988).
GROWTH HORMONE	- Antler development - Rate of body growth	Ryg & Jacobsen (1982a); Suttie et al. (1989)
IGF-I	- Antler development - Rate of body growth	Suttie et al. (1989)
IGF-II	- Antler development - Rate of body growth	Suttie et al. (1989)
THYROID HORMONES	- Rate of body growth - Voluntary feed intake - Heart rate and activity	Rindberg et al. (1978); Ryg & Jacobsen (1982a; 1982b).
TESTOSTERONE	- Sexual behaviour	Fennessy et al. (1985); Suttie & Kay (1985); Barrell et al. (1985)

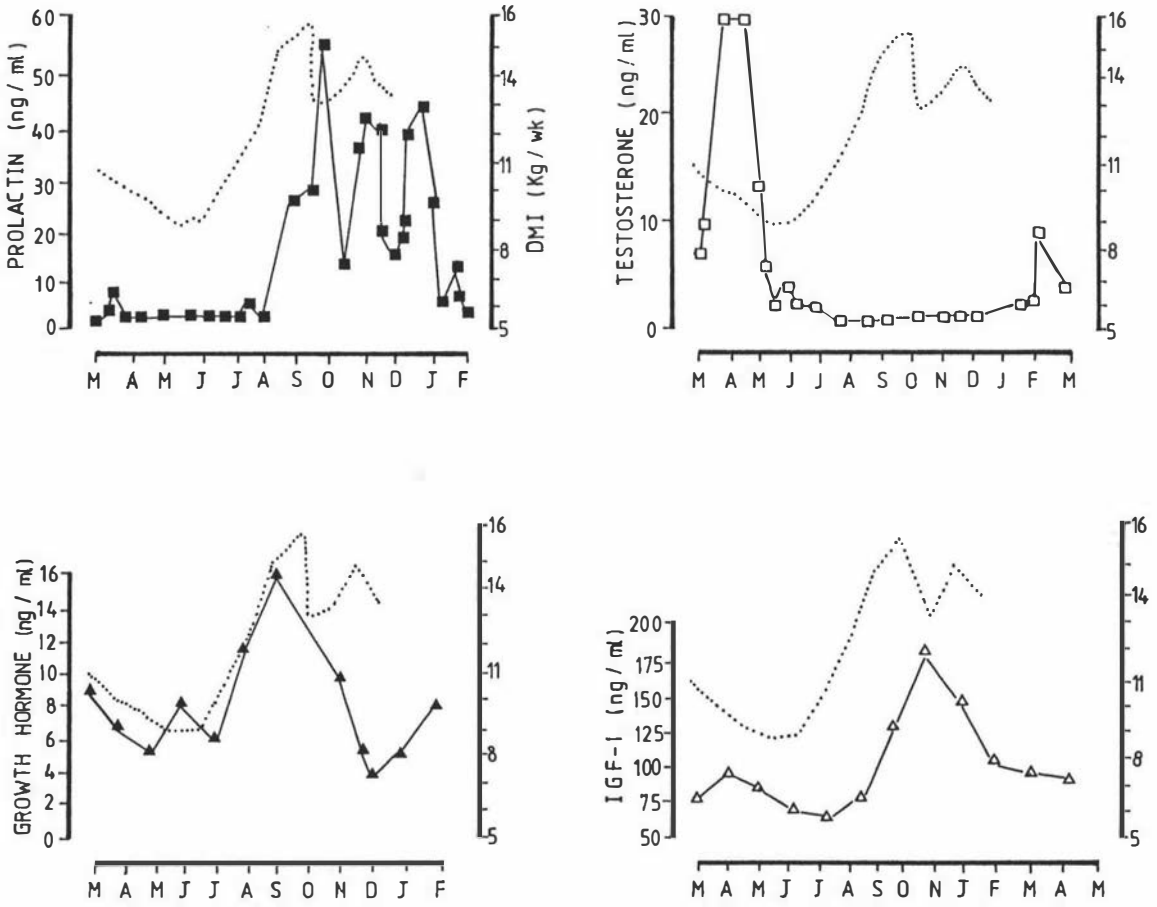


Figure 1.3. Seasonal hormonal status of Red Deer: the seasonal hormonal profiles of prolactin (■), Testosterone (□) (Barrell et al., 1985), growth hormone (▲) and IGF-I (△)(Suttie et al., 1989), together with the seasonal VFI (Suttie et al., 1989).

The annual pattern of T consists of low plasma levels throughout winter and spring, following an increase in plasma concentration in late summer, and reaching peak levels in mid-autumn (Barrell, Muir and Sykes, 1985). Elevated concentrations of plasma P occur between spring and autumn, with peak values occurring during summer. Plasma P level is reduced to base-line levels in winter (Mirarchi, Howland, Scanlon, Kirkpatrick and Sanford, 1978; Barrell et al., 1985; Fennessy and Suttie, 1985). High P plasma levels have been associated with an increase in body growth and VFI (Suttie, 1980; Ryg and Jacobsen, 1982b). Growth hormone secretion is highest in late winter and early spring, and is associated with a high pulse amplitude and high pulse frequency of the hormone (Suttie, Fennessy, Corson, Laas, Crosbie, Butler and Gluckman, 1989). Elevated plasma concentration of GH is followed one month later by a seasonal elevation of IGF-I (September), which correlates positively with an increase in body growth and VFI (Suttie et al., 1989).

Although correlations do not imply causation, the seasonal cycles of hormonal secretions in deer can be correlated with seasonal changes in VFI (Figure 1.3), and growth. The correlations indicate associated dependent relationships between the seasonal cycles of growth, VFI and reproduction in the deer. Published data on the seasonal physiology of deer and summarised in Table 1.15 and Figure 1.3 indicate that all aspects of seasonal physiology are linked in the deer, namely the cyclicity of reproduction (gonadal activity and regression), peaks and troughs in VFI, changes in body weight, antler casting and growth, and coat growth. However the direct mechanisms involved in the hormonal daylength control of VFI in the deer are unknown at present, as well as the digestive functions which would accompany the seasonal changes in VFI. It is concluded that the seasonal cycle of VFI in deer is not a separate entity, but occurs as part of their seasonal cycles of metabolism, body growth and reproduction. There is no published evidence of strong physiological cycles in the domestic sheep or goat.

1.4 HORMONAL MANIPULATION OF FEED INTAKE IN DEER

Three hormonal manipulation techniques have been investigated to control the seasonal VFI in deer, namely:

1. Active immunisation against melatonin,

2. Manipulation of plasma prolactin levels, and

3. Active immunisation against Luteinising Hormone Releasing Hormone (LHRH).

1.4.1 Active immunisation against melatonin

The objectives of an active immunisation against Me are to coincide long hours of darkness in late autumn/winter with low Me secretion, and hence reduce winter depressions of VFI and body growth in deer since Me possibly entrains these cycles to photoperiod.

Antibodies against Me have been successfully raised in the deer, but the titres obtained were low and the antibody response very slow (Ataja, Wilson, Purchas, Hay, Hodgson and Barry, 1989). Currently work is being conducted at Massey University to achieve a peak antibody production and high titres by late autumn, by immunising the deer calves at birth (Ataja, unpl. data). Preliminary data have shown that Red Deer calves which had been immunised against Me at birth, were 7-10% heavier than the Control group, between 9-11 months of age (Duckworth and Barrell, 1989).

1.4.2 Manipulation of plasma prolactin concentration

In view of the association of P with long daylength and an increase in VFI in deer, hormonal manipulation to elevate plasma P in winter has been investigated to reduce the winter depression of VFI.

Two methods have been used to increase plasma P concentration in winter, namely:

1. Daily intramuscular (IM) injections of ovine P (Ryg and Jacobsen, 1982b; Milne, unpl. data)

2. Daily domperidone injections to elevate the level of plasma P (Loudon, Milne, Curlewis and McNeilly, 1986)

Daily IM injections of bromocryptine (a dopamine agonist and inhibitor of P secretion), have also been given in summer to suppress P secretion, to elucidate whether P has a mediating role in the seasonal cycle of VFI in deer (Curlewis, Loudon, Milne and McNeilly, 1988).

Ryg and Jacobsen (1982b), reported that P injections in winter were followed by an increase in VFI in early spring. However, most of the work on P manipulation (increase in winter or decrease in summer of plasma P levels), has shown no response to VFI in the deer (Loudon et al., 1986; Curlewis et al., 1988). There is no clear evidence, yet, that P mediates the increase in VFI in spring/summer in deer. Further experiments are being conducted by comparing melatonin-treated animals with animals given bromocryptine, to provide a role for P in the control of VFI in deer (Milne, pers. comm.).

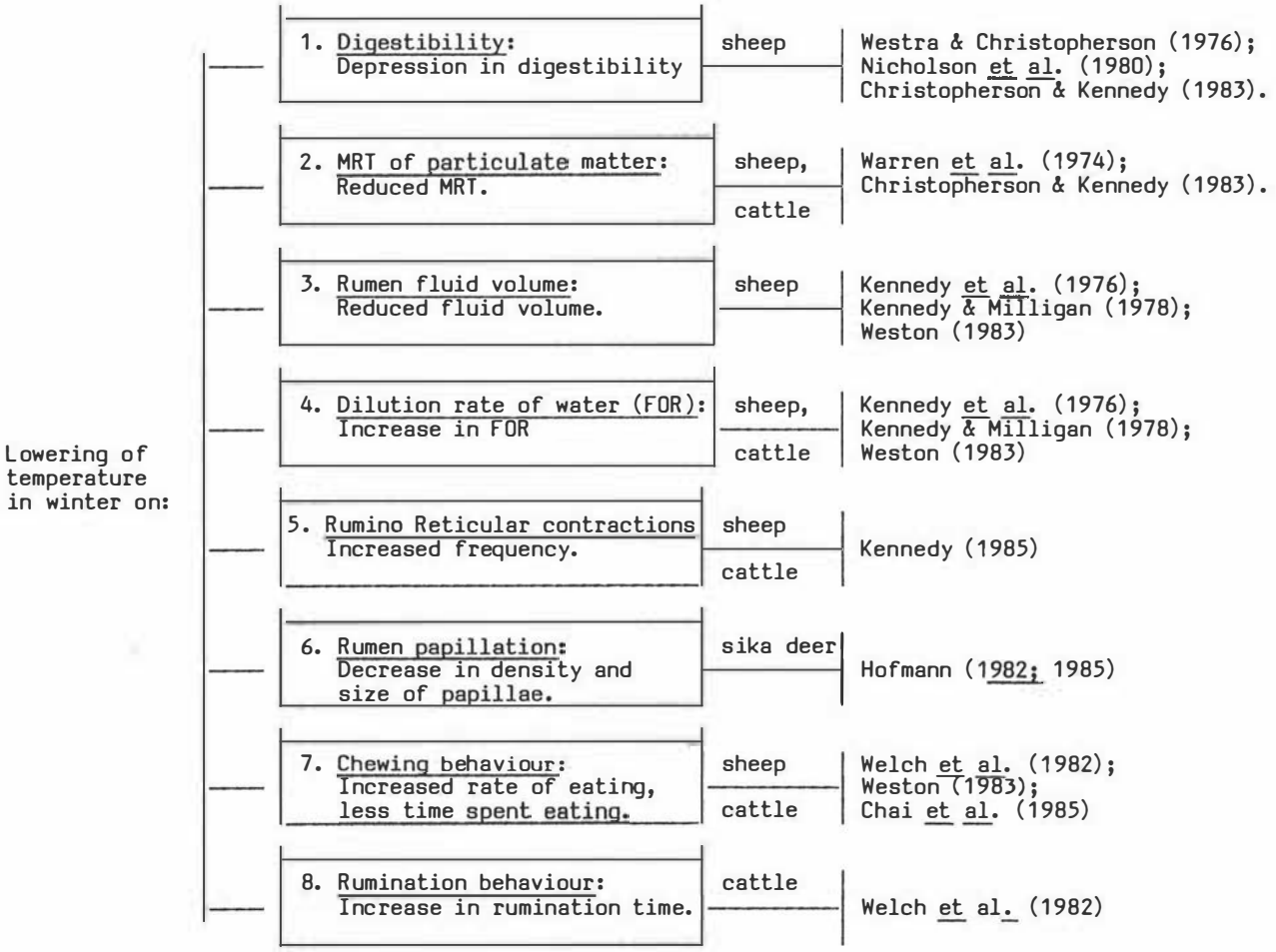
1.4.3 Active immunisation against LHRH

The seasonal cycle of rutting in deer is regulated by the seasonal cycle in the secretion of testosterone, an effect dependent on the secretion of LHRH (Lincoln, Youngson and Short, 1970; Lincoln, 1971; Lincoln, Guinness and Short, 1972). Active immunisation against LHRH has been shown to effectively suppress the rut and testosterone secretion in stags (Lincoln, Fraser and Fletcher, 1984). Hormonal manipulation of low testosterone in late autumn/early winter by active immunisation against LHRH in yearling stags, may prevent the testosterone-associated LWT loss and reduction in feed intake in winter. The technique is being currently investigated at Massey University (Ataja, unpl. data).

1.5 SEASONAL VARIATIONS IN RUMEN FUNCTIONS

Seasonal variations in temperature have been associated with changes in rumen function, namely in: (i) digestibility, (ii) rumen volume, (iii) MRT of particulate matter in the rumen, (iv) dilution rate of water in the rumen, (v) rumino-reticular contractions, (vi) changes in the rumen papillation and, (vii) eating and rumination behaviour. Data in Table 1.16 summarise the associations observed between rumen digestion and changes in temperature.

Table 1.16. Seasonal variations in temperature and associated changes in rumen digestion.



Data in Table 1.16 show that most of the data have been derived for sheep, with almost no data on goats and deer. Although temperature was the only measured variable parameter in the experiments reported in Table 1.16, changes in daylength with season could have had a confounding effect on the results.

1.6 CLEARANCE OF DIGESTA FROM THE RUMEN, AND CONTROL OF INTAKE

Three processes affect the clearance of digesta from the rumen, as described by Ulyatt, Dellow, John, Reid and Waghorn (1986), namely:

1. The passage of particles through the reticulo-omasal orifice,

2. The breakdown of particulate matter in the rumen, and

3. Microbial digestion.

The three processes interact to control VFI and digestibility, by imposing a delay in transit on the passage of the feed particles out of the rumen (Ulyatt *et al.*, 1986).

1.6.1 Passage of particles through the reticulo-omasal orifice

Particles cannot leave the reticulo-omasal orifice until they have been reduced to below a certain critical particle size, as threshold to passage through the reticulo-omasal orifice. In sheep, the particle size as threshold to passage is 1.0 mm (Reid, Ulyatt and Munro, 1977; Troelsen and Campbell, 1968; Poppi, Norton, Minson and Hendricksen, 1980). One limited study indicates that the critical size is 1.0 mm in goats (Uden and Van Soest, 1982). There are no data for deer.

There is a differential rate of passage for particles <1.0 mm through the reticulo-omasal orifice, and it appears that the density of the particles controls the process.Indirect evidence can be obtained from the data (Table 1.17) of rumen FOR (%/h) of particles in sheep (Egan and Doyle, 1984). Particle density was not measured, but data in Table 1.17 suggest the smaller the particles, the denser they are. Small particles have a larger surface area and pack more densely

Table 1.17. "Apparent" fractional outflow rates (FOR, %/h) and "apparent" mean retention time (h) of particles in the rumen of sheep fed a forage diet.

Particle size	FOR (%/h)	MRT (h)
>2.0 mm	0.25	400
2.0 - 1.0 mm	0.58	172
1.0 - 0.71 mm	1.91	52.4
0.71 - 0.50 mm	2.80	35.7
0.50 - 0.25 mm	6.38	15.7
0.25 - 0.15 mm	6.07	16.5
<0.15 mm	5.43	18.4
Cr-EDTA†	10.75	9.3

Calculated from Egan & Doyle (1984)

† for reference of liquid flows from the rumen.

than larger particles (Martz and Belyea, 1986). Dense particles can resist escape and sink to the bottom of the rumen. Hence, the MRT of particles <0.15 mm was longer than that of the fraction 0.50-0.15 mm (Table 1.17). Ehle and Stern (1986), made similar observations with the cow. There are no data for goats and deer in the proportions of feed particles in the rumen contents.

1.6.2 Breakdown of particulate matter in the rumen

Feed particulate matter can be reduced in particle size by two processes (Ulyatt et al., 1986), namely:

1. Physical breakdown by chewing, during initial eating,

2. Further physical breakdown, by chewing during rumination.

The two processes are well documented for sheep. There is one limited goat vs sheep comparison study (Geoffroy, 1974), and no data for deer.

The effectiveness of chewing during eating can be assessed by 4 factors, as summarised by Ulyatt et al. (1986), namely: (i) frequency of chewing during eating, (ii) rate of eating, (iii) particle size breakdown during eating and (iv) anatomy of teeth and jaws, which determine the forces applied during eating.

Limited data (Table 1.18) of goat vs sheep comparison studies indicate that goats compared to sheep have a slower rate of eating (g DM/min spent eating). Goats appear to spend more time eating than sheep, with the difference not attaining significance ($P>0.05$).

The effectiveness of chewing during rumination can be assessed by 5 factors, as summarised by Ulyatt et al. (1986), namely: (i) time spent ruminating, (ii) frequency of chews during ruminating, (iii) particle size breakdown during ruminating, (iv) mean bolus weight regurgitated and (v) anatomy of the teeth and jaws.

Limited data in Table 1.19 show that goats spend less time ruminating than sheep. At present, there are no data on the efficiency of

Table 1.18. Comparison of eating behaviour by goats and sheep.

	Feed offered	Goats	Sheep	Sig	Author
Rate of eating					
g DM/min/$W^{1.0}$	Chopped rye-	1.14	1.63	**	Geoffroy (1974)
g DM/min/$W^{0.75}$	grass straw	2.96	4.44	**	" "
Time spent eating					
(h/d)	" "	5.7	5.0	NS	" "
Eating bouts					
(d)	" "	9.2	5.4	*	" "
Rate of parotid salivation					
(ml/g DMI/d)	Fresh forage	1.19	0.895	**	Seth et al. (1976)

** $P<0.01$; * $P<0.05$; NS Non-significant.

Table 1.19. Comparison of rumination behaviour by goats and sheep fed chopped ryegrass straw.

Rumination behaviour	Goats	Sheep	Sig
Time spent ruminating (min)	504	602	**
Ratio Rum/Eat	1.4	1.6	ND
Number of Rum periods	16.8	16.1	NS
Duration of each Rum period (min)	30.0	37.4	**
Duration of one Rum episode (sec)	66	53	**

Calculated from Geoffroy (1974)

Rum = ruminating Eat = eating
** P<0.01; NS Non-significant.

breakdown of feed particles during eating and/or ruminating in goats or deer. This area requires further study to understand the contributions of the 2 processes to breakdown of feed particles, clearance of digesta and VFI, and digestibility in deer, goats and sheep.

1.7 CONCLUSIONS AND AREAS REQUIRING FURTHER STUDY

1.7.1 Goats vs Sheep

1.7.1.1 Both species utilise high/medium quality forages (37.0-15.0 gN/Kg DM) with the same efficiency, with no differences in voluntary OMI and DOMI (g/Kg $W^{0.75}$/d).

1.7.1.2 Goats are superior to sheep in utilising low quality forages (15.0-5.1 gN/Kg DM), and browse diets, with a significantly higher OMI and DOMI (g/Kg $W^{0.75}$/d), as the fibre component increases.

1.7.1.3 When fed on low quality forages, a higher OMD and DOMI in goats can only be associated with a longer MRT of particulate matter in the rumen, and a concurrent larger rumen volume (as a proportion of $W^{0.75}$) in goats, compared to sheep.

1.7.1.4 Goats digest fibre more efficiently than sheep, especially the lignin component.The differences between the 2 species become more apparent as the roughage component of the diet increases. A longer MRT of particulate matter and of water in the rumen of goats than sheep, may be a partial explanation for increased fibre digestion in goats.

1.7.1.5 One limited goat vs sheep comparison study indicates that goats tend to spend more time eating and less time ruminating than sheep. The efficiency of chewing of goats compared to sheep, in breaking down feed particles is not known. A greater efficiency of chewing by goats would indicate a superior breakdown of the cell wall component and partially explain a better fibre digestion in goats.

1.7.1.6 When fed on low quality forages, goats can maintain a higher rumen NH_3-N concentration, than sheep. This may indicate a higher fermentation rate, and a more efficient N recycling within the

rumen, or into the rumen via saliva and diffusion in goats, compared to sheep.

1.7.1.7 Goats have higher metabolisable energy requirements for maintenance than sheep. Any seasonal diference in requirements for maintenance equilibrium are unknown.

1.7.1.8 It is not known at present, if goats have a seasonal VFI, and any associated effects on OMD, MRT of digesta, and rumen volume.

1.7.2 Deer vs Sheep

1.7.2.1 Deer show a markedly seasonal VFI (g/Kg $W^{0.75}$/d), with a low appetite in winter, and a sharp increase in appetite in summer. The domestic sheep also shows seasonal cycles of VFI, which are much more attenuated than deer.

1.7.2.2 Both deer and sheep digest fibre more efficiently in summer than in winter, with the magnitude being greater in deer than in sheep. The increase in fibre digestibility in summer is associated with a longer rumen MRT of particulate matter in deer.

1.7.2.3 It is postulated that the deer, in contrast to the sheep, can show a compensatory enlargement of the rumen volume in summer, to compensate a greater OMI, DOMI, with a longer rumen MRT of particulate matter and apparent fibre digestibility. This has not been determined experimentally yet.

1.7.2.4 Changing daylength is the stimulus to the changes in the observed appetite cycle in the deer and in the sheep. Melatonin, secreted by the pineal gland, possibly synchronises the seasonal rhythms in the deer.

1.7.2.5 Correlations between seasonal hormone secretions of Me, GH, IGF-I, T and P, and growth/VFI in spring-summer, indicate possible underlying causal or associated dependent relationships, and show a functional linkage between the seasonal hormonal status and VFI in deer. The direct mechanism involved is not clearly understood yet.

1.7.2.6 A control of the winter VFI in the deer appears to lie in an understanding of the mechanisms and regulations involved in the seasonal hormone secretion and requires more study.

1.7.2.7 The energy requirements of deer for maintenance (ME) are greater than sheep. Deer show marked seasonal cycles of ME, heart rate and activity, which are all greater in summer than in winter.

1.7.2.8 Seasonal changes in rumen fermentation rate, dilution rate of water in the rumen, rumen NH_3-N and N recycling within and into the rumen, have not been determined in the deer.

1.7.2.9 There are no data on the physical breakdown of feed particles in the rumen of deer.

1.7.3 Areas requiring further study

The Review of Literature has indicated 4 major areas where further studies are required, and are summarised as follows:

1.7.3.1 The reasons for a superior degradation of fibre, especially lignin, by goats compared to sheep. A study of the kinetics of NH_3-N production in the rumen, using ^{15}N, could explain some of the differences in apparent fibre digestibility between the two species.

1.7.3.2 The relative efficiencies of chewing during eating and/or ruminating by goats and sheep, and the effects on particle size breakdown in the rumen.

1.7.3.3 Seasonal cycles of VFI in deer, goats and sheep, and the possible associated seasonal cycles in the rumen digestive functions.

1.7.3.4 The role of melatonin in the hormonal control of seasonal VFI in deer, in particular its role in entraining the seasonal cycles associated with VFI in deer to changes in photoperiod.

CHAPTER TWO. MATERIALS AND METHODS.

The details of materials and methods, common to all the experiments reported in the present thesis, are described in this Chapter.

2.1 ANIMALS

(i) Border Leicester-Romney cross wethers, (ii) castrated Angora-NZ feral goats, and (iii) castrated hand-reared Red Deer were used as experimental animals. All the animals were weighed after a 24 h fast at the start and end of each experiment, and the mean liveweight (W) and metabolic liveweight ($W^{0.75}$) used in the calculations. The mean weights and age of the animals are reported for each experiment, with the goats, sheep and deer being all of the same age.

The castrated goats and sheep were fistulated in the rumen, according to routine procedures (Hecker, 1974), and fitted with permanent rubber cannulae (25 mm internal diameter (ID)), after surgery. The size of the cannula was gradually increased from 25 mm to 65 mm (ID).

The fistulation procedures for the deer were as follows:

(i) The hand-reared deer were castrated two months prior to fistulation.

(ii) The animals were then kept in metabolic crates for 12-15 days, and the animals' temperament and adaptation to the crates assessed.

(iii) On the basis of a positive response to the criteria in (ii), the animals were fistulated. The incision made was 70-80 mm long. After surgery, the animals were fitted with a 35 mm (ID) rubber cannula. The size of the cannula was gradually increased from 35 to 83 mm (ID).

All the animals were fistulated at least six months prior to the start of the experiments. In between trials, the animals were allowed to graze on a perennial ryegrass/white clover pasture, and drenched on

a two-monthly basis, alternatively with 6 ml of Nilverm oral drench (levamisole hydrochloride; Coopers Animal Health (NZ) Ltd.); Ivomec liquid (ivermectin; Merck Sharp and Dohme B.V.(NZ) Ltd.), and Valbazen minidose cattle and deer drench (albendazole; SmithKline Animal Health Products).

2.2 DIET

All animals were fed on (i) lucerne hay, for Experiments 2a, 2b, 3, 4, and (ii) threshed prairie grass straw for Experiments 1a, 1b.

Each type of hay was purchased in bulk from one source, to cover the feeding requirements of all the experiments, and to avoid any fluctuations in the chemical composition of the diet. The hay was chaffed through a chaff-cutter, and reduced to 40-80 mm portions. The chemical composition of the diet under offer is given for each experiment.

When fed on lucerne chaff, the animals had free access to a multimineral salt block (50 g) placed in the feed bin (Summit Multi-mineral Salt Block; Dominion Salt (NZ), Ltd.). When fed on the prairie grass roughage, the animals were given a daily supplement (10 g) of a mineral pre-mix (Pfizer Laboratories (NZ) Ltd.), and a weekly oral dose (5 ml) of a liquid multi-vitamin supplement (Hydrovit, May and Baker (NZ), Ltd.). All formulations are given in Appendices A-C. All animals were allowed free access to water in all experiments.

2.3 HOUSING

All animals were housed individually in metabolic crates, fitted with automatic overhead feeders, under natural ambient conditions of temperature and illumination. The feeders delivered the diet at hourly intervals.

The goats and sheep were kept together in conventional metabolic crates, which allowed for separate collection of faeces and urine. The deer were kept separately from the goats and sheep, to prevent any outbreaks of malignant cattarrhal fever (MCF).

A deer crate prototype (specifications as per Milne et al., 1978) was built ten months prior to the start of Experiment 2a. The prototype was modified twice subsequently to produce a metabolic crate (Plates 1, 2, 3), with the following characteristics: (i) doors on the two lateral sides of the crate to allow for rumen fluid sampling, rumen emptying ("bailing") and blood sampling, (ii) a sliding side door to restrain the animal when required, (iii) separate collection of the faeces and urine by a separating funnel device placed below the shute, (iv) easy access to a larger feed bin and water trough, and (v) smooth galvanised floor netting (30 x 15 mm) to prevent any foot injury.

Antlers were removed prior to moving into the crates to prevent damage from the mesh top of the cage. During this operation, the animals were sedated with 1 ml of 2% Rompun given intramuscularly (IM) (xylazine; Haverlockhart; Bayvet (USA) Division), and with 20 ml of Xylotox (lignocaine; Willows Francis Veterinary Division of A.H. Robins Co.(Ltd.), U.K.) given at the base of the antler as a local anaesthesia. The animals were tranquilised (1 ml (2%) Rompun IM) prior to any movement to and from the crates.

2.4 EXPERIMENTAL DESIGN

The design for each experiment is given schematically for each experiment in the appropriate Chapters.

2.5 MEASUREMENT OF VOLUNTARY FEED INTAKE

The following procedures were used for the measurement of voluntary feed intake (VFI) in all experiments. The animals were offered the experimental feed "ad-lib", with that offered being 1.15 of the previous day's consumption. The first 12 days were used as the pre-feeding period, until VFI stabilised. VFI was then recorded over the next 8 days (or 12 days for Experiment 1a). The animals were accustomed to hourly feeding from day 2 of the pre-feeding period.

Representative samples of the feed offered were taken daily, and duplicate DM determined on 100 g subsamples, in forced draught oven at 100 C, for 24 h. Two further 100 g subsamples were taken daily, and

Plate 1. Front view of a deer metabolic crate used in the present study.

Plate 2. Side view of deer metabolic crate.

Plate 3. Deer metabolic crate showing the side closed in, restraining the animal.

pooled separately at -20 C. They were subsequently freeze-dried, ground and used for laboratory analysis.

2.6 DETAILS OF DIGESTIBILITY TRIAL

During the 8-day digestibility trial, the weights and oven DM of the following components were recorded, namely: (i) feed offered, (ii) feed refusals, (iii) undercrate residues, and (iv) faeces.

Representative samples of the feed offered were taken daily, and duplicate DM determined, as described in Section 2.5. The bin refusals (feed refusals) and undercrate residues were collected daily, weighed and pooled separately at 4 C for each animal. An oven DM determination was done every 2 days.

Faeces from each animal were weighed daily, and pooled separately at -20 C. At the end of the trial, the faeces were allowed to thaw and mixed thoroughly. A 600 g subsample was taken, and the faecal pellets broken down in a food mixer (Kenwood Peerless; Peerless and Ericsson (UK) Ltd.). Triplicate DM determinations were done on 100 g subsamples, in a forced draught oven at 100 C, for 48-72 h, until constant weight was attained.

Subsamples of (i) feed offered, (ii) feed refusals per animal, and (iii) faeces per animal, were pooled over the 8-day trial at -20 C. They were later freeze-dried, ground and stored for chemical analysis of OM, N, hemicellulose, cellulose, lignin and energy. The chemical composition (DM) of the undercrate residues was assumed to be the same as the feed offered. A subsample of faeces was stored at -20 C, and kept for particle size analysis.

Urine was collected for each animal over the 8-day digestibility trial. The urine was voided into buckets placed under the shutes, and collected over 100 ml of 25% (v/v) H_2SO_4 acid. The pH of the urine was kept below 3, to prevent any N losses. The daily weight of urine/animal was recorded, and 10% of the daily amount pooled over 8 days, and stored at -20 C for total N determination.

2.7 INFUSION PROCEDURES

2.7.1 Infusion of the dual-phase marker, Cr-EDTA/Ru-Phen

2.7.1.1 Preparation of markers

The inert marker, chromium complex of ethylenediamine tetraacetic acid (Cr-EDTA), was prepared by the method of Binnerts, Van't Klooster and Frens (1968), with a concentration of 4000 mg Cr/Kg of marker solution. The inert marker, ruthenium tris (1, 10-phenanthroline)-ruthenium (II) chloride (Ru-Phen), was prepared by the method of Tan, Weston and Hogan (1971), with a concentration of 99.6 mg Ru/Kg of marker solution. The Cr-EDTA and Ru-Phen markers were then combined in equal volumes, with a final (theoretical) Cr concentration of 2000 mg/Kg, and a Ru concentration of 49.8 mg/Kg of dual-phase marker solution, and the pH adjusted to 6.5-7.0 with NaOH. The level of N contamination was determined and was negligible (0.107%).

The dual-phase marker was infused continuously into the rumen, for 120 hr, with the animals fed hourly, at 90% of "ad-lib". A priming dose of 40 ml of the dual marker was administered in the rumen, at the beginning of the infusion (Faichney, 1975). The infusion rate adopted was 12 mg Ru in dual-phase marker/Kg DMI, with the actual infusion rates for goats, sheep and deer given for each experiment.

500 ml of the infusate were kept prior to infusion, stored at 4 C, and used later for spiking unlabeled rumen digesta samples, in the preparation of the analytical standards for Cr and Ru. The unlabeled rumen digesta samples were taken during the pre-feeding period from 4 animals/species, pooled together for each species, and stored at -20 C until required.

2.7.2 Infusion of $^{15}NH_4Cl$

The stable isotope tracer $^{15}NH_4Cl$ was added to the dual marker solution, and infused continuously into the rumen for the last 41-43 hr of dual-phase marker infusion before rumen emptying ("bailing"). The infusion rate of the tracer is given for each species in the experimental procedures for each experiment.

Triplicate subsamples of the infusate were taken prior to the start of the infusion, stored at -20 C, and later analysed for enrichment with ^{15}N.

2.7.3 Infusion techniques

A peristaltic pump was used for infusion (PLG-multipurpose pump, Desaga (Heidelberg) W.Germany). Silicone rubber tubing (Desaga, 1mm ID) was used on the pump, and allowed for a minimum pulsation delivery per tube. Separate peristaltic pumps were used for each species, and calibrated to the required delivery rate (g/min).

The infusates were stored in 1 L brown bottles, and the daily infusion rates recorded for each animal. The infusate was pumped through infusion lines (polyethylene tube; medical grade, 1 mm ID, 1.5 mm OD; Dural Plastics and Engineering; NSW, Australia). The infusion line was then connected to a rubber expandex tubing (366 cm long; 3 mm ID, 7 mm OD; Cenvet Pty (Ltd.) Australia), the other end of which was inserted into the bung of the cannula (see Figure 2.1). The expandex tubing allowed the animals free movement, and was regularly covered with a barrier cream to prevent the deer and goats from chewing the tubing (Stop Crib; pelargonic acid vanillylamide, aloes and capsicum; Medical Research (Marketing) Pty (Ltd.) Australia).

2.8 SAMPLING PROCEDURES AND SAMPLING PREPARATION

2.8.1 Rumen Fluid Sampling

Rumen fluid (for NH_3-N, enrichment of NH_3-N with ^{15}N, volatile fatty acids (VFA) and pH determination) was sampled through a rumen sampler (a hollow brass cylinder, 100 mm long, 15 mm ID, with a series of holes (2 mm diameter) along its length, and glued to a plastic tubing (3 mm diameter), as seen in Figure 2.1 (Agricultural Engineering Workshop; Massey University). The length of the plastic tube was 270 mm for goats and sheep, and 330 mm for deer, to obtain a representative positioning of the sampler in the rumen.

The rumen sampler was encased in a polyester bag, which acted as a filter, with a pore size of 47 µm (Estal Mono; Swiss Screens (Ltd.)

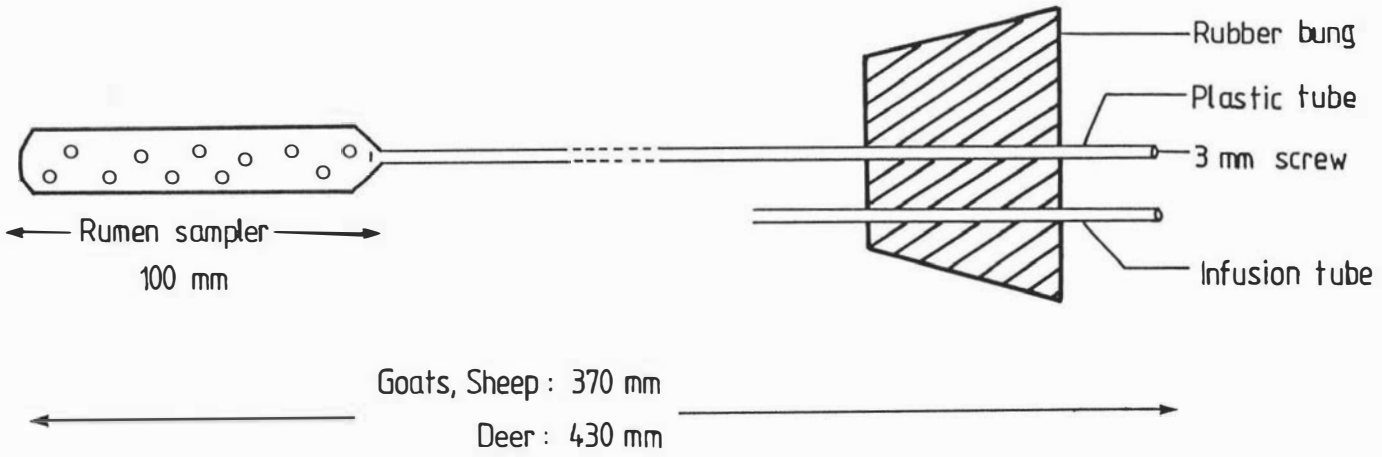


Figure 2.1. Rumen sampler (Agricultural Engineering Workshop; Massey University)

Australia), prior to placement in the rumen. Samples of rumen fluid were taken by attaching a 30 ml syringe to the plastic tube, and drawing the fluid through the rumen sampler. The first 30 ml of rumen fluid were returned to the rumen via the return tube, or discarded.

2.8.2 Ammonia in rumen fluid

Duplicate samples (10ml) were added to 2.5 ml of deproteinising reagent (1M H_2SO_4, saturated with magnesium sulphate), centrifuged at 1895 *g*, for 15 mins and stored at -20 C until analysed. The samples were taken three times during the digestibility trial, at 2-day intervals, at 10.00 and 15.00 hours.

2.8.3 VFA in rumen fluid

Duplicate samples (5 ml) were added to 1 ml of protein precipitant (metaphosphoric acid/formic acid: 18.75% w/v / 25% v/v). One ml of the internal standard (isocaproic acid; 0.52% v/v) was added to one sample (internal standard sample), and 1 ml of distilled water added to the other sample (control sample). Both samples were centrifuged at 1895 *g*, for 15 mins and stored at -20 C until analysed.

2.8.4 pH of rumen fluid

The pH of rumen fluid was determined immediately on a PHM 61, Laboratory pH meter (Radiometer (Copenhagen) Ltd.), after calibration with pH 7.0 and pH 4.0 buffers.

2.8.5 Rumen Emptying ("bailing")

Rumen emptying ("bailing") was done through a large rumen fistula (ID 63 mm for goats and sheep, and ID 83 mm for deer). The deer were lightly tranquilised 5 mins before "bailing", with 1 ml of 2% Rompun IM, which kept the animals in a "standing" position.

The rumen contents were emptied into a tared bucket, placed over a larger container containing warm water (temp 70 C), to keep the digesta warm throughout the sampling. The rumen contents were weighed, thoroughly mixed and subsampled. The warmed rumen digesta

was then returned back to the animal. The whole process was completed in 10-12 mins for goats and sheep, and 15-18 mins for deer.

At "bailing", subsamples of rumen digesta were taken for: (i) triplicate DM determination, by freeze-drying, (ii) Cr and Ru concentration, (iii) particle size analysis, (iii) chemical analysis for cellulose, hemicellulose, and lignin, (iv) determination of pH, NH_3-N, VFA and enrichment of NH_3-N with ^{15}N, after squeezing a subsample of the rumen digesta through muslin cloth, and (v) rumen bacterial sample.

2.8.6 Sampling for enrichment of N with ^{15}N

2.8.6.1 Sampling Protocol: The following samples were taken for the estimation of enrichment with ^{15}N:

(i) Rumen fluid sample,

(ii) Rumen bacterial sample,

(iii) Rumen digesta sample.

The sampling protocol is shown in Table 2.1.

2.8.6.2 Sample preparation

2.8.6.2.1 Rumen fluid sample: Ten ml of rumen fluid samples (RF 1-RF 4) were taken through the rumen sampler into 0.2 ml of 18M H_2SO_4, centrifuged at 7850 *g*, for 15 mins, and stored at -20 C until analysed for ^{15}N enrichment and NH_3-N (Nolan and Stachiw, 1979). Sample RF 5 was obtained at "bailing" (See Section 2.8.5), and a 10 ml sample taken, and prepared as above.

2.8.6.2.2 Rumen bacterial sample: Rumen bacterial samples were processed as shown in Figure 2.2 (modified from Nolan and Leng, 1972).

2.8.6.2.3 Rumen digesta sample: 100 g of rumen digesta was subsampled at "bailing", stored at -20 C until analysed.

Table 2.1. Sampling protocol for [^{15}N] samples.

Time	Sample taken
30 mins before CI[!] commenced	Background sample RF 1
> 24 h CI	RF 2
> 36 h CI	RF 3
> 40 h CI	RF 4
> 40-42 h CI	RF 5, RBS, RD (at "bailing")

[!] CI Continuous infusion of $^{15}NH_4Cl$.
RF Rumen fluid
RBS Rumen bacterial sample
RD Rumen digesta sample.

2.9 CHEMICAL ANALYSIS

All chemicals used were of ANALAR (BDH) grade. Samples of feed offered, refusals, faeces, rumen digesta used for chemical analysis were freeze-dried (FD 57 freeze-dryer; WGG Cuddon (NZ) Ltd.). The samples were then ground, using sieve sizes of 1mm openings (and 0.5mm openings with samples for Cr and Ru determinations), on a grinding mill (Thomas Wiley Mill, Model ED-5, Thomas Scientific (Milling) USA). All analyses were made in duplicate, and expressed on a DM basis.

2.9.1 Organic Matter

OM was determined on 2 g DM samples, as a loss in weight, after heating the samples at 500 C, for 18 h in a muffle furnace (Mc Gregor Lab; Mc Gregor and Sons (NZ) Ltd.), (Association of Official Agricultural Chemists, 1975).

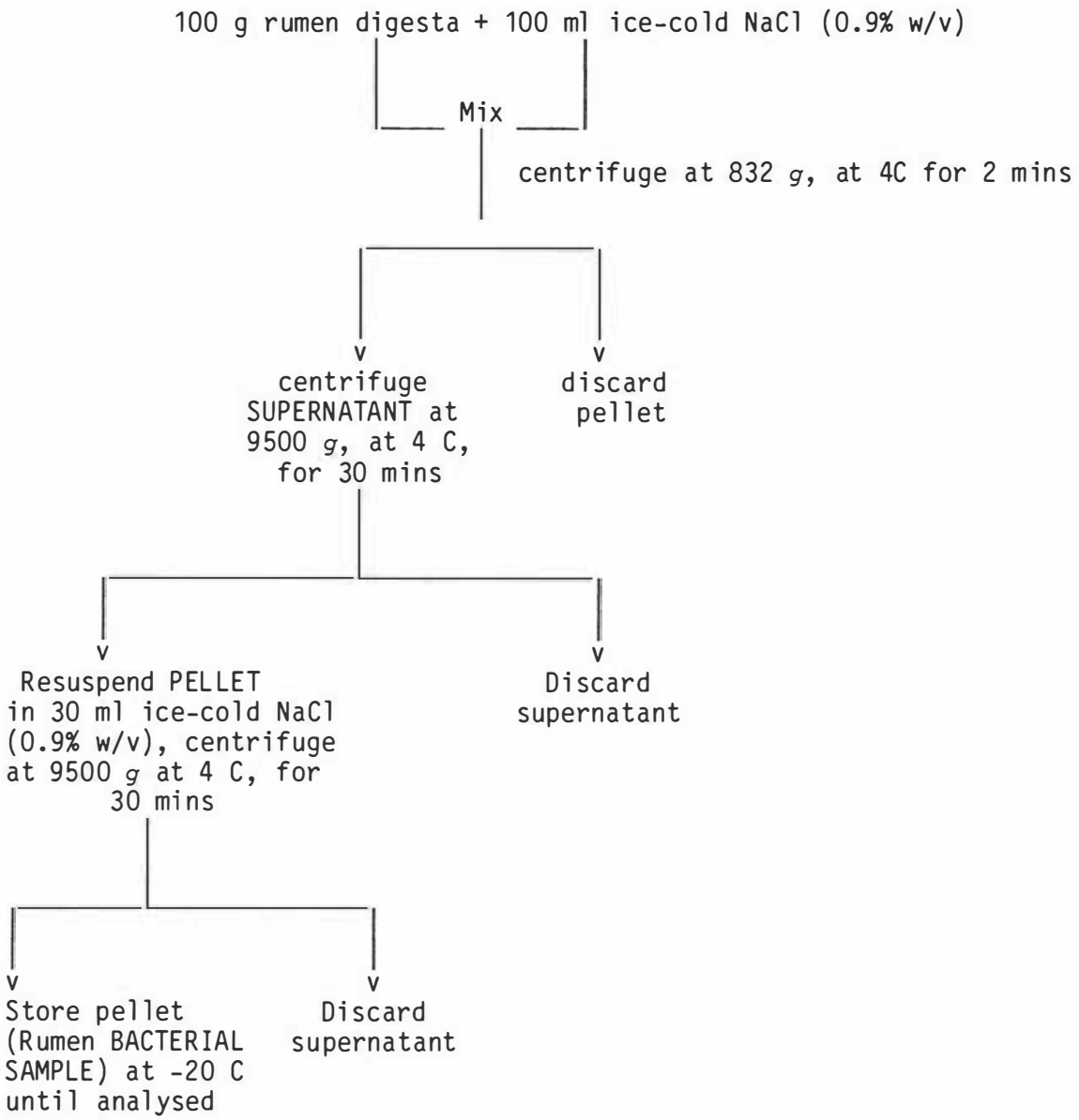


Figure 2.2. Preparation of rumen bacterial sample (modified from Nolan and Leng, 1972).

2.9.2 Total Nitrogen

Total N was determined by the Kjeldahl procedure, using 0.3-0.35 g DM for the feed samples, and 5 g for the urine samples. The samples were digested (Digestion System 20; 1015 Digester; Tecator (Sweden) Ltd.) in 10 ml of concentrated H_2SO_4 for 25-50 mins at 420 C, using a selenium (Se) catalyst (Macrokjeltab; 15 mg Se; 3000 mg K_2SO_4; Tecator (Sweden)). After digestion, the samples were cooled, diluted with 30 ml distilled water, and steam-distilled on the Kjeltec Auto 1030 Analyser (Tecator (Sweden) Ltd.). The acid digest was made strongly alkaline by the automatic dispensing of 50 ml of NaOH (40% w/v). The ammonia was distilled in 25 ml of boric acid (1% w/v) containing the mixed indicator (bromocresol green and methyl red), and automatically titrated with HCl (0.1M).

The % ammonia recovery by the distillation process was determined by using ovendried (temp 100 C) $(NH_4)_2SO_4$, and was 99-101%.

2.9.3 Heat of Combustion

Heat of combustion was determined using an adiabatic bomb calorimeter (Gallenkamp autobomb; Watson Victor(U.K) Ltd.). The feed and faeces samples were made into 0.6-0.8 g (DM basis) pellets, on a briquette press (12 mm diameter) prior to bombing.

2.9.4 Carbohydrate Analysis

Cellulose, hemicellulose, and lignin were extracted from 0.4-0.5 g DM (of feed, faeces and rumen digesta samples) by the sequential carbohydrate extraction of Bailey (1967), and summarised in Figure 2.3.

Concentrations of hemicellulose and cellulose were determined in the neutralised extracts, by photometric method of reducing sugars (Nelson, 1944), using copper sulphate and arsenomolybdate solutions on a spectrophotometer (Ultrospec II 4050; LKB Biochrom (UK) Ltd., attached to an autofill aspirator, Autofill 4070; LKB Biochrom (UK) Ltd.). The wavelength used was 520 nm for hemicellulose and cellulose.

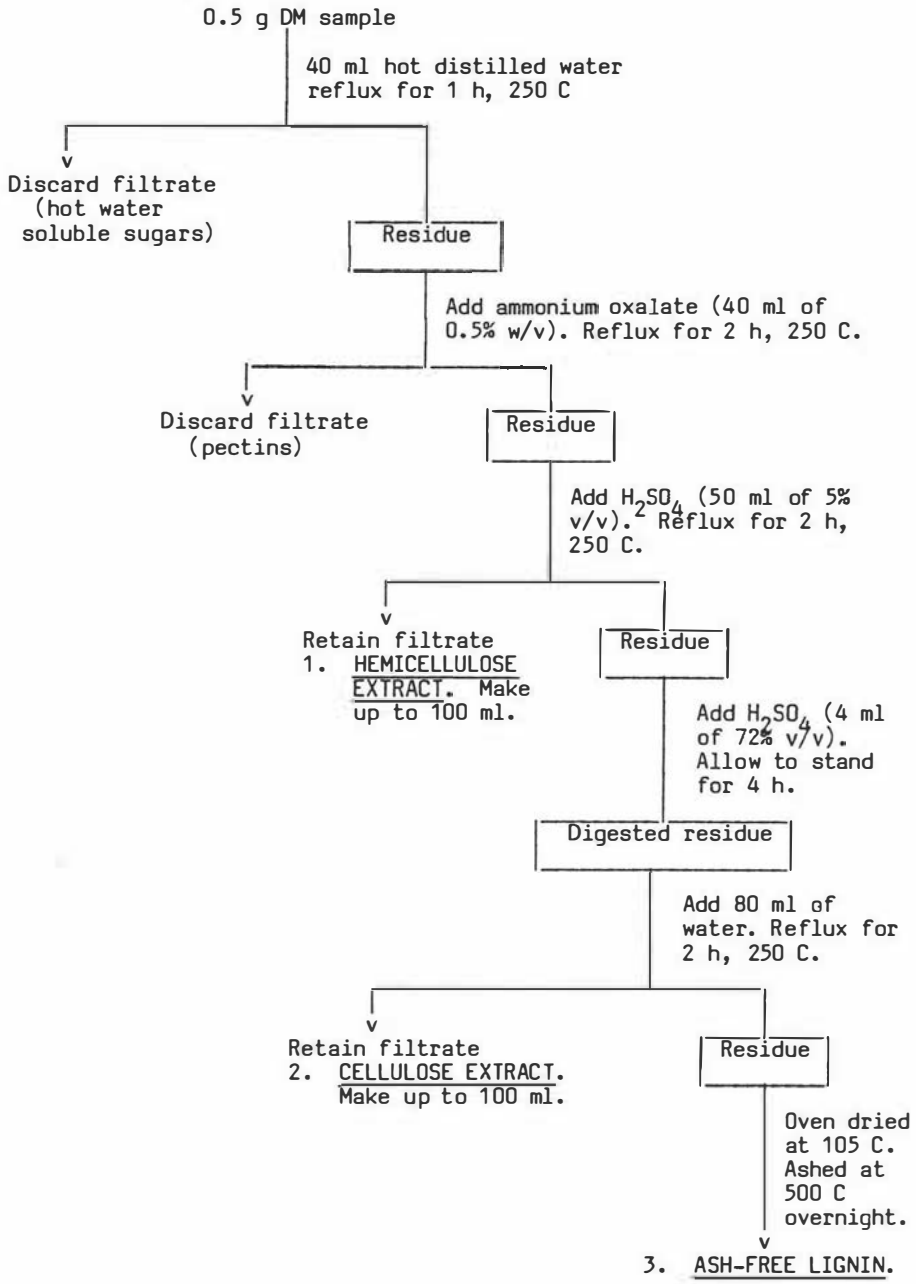


Figure 2.3. Sequential carbohydrate extraction (from Bailey, 1967).

Hemicellulose concentration was determined from a standard curve of xylose (0-200 ppm) using a correction factor of 0.88. Cellulose concentration was calculated from a standard curve of glucose (0-400 ppm), using a correction factor of 0.90.

Ash-free lignin was determined as the organic matter remaining after sequential extraction of all carbohydrates.

2.9.5 Ammonia in Rumen Fluid Samples

The deproteinised rumen fluid samples were thawed, weighed, and stored over ice until analysis was completed, to reduce N losses. NH_3-N was determined on 6 g rumen fluid samples by steam distillation on the Kjeltec Auto 1030 Analyser. The rumen fluid samples were made weakly alkaline (pH 9.5) by the addition of 25 ml of saturated sodium tetraborate (8-10% w/v). The ammonia was distilled into 10 ml of boric acid (4% w/v), containing mixed indicator (bromocresol green and methyl red), and then titrated automatically with 0.03M HCl.

The efficiency of the distilling process was determined by a N recovery test on ovendried $(NH_4)2SO_4$ (temp 100C), and was 99-101%.

2.9.6 Volatile Fatty Acids in Rumen Fluid Samples

2.9.6.1 Gas-Liquid chromatography

VFA analysis was carried out by gas-liquid chromatography (GLC) (Shimadzu Gas Chromatograph; GC-8A). Separation was made on a 1500 mm x 3.1 mm OD glass column, packed with 80-100# chromosorb 101. A flame ionisation detector (hydrogen gas and air, (Gas Industrial (Ltd.) NZ) was used. The operating conditions were:

1. Temperatures: (i) Column 190 C
   (ii) Injector port 200 C
   (iii) Detector 250 C

2. Gas flow: (i) Carrier gas (N) 15 ml/min
   (ii) Hydrogen 30 ml/min
   (iii) Air 300 ml/min.

3. Sample size: 0.5 µl (airtight syringe; 7001 Microliter; Hamilton Co., Reno Nevada (USA)).
4. Attenuator: 32-512.
5. Separation time: 15-20 mins.

The chromatographs were recorded on a Sekonic SS-250 F recorder, and the area under the peaks determined manually.

2.9.6.2 Preparation of standard VFA solutions

A standard VFA mixture was prepared with the following concentrations: (i) acetic acid (0.02M), (ii) propionic acid (0.005M), (iii) n-butyric acid (0.01M), (iv) iso-butyric acid (0.0005M), (v) iso-valeric acid (0.001M), and (vi) n-valeric acid (0.001M). A working standard solution was then prepared with graded quantities of the stock solution, and the concentrations (mmol/L) are given in Table 2.2. Metaphosphoric acid/formic acid protein precipitant, and iso-caproic acid internal standard were added to the standard solutions, using similar procedures to the processed rumen fluid samples (Section 2.8.3.)

Table 2.2. Concentrations (mmol/L) of VFA in the working standard solution.

	VFA working solution (mmol/L)					
Standard	Acetic	Propionic	n-Butyric	iso-Butyric	n-Valeric	iso-Valeric
0	0	0	0	0	0	0
1	20	5	10	0.5	1.0	1.0
2	40	10	20	1.0	2.0	2.0
3	60	15	30	1.5	3.0	3.0
4	80	20	40	2.0	4.0	4.0
5	100	25	50	2.5	5.0	5.0

The standards were used to establish response factors for each VFA.

2.9.6.3 Analysis of rumen fluid samples

The control rumen fluid samples (Section 2.8.3) were pooled together for each animal, and analysed on the GLC to check for the presence of peaks coincident with the internal standard isocaproic acid, and none were detected. The samples containing internal standard were then run for each animal, at all the sampling times.

2.9.7 Chromium and Ruthenium Determinations

Inert Cr and Ru in the rumen digesta samples were analysed by X-ray Fluorescence Spectrometry, XRFS (Philips RW1404 Automatic Sequential X-ray Fluorescence Spectrometer)(Evans, MacRae and Wilson, 1977).

2.9.7.1 Preparation of analytical standards

Reference standards were prepared separately for goats, sheep and deer, and for each experiment. The concentrations are given in the experimental procedures for each experiment. Ru and Cr analytical standards were prepared by incremental additions of the dual-phase marker Cr-EDTA/Ru-Phen (primary standard) to 140 g of rumen digesta (Section 2.7.1.1). The labeled samples were then freeze-dried, and ground to pass a 0.5 mm sieve.

2.9.7.2 Preparation of samples for XRFS

The freeze-dried and ground samples (0.5 mm sieve) for the, (i) analytical standard samples, and (ii) the unknowns (rumen digesta samples), were compressed into self-supporting disks. The disks (40 mm diameter, 3-3.5 mm depth, 5 g DM) were made using a steel holder with pressing plate and plunger (Massey University; Agricultural Engineering Department), at 150, 000 Newtons pressure on an hydraulic press (Shimadzu Universal Testing Machine; Japan).

Correlation coefficient values showed excellent agreement of all standards to the calibration curve, for Cr (r=1.000) and Ru (r=0.999).

The sensitivity of the XRFS was, for Ru analysis: 1 mg/kgDM, and for Cr analysis: 5 mg/KgDM.

2.9.8 Estimation of Enrichment with ^{15}N

The rumen fluid, rumen bacterial and rumen digesta samples were processed to transfer their N to $(NH_4)_2SO_4$, as required for estimation of enrichment with ^{15}N by mass spectrometry (Nolan and Leng, 1974).

2.9.8.1 Rumen fluid samples

5-7 ml of rumen fluid samples were steam-distilled with 7 ml of NaOH (20% w/v). The ammonia (0.6-1.0 mg N) was collected into 5 ml boric acid (2% w/v) without indicator, and titrated to pH 5.0 with 0.0175M H_2SO_4, using an ABU 80 Autoburette with a PHM 82 standard pH meter and a TTT 80 Auto-titrator (Metrohm, Switzerland). The titre was recorded, and the distillate acidified further to a pH of 4.0. The samples were then oven-dried (95 C for 24 h), and transferred to spectrometer vials (Wheaton Scientific (USA)) with distilled water, and re-dried (95 C for 24 h) for mass spectroscopy (Model MS 10; GEC-AEI Electronics (Ltd.) England).

2.9.8.2 Rumen bacterial and digesta samples

0.2 g DM of rumen digesta and rumen bacterial samples were digested by normal Kjeldahl procedures, and diluted to a concentration of 0.2 mg N/ml. A 5 ml aliquot of the diluted solution was then distilled as per procedures for rumen fluid samples and processed for mass spectroscopy.

Precautions were taken to prevent any "memory effects" and cross-contamination of samples, during the distillation process, as described by Nolan and Leng (1974).

2.9.9 Particle Size Analysis

The particle size distribution in feed, rumen digesta and faeces samples was determined by wet sieving, using the apparatus described by Evans, Pearce, Burnett and Pillinger (1973), (Turner and Newall,

(Ltd.)). Sieve sizes (length of side of square hole) were 4.0, 2.0, 1.0, 0.5 and 0.25 mm.

Rumen digesta (30 g wet weight), faeces (20 g wet weight), and feed samples (10 g wet weight) were washed by recirculation of 1300 ml of water, at a flow rate of 4 L/min through the sieves, for 5 mins. Faeces samples were soaked in 100 ml of water overnight prior to sieving, to prevent flotation. Feed samples were soaked in 100 ml artificial saliva (Baumgardt, Taylor and Cason, 1962), for 15 mins prior to sieving.

Material retained on the sieves was washed onto tared filter paper (Whatman No 21) in a Buchner funnel, and oven-dried at 100 C, for 24 h to determine the dry weight of each particle size fraction. Material not retained on the sieves (<0.25 mm particles) was determined by difference from the initial sample dry weight and the sum of recovered particulate DM fractions.

Results for each particulate fraction were expressed as the % of the total initial DM in each sample.

2.10 TERMINOLOGY AND CALCULATIONS

2.10.1 Marker Kinetics

Three markers were used to determine the kinetics of digesta flows from the rumen, namely (i) indigestible lignin, (ii) inert Ru-Phen and (iii) inert Cr-EDTA.

Lignin, as an internal dietary marker, constitutes a particulate-phase marker. It is a component of the feed particles, and is distributed throughout the range of particles produced when the feed is chewed and swallowed (Faichney, 1980, 1984; Fahey and Jung, 1983). Ru-Phen, as an external marker, is a particulate-phase marker. Ru-Phen moves from particle to particle (Faichney and Griffiths, 1978; Dixon, Kennelly and Milligan, 1983), and is found at highest concentrations in the smaller particles with a larger surface area (Dixon and Milligan, 1980). Cr-EDTA is a near "ideal" marker for the liquid-

phase of the digesta, and associates closely with liquid in the rumen (Faichney, 1975).

2.10.1.1 Fractional Outflow Rate (FOR, %/h)

Individual FOR (%/h) of Cr-EDTA and Ru-Phen was calculated separately (Equations 1 and 2), as the proportion of the total rumen contents (i.e the pool), that leaves the rumen per unit time (Faichney, 1975).

$$\text{FOR of Cr-EDTA (\%/h)} = \frac{\text{Infusion Rate of Cr (mg/h)} \times 100}{\text{Rumen Pool Size of Cr (mg)}} \qquad (1)$$

$$\text{FOR of Ru-Phen (\%/h)} = \frac{\text{Infusion Rate of Ru (mg/h)} \times 100}{\text{Rumen Pool Size of Ru (mg)}} \qquad (2)$$

The FOR (%/h) of lignin (L) was calculated from Equation (5) of Faichney (1980).

$$\text{FOR of Lignin (L) (\%/h)} = \frac{\text{Faeces L output (mg/h)} \times 100}{\text{Rumen L Pool size (mg)}} \qquad (3)$$

where (i) Rumen outflow of L (mg/h) was assumed to equal L faecal output (mg/h), i.e digestion of L occurs solely in th rumen, and all the L leaving the rumen is recovered in the faeces.

(ii) Rumen L pool (mg) was determined at "bailing".

(iii) Faecal L output (mg/h) was determined during the infusion experiment.

2.10.1.2 Mean Retention Time (MRT, h)

MRT (h) of Cr-EDTA, Ru-Phen and lignin was calculated as the reciprocal of their respective FOR (/h), and represent the amount of time the markers (hence, the phase of the digesta which is associated with the markers), spend in the rumen (Faichney, 1975).

$$\text{MRT (h) of Cr-EDTA} = \frac{\text{Rumen Pool Size of Cr (mg)}}{\text{Infusion Rate of Cr (mg/h)}} \quad (4)$$

$$\text{MRT (h) of Ru-Phen} = \frac{\text{Rumen Pool of Ru (mg)}}{\text{Infusion Rate of Ru (mg/h)}} \quad (5)$$

$$\text{MRT (h) of Lignin} = \frac{\text{Rumen Lignin Pool Size (mg)}}{\text{Faeces Lignin Output (mg/h)}} \quad (6)$$

2.10.1.3 Fractional Disappearance Rate (FDPR, %/h)

The Fractional Disappearance Rate (FDPR, %/h) of each of the carbohydrate constituents (cellulose, hemicellulose and lignin) was defined and calculated as (Equation 7):

$$\text{FDPR (\%/h)} = \frac{\text{Intake (g/h)} \times 100}{\text{Rumen Pool Size (g)}} \quad (7)$$

2.10.1.4 Fractional Outflow Rate of lignin (FOR, %/h)

The Fractional outflow rate of lignin (FOR, %/h) was defined and calculated (Equation 8) as:

$$\text{FOR of Lignin (\%/h)} = \frac{\text{Faecal Lignin Output (mg/h)} \times 100}{\text{Rumen Pool Size of Lignin (mg)}} \quad (8)$$

2.10.1.5 Fractional Degradation Rate of Lignin (FDR, %/h)

The Fractional degradation rate of lignin (FDR, %/h), was defined (Equation 9) as:

$$\text{FDR of Lignin (\%/h)} = \frac{\text{Intake of Lignin (mg/h) - Faecal Output (mg/h) x100}}{\text{Rumen Pool Size of Lignin (mg)}} \quad (9)$$

FDR (%/h) of lignin can also be calculated (Equation 10) as the difference between FDPR (%/h) and FOR (%/h) of lignin.

$$\text{FDR of Lignin (\%/h)} = \text{FDPR (\%/h) of Lignin - FOR (\%/h) of Lignin} \quad (10)$$

It was assumed that there was no net synthesis of lignin in the rumen and no input into the rumen other than by the diet.

2.10.2 ^{15}N TRACER KINETICS

2.10.2.1 Irreversible Loss Rate of NH_3-N (IRL, g N/d)

The IRL of NH_3-N (g N/d) with respect to the rumen pool is expressed as the rate (mass/unit time) that NH_3-N leaves the compartment and does not return during the experimental period (Nolan and Leng, 1974). IRL of NH_3-N (g N/d) from the rumen pool was calculated as shown in Equation 11.

$$\text{IRL (g N/d)} = \frac{\text{Infusion Rate of } ^{15}N \text{ (g/d)}}{\text{Enrichment at "plateau" of rumen } NH_3\text{-N with } ^{15}N \text{ (atoms \% excess)}} \quad (11)$$

(i) All the enrichment values were corrected for the background abundancies, determined prior to infusion of the ^{15}N tracer.

(ii) The characterisation of the "plateau" was determined by plotting the enrichment values for each animal at 24, 36, 40, 42 h of continuous infusion of the tracer ^{15}N.

(iii) IRL of NH_3-N (g N/d) was calculated from a single estimate of enrichment of N at "plateau", as determined at "bailing".

2.10.2.2 Proportion of bacterial-N from NH_3-N (%)

The proportion of bacterial-N arising from NH_3-N in the rumen pool was calculated from Equation 12.

$$\frac{\text{Enrichment at "plateau" of bacterial-N with } ^{15}N \times 100}{\text{Enrichment at "plateau" of rumen } NH_3\text{-N with } ^{15}N.} \quad (12)$$

Both enrichment values were determined at "bailing".

2.10.2.3 Proportion of bacterial-N from digesta-NAN

The proportion of bacterial-N arising from digesta-NAN was calculated from Equation 13:

$$\frac{\text{Enrichment at "plateau" of bacterial-N with } ^{15}N \times 100}{\text{Enrichment at "plateau" of rumen digesta-NAN with } ^{15}N} \quad (13)$$

CHAPTER 3. VOLUNTARY INTAKE AND RUMEN DIGESTION OF A LOW QUALITY ROUGHAGE BY GOATS AND SHEEP.

3.1 INTRODUCTION

Comparative studies of digestion in goats and sheep fed on low quality forages (low in N, high in fibre) have shown that goats achieve superior voluntary DMI (g/Kg $W^{0.75}$/d) to sheep, and digest the fibre component of the diet better than sheep (Jones et al., 1972; El Hag, 1976; Gihad, 1976; Gihad et al., 1980; Doyle and Egan, 1980; Howe et al., 1988).

The increased fibre digestion by goats compared to sheep, has been partially attributed to a longer MRT (h) of particulate dry matter (labeled with ^{103}Ru-Phen) in the rumen of goats, and hence to a longer exposure of the rumen cell-wall pool to microbial attack (Doyle and Egan, 1980; Watson and Norton, 1982; Doyle et al., 1984). Goats, compared to sheep, sustain higher levels of rumen ammonia concentration when fed on low quality forages, and this has been related to higher rumen microbial growth rates and greater fibre digestion (Watson and Norton, 1982; Alam et al., 1985). The mechanism, however, by which goats maintain a higher rumen ammonia concentration is not clear, and Alam, Borens, Poppi and Sykes (1984) suggested that the lower water intake observed in goats (Owen and Ndosa, 1982; Alam et al., 1983), would increase the rumen ammonia concentration, and predispose the goats to a greater N retention. Goats tend to have a larger rumen volume per Kg $W^{0.75}$ than sheep, when fed on low quality forages (Watson and Norton, 1982; Tan, 1988). The effects of a larger rumen volume, on the voluntary DMI and DOMI, and MRT of rumen digesta in goats are not clear. Watson and Norton (1982) postulated that there is a greater degradation of dietary protein in the rumen of goats than in sheep, as a result of a longer MRT of digesta in the rumen of goats.

The objective of the first experiment (Expt 1a) was to investigate the voluntary intake and digestion of a low quality roughage by goats and sheep. The second experiment (Expt 1b) used an integral approach to study simultaneously the kinetics of rumen ammonia production, and investigated mechanisms for any differences in fibre

digestion between goats and sheep, when fed on a low quality roughage diet. Further objectives of the study were to measure the critical particle size as threshold to passage through the reticulo-omasal orifice. It is known to be 1.0 mm in sheep (Reid et al., 1977; Reid, John, Ulyatt, Waghorn and Milligan, 1979; Poppi et al., 1980). There is one limited study on goats (Uden and Van Soest, 1982). The "apparent" FOR (%/h) of particles from the rumen was also determined.

3.2 EXPERIMENTAL

3.2.1 Diet

Threshed prairie grass straw *(Bromus catharticus)* was fed to the animals. A daily supplement (10 g) of a mineral pre-mix (no N, see Appendix B), and a weekly oral dose (5 ml) of a liquid multi-vitamin supplement (Appendix C), were given in Expt 1b only. The straw was chaffed into 50-80 mm lengths and placed upon belt feeders which delivered the day's ration in 24 feeds, at 1h interval.

3.2.2 Animals

Seven Border-Leicester/Romney cross wethers, aged 2 years and weighing 44.2 Kg LWT (SD 4.16) were used in Expt 1a; eight wether sheep, including all those used in Expt 1a, aged 3 years and weighing 60.7 Kg LWT (SD 3.43) were used in Expt 1b. Six castrated Angora-NZ feral goats, aged 2 years and weighing 29.9 Kg LWT (SD 3.16) were used in Expt 1a; six goats, including four from Expt 1a and two replacement ones, aged 3 years and weighing 40.9 Kg LWT (SD 4.15) were used in Expt 1b.

3.2.3 Experimental Design

Expt 1a was conducted in the summer of 1986 and Expt 1b in the summer of 1987, and the experimental design is shown schematically in Figure 3.1.

3.2.3.1 Expt 1a: VFI was measured, with the animals fed "ad-lib", with the feed offered being 1.15 of the previous day's DM intake. VFI was recorded over d16-d28, after a pre-feeding period of 15 days. The

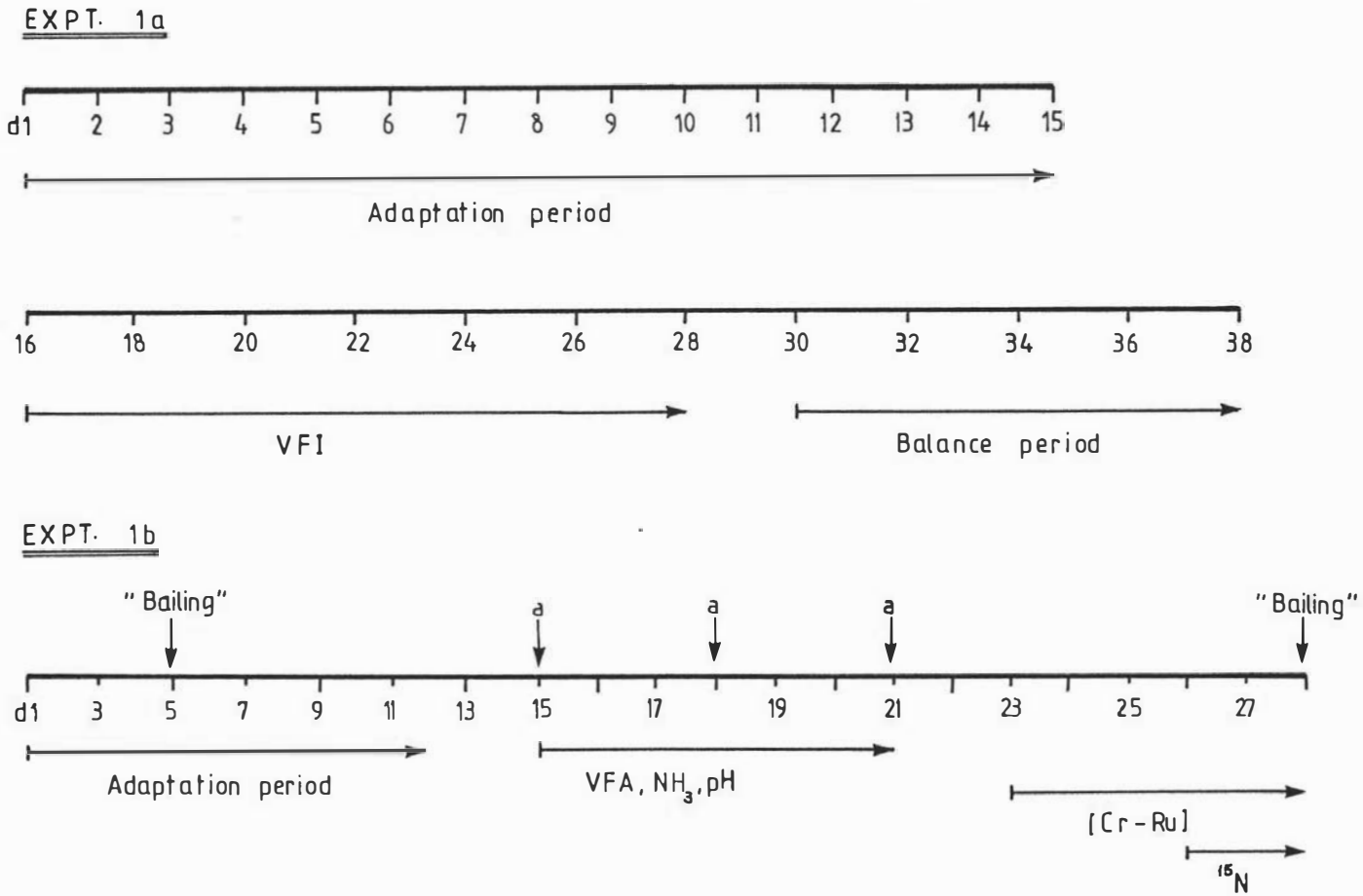


Figure 3.1. Schematic representation of the experimental design (Experiment 1).

digestibility and N-balance trials were carried out over d30-d38, with the animals maintained at 90% of VFI.

At the end of Expt 1a, the goats lost body condition, and 3 goats died as a result of a severe depletion of body reserves. Expt 1a was then stopped and Expt 1b carried out 12 months later, with the goats in better condition at the start of the trial.

3.2.3.2 Expt 1b: After a pre-feeding period of 12 days (fed "ad-lib"), the animals were restricted to 90% of "ad-lib" intake. Rumen fluid samples were taken during the period d15-d21, for NH_3-N, VFA and pH determinations. The non-radioactive dual-marker Cr-EDTA/Ru-Phen infusion trial commenced on d-23 and continued until d-28. The ^{15}N infusion trial was carried out over d26-d28. The animals had their rumen contents emptied out ("bailing") on d28, and subsamples taken before returning the warmed rumen digesta back to the rumen.

3.2.4 Marker Infusion Procedures

All infusions were administered by a peristaltic pump, fitted with silicone rubber tubing. Following a priming dose of 40 g, the dual marker Cr-EDTA/Ru-Phen (containing 2mg Cr/g; 0.0498mg Ru/g) was continuously infused into the rumen for 5 days, at a constant rate of 10.0 g/h for the goats and 8.73 g/h for the sheep. Infusion rates were 20 mg Cr/h and 0.498 mg Ru/h for goats and 17.46 mg Cr/h and 0.435 mg Ru/h for sheep.

^{15}N-ammonium chloride salt (94.74 atoms % excess) was added to the dual-marker solution (640 mg $^{15}NH_4Cl$/Kg of dual marker solution; pH 6.8), and infused continuously for the last 42 hours of infusion into the rumen, from 18.00 hours on d-26, until 12.00 hours on d-28. The infusion rate was 41.09 mg ^{15}N/d for goats and 34.71 mg ^{15}N/d for sheep.

3.2.5 Sampling

Composite samples of feed offered were collected daily during Expt 1a and Expt 1b and pooled on a weekly basis. The refusals, faeces and urine samples for each animal, were taken daily during the

digestibility trial of Expt 1a and pooled at -20 C. A representative sample of the rumen digesta was taken from 4 goats and 4 sheep, on d-6 of the pre-feeding trial (Expt 1b), and used to form a matrix for the preparation of Cr and Ru standard curves.

Rumen fluid samples for NH_3-N, pH and VFA were taken on d-15, d-18, d-21 of Expt 1b, at 10.00 hours and 15.00 hours. Rumen fluid samples were taken for determination of enrichment (atoms % excess) of rumen NH_3-N with ^{15}N: on d-26, before the start of ^{15}N infusion, at 17.30 hours (background sample); on d-27, at 18.00 (after 24h infusion) and 24.00 hours (after 30h infusion); on d-28, at 07.00 (after 37h infusion) and 12.00 hours (after 42h infusion). At "bailing", on d-28 (12.00-14.30 hours, corresponding to 42-44½ h after infusion), a representative sample of rumen fluid was obtained from the whole rumen digesta (see Section 2.8.5.), and the enrichment of NH_3-N with ^{15}N determined, as well as NH_3-N, VFA and pH. Samples for rumen bacterial-N, and rumen digesta-NAN were taken at "bailing" for determination of enrichment with ^{15}N, together with samples for particle size and chemical analyses.

Samples of rumen fluid, rumen digesta, rumen bacteria, faeces, feed offered, refusals and urine were prepared and stored, as per procedures described in Section 2.8.

3.2.6 Chemical Analysis

Chemical analysis was carried out using the methods described in detail in Section 2.9. The following analyses were performed. Samples of feed offered, refusals, and faeces were analysed for OM, total N, cellulose, hemicellulose, lignin and heat of combustion. Urine samples were analysed for total N. Rumen fluid samples were analysed for NH_3-N, pH, enrichment of NH_3-N with ^{15}N, and VFA (acetate, propionate, n-butyrate, iso-butyrate, n-valerate and iso-valerate). Rumen bacterial-N samples isolated from whole rumen digesta, and sub-samples of rumen digesta-NAN were analysed for enrichment with ^{15}N. Particle size analysis was determined on sub-samples of whole rumen digesta and faeces. Cr and Ru in rumen digesta were analysed by XRF spectrometry, using the preparation of standard curves. Correlation coefficients (r) were, for Cr: r=1.000 for both goat and sheep

matrix; for Ru: r=0.999 and 1.000 for goat, and sheep matrix respectively).

3.2.7 Calculations of Data

The FOR (%/h) and MRT (h) of Cr-EDTA, Ru-Phen and lignin, and the FDR (%/h) of lignin were calculated, as described in Section 2.10.1. The "apparent" FDR (%/h) of cellulose (C) and hemicellulose (H) have been calculated from Equations 1 and 2, respectively.

$$\text{FDR (C), \%/h} = \text{FDPR (C)} - \text{FOR (Lignin)} \quad (1)$$

$$\text{FDR (H), \%/h} = \text{FDPR (H)} - \text{FOR (Lignin)} \quad (2)$$

The calculation was based on the assumption that both cellulose and hemicellulose leave the rumen on the same particle as lignin, and hence have the same FOR (%/h) as lignin (Van Soest, 1975).

The IRL of NH_3-N (mg N/d) from the rumen, and the proportion of bacterial-N from NH_3-N and the proportion of bacterial-N as a proportion of total digesta NAN, were calculated as shown in Section 2.10.2.

The "apparent" FOR (%/h) of particles from the rumen (>2.0 mm, 2-1 mm, 1.0-0.5 mm, 0.5-0.25 mm, <0.25 mm), have been calculated from Equation 3.

$$\text{"Apparent" FOR (\%/h) of particle (A)} = \frac{\text{Particle(A) excreted in faeces (g/h) x 100}}{\text{Pool size of particle (A) in rumen (g)}} \quad (3)$$

where (A) is particle size for which measurement is being made.

The "apparent" MRT (h) of particles were calculated as the reciprocal of their respective FOR's (/h). The calculation is based on the assumption that there is no further breakdown in particle size once digesta has left the rumen (Grenet, 1970; Poppi et al., 1980).

Metabolisable energy for maintenance was taken as 0.39 MJ/Kg $W^{0.75}$, both for sheep (Agricultural Research Council, 1980), and for goats (Holmes and Moore, 1981).

3.2.8 Statistical Design and Analysis

A complete randomised design was used. Comparisons between goats and sheep were made, using one-way analysis of variance. Mean values with the standard error of the difference (SED) are presented. Regression relationships were derived between the DMI (g/Kg $W^{0.75}$/d) versus the total rumen (fluid + DM) pool size (g/Kg $W^{0.75}$), and between the rumen "apparent" FOR (%/h) of particles <0.25 mm and 0.10-0.5 mm versus that of lignin, for both goats and sheep. The differences in slopes between the regression lines for goats and sheep were tested using a t-test.

The values presented for NH_3-N, VFA and pH, are the means of seven observations per animal, since there were no significant differences ($P>0.05$) between day/or time of the day at which sampling occurred. There was no significant difference ($P>0.05$) between the enrichment values of the rumen fluid NH_3-N samples with ^{15}N, taken at 30, 36, 40-h after infusion of the ^{15}N-tracer commenced, and the sample taken at "bailing". The ^{15}N-enrichment value of the rumen fluid NH_3-N taken at "bailing" was used in the calculations of the IRL of NH_3-N in the rumen (gN/d).

3.3 RESULTS

3.3.1 Chemical Composition of Diet and Selection of Feed Offered

The chemical composition (g/Kg DM) of the prairie grass straw did not change over one year, from Expt 1a to Expt 1b, with constant values for the fibre components and total N (Table 3.1a).

The refusals of sheep, when compared to goats (Table 3.1b), showed significantly lower contents (g/Kg OM) of total N and lower heat of combustion values ($P<0.05$). The fibre content, however, was higher ($P<0.1$), with cellulose attaining significance ($P<0.05$). These observations were due to sheep selecting a diet lower in fibre and

Table 3.1a. Chemical composition (g/Kg dry matter (DM)) of mature prairie grass straw *(Bromus catharticus)* fed to goats and sheep during Experiments 1a and 1b.

	Experiment 1a[@]	Experiment 1b[$]
Organic matter	893	887
Heat of combustion (MJ/Kg DM)	17.8	17.6
Total Nitrogen	13.7	13.6
Cellulose	317	301
Hemicellulose	123	120
Lignin	128	128
Total fibre[†]	568	550

† Cellulose + hemicellulose + lignin

@ Summer 1986

$ Summer 1987

Table 3.1b. Chemical composition (g/Kg organic matter (OM)) of mature prairie grass straw, and the feed refusals by goats and sheep when fed at "ad-lib" intake.

(Mean values with their standard error of the difference (SED) for six goats and seven sheep.)

	Feed Offered[@]	Refusals		
		Goats	Sheep	SED
Heat of combustion (MJ/Kg OM)	20.0	24.4	17.8	2.64 *
Total Nitrogen	15.4	16.2	12.1	1.62 *
Cellulose	355	333	386	21.1 *
Hemicellulose	138	183	187	6.8 NS
Lignin	144	138	133	4.9 NS
Total fibre[†]	637	654	706	24.5 (*)

† Cellulose + hemicellulose + lignin

@ Experiment 1a

* P<0.05; (*) P<0.1; NS Non-significant.

higher in N than the feed offered, whereas goats showed no evidence of selection.

3.3.2 Voluntary Intake and Nitrogen Retention

The voluntary DMI and OMI (g/Kg $W^{0.75}$/d) of goats were significantly higher ($P<0.001$) than sheep, with both DMI and OMI being 1.65 of that of sheep (Table 3.2).

Goats also digested the DM of the feed better than sheep ($P<0.05$), with a difference of 6.8 units between the two species. However, the digestibility of OM was not significantly different between the two species ($P>0.1$), although goats appeared to digest OM better than sheep by 3.0 units. The net effects were significantly higher ($P<0.001$) DDMI and DOMI (g/Kg $W^{0.75}$/d) by goats compared to sheep. Digestible DMI and OMI by goats were 2.12 and 1.81 that of sheep, respestively.

ME intake (MJ/Kg $W^{0.75}$/d) of goats was 0.245, and that of sheep was 0.145 ($P<0.01$). ME intakes, expressed as a function of the amount of ME required for maintenance, were 0.63 for goats and 0.37 for sheep.

Voluntary intake of N (mg/Kg $W^{0.75}$/d) was higher ($P<0.01$) by goats (Table 3.3). There were no differences in the apparent digestibility of N between the two species ($P>0.1$). Both species were in negative N balance, although goats tended to lose more N (mgN/100g DMI/d) than sheep ($P>0.1$). When expressed as a % of dietary N intake, both faecal and urinary losses were not significantly different ($P>0.1$) between goats and sheep.

3.3.3 Fibre Digestion

Data in Table 3.4 show that goats digested total fibre better ($P<0.1$), than sheep, and had a superior voluntary intake (g/kg $W^{0.75}$/d) of total fibre ($P<0.001$).Goats had a larger ($P<0.05$) rumen total fibre pool size (g/Kg $W^{0.75}$).

Table 3.2. Voluntary and digestible intakes of dry matter and organic matter (g/Kg $W^{0.75}$/d), metabolisable energy intake (MJ/Kg $W^{0.75}$/d), and apparent digestibilities of dry matter and organic matter (%) by goats and sheep fed on mature prairie grass in summer.

(Mean values with their standard error of the difference (SED) for six goats and seven sheep.)

	Goats	Sheep	SED	
Intake (g/Kg $W^{0.75}$/d):				
Dry matter	55.6	33.8	4.43	***
Organic matter	49.7	30.2	3.96	***
Digestible dry matter	17.4	8.2	1.93	***
Digestible organic matter	18.1	10.0	2.16	***
Metabolisable energy intake†	0.245	0.145	0.0292	**
Apparent digestibility of dry matter@	31.2	24.3	2.51	*
Apparent digestibility of organic matter@	36.0	33.0	2.29	NS

† Digestible energy intake x 0.82

@ Animals fed at 90% "ad-lib".

*** P<0.001; ** P<0.01; * P<0.05; NS Non-significant.

Table 3.3. Nitrogen (N) intake, faecal N and urinary N excretions, N balance, and apparent N digestibility by goats and sheep fed on mature prairie grass straw, at 90% of "ad-lib" intake.

(Mean values with their standard error of the difference (SED) for six goats and seven sheep.)

	Goats	Sheep	SED	
Intake (mg/Kg $W^{0.75}$/d):	516	328	42.9	**
Faecal excretion (mg/Kg $W^{0.75}$/d)	359	236	28.5	**
Urinary excretion (mg/Kg $W^{0.75}$/d)	237	117	41.3	*
Nitrogen balance:				
mg N/Kg $W^{0.75}$/d	-96	-38	25.0	*
mg N/100 g DMI/d	-171	-119	62.0	NS
Apparent digestibility (%)	30.5	28.2	1.37	NS
Faeces N (percentage intake)	69.6	71.9	1.48	NS
Urine N (percentage intake)	45.5	37.9	9.87	NS

** $P<0.01$; * $P<0.05$; NS Non-significant.

Table 3.4. Voluntary and digestible intakes of total fibre [†], rumen pool, fractional disappearance rate (FDPR) and "apparent" fractional degradation rate (FDR) of total fibre in the rumen of goats and sheep, fed on mature prairie grass straw.

	Goats	Sheep	SED	
Intake (g/Kg $W^{0.75}$/d): [@#]				
Voluntary intake	31.6	19.2	2.52	***
Digestible intake	11.7	6.3	1.29	**
Apparent digestibility (%) [#α]	36.8	32.6	2.19	(*)
Rumen pool: g/Kg $W^{1.0}$ [αβ]	7.0	3.9	0.88	**
g/Kg $W^{0.75}$	17.7	11.0	2.24	*
FDPR (%/h) [αβ]	6.63	6.64	0.85	NS
"Apparent" FDR (%/h) [¶αβ]	4.05	3.30	0.58	NS

[†] Cellulose + hemicellulose + lignin

[#] Mean values with their standard error of the difference (SED) for six goats and seven sheep.

[α] Mean values with their standard error of the difference (SED) for six goats and eight sheep.

[@] Animals fed "ad-lib".

[β] Animals fed at 90% "ad-lib".

[¶] FDPR (%/h of fibre) - FOR (%/h of lignin).

*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1; NS Non-significant

Tables 3.5-3.7 show relative differences in the intakes and apparent digestibilities of the constituents of total fibre, namely: cellulose, hemicellulose and lignin.Both species had higher intakes (g/Kg $W^{0.75}$/d) of cellulose, intermediate intakes for hemicellulose, and lowest intakes for lignin. Goats were, however, superior to sheep in the voluntary intakes ($P<0.001$) of all the three components of fibre (expressed on a g/Kg $W^{0.75}$/d basis), and maintained larger rumen pools (g/Kg $W^{0.75}$) of cellulose ($P<0.05$), hemicellulose ($P<0.05$) and lignin ($P<0.01$).

Goats digested cellulose, hemicellulose and lignin better than sheep, but the difference attained significance ($P<0.1$) only for lignin, the least digestible dietary component of fibre. The rumen "apparent" FDR (%/h) of cellulose ($P<0.05$), hemicellulose ($P<0.001$) and the FDR of lignin ($P<0.1$) were faster in goats, compared to sheep.

3.3.4 Rumen Pool Size

When restricted to 90% of "ad-lib" intake, the DMI (g/Kg $W^{0.75}$/d) of goats was superior to that of sheep ($P<0.001$) by 1.68 (Table 3.8). The rumen total digesta (DM+liquid), rumen DM and liquid pool sizes were all larger in goats than in sheep, when expressed on a Kg $W^{1.0}$ or Kg $W^{0.75}$ basis ($P<0.01$). The rumen pool of goats (both DM and liquid pools) was 1.73 that of sheep (g/Kg $W^{0.75}$). The percentage of DM in the rumen digesta did not differ between the two species ($P>0.1$).

Table 3.9 gives the distribution (% particulate DM retained on sieve size) of particles in the rumen digesta and faeces. The rumen digesta of goats had a higher proportion of particles broken down to < 0.25 mm ($P<0.05$), and a markedly lower proportion ($P<0.001$) of particles >4.0 mm than sheep. Figure 3.2 shows that the particle size as threshold to passage through the reticulo-omasal orifice was 1.0 mm, in both goats and sheep, since 98.6% of the particulate DM in the faeces of both species were recovered from particles <1.0 mm. However, if the threshold to passage from the rumen was <1.0 mm it would appear that goats were able to pass a significantly larger proportion ($P<0.01$) of particles of size 1.0-0.5 mm in the faeces, compared to sheep. The data in Table 3.9 indicate that, the proportion of particles broken to <1.0 mm in the rumen was higher in goats ($P<0.1$), and

Table 3.5. Voluntary and digestible intakes of cellulose, rumen pool, fractional disappearance rate (FDPR) and "apparent" fractional degradation rate (FDR) of cellulose in the rumen of goats and sheep fed on mature prairie grass straw.

	Goats	Sheep	SED	
Intake (g/Kg $W^{0.75}$/d): @!				
Voluntary intake	17.6	10.7	1.40	***
Digestible intake	9.2	5.1	0.97	**
Apparent digestibility (%) $^{\$!}$	52.1	47.5	3.42	NS
Rumen pool: g/Kg $W^{1.0}$ $^{\#\$}$	3.1	1.8	0.41	**
g/Kg $W^{0.75}$	7.7	4.9	1.04	*
FDPR (%/h)$^{\$\#}$	8.41	6.95	1.34	NS
"Apparent" FDR (%/h)$^{a\$\#}$	5.83	4.39	0.58	*

! Mean values with their standard error of the difference (SED) for six goats and seven sheep.

\# Mean values with their standard error of the difference (SED) for six goats and eight sheep.

@ Animals fed "ad-lib".

$ Animals fed at 90% "ad-lib".

a FDPR, (%/h of cellulose) - FOR, (%/h of lignin).

*** P<0.001; ** P<0.01; * P<0.05; NS Non-significant.

Table 3.6. Voluntary and digestible intakes of hemicellulose, rumen pool, fractional disappearance rate (FDPR) and "apparent" fractional degradation rate (FDR) of hemicellulose in the rumen of goats and sheep fed on mature prairie grass straw.

	Goats	Sheep	SED	
Intake (g/Kg $W^{0.75}$/d): @!				
Voluntary intake	7.1	4.3	0.55	***
Digestible intake	3.2	1.9	0.34	**
Apparent digestibility (%) $!	47.0	45.0	2.78	NS
Rumen Pool: g/Kg $W^{1.0}$ $#	1.7	1.0	0.23	*
g/Kg $W^{0.75}$	4.3	2.9	0.58	*
FDPR (%/h) $#	5.97	5.58	0.71	NS
"Apparent" FDR (%/h) $#	3.39	2.09	0.30	***

! Mean values with their standard error of the difference (SED) for six goats and seven sheep.

Mean values with their standard error of the difference (SED) for six goats and eight sheep.

@ Animals fed "ad-lib".

$ Animals fed at 90% "ad-lib".

FDPR, (%/h of hemicellulose) - FOR, (%/h of lignin).

*** P<0.001; ** P<0.01; * P<0.05; NS Non-significant.

Table 3.7. Voluntary and digestible intakes of lignin, rumen pool, fractional disappearance rate (FDPR) and fractional degradation rate (FDR) of lignin in the rumen of goats and sheep, fed on mature prairie grass straw.

	Goats	Sheep	SED	
Intake (g/Kg $W^{0.75}$/d): †α				
Voluntary intake	7.1	4.3	0.57	***
Digestible intake	0.8	0.3	0.22	**
Digestibility (%) †β	11.3	5.3	2.98	(*)
Rumen pool (g/Kg $W^{1.0}$)	2.3	1.2	0.26	**
(g/Kg $W^{0.75}$)	5.7	3.2	0.65	**
FDPR (%/h) #	4.79	5.26	0.648	NS
FDR (%/h) #	2.21	1.61	0.323	(*)

† Mean values with their standard error of the difference for six goats and seven sheep.

Mean values with their standard error of the difference for six goats and eight sheep.

α Animals fed "ad-lib".

β Animals fed at 90% "ad-lib".

*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1; NS Non-significant

Table 3.8. Rumen total pool (DM + liquid), rumen dry matter (DM), and rumen liquid pool sizes (g/Kg $W^{1.0}$ and g/Kg $W^{0.75}$), and percentage of DM in the rumen contents of goats and sheep fed on mature prairie grass straw, at 90% "ad-lib" intake. (Mean values with their standard error of the difference (SED) for six goats and eight sheep.)

	Goats	Sheep	SED	
Intake at 90% "ad-lib":				
gDM/Kg $W^{1.0}$/d	19.7	10.7	1.56	***
gDM/Kg $W^{0.75}$/d	49.6	29.6	3.90	***
Rumen pool size:				
Rumen total pool (DM + liquid):				
g/Kg $W^{1.0}$	132.8	76.7	13.7	**
g/Kg $W^{0.75}$	334.7	213.5	35.3	**
Rumen DM pool:				
g/Kg $W^{1.0}$	15.5	8.9	1.8	**
g/Kg $W^{0.75}$	39.0	24.9	4.6	**
Rumen liquid pool:				
g/Kg $W^{1.0}$	117.3	67.8	12.0	**
g/Kg $W^{0.75}$	295.7	188.6	31.1	**
Dry matter percentage (%)	11.61	11.75	0.75	NS

*** $P<0.001$; ** $P<0.01$; NS Non-significant.

Table 3.9. Particle size distribution (% particulate dry matter (DM) retained on sieve size) in the rumen and faeces of goats and sheep fed on mature prairie grass straw, at 90% "ad-lib" intake.

(Mean values with their standard error of the difference (SED) for six goats and eight sheep.)

Sieve size (mm)	Goats	Sheep	SED	
Rumen digesta:				
4.0	5.1	9.6	0.76	***
2.0	3.1	3.1	0.47	NS
1.0	7.9	6.7	0.75	NS
0.5	13.8	13.0	0.87	NS
0.25	31.7	34.1	1.42	NS
<0.25 @	38.5	33.5	1.80	*
<1.0	83.9	80.6	1.62	(*)
>1.0	16.1	19.4	1.62	(*)
Faeces:				
4.0	-	-	-	
2.0	0.57	0.66	0.12	NS
1.0	0.79	0.68	0.19	NS
0.5	11.2	6.0	1.25	**
0.25	50.7	51.8	1.44	NS
<0.25 @	36.7	40.8	2.06	(*)
<1.0	98.6	98.6	0.21	NS
>1.0	1.4	1.4	0.21	NS

@ Initial sample D.WT - sum of recovered particulate DM fractions.

*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1; NS Non-significant.

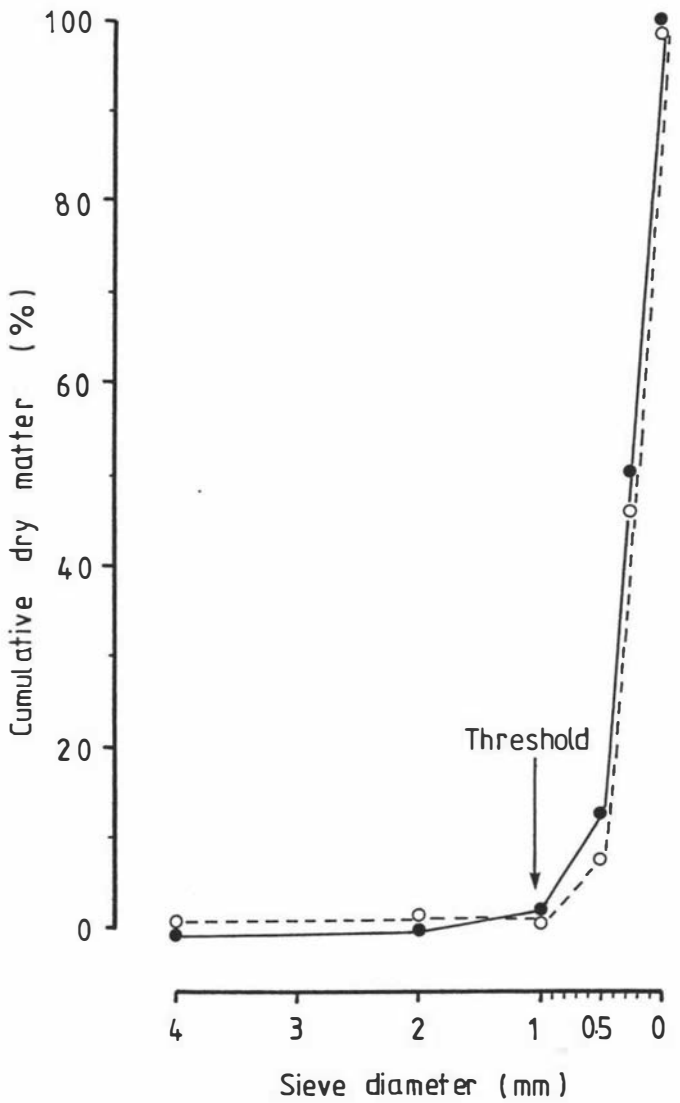


Figure 3.2. Cumulative dry matter distribution of faecal samples from goats (•) and sheep (o).

the proportion >1.0 mm and resisting escape through the reticulo-omasal orifice was lower in goats ($P<0.1$), compared to sheep.

3.3.5 MRT (h) and FOR (%/h) of Cr-EDTA, Ru-Phen, and Lignin from the Rumen

The data in Table 3.10 show that goats compared to sheep, had a longer MRT (h) of Cr-EDTA, Ru-Phen and lignin in the rumen, although the differences were not significant ($P>0.1$). In both goats and sheep, the MRT of Cr-EDTA (which labels the liquid pool of the rumen) was lowest, with intermediate values for the MRT of the particulate marker Ru-Phen, and longer MRT values for the indigestible dietary marker, lignin.

3.3.6 "Apparent" MRT (h) and "Apparent" FOR (%/h) of Feed Particles from the Rumen

Table 3.10 shows the "apparent" MRT (h) and their respective "apparent" FOR's (%/h) of particles retained on sieves of sizes >2.0 mm to <0.25 mm. In both goats and sheep, the "apparent" MRT (h) of particulate DM in the rumen decreased as the particles were reduced in size from 2.0 mm to 0.25 mm. Particles that were <0.25 mm had a greater resistance to flowing out of the rumen in both species, compared to particles 0.50-0.25 mm. However, goats showed a tendency to retain the particles <0.25 mm for a longer time in the rumen than sheep, although the difference was not significant ($P>0.1$).

The "apparent" MRT (h) of particles >1.0 mm in the rumen of goats and sheep tended to reach infinity (395 h and 539 h, for goats and sheep, respectively), indicating that the breaking down of these particles to <1.0 mm was a pre-requisite to passage through the reticulo-omasal orifice. Goats showed a significantly shorter "apparent" MRT of particles 1.0-0.5 mm in the rumen than sheep ($P<0.05$). This contributed to a higher proportion of these particles in the faeces of goats.

Table 3.10. Mean retention time (MRT, h) and fractional outflow rate (FOR, %/h) of Cr-EDTA, Ru-Phen and lignin, and the "apparent" MRT (h) and "apparent" FOR (%/h) of particulate DM (>2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm, <0.25 mm, <1.0 mm, >1.0 mm) from the rumen of goats and sheep fed on mature prairie grass straw, at 90% "ad-lib" intake.

(Mean values with their standard error of the difference (SED) for six goats and eight sheep.)

	Goats	Sheep	SED	
Mean retention time, MRT (h):				
Cr-EDTA	12.6	11.7	0.80	NS
Ru-Phen	15.3	14.7	1.13	NS
Lignin	40.7	33.0	4.91	NS
Fractional outflow rate, FOR (%/h):				
Cr-EDTA	8.0	8.7	0.58	NS
Ru-Phen	6.7	6.9	0.51	NS
Lignin	2.6	3.3	0.53	NS
"Apparent" MRT of particulate DM (h):				
>2.0 mm	245	173	43.7	(*)
2.0-1.0 mm	374	359	73.6	NS
1.0-0.5 mm	46	86	13.8	*
0.5-0.25 mm	22.6	23.7	3.7	NS
<0.25 mm	36.6	30.9	5.7	NS
<1.0 mm	30.3	29.9	4.8	NS
>1.0 mm	395	539	87.8	(*)
"Apparent" FOR of particulate DM (%/h):				
>2.0 mm	0.48	0.61	0.10	NS
2.0-1.0 mm	0.27	0.29	0.11	NS
1.0-0.5 mm	2.53	1.36	0.52	*
0.5-0.25 mm	4.82	4.56	0.88	NS
<0.25 mm	2.78	3.76	0.65	NS
<1.0 mm	3.48	3.69	0.85	NS
>1.0 mm	0.32	0.20	0.65	NS

* P<0.05; (*) P<0.1; NS Non-significant.

3.3.7 Rumen Volatile Fatty Acids and pH

There was no difference ($P>0.1$) in the concentration of total VFA (mmol/L) in the rumen of goats and sheep, although the goats appeared to maintain higher concentrations of total VFA (Table 3.11). Both goats and sheep had similar molar proportions ($P>0.1$) of acetate, with a tendency for goats to maintain a higher concentration in the rumen. The molar proportion of propionate was significantly lower ($P<0.05$) in goats.

The concentrations of butyrate and of valerate were all greater ($P<0.05$), in goats. The molar proportions of n-valerate and iso-valerate were also higher in the rumen of goats compared to sheep ($P<0.05$ and $P<0.1$, respectively). The molar proportions of butyrate (n- and iso-), however, were not different between the two species ($P>0.1$).

The acetate/propionate ratio showed no differences ($P>0.1$) between the two species. The ratio of (butyrate+valerate) to total VFA in the rumen, showed a difference ($P<0.1$) between the two species, with the goats having greater valerate and butyrate concentrations, as a proportion of the total VFA.

The pH of rumen fluid was significantly lower ($P<0.05$) in goats, than in sheep.

3.3.8 Water Transactions in the Rumen

Voluntary intake of supplementary water (drinking water, g/g DMI/d) was significantly lower in goats ($P<0.05$), with the intake of goats being 77% that of sheep. Total water consumed by goats (g/g DMI/d) was also significantly lower ($P<0.05$) than by sheep (Table 3.12).

Data in Table 3.12 indicate that there was no difference in the water outflow (g/g DMI/d) from the rumen of goats and sheep. However, there was a tendency for it to be slower in goats ($P>0.1$).

Table 3.11. Total VFA (mmol/L), and concentrations of acetate, propionate, n-butyrate, iso-butyrate, n-valerate and iso-valerate in the rumen contents of goats and sheep fed on mature prairie grass, at 90% "ad-lib" intake (mmol/L and moles %) and pH of rumen.

(Mean values with their standard error of the difference (SED) for six goats and eight sheep.)

	Goats	Sheep	SED	
Total VFA (mmol/L)	96.1	86.9	8.9	NS
Acetate (mmol/L)	68.0	61.9	6.9	NS
(moles %)	70.6	71.2	0.71	NS
Propionate (mmol/L)	18.2	17.4	1.7	NS
(moles %)	18.9	20.0	0.41	*
n-butyrate (mmol/L)	5.8	4.7	0.45	*
(moles %)	6.2	5.6	0.45	NS
iso-butyrate (mmol/L)	1.7	1.5	0.07	*
(moles %)	1.80	1.78	0.15	NS
n-valerate (mmol/L)	1.0	0.60	0.06	***
(moles %)	1.05	0.75	0.10	*
iso-valerate (mmol/L)	1.1	0.80	0.14	*
(moles %)	1.25	0.89	0.17	(*)
Ratio:				
Acetate/Propionate	3.75	3.56	0.133	NS
(Butyrate + valerate)/total VFA	0.102	0.090	0.007	(*)
pH of rumen	6.73	6.90	0.097	*

*** $P<0.001$; * $P<0.05$; (*) $P<0.1$; NS Non-significant.

Table 3.12. Water flows into and out of the rumen: drinking water and total water intakes, water outflow from rumen and net rumen water balance in goats and sheep fed on mature prairie grass straw, at 90% of "ad-lib" intake.

(Mean values with their standard error of the difference (SED) for six goats and eight sheep.)

	Goats	Sheep	SED	
Drinking water:				
$g/W^{1.0}/d$	31.6	22.4	2.66	**
g/g DMI/d	1.63	2.13	0.16	*
Total water intake: !				
$g/W^{1.0}/d$	34.2	23.7	2.80	**
g/g DMI/d	1.76	2.26	0.16	*
Water outflow: @				
$g/W^{1.0}/d$	224.5	139.2	25.0	**
g/g DMI/d	11.4	12.8	1.11	NS
Net rumen water balance: $				
$g/W^{1.0}/d$	190.3	115.5	23.4	**
g/g DMI/d	9.7	10.6	1.15	NS

! Drinking water + water in feed.

@ Rumen liquid pool x FOR (/d of Cr-EDTA).

$ Rumen outflow - total water intake = salivary secretion + net inflow of water across rumen wall.

** $P<0.01$; * $P<0.05$; NS Non-significant.

The net rumen water balance (g/g DMI/d), which represents the combined effects of both salivary secretion and net inflow of water across the rumen, indicated no differences between the two species, although it appeared to be slightly lower in goats than in sheep, with the difference not attaining significance ($P>0.1$). The water transactions in the rumen of goats and sheep are represented diagrammatically in Figure 3.3.

3.3.9 Rumen Ammonia Kinetics

Ammonia kinetic data are summarised in Table 3.13. Enrichment of rumen fluid NH_3-N, rumen bacterial-N and digesta-NAN with ^{15}N are shown in Figures 3.4 and 3.5, for goats and sheep respectively.

Dietary N intake (g N/d and g N/Kg $W^{0.75}$/d) was significantly higher in goats ($P<0.001$), compared to sheep, with both species being fed at 90% that of "ad-lib" intake.

NH_3-N concentration (mg N/L) in the rumen and rumen NH_3-N pool size (mg N), outflow of NH_3-N in water leaving the rumen (mg N/d), and the Irreversible Loss Rate (IRL) of NH_3-N (g N/d) from the rumen NH_3-N pool were all significantly higher ($P<0.05$) in goats, compared to sheep. However, when corrected for differences in dietary N intake per day, no differences were observed between goats and sheep ($P>0.1$), in either the IRL, rumen NH_3-N pool or outflow of NH_3-N from the rumen. IRL minus the rumen NH_3-N outflow rate was not different ($P>0.1$), between goats and sheep. It represents the combined values for NH_3-N incorporated into microbial-N and total NH_3-N absorbed from the rumen, with both components leaving the rumen and not returning to that compartment during the sampling period.

The proportion of rumen bacterial-N derived from rumen NH_3-N showed no significant differences ($P=0.11$), between goats and sheep. The proportion, however, was lower in goats than in sheep (0.47 vs 0.63). This indicates that a large proportion of N in the rumen bacteria of goats was derived from digesta-NAN, such as peptides and amino acids.

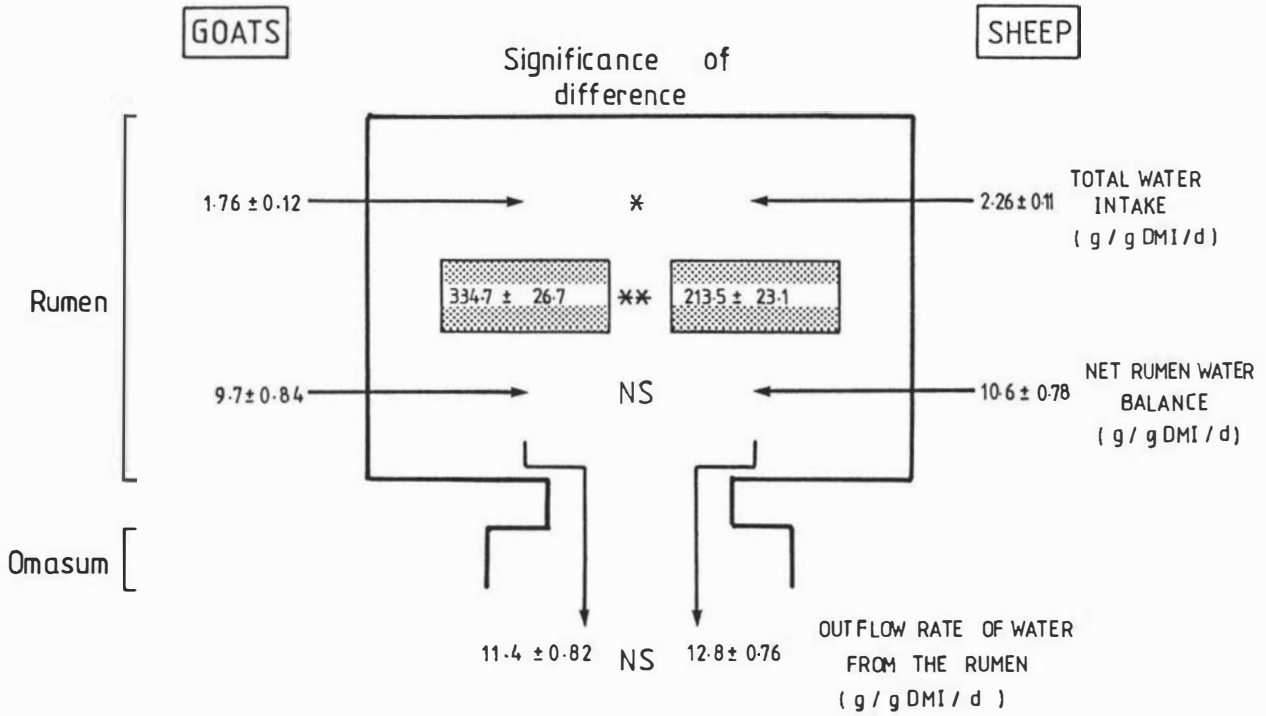


Figure 3.3. Water flows (g/g DMI/d) into and out of the rumen of goats and sheep fed on mature prairie grass straw, at 90% "ad-lib" intake (values in boxes represent rumen pool size (g/Kg $W^{0.75}$)).

Table 3.13. Kinetics of ammonia (NH_3-N) production in the rumen of goats and sheep fed on mature prairie grass straw, at 90% "ad-lib" intake.

(Mean values with their standard error of the difference (SED) for six goats and eight sheep.)

	Goats	Sheep	SED	
Total N intake (NI):				
g NI/d	10.9	8.7	1.10	***
g NI/Kg $W^{0.75}$/d	0.68	0.40	0.05	***
Rumen ammonia (NH_3-N) kinetics:				
NH_3-N concentration (mg N/L)	115	80	12.0	*
Pool size: mg N !	612	371	82.8	*
mg N/g NI	56.3	42.7	8.48	NS
Outflow in water: mg N/d @	1046	630	145.5	*
mg N/g NI/d	96.3	72.6	14.26	NS
Irreversible loss rate (IRL): g N/d	13.6	10.7	1.07	**
g N/g NI/d	1.26	1.25	0.14	NS
IRL - outflow in water: g N/d	12.5	10.1	1.40	(*)
g N/g NI/d	1.16	1.17	0.142	NS
Bacterial-N from NH_3-N (%)	47.1	63.3	9.48	NS
Bacterial-N (% digesta NAN)	53.0	36.7	9.48	NS
Total N in rumen digesta (g/100 g DM)	2.19	1.69	0.119	***
Total N in rumen bacterial cells (g/100 g DM)	5.73	4.61	0.454	*

! Rumen liquid (L) x NH_3-N (mg N/L).

@ Water outflow from rumen (L/d) x NH_3-N (mg N/L), calculated from rumen FOR (/d) of Cr-EDTA.

*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1;
NS Non-significant.

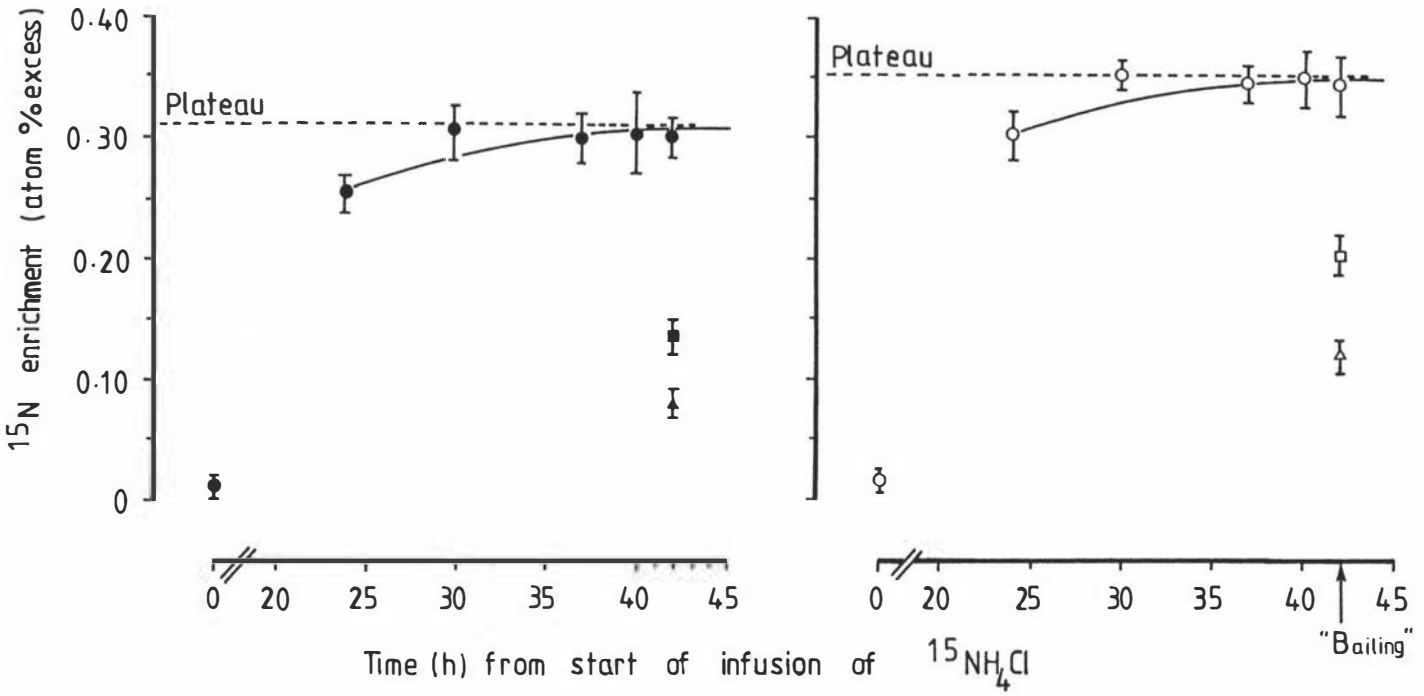


Figure 3.4. Enrichment with ^{15}N (atoms % excess) of rumen fluid NH_3-N (•), bacterial-N (■) and rumen digesta-NAN (▲) samples for goats (± SEM), fed on mature prairie grass straw.

Figure 3.5. Enrichment with ^{15}N (atoms % excess) of rumen fluid NH_3-N (o), bacterial-N (□) and rumen digesta-NAN (△) samples for sheep (± SEM), fed on mature prairie grass straw.

Total N in the rumen digesta of goats ($P<0.001$), and total N in the isolated rumen bacterial cells of goats ($P<0.05$), were significantly higher than corresponding values for sheep.

3.4 DISCUSSION

3.4.1 Voluntary Feed Intake and Digestibility

The results of this experiment confirm previous studies, reported in the Literature Review, where goats consumed more (g/Kg $W^{0.75}$/d) of a low N high fibre forage diet than sheep (El Hag, 1976; Doyle and Egan, 1980; Gihad et al., 1980; Watson and Norton, 1982; Alam et al., 1983). Howe et al. (1988) fitted a regression relationship (Equation 4), between the ratio of voluntary DDMI (g/Kg $W^{0.75}$) goats/sheep versus the DMD (sheep), %. The regression was based on comparison studies published in literature between the two species and involving 14 forage diets. The fitted regression equation was:

$$\text{DDMI (goats/sheep) (g/g Kg } W^{0.75}\text{)} = 1.84(\text{SE } 0.29) - 0.013\ (\text{SE } 0.0049)\ \text{DMD(sheep)} \quad (4)$$

$r=0.58$; $P<0.05$.

When substituting the DMD (sheep) of the present experiment in Equation 4, the predicted DDMI (goats/sheep) value is 1.52. The ratio obtained in the present experiment was 2.12, and appears to be higher than the values published in the literature, indicating greater than expected superiority of goats on the low quality roughage.

The superiority of goats over sheep, when fed on low quality forages, is possibly due to differences between the two species in four factors:

1. Rumen pool size,

2. MRT of digesta in the rumen,

3. Particle size distribution of rumen contents,

4. Threshold of particle size to passage from the rumen.

The rumen (DM + Fluid) pool size (g/Kg $W^{0.75}$) was larger in goats than in sheep (Table 3.8), and hence may have allowed space for increased VFI. Figure 3.6 shows the relationship between DMI (g/Kg $W^{0.75}$/d) and the rumen (DM + Fluid) pool size (g/Kg $W^{0.75}$) for goats and sheep. The relationships are:

$$\text{DMI (goats)} = 14.1(\text{SE } 18.4) + 0.11\ (\text{SE } 0.05)\ \text{Rumen pool} \quad (5)$$
$$r=0.70;\ P=0.12$$

$$\text{DMI (sheep)} = 17.2(\text{SE } 4.70) + 0.058\ (\text{SE } 0.02)\ \text{Rumen pool} \quad (6)$$
$$r=0.78;\ P<0.05$$

Equations 5 and 6 show that the increase in DMI (g/Kg $W^{0.75}$/d) per unit increase in rumen pool size (g/Kg $W^{0.75}$) is greater for goats than for sheep, as shown by the significant difference in the two slopes ($P<0.1$). However, the tendency for goats to have a longer MRT (h) of the digesta in the rumen (Table 3.10), goes against the inverse relationship which is known to exist between DMI and MRT (Ulyatt, 1971; Thornton and Minson, 1973; Faichney, 1983; Shaver, Nytes, Satter and Jorgensen, 1986). It appears that these effects are counteracted by goats having a larger rumen pool size (g/Kg $W^{0.75}$) than sheep. Watson and Norton (1982) and Tan (1988) have also reported that goats have a larger rumen pool size (g/Kg $W^{0.75}$) than sheep when fed on low quality forages.

Figure 3.6 also indicates that at a constant rumen pool size (g/Kg $W^{0.75}$), say 280 units, goats achieve a higher VFI (45 g/Kg $W^{0.75}$/d), than sheep (34 g/Kg $W^{0.75}$/d). Two main factors are known to affect clearance of digesta from the rumen and voluntary feed intake, namely the breakdown of particles in the rumen, and rate of passage of particles through the reticulo-omasal orifice (Ulyatt *et al.*, 1986). Figure 3.2 showed that the threshold to passage of particles through the reticulo-omasal orifice was 1.0 mm, both for goats and sheep. Table 3.9 indicated that goats can pass a larger proportion of particles of size 1.0-0.5 mm in the faeces than sheep, when fed on the roughage used in the present experiment. If it is assumed that there is no further breakdown in particle size after the particles have left the rumen (Smith, Waldo, Moore, Leffel and Van Soest, 1967; Grenet,

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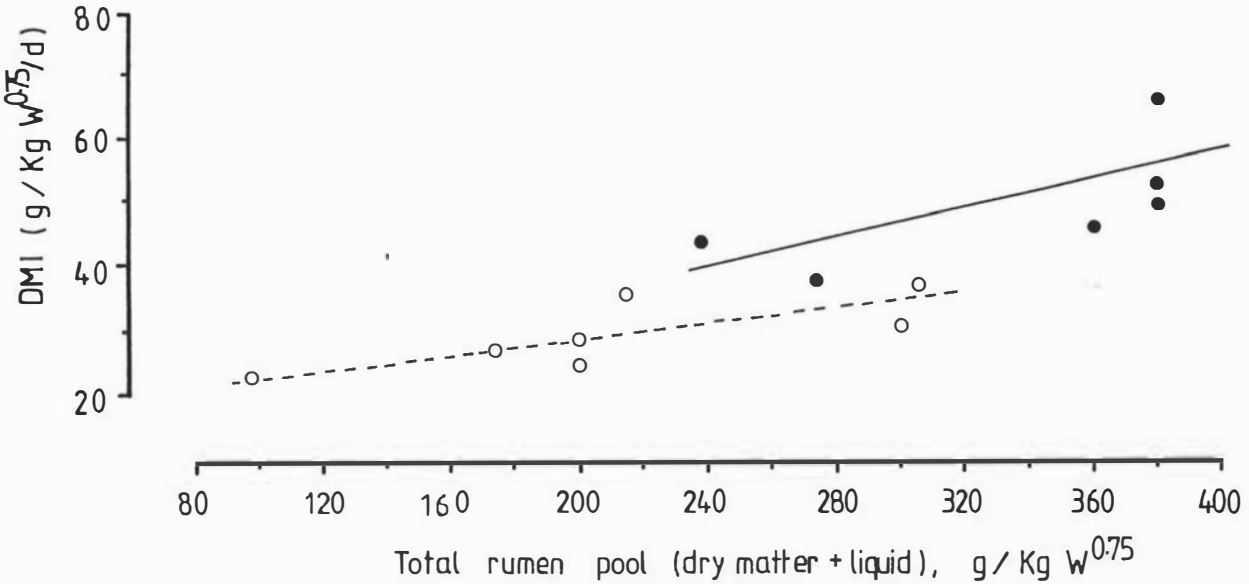

Figure 3.6. Relationship between the dry matter intake (g/Kg $W^{0.75}$/d) and total rumen pool (DM + liquid) (g/Kg $W^{0.75}$) by goats (•) and sheep (o) fed on mature prairie grass straw, at 90% "ad-lib" intake.

1970; Poppi et al., 1980), goats appeared to alleviate rumen fill by allowing a larger size of particles to escape the rumen than sheep, in the present experiment. Van Soest (1982) postulated that at higher intakes and larger ruminal volumes, ruminants are expected to pass a larger size of particles in the faeces.

Goats had a larger proportion of small particles (<1.0 mm) in the rumen contents than sheep (Table 3.9), which could indicate a greater efficiency of chewing by goats in reducing particle size. It is known that a rapid reduction in feed DM to the critical particle size of 1.0 mm as threshold to passage, results in an increased voluntary intake in ruminants (Reid et al., 1979; Black, Faichney and Sinclair, 1982; Ulyatt et al., 1986). Small particles have an increased surface area and pack more densely than larger particles (Martz and Belyea, 1986).

The results discussed above indicate possible differences in the chewing behaviour during eating and/or rumination by goats and sheep. Further studies should look at the comparative efficiencies of chewing and rumination in relation to particle breakdown and the clearance of digesta from the rumen in goats and sheep, to investigate if this is superior in goats.

3.4.2 Rumen Fermentation

Goats maintained higher total concentrations of butyrate (iso- and n-), and valerate (iso- and n-), in the rumen fluid than sheep (Table 3.11). Butyrate and valerate are growth factors for many cellulolytic rumen bacteria (Hungate, 1966; Bryant, 1973; Russell, 1983). Higher rumen concentrations of NH_3-N ($P<0.05$), lower pH ($P<0.05$) and higher concentrations of valerate and butyrate ($P<0.05$) in goats, compared to sheep, indicate differences in the rumen environment between the two species. Watson and Norton (1982) and Cabrera, Villarroel, Vial and Castillo (1983) have also reported higher concentrations of butyrate and valerate in the rumen contents of goats compared to sheep, when fed on low quality forages. Higher rumen NH_3-N concentrations in the rumen of goats as observed in the present experiment are consistent with other studies cited in the Literature Review (Watson and Norton, 1982; Cabrera et al., 1983; Alam et al., 1985; Antoniou and Hadjipanayiotou, 1985).

In a review of comparative fibre digestibility by goats and sheep, Gihad et al. (1980), reported that goats had significantly larger populations of cellulolytic bacteria than sheep in the rumen, when fed on low quality forages. It seems probable that, when fed on low quality forages, goats can maintain larger populations of fibre-digesting bacteria than sheep, and a possible contributing factor could be the previously mentioned difference in rumen environment between the two species.

3.4.3 Particulate Marker Methodology

The relationship between the "apparent" FOR (%/h) of particles <0.25 mm and 1.0-0.5 mm with that of lignin are given in Equations 7-10, and are shown in Figures 3.7 and 3.8.

"Apparent" FOR 1.0-0.5mm = -1.62 (SE 0.85) + 1.61 (SE 0.32) FOR Lignin
(goats) r=0.93; P<0.01 (7)

"Apparent" FOR 1.0-0.5mm = -0.90 (SE 3.41) + 0.42 (SE 0.63) FOR Lignin
(sheep) r=0.29; P>0.05 (8)

"Apparent" FOR <0.25mm = 1.60 (SE 0.39) + 0.45 (SE 0.15) FOR Lignin
(goats) r=0.84; P<0.05 (9)

"Apparent" FOR <0.25mm = -1.06 (SE 7.00) + 0.90 (SE 1.30) FOR Lignin
(sheep) r=0.29; P>0.05 (10)

The regression relationships (7) and (9), derived for goats, are significant, showing that particulate matter FOR (%/h) as measured with lignin correlated well with the "apparent" FOR (%/h) as measured using the particles themselves. However, the FOR (%/h) of particulate matter in sheep as measured with lignin correlated poorly (P>0.05) with the "apparent" FOR (%/h) as measured with the particles. The slope of the regression line of FOR (%/h) 1.0-0.5 mm with the FOR (%/h) of lignin was significantly greater (P<0.1) in goats than in sheep. The slope of the regression line of the "apparent" FOR (%/h) <0.25 mm with the FOR (%/h) of lignin was significantly smaller for

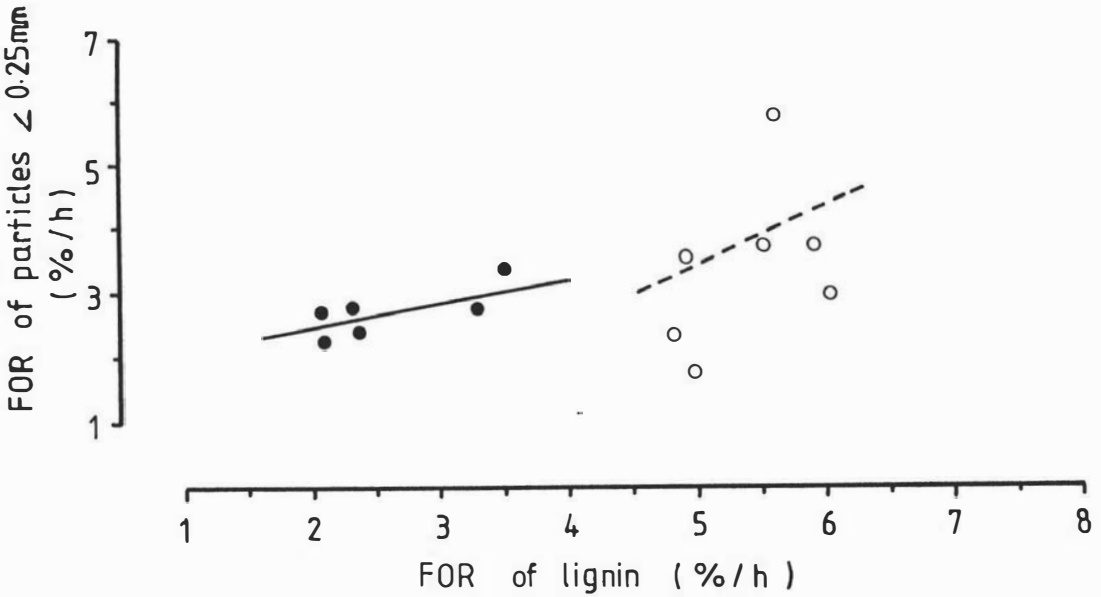

Figure 3.7. Relationship between the "apparent" fractional outflow rate (FOR, %/h) of particles <0.25 mm and the FOR (%/h) of lignin by goats (•) and sheep (o), fed on mature prairie grass straw, at 90% "ad-lib" intake.

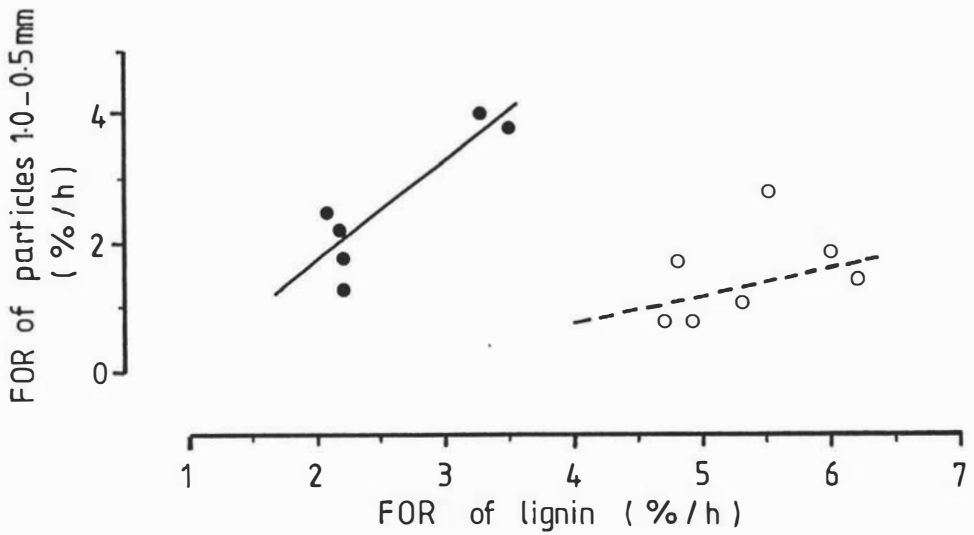

Figure 3.8. Relationship between the "apparent" fractional outflow rate (%/h) of particles 1.0-0.5 mm and the FOR (%/h) of lignin by goats (•) and sheep (o), fed on mature prairie grass straw, at 90% "ad-lib" intake.

goats than for sheep ($P<0.01$). It can therefore be concluded from the regression relationships that lignin as a particle-associated marker behaves differently for goats and sheep, in relation to the above particle sizes, when fed on the roughage used in the present experiment.

Although lignin as an index of the total particulate FOR was slower for goats, the fraction of particles 1.0-0.5 mm (as % DM in the rumen), actually left the rumen faster in goats, than in sheep. Hence the top end of particles, constituting the threshold to passage, left the rumen of goats at a faster rate than that of sheep. This indicates differences between the two species in the mechanisms controlling passage of particles which are below the critical threshold size in the rumen, and should be repeated in other studies with low quality roughages.

The finest particulate plant cell-wall fractions in the rumen and faeces contain 50% or more in lignin (Uden, Parra and Van Soest, 1974; Van Soest, 1975). The "apparent" FOR (%/h) of particles <0.25 mm was slower in goats than in sheep, with the difference not attaining significance ($P>0.1$). This indicates that the overall FOR of lignin as a particulate marker measures slightly different things in goats and sheep, and is not therefore the best marker in inter-species comparisons between goats and sheep, fed on the low quality diet used in the present study.

3.4.4 Fibre Degradation

The results of this study have shown the superiority of goats over sheep in digesting fibre, as shown by the faster rumen FDR (%/h) of cellulose, hemicellulose and lignin. The apparent digestibility of lignin was significantly greater ($P<0.1$)in goats, compared to sheep and the apparent digestibilities of cellulose and hemicellulose tended to be greater in goats than in sheep, with the differences not attaining significance ($P>0.1$) (Tables 3.5-3.6). Previous comparison studies of fibre digestion by goats and sheep, as reported in the Literature Review, support the findings of the present experiment, where goats digest the fibre of low quality forages better than sheep (Jones et al., 1972; El Hag, 1976; Gihad, 1976; Doyle et al., 1984).

It is known that as the fibre percentage of forages increases, voluntary intake decreases, together with a decrease in both ruminal and total tract digestion (Sutton, 1980; Hogan, 1982; Zinn and Owens, 1983). The reasons for a greater digestion of fibre in goats, despite a higher intake, are possibly due to three factors:

1. Longer MRT (h) of digesta in the rumen,

2. Larger proportion of small particles (larger surface area) in the rumen,

3. A more active fibre-digesting microbial population.

Goats showed a tendency to have a longer MRT (h) of both the liquid (Cr-EDTA), and the particulate components of the diet (Ru-Phen, Lignin, particulate pool <0.25 mm), compared to sheep (Table 3.10). This could result in a greater digestibility of fibre due to a longer time of exposure to microbial attack.

Goats had a larger proportion of small particles (<1.0 mm) in the rumen than sheep (Table 3.9). Hence a larger surface area of the fibrous substrates was possibly available for microbial attachment and fibre digestion in goats, compared to sheep. The role of an adherent bacterial population involved in fibre digestion is well established (Hungate, 1966; Akin, 1976). Scanning and electron microscopy have shown that "chewed" feed particles entering the rumen are colonised within five minutes by bacteria (Cheng et al., 1977; Akin, 1979; Elliott and Norton, 1985). Dehority and Johnson (1964) reported that the "in-vitro" digestibility of cellulose was increased by reducing the feed particle size to <1.0 mm.

It seems probable that goats are more efficient "chewers" during eating than sheep. This would present the rumen with smaller particles larger in surface area, and would explain the faster rumen "apparent" FDR (%/h) of fibre, and greater apparent fibre digestibility observed in goats, compared to sheep in the present study. From Section 3.4.2, it was observed that the rumen environment of goats possibly favoured the development of a more active fibre-

digesting microbial population. This would also allow goats to digest fibre better than sheep.

3.4.5 Validity of Assumptions for ^{15}N Marker Methodology

A basic assumption for the interpretation of isotope kinetic data is that the animal, and therefore the N pools and the N transactions in the pools sampled, are in a steady-state condition throughout the infusion period (Nolan and Leng, 1972; Nolan, 1975).

This was achieved during the present experiment by a hourly feeding regimen, with the animals fed at 90% of "ad-lib" intake. Feed refusals were therefore kept low, and daily feed intake was constant. Coefficients of variation (CV) for feed intake (g DMI/Kg $W^{0.75}$/d) for goats ranged from 1.5 to 5.4% (mean 3.4%), and CV for feed intake (g DMI/Kg $W^{0.75}$/d) in sheep ranged from 5.4 to 14.8% (mean 8.9%). Further indications of the validation of the assumption were obtained from relatively constant concentrations (mg N/L) of rumen NH_3-N (Figure 3.9) and pH during the ^{15}N infusion period.

3.4.6 Kinetics of Rumen Ammonia Production

Rumen NH_3-N concentration was higher in goats, than in sheep (Table 3.13), although the IRL of NH_3-N from the rumen expressed as g N/g dietary N/d, was not different between goats and sheep.

Four factors might have contributed to this situation, namely differences between species in:

1. Water transactions in the rumen,

2. Net outflow of NH_3-N to the abomasum,

3. Incorporation of NH_3-N into bacterial cells, and

4. Absorption of NH_3-N from the rumen wall.

The rumen liquid pool (g/Kg $W^{0.75}$) was larger in goats than in sheep (Figure 3.3). A larger rumen liquid pool (g/Kg $W^{0.75}$) will have

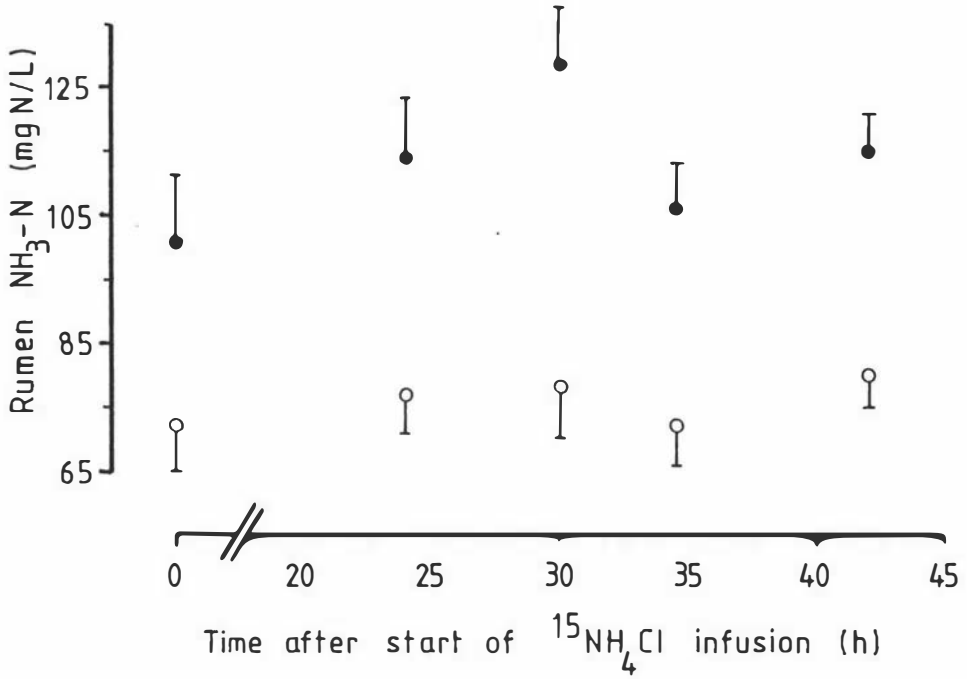

Figure 3.9. Ammonia concentration (mg N/L) in the rumen of goats (•) and sheep (o) during continuous intraruminal infusion of $^{15}NH_4Cl$ (± SEM).

a diluting effect, and at constant rumen NH_3-N IRL (g/g N intake) will lower the rumen NH_3-N concentration (mg N/L). Despite this, the higher rumen NH_3-N concentration observed in goats compared to sheep, indicates that goats must have a mechanism for concentrating NH_3-N in the rumen when fed on low quality roughages. Figure 3.3 indicated that goats had slower rumen water inflow and outflow (g/g DMI/d) than sheep. This might have contributed partly to a concentrating effect of NH_3-N in the rumen of goats, compared to sheep. The lower water intake of goats (g/g DMI/d) than sheep, would appear to be the most important component.

NH_3-N is lost irreversibly from the rumen fluid (IRL, g N/d) by three routes, namely:

1. Absorption of NH_3-N through the rumen epithelium,

2. Incorporation into microbial cells which leave the rumen,

3. Flowing into the fluid passing out of the rumen.

All the routes (1-3) defined above occur within the time of the experiment.

The amount of NH_3-N (mg N/gN intake/d) flowing to the abomasum in the fluid leaving the rumen, was not different between goats and sheep ($P>0.1$). It represents only a small proportion of the total IRL (0.08 in goats; 0.06 in sheep). This pathway of IRL should not have affected the differences in rumen NH_3-N concentrations observed between goats and sheep.

A lower proportion of NH_3-N was incorporated into the microbial cells of goats, compared to sheep ($P=0.11$), indicating that goats obtained a higher proportion of their N requirements from NAN sources when fed on the roughage used in the present study (Table 3.13). This would contribute to a higher NH_3-N concentration in the rumen of goats, and perhaps allow a limited amount of NH_3-N to be used to synthesise more microbial protein.

However, a mention must be made here of the methodology used for the isolation of bacteria (Nolan et al., 1976). The differential centrifugation used to isolate the rumen bacteria (Section 2.8.6.2.2) would tend to selectively remove the fibre-digesting bacteria which adhere closely to plant materials (Hungate, 1966). It is assumed that the populations of bacteria in goats and sheep have been affected in the same way.

NH_3-N absorption through the rumen wall was not measured in this experiment. It is known that NH_3-N absorption increases with increases in the concentration of unionised NH_3 in the rumen fluid (Siddons, Nolan, Beever and MacRae, 1985). A tendency for the rumen pH to rise towards 7.0 or above, would tend to facilitate the absorption of unionised NH_3 through the rumen wall (Nolan, 1981). The pH of the rumen was significantly lower ($P<0.05$), in goats than in sheep (6.7 vs 6.9, Table 3.11), which would tend to reduce NH_3-N absorption, and therefore increase rumen NH_3-N concentration.

The pool sizes of microbial-NAN have been calculated from the total rumen NAN pool size and the proportion of this as microbial protein, using ^{15}N data, and the nonmicrobial-NAN pool size was calculated by difference (Table 3.14). The protein supply to the small intestines of goats and sheep has been calculated with the following assumptions:

1. Estimates of the microbial-NAN flowing to the abomasum (Equation 11) were based on the assumption that the microbial population would leave the rumen with the same FOR (%/h) as Ru-Phen (Faichney, 1980).

Microbial-NAN outflow (g/d) =

Microbial-NAN pool (g) x FOR(/d) of Ru-Phen (11)

Ru-Phen is known to move from particle to particle (Faichney and Griffiths, 1978; Dixon and Milligan, 1980), and is mostly associated with small particles (Dixon and Millligan, 1980). A proportion of small particles leaves the rumen flowing close to the rate of water, and a proportion also leaves the rumen flowing close to the rate of particulate dry matter. Hence the FOR (%/h) of Ru-Phen is

Table 3.14. Calculated microbial-NAN (g) and calculated nonmicrobial-NAN (g) in the rumen of goats and sheep, fed on mature prairie grass straw at 90% "ad-lib", with the abomasal flows.

(Mean values with the standard error of difference (SED) for six goats and seven sheep.)

		Goats	Sheep	SED	
Rumen pool size:					
Microbial-NAN:	g	6.00	2.79	0.866	**
	g/g NI†	0.56	0.31	0.082	*
Nonmicrobial-NAN:	g	6.31	5.88	1.115	NS
	g/g NI	0.59	0.68	0.100	NS
Total-NAN:	g	12.31	8.67	1.189	*
	g/g NI	1.15	0.99	0.096	NS
NAN flow to the abomasum:					
Microbial-NAN:	g/d ¶	9.65	4.51	1.517	**
	g/g NI/d	0.89	0.51	0.134	*
Nonmicrobial-NAN:	g/d #	3.76	3.99	0.448	NS
	g/g NI/d	0.35	0.46	0.049	(*)
Total-NAN:	g/d	13.32	8.50	1.371	**
	g/g NI/d	1.24	0.98	0.123	(*)
Proportion of microbial-NAN/Total-NAN flowing to abomasum		0.72	0.53	0.075	*

¶ Microbial-NAN (g) x FOR (/d) of Ru-Phen.

\# Nonmicrobial-NAN (g) x FOR (/d) of lignin.

† Dietary N intake.

** P<0.01; * P<0.05; (*) P<0.1; NS Non-significant

intermediate between the value for solutes and particles (Faichney, 1980; Dixon et al., 1983). Microbial material which leaves the rumen is also derived from a free-floating population (Cheng and Costerton, 1979), and a population attached to particulate matter (Egan, Walker, Nader and Storer, 1975; Akin, 1976; Faichney, 1980). Hence, Faichney (1980) concluded that the FOR (%/h) of microbial material, like that of Ru-Phen, was intermediate between the values for solutes and particles.

2. It was assumed that all undegraded plant NAN left the rumen (Equation 12) on the same particle as lignin.

Nonmicrobial-NAN outflow (g/d) =

Nonmicrobial-NAN pool (g) x FOR (/d) of Lignin (12)

By definition, any undegraded N would leave the rumen on the same particle as lignin.

Based on the assumptions made in (11) and (12), the following conclusions can be drawn from the calculations shown in Table 3.14. The rumen microbial NAN pool size (g/g N intake), was significantly greater in goats ($P<0.05$) than in sheep. The total NAN pool size (g/g N intake) was greater in goats but the difference did not attain significance ($P>0.1$). The calculated microbial NAN flow to the abomasum (g/g N intake/d), was significantly higher in goats. The calculated degradability of dietary protein appeared to be greater ($P>0.1$) in goats (0.65), than in sheep (0.54). The calculated flows of total NAN (g/g N intake/d) to the abomasum tended to be greater in goats than in sheep. The calculated proportion of microbial NAN/total NAN in digesta leaving the rumen was higher in goats, compared to sheep ($P<0.05$).

The greater calculated degradability of dietary protein by goats than sheep, could be explained by the longer MRT (h) of digesta in the rumen of goats. Watson and Norton (1982), postulated that goats degraded dietary protein to a greater extent than sheep, and would explain the superior utilisation of fibre by goats. It is probable that the higher rumen concentration of NH_3-N in goats is a factor in their greater rumen bacterial growth and fibre digestion, as compared

to sheep. It has been reported that concentrations of 50 mg NH_3-N/L are apparently required to maintain normal rumen microbial growth (Satter and Slyter, 1974). However, the optimal concentration of NH_3-N for maximal rumen fermentation was estimated as 235 mg NH_3-N/L (Mehrez, Ørskov and McDonald, 1977). This implies that on low quality forages, with a slow rate of fermentation of the cell-wall carbohydrates, such as the low quality prairie grass straw used here, low concentrations of NH_3-N are limiting to microbial activity. Evidence to support this statement can be obtained from the improved utilisation of low quality forages by sheep when given a urea supplement, which is rapidly degraded in the rumen (Elliott, McMeniman, Norton and Cortes, 1983; McMeniman and Elliott, 1984). Rumen NH_3-N concentration (mg N/L) in sheep was raised from 39 to 74 mg N/L, and was associated with a 18% increase in voluntary DMI, when fed on oaten chaff, supplemented with 8 g of urea/d (McMeniman and Elliott, 1984). Goats, in contrast to sheep, can maintain higher rumen NH_3-N concentrations, and utilise the low quality forages better than sheep.

3.5 CONCLUSIONS

3.5.1 Goats were markedly superior to sheep in utilising the low quality prairie grass straw, with a greater voluntary intake (g/Kg $W^{0.75}$/d) of DM and OM ($P<0.001$). The ratio of DDMI(g/Kg $W^{0.75}$) (goats/sheep) was calculated to be 2.12.

3.5.2 The apparent digestibilities of DM ($P<0.05$) and OM ($P>0.1$) were greater by goats than sheep.

3.5.3 Sheep selected a diet (g/Kg OM) lower in fibre and higher in total N than the feed offered. Goats showed no evidence of selection.

3.5.4 Goats digested the fibre components better than sheep, with the superiority being greater for the least digestible component, lignin ($P<0.1$). Goats had faster rumen FDR (%/h) for cellulose ($P<0.05$), hemicellulose ($P<0.001$), and lignin ($P=0.09$).

3.5.5 Goats tended ($P>0.1$) to have a longer MRT (h) for Cr-EDTA, Ru-Phen and lignin in the rumen, than sheep. The "apparent" MRT (h)

of particles 1.0-0.5 mm was shorter in the rumen of goats ($P<0.05$) than in sheep. The "apparent" MRT (h) of particles <0.25 mm was longer in goats than in sheep ($P>0.05$).

3.5.6 Goats had a larger rumen pool size (g/Kg $W^{0.75}$) of DM and liquid than sheep ($P<0.01$). This was shown to be a factor in the increased feed intake of goats compared to sheep, despite the longer MRT of digesta in the rumen of goats.

3.5.7 The particle size as threshold to passage through the reticulo-omasal orifice was 1.0 mm in goats and sheep, but goats were able to pass a larger ($P<0.05$) proportion of particles 1-0.5 mm in size out of the rumen than sheep, when fed on the roughage diet used in the present study.

3.5.8 Goats had a larger proportion of particles <0.25 mm in the rumen than sheep ($P=0.07$). This would provide a larger surface area for microbial attachment and attack of the fibrous substrates.

3.5.9 Goats had higher concentrations of NH_3-N, butyrate and valerate ($P<0.05$) in the rumen than sheep. The rumen environment of goats, together with a pH of 6.73, would be favourable to the potential growth of fibre-digesting bacteria, more so than sheep.

3.5.10 Despite higher rumen NH_3-N concentration in goats, the IRL of NH_3-N from the rumen (g/g N intake/d) was not different between the two species. Although the production rates of NH_3-N were not different between the two species when compared per g dietary N intake/d, goats had a concentrating mechanism which increased the NH_3-N (mg N/L) concentration in the rumen.

3.5.11 Goats obtained a lower proportion of their N requirements for microbial growth from NH_3-N ($P=0.11$), so a limited amount of NH_3-N was used to synthesise more bacterial protein.

3.5.12 It was calculated that the proportion of microbial NAN/total NAN flowing to the abomasum was higher in goats, than in sheep ($P<0.05$). The calculated total NAN flow to the abomasum (g/g N intake/d) tended to be greater in goats than in sheep ($P<0.1$).

3.5.13 It was concluded that the ability of goats to maintain a higher rumen NH_3-N concentration is probably a contributing factor to a greater bacterial growth and fibre digestion in goats, as compared to sheep when fed on low quality forages.

CHAPTER 4. VOLUNTARY INTAKE AND RUMEN DIGESTION OF A MEDIUM QUALITY FORAGE BY DEER, GOATS AND SHEEP. A SEASONAL STUDY.

4.1. INTRODUCTION

Comparative studies of voluntary feed intake (g/Kg $W^{0.75}$/d) in deer and sheep have shown that both species have seasonal cycles of feed intake. Deer have a dramatic decrease in appetite in winter, and show a marked increase in feed intake in early spring/summer (Milne et al., 1978; Fennessy, 1981; Suttie and Simpson, 1985). Domestic sheep show a similar pattern of seasonal feed intake, but the trend is very much attenuated, when compared to deer (Kay, 1979; Blaxter and Boyne, 1982). Goats enter a period of growth stasis in winter (McCall, Clayton and Dow, 1989), but there are no published reports on the seasonal feed intake in goats.

The seasonal cycles in feed intake in deer have been associated with changes in photoperiod, with the hormone melatonin (Me) acting as a transducer (Kay, 1979; Simpson et al., 1984; Bubenik and Smith, 1985; Suttie and Simpson, 1985). It has been postulated that Me synchronises the body internal rhythm with changes in daylength (Barry et al., 1989). Me is secreted by the pineal gland during the hours of darkness (Bubenik, 1983). Hence, photoperiods with longer hours of darkness lead to longer periods where Me concentration is high. During winter the period of elevated Me concentration is long, during summer short (Wurtman and Anton-Tay, 1969; Plotka et al., 1981; Kennaway, Dunstan, Gilmore and Seamark, 1983; Lincoln, 1983). The nutritional mechanisms associated with the seasonal cycles are not clear. Milne et al. (1978), reported that an increase in feed intake in summer in deer occurred without any effects on the digestibility of the feed, nor the MRT (h) of digesta in the rumen.It was postulated that a possible increase in the rumen volume of deer in summer would be a factor in regulating the seasonal feed intake, but this has never been directly measured. Hofmann (1985), reported that the chamois had a maximum rumen volume in summer (10-10.5 L), compared to 3.5-4.0 L in winter.

Objectives of the present experiment were to measure seasonal changes in the voluntary feed intake of a standard medium quality

forage fed to deer, goats and sheep both in summer and in winter. Seasonal differences between species, and within species were determined. The mechanisms for the seasonal cycles in voluntary feed intake were studied in relation to MRT (h) of digesta in the rumen, rumen pool size, and apparent digestibility.

Rumen ammonia (NH_3-N) production is fully documented for the sheep (Nolan et al., 1972; 1976), and Chapter 3 has provided data for the goats, when fed on low quality forages. There are no published data for Red Deer, and in the present investigation the kinetics of rumen NH_3-N production were measured in deer, goats and sheep fed a medium quality forage. Further objectives of the study were to investigate particle size breakdown in the rumen of the three species, and to establish the critical particle size as threshold to passage through the reticulo-omasal orifice. This is known for sheep (Reid et al., 1979; Poppi et al., 1980), and has been investigated for goats in Chapter 3, but there are no published data for deer. The "apparent" rumen FOR (%/h) of particles was also determined for the deer, goats and sheep, and compared with that of lignin.

4.2 EXPERIMENTAL

4.2.1 Diet

Lucerne hay *(Medicago sativa)*, purchased in bulk from a single source, was fed to the animals in summer, and in winter. The animals were allowed free access to a multimineral salt block (50 g) (Appendix A), placed in the feed bin. The hay was chaffed into 50-80 mm lengths and placed upon belt feeders which delivered the day's ration in 24 feeds, at 1h-interval.

4.2.2 Animals

Five castrated hand-reared Red Deer were used; these were aged 2½ years and weighed 94.8 Kg LWT (SD 5.46) in winter, and were aged 3 years and weighed 96.2 Kg LWT (SD 5.60) in summer. Seven castrated Angora-NZ feral goats were used; these were aged 2½ years and weighed 42.5 Kg LWT (SD 4.83) in winter, and were aged 3 years and weighed 43.4 Kg LWT (SD 4.93) in summer. Eight Border-Leicester/ Romney cross

wethers were used; these were aged 2½ years and weighed 57.5 Kg LWT (SD 6.58) in winter and were aged 3 years and weighed 60.7 Kg LWT (SD 7.18) in summer. All animals were fistulated in the rumen, and were fitted with permanent rubber cannulae (63 mm ID for goats and sheep; 83 mm ID for deer). All animals were kept individually in metabolic crates. Goats and sheep were housed in conventional metabolic crates. Deer were kept in metabolic crates as designed by Milne et al. (1978), and modified as described in Section 2.3.

4.2.3 Experimental Design

The experimental design is shown schematically in Figure 4.1.

The winter experiment was conducted in May-June 1987, and the summer experiment in November-December 1987. VFI was measured with the animals fed "ad-lib", with the feed offered being 1.15 that of the previous day's DMI. VFI was measured for 8 d over d13-d20, after a pre-feeding period of 12 d. The apparent digestibility and N balance measurements were carried out over d13-d20, with the animals being fed at "ad-lib". At the end of the VFI and apparent digestibility measurements, the animals were restricted to 90% "ad-lib" intake.

The non-radioactive dual-marker Cr-EDTA/Ru-Phen infusion trial commenced on d-25 and continued until d-30. After 5 d of continuous infusion, the rumen contents were emptied out ("bailing") on d-30, and subsamples taken before returning the warmed rumen digesta back to the rumen. The ^{15}N infusion trial was carried out in winter only, over d28-d30.

4.2.4 Marker Infusion Procedures

All infusions were administered by a peristaltic pump, fitted with silicone rubber tubing. Following a priming dose of 40 g (Faichney, 1975), the dual-marker Cr-EDTA/Ru-Phen (containing 2 mg Cr/g and 0.0498 mg Ru/g), was continuously infused at a constant rate into the rumen for 5 d. The infusion rates were calculated on the DMI/d, and administered at a rate of about 12 mg Ru/Kg DMI/d. The infusion rates of Cr-EDTA/Ru-Phen (g/h), and of Cr (mg/h) and Ru

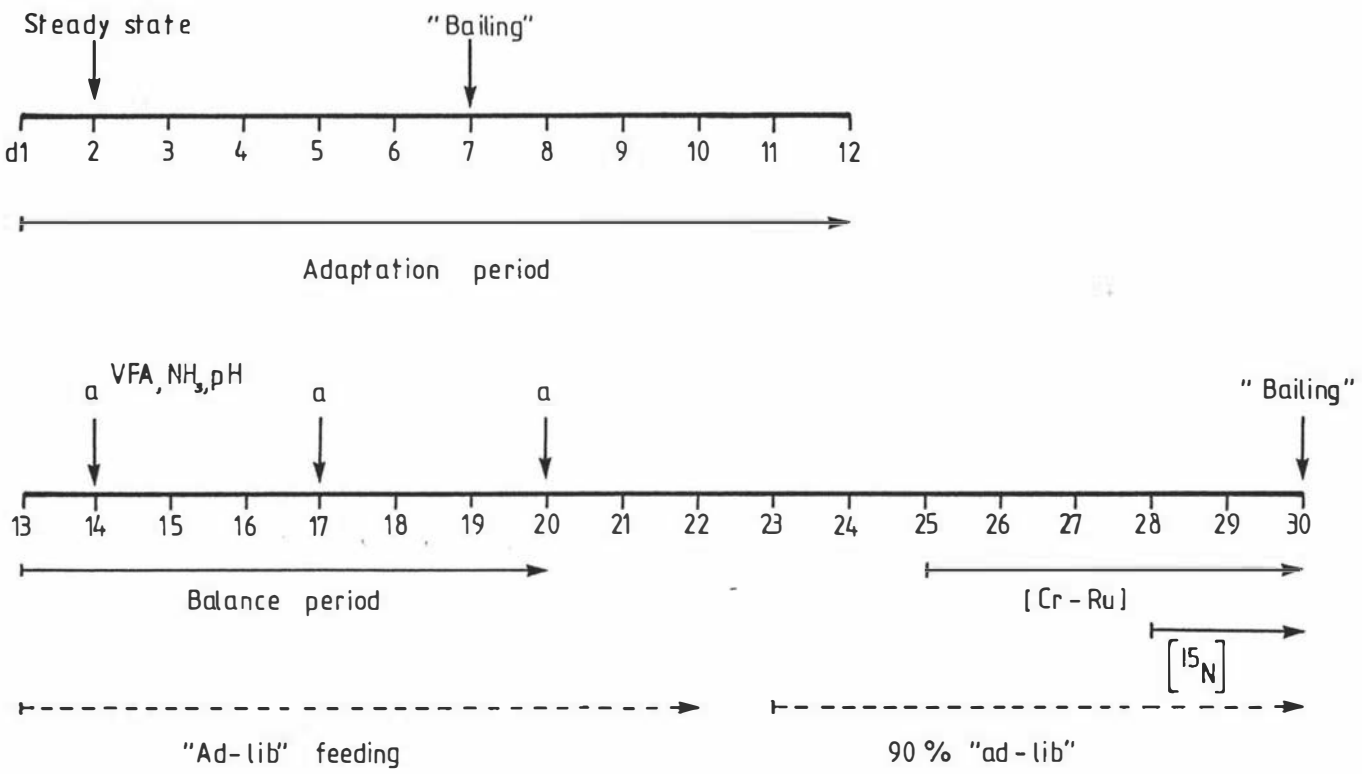

Figure 4.1. Schematic representation of the experimental design (Experiment 2).

(mg/h) are given in Table 4.1 for deer, goats and sheep, in summer and in winter.

^{15}N ammonium chloride salt (95.55 atoms % excess), was added to the dual-marker solution (589.3 mg $^{15}NH_4Cl$/Kg of dual-marker solution; pH=6.7), and infused continuously for the last 42 hours of marker infusion period into the rumen, during the winter experiment only. Infusion commenced from 18.00 hours on d-28, and continued until 12.00 hours on d-30. The infusion rate was 63.25 mg ^{15}N/d for deer, 41.93 mg ^{15}N/d for goats, and 51.62 mg ^{15}N/d for sheep.

4.2.5 Sampling

Composite samples of feed offered were collected daily during the summer and winter experiments, and pooled on a weekly basis. Feed refusals, faeces and urine samples were taken daily during d13-d20 and pooled at -20 C, separately for each animal. A representative sample of the rumen digesta was taken from 2 deer, 4 goats and 4 sheep, on d-7 of the pre-feeding period in each of the summer and winter experiments. The rumen digesta was used as a matrix for the preparation of separate summer and winter Cr and Ru standard curves for deer, goats and sheep.

Rumen fluid samples for NH_3-N, pH and VFA were taken on d-14, d-17 and d-20, at 10.00 and 15.00 hours, using brass probes placed in the rumen (as per specifications in Section 2.8.1). At "bailing", subsamples of the whole rumen digesta were taken for NH_3-N, VFA, pH, particle size and chemical analyses.

In winter rumen fluid samples were taken for NH_3-N determination and enrichment of NH_3-N with ^{15}N, before the start of the infusion of the ^{15}N isotope, at 17.30 hours on d-28 (background sample); on d-29, at 18.00 hours (after 24 h infusion) and 24.00 hours (after 30 h infusion); on d-30, at 07.00 hours (after 37 h infusion), at 12.00 hours (after 42 h infusion). At "bailing" (after 42-42½ h infusion) on d-30, a representative sample of the whole rumen digesta was taken for determination of enrichment of NH_3-N, bacterial-N and rumen digesta-NAN with ^{15}N.

Table 4.1. Infusion rates of Cr-EDTA/Ru-Phen (g/h), Cr and Ru (mg/h) in the rumen of deer, goats and sheep fed on lucerne hay, at 90% "ad-lib" intake, in summer and in winter.

	Deer	Goats	Sheep
Summer:			
Cr-EDTA/Ru-Phen (g/h)	20.8	12.5	13.5
Cr (mg/h)	41.6	25.0	27.0
Ru (mg/h)	1.04	0.62	0.67
Winter:			
Cr-EDTA/Ru-Phen (g/h)	16.7	11.7	14.6
Cr (mg/h)	33.4	23.4	29.2
Ru (mg/h)	0.83	0.58	0.73

Samples of rumen fluid, rumen digesta, bacterial cells, faeces, feed offered, refusals and urine were prepared and stored, as per procedures described in Section 2.8.

4.2.6 Chemical Analysis

The following analyses were performed using the methods described in detail in Section 2.9. Samples of feed offered, feed refusals and faeces were analysed for OM, total N, cellulose, hemicellulose, lignin and heat of combustion. Urine samples were analysed for total N. Rumen fluid samples were analysed for NH_3-N, pH, enrichment of NH_3-N with ^{15}N and VFA (acetate, propionate, n-butyrate, iso-butyrate, n-valerate and iso-valerate). Rumen bacterial-N samples and samples of rumen digesta-NAN were analysed for enrichment with ^{15}N. Particle size analysis was determined on subsamples of whole rumen digesta and faeces. Cr and Ru in rumen digesta were analysed by XRF-spectrometry, using the preparation of separate standard curves in summer and in winter. Table 4.2 gives the correlation coefficient values (r), of the calibration curves for Cr and Ru.

4.2.7 Calculations of Data

The FOR (%/h) and MRT (h) of Cr-EDTA, Ru-Phen and lignin, and the FDR (%/h) of lignin were calculated, as described in Section 2.10.1. The FDR (%/h) of cellulose and hemicellulose have been calculated, as described by Equations 1 and 2, Section 3.2.7. The calculations were based on the assumption that cellulose, hemicellulose and lignin are all bound on the same matrix, and therefore leave the rumen on the same particle (Van Soest, 1975). The calculations assume that cellulose and hemicellulose leave the rumen on the same particle as lignin, and hence have the same FOR (%/h) as lignin.

The IRL of NH_3-N (mg N/d) from the rumen, and the proportion of bacterial-N from NH_3-N and the proportion of bacterial-N from total digesta-NAN, were calculated as shown in Section 2.10.2. ✓

The "apparent" FOR and MRT of particles from the rumen (>2.0 mm, 2.0-1.0 mm, 1.0-0.5 mm, 0.5-0.25 mm, <0.25 mm), have been calculated as described by Equation 3, Section 3.2.7. The calculation was based

Table 4.2. Correlation coefficient values (r) of the calibration curves for Cr and Ru (summer and winter), made in the rumen digesta as matrix, for deer, goats and sheep.

	Rumen digesta as matrix		
r value	Deer	Goats	Sheep
Ruthenium:			
Summer			
Winter	0.998	0.999	0.999
Chromium:			
Summer			
Winter	1.000	1.000	1.000

on the assumption that there is no further breakdown in particle size once digesta has left the rumen (Grenet, 1970; Poppi et al., 1980).

Metabolisable energy for maintenance was taken as 0.39 MJ/Kg $W^{0.75}$/d), both for sheep (ARC, 1980), and for goats (Holmes and Moore, 1981). The metabolisable energy required for maintenance for deer was taken as 0.45 MJ/Kg $W^{0.75}$/d in winter and 0.55 MJ/Kg $W^{0.75}$/d in summer (Simpson et al., 1978).

4.2.8 Statistical Design and Analysis

A split-plot design was used, with animal species as main plots (x3), and season (x2) as sub-plots. Analysis of variance procedures were used to determine differences between the species with season, and species/season interactions. 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, since there were no significant differences ($P>0.1$), between day/or time of the day at which sampling occurred. There were no differences for goats and sheep ($P>0.1$) between the enrichment of the rumen fluid NH_3-N samples with ^{15}N, taken at 30, 36, and 42 h after commencement of the ^{15}N infusion, and the sample taken at "bailing". For deer, however, the differences between the enrichment values of the rumen fluid NH_3-N samples with ^{15}N, did not attain significance ($P>0.1$), for samples taken at 36, 42 h after commencement of ^{15}N infusion, and sample taken at "bailing". Hence, it can be concluded that the rumen NH_3-N in deer, in contrast to sheep and goats, takes more than 30 h to reach towards "plateau" enrichment of NH_3-N with ^{15}N. The ^{15}N enrichment value of the sample taken at "bailing" was used in the calculations of rumen NH_3-N irreversible loss rate (IRL).

4.3 RESULTS

4.3.1 Chemical Composition of Diet and Selection of Feed Offered

The chemical composition (g/Kg DM) of the lucerne hay did not change from winter to summer, with constant values for OM, total N and total fibre (Table 4.3 a).

The refusals of sheep and deer (g/Kg OM) were not significantly different in composition ($P>0.1$), both in summer and in winter, and contained lower contents of total N and higher proportions of total fibre than the feed offered (Table 4.3 b). The refusals of goats contained significantly higher proportions of total N than sheep ($P<0.01$) and deer ($P<0.1$), and lower contents of total fibre both in summer and in winter. Both deer and sheep appeared to select for a diet higher in total N and lower in total fibre than the feed offered, whereas goats showed no evidence of any feed selection.

4.3.2 Voluntary Feed Intake and Apparent Digestibility of DM and OM

4.3.2.1 Seasonal Effects

Sheep showed no seasonal differences ($P>0.1$) in voluntary DMI, OMI, DDMI, DOMI (g/Kg $W^{0.75}$/d), or MEI (MJ/Kg $W^{0.75}$/d). This was associated with no significant changes ($P>0.1$) in the apparent digestibilities of DM and OM, and in the rumen pool sizes (g/Kg $W^{0.75}$) of DM and liquid (Tables 4.4 and 4.5).

In contrast to sheep, deer increased significantly ($P<0.1$) their voluntary DMI, OMI, DDMI and DOMI(g/Kg $W^{0.75}$/d) from winter to summer by about 30%, and the MEI (MJ/Kg $W^{0.75}$/d) was increased by about 25%. The significant increase in intake from winter to summer was associated with a significant increase in the rumen pools of DM ($P<0.05$) and liquid ($P<0.01$), when expressed as g/Kg $W^{0.75}$.
The total rumen pool (DM + liquid) (g/Kg $W^{0.75}$), was significantly increased ($P<0.01$) by 51% from winter to summer. There were no seasonal effects on the apparent digestibilities of DM and OM in the deer, despite the dramatic increase in voluntary feed intake in summer.

Table 4.3a. Chemical composition (g/Kg dry matter (DM)) of lucerne hay *(Medicago sativa)* fed to deer, goats and sheep in summer and in winter.

	Summer [@]	Winter [$]
Organic matter	906	911
Heat of combustion (MJ/Kg DM)	18.6	18.7
Total Nitrogen	28.5	28.2
Cellulose	223	208
Hemicellulose	75	76
Lignin	105	103
Total Fibre [#]	403	387

[#] cellulose + hemicellulose + lignin
[@] summer 1987
[$] winter 1987

Table 4.3b. Chemical composition (g/Kg organic matter (OM)) of lucerne hay, and the feed refusals by deer, goats and sheep when fed "ad-lib" in summer and in winter.
(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Lucerne hay	Deer	Goats	Sheep	SEM
Heat of combustion	S	20.5	20.0	20.2	20.2	0.03
(MJ/Kg OM)	W	20.5	20.0	20.4	20.2	0.08
Total Nitrogen	S	31.5	21.2	28.6	22.3	0.78
	W	31.0	20.8	30.2	24.6	1.42
Cellulose	S	246	276	244	306	5.9
	W	228	302	244	250	8.2
Hemicellulose	S	83	99	87	97	1.7
	W	83	104	97	109	2.1
Lignin	S	116	126	125	132	0.93
	W	113	124	120	123	1.4
Total Fibre !	S	445	500	457	535	8.1
	W	425	530	461	488	10.4

S = summer
W = winter
! cellulose + hemicellulose + lignin

Table 4.4. Voluntary and digestible intakes of dry matter and organic matter (g/Kg $W^{0.75}$/d) together with their apparent digestibilities (%), and metabolisable energy intake (MJ/Kg $W^{0.75}$/d) of deer, goats and sheep fed on lucerne hay in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Voluntary intake : (g/Kg $W^{0.75}$/d)					
Dry matter	S	62.5	68.7	52.2	3.20
	W	46.7	57.4	54.8	4.24
Organic matter	S	56.6	62.2	47.2	2.90
	W	45.7	54.7	52.0	5.52
Digestible dry matter	S	35.6	38.6	28.2	1.88
	W	27.4	36.9	31.6	1.77
Digestible organic matter	S	34.2	36.4	27.0	1.79
	W	27.0	35.4	31.0	1.73
Metabolisable energy intake ! (MJ/Kg $W^{0.75}$/d)	S	0.50	0.58	0.43	0.029
	W	0.40	0.56	0.49	0.028
Apparent digestibility of dry matter (%)	S	56.7	55.9	54.2	0.44
	W	54.7	62.0	55.9	0.78
Apparent digestibility of organic matter (%)	S	60.2	58.2	57.2	0.46
	W	59.0	65.3	60.1	0.75

! Digestible energy intake x 0.82.

S = summer.

W = winter.

Table 4.5. Total rumen (DM + liquid) pool size, DM and liquid pool sizes (g/Kg $W^{0.75}$) of deer, goats and sheep fed on lucerne hay in summer and in winter, and the dry matter content (%) of the rumen digesta.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Rumen pool size: ($g/Kg\ W^{0.75}$)					
Total rumen pool (DM + liquid)	S	289	340	275	17.5
	W	191	268	307	13.4
Rumen DM pool	S	43.3	45.7	37.6	2.41
	W	31.8	37.1	40.4	1.88
Rumen liquid pool	S	245	294	237	15.2
	W	159	231	267	11.7
Dry matter of rumen digesta (%)	S	15.1	13.4	13.7	0.19
	W	16.6	13.8	13.2	0.26

S = summer.
W = winter.

Goats showed a 17% increase ($P>0.1$) in voluntary DMI and OMI (g/Kg $W^{0.75}$/d) in summer, compared to winter. The increase in intake was associated with a significant decrease in the apparent digestibilities of DM ($P<0.01$), and OM ($P<0.001$). This resulted in no seasonal changes ($P>0.1$) in the DOMI (g/Kg $W^{0.75}$/d) and MEI (MJ/Kg $W^{0.75}$/d) in goats. The rumen pool sizes (g/Kg $W^{0.75}$) of DM ($P<0.01$) and liquid ($P<0.05$) increased significantly from winter to summer. The total rumen pool (DM + liquid) (g/Kg $W^{0.75}$) in goats increased significantly ($P<0.01$) by 27%, from winter to summer.

4.3.2.2 Species Effects

The voluntary DMI (g/Kg $W^{0.75}$/d) of deer in winter was 15% lower than that of sheep, although the difference did not attain significance ($P>0.1$). Deer and sheep digested DM and OM with similar efficiencies in winter ($P>0.1$), despite the differences in voluntary DMI and OMI (g/Kg $W^{0.75}$/d) between the two species. The summer DMI and OMI (g/Kg $W^{0.75}$/d) of deer was 20% greater than that of sheep ($P<0.05$), yet deer digested the DM ($P=0.06$) and the OM ($P<0.05$) components of the feed better than sheep at this time.

The MEI (MJ/Kg $W^{0.75}$/d) of deer and sheep in winter were 0.80 and 1.26 that of their maintenance requirements, respectively; in summer the MEI of deer and sheep were 0.91 and 1.19 that of their maintenance requirements, respectively. The low appetite in deer in winter was associated with a significantly ($P<0.01$) smaller total (DM + liquid) rumen pool size (g/Kg $W^{0.75}$) than sheep. The total (DM + liquid) rumen pool size (g/Kg $W^{0.75}$) in deer was 60% that of sheep in winter, but similar to that of sheep during summer.

The DMI and OMI (g/Kg $W^{0.75}$/d) of goats and sheep were similar in winter ($P>0.1$). At similar DMI and OMI, goats digested DM and OM ($P<0.01$) better than sheep in winter. Hence the DDMI and DOMI (g/Kg $W^{0.75}$/d) of goats in winter were about 15% greater than sheep, although the differences did not attain significance ($P>0.1$). In summer, the DMI and OMI (g/Kg $W^{0.75}$/d) of goats were significantly greater than sheep ($P<0.05$). At greater intakes of DMI and OMI (g/Kg $W^{0.75}$/d), the goats digested the DM and OM ($P>0.1$) with similar efficiencies to sheep. Hence, in summer, the DDMI and DOMI (g/Kg

$W^{0.75}$/d) were 36% greater than sheep ($P<0.05$). The MEI (MJ/Kg $W^{0.75}$/d) of goats and sheep were 1.44 and 1.26 that of maintenance requirement, respectively; in summer, the MEI of goats and sheep (MJ/Kg $W^{0.75}$/d) were 1.49 and 1.19 that of their maintenance requirements, respectively. Compared to sheep, the total (DM + liquid) rumen pool size (g/Kg $W^{0.75}$) in goats tended to be smaller in winter and greater in summer, with the differences not attaining significance.

4.3.3 MRT of Digesta in the Rumen

There were no indications of seasonal effects in the rumen MRT (h) of the liquid marker Cr-EDTA and the particulate markers Ru-Phen and lignin in goats and sheep (Table 4.6). Deer showed no seasonal changes in the MRT (h) of Cr-EDTA and Ru-Phen in the rumen, but the rumen MRT (h) of lignin tended to be longer (26%) in summer than in winter, although the difference did not attain significance ($P=0.16$). The MRT (h) of lignin in the rumen of deer in summer, was significantly longer than in sheep ($P=0.13$) and goats ($P<0.05$). All three species retained lignin for a longer time in the rumen, with intermediate values for Ru-Phen, and least values for Cr-EDTA. The deer had a faster FOR (%/h) of liquid (Cr-EDTA) from the rumen than sheep ($P<0.01$) and goats ($P<0.01$), both in summer and in winter.

4.3.4 Particle Size Breakdown in the Rumen in Winter

Figure 4.2 shows that the critical particle size as threshold to passage through the reticulo-omasal orifice was 1.0 mm in sheep, deer and goats. Hence, more than 98% of the particles which appeared in the faeces of all three species were below the critical threshold size of 1.0 mm.

The data in Table 4.7 indicate that there were no significant differences ($P>0.1$) between sheep and deer in the proportions of large particles (>4.0 mm, 4.0-2.0 mm), and of small particles (<0.25 mm) in the rumen contents. Sheep tended to have greater proportions of particles of size 1.0-0.5 mm ($P<0.01$) and 0.5-0.25 mm ($P<0.05$) in the rumen contents, than deer.In contrast to sheep and deer, goats had significantly lower proportions of large particles (>4.0 mm, 4.0-2.0 mm) in the rumen contents than both sheep and deer ($P<0.01$), and a

Table 4.6. Mean retention time (MRT, h) and fractional outflow rate (FOR, %/h) of Cr-EDTA, Ru-Phen and lignin from the rumen of deer, goats and sheep fed on lucerne hay in summer and in winter, at 90% "ad-lib".

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Mean retention time (h):					
Cr-EDTA	S	6.4	10.4	10.0	0.43
	W	6.4	10.6	9.8	0.30
Ru-Phen	S	14.5	13.5	15.8	0.92
	W	14.0	15.0	14.8	0.73
Lignin	S	37.6	28.0	31.0	1.5
	W	29.9	29.4	30.9	1.2
Fractional outflow rate (%/h):					
Cr-EDTA	S	15.8	10.8	10.4	0.54
	W	16.3	9.6	10.3	0.56
Ru-Phen	S	7.0	7.6	6.9	0.38
	W	7.6	6.8	6.9	0.34
Lignin	S	2.77	3.66	3.32	0.163
	W	3.47	3.47	3.29	0.142

S = summer
W = winter

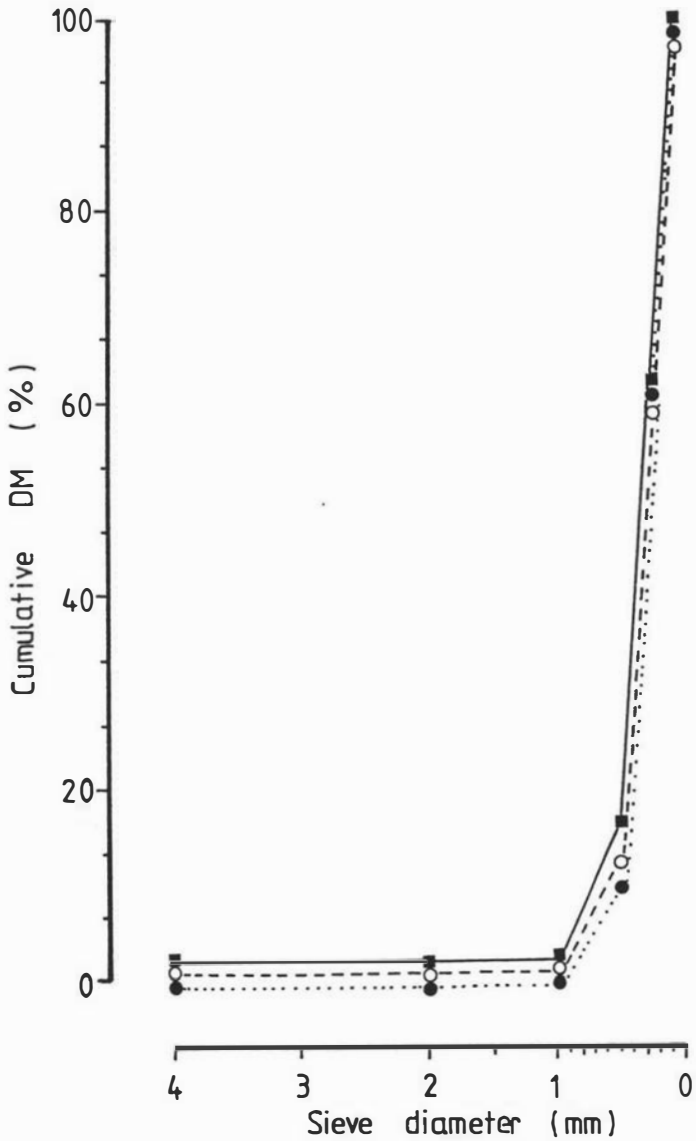

Figure 4.2. Cumulative dry matter distribution of faecal samples from deer ( ), goats (•) and sheep (o).

Table 4.7. Particle size distribution (% particulate DM retained on sieve size) in the rumen digesta and faeces of deer, goats and sheep fed on lucerne hay in winter, at 90% "ad-lib". (Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

Sieve size (mm)	Deer	Goats	Sheep	SEM
Rumen digesta:				
4.0	7.1	2.9	8.5	0.73
2.0	8.4	3.9	6.4	0.44
1.0	17.1	8.5	11.2	0.68
0.5	18.8	17.0	16.3	0.43
0.25	19.1	28.5	23.6	0.56
<0.25 @	29.5	39.4	34.1	1.24
<1.0	67.4	84.9	74.0	1.45
>1.0	32.6	15.1	26.0	1.45
Faeces:				
4.0	-	-	-	
2.0	0.20	0.08	0.14	0.025
1.0	1.04	0.22	0.42	0.096
0.5	15.2	9.3	11.6	0.78
0.25	45.5	51.0	46.9	1.02
<0.25 @	38.1	39.5	41.0	0.74
<1.0	98.8	99.7	99.4	0.09
>1.0	1.22	0.27	0.59	0.094

@ Initial sample D.WT - Sum of recovered particulate DM fractions

significantly greater proportion of small particles (0.5-0.25 mm and <0.25 mm) than sheep ($P<0.01$), and deer ($P<0.001$).

The rumen contents of both deer and sheep contained significantly ($P<0.01$) larger proportions of particles which were above the critical threshold size to passage (>1.0 mm) than goats. The rumen contents of deer contained significantly greater proportions of particles 2.0-1.0 mm than both sheep ($P<0.01$), and goats ($P<0.01$).

4.3.5 "Apparent" Fractional Outflow Rate of Particles from the Rumen in Winter

In all three species, the "apparent" FOR (%/h) of particles from the rumen consistently increased as the particles were reduced in size from >2.0 mm to 0.25-0.5 mm (Table 4.8). There was also a consistent decrease in the "apparent" FOR (%/h) of particles as they were broken down to <0.25 mm in all three species. Particles which were >1.0 mm had a greater resistance to passage through the reticulo-omasal orifice.

When fed on the diet used in the present experiment, the deer had faster "apparent" rumen FOR (%/h) for all the spectrum of particle sizes than sheep and goats, with the differences attaining significance for particles 2.0-1.0 mm ($P<0.10$, for both goats and sheep), and particles 0.5-0.25 mm (for goats, $P<0.01$; for sheep, $P<0.05$). The deer passed a greater fraction of particles 0.5-0.25 mm in size in the faeces, than both goats ($P<0.01$) and sheep ($P<0.05$). Goats had the slowest "apparent" rumen FOR (%/h) for all the spectrum of particle sizes than sheep and deer.

4.3.6 Fibre Digestion

4.3.6.1 Seasonal Effects

Tables 4.9-4.12 show the apparent digestibilities of total fibre, cellulose, hemicellulose and lignin, together with their FDR's (%/h) with season for sheep, deer and goats. Sheep digested the total fibre of the diet better in summer than in winter ($P<0.001$). This was reflected in greater apparent digestibilities for cellulose ($P<0.001$),

Table 4.8. "Apparent" mean retention time (MRT, h) and "apparent" fractional outflow rate (FOR, %/h) of particulate DM (>2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm, and <0.25 mm) from the rumen of deer, goats and sheep fed on lucerne hay at 90% "ad-lib" intake, in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

	Deer	Goats	Sheep	SEM
"Apparent" MRT of particulate DM (h):				
>2.0 mm	2430	2414	2158	390
2.0-1.0 mm	547	1641	1525	253
1.0-0.5 mm	42	62	56	3.6
0.5-0.25 mm	14.1	20.6	19.6	0.89
<0.25 mm	26.9	36.8	32.5	2.25
<1.0 mm	22.9	31.1	29.0	1.40
>1.0 mm	982	2389	2111	293
"Apparent" FOR of particulate DM (%/h):				
>2.0 mm	0.06	0.07	0.07	0.011
2.0-1.0 mm	0.30	0.06	0.10	0.038
1.0-0.5 mm	2.55	1.69	1.93	0.14
0.5-0.25 mm	7.30	4.96	5.27	0.269
<0.25 mm	4.09	2.84	3.41	0.292
<1.0 mm	4.36	3.30	3.58	0.200
>1.0 mm	0.11	0.05	0.08	0.011

Table 4.9. Voluntary intake of total fibre [!], rumen pool (g/Kg $W^{0.75}$), fractional disappearance rate (FDPR, %/h) and "apparent" fractional degradation rate (FDR, %/h) of total fibre by deer, goats and sheep fed on lucerne hay in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Voluntary intake [@]	S	26.4	27.7	21.0	1.36
(g/Kg $W^{0.75}$/d)	W	19.4	23.2	22.0	1.29
Apparent digestibility [@]	S	44.6	42.6	41.3	0.65
(%)	W	40.1	45.2	36.6	0.80
Rumen pool [$]	S	29.2	25.4	21.5	1.41
(g/Kg $W^{0.75}$)	W	18.2	18.8	20.1	1.01
FDPR [$]	S	3.71	4.26	3.63	0.18
(%/h)	W	5.11	4.93	4.64	0.18
"Apparent" FDR [#$]	S	1.12	1.08	0.76	0.090
(%/h)	W	1.64	1.71	1.35	0.104

[@] Animals fed "ad-lib".
[$] Animals fed at 90% "ad-lib".
[!] Cellulose + hemicellulose + lignin.
[#] FDPR (total fibre) - FOR (lignin).
S = summer.
W = winter.

Table 4.10. Voluntary intake of cellulose, rumen pool (g/Kg $W^{0.75}$), fractional disappearance rate (FDPR, %/h) and "apparent" fractional degradation rate (FDR, %/h) of cellulose by deer, goats and sheep fed on lucerne hay in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Voluntary intake [@]	S	14.6	15.3	11.6	0.75
(g/Kg $W^{0.75}$/d)	W	10.5	12.5	11.9	0.69
Apparent digestibility [@]	S	63.6	59.1	59.7	0.64
(%)	W	57.0	61.0	53.8	1.05
Rumen pool [$]	S	15.5	13.0	11.1	0.72
(g/Kg $W^{0.75}$)	W	9.0	9.2	9.9	0.49
FDPR [$]	S	3.89	5.11	4.38	0.19
(%/h)	W	5.57	5.44	5.08	0.19
"Apparent" FDR [!$]	S	1.28	1.44	1.24	0.17
(%/h)	W	2.10	2.38	1.79	0.11

[@] Animals fed "ad-lib".

[$] Animals fed at 90% "ad-lib".

[!] FDPR (cellulose) - FOR (lignin).

S = summer.

W = winter.

Table 4.11. Voluntary intake of hemicellulose, rumen pool (g/Kg $W^{0.75}$), fractional disappearance rate (FDPR, %/h) and "apparent" fractional degradation rate (FDR, %/h) of hemicellulose by deer, goats and sheep fed on lucerne hay, in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Voluntary intake [@]	S	4.92	5.17	3.92	0.253
(g/Kg $W^{0.75}$/d)	W	3.80	4.54	4.31	0.258
Apparent digestibility [@]	S	51.5	49.8	49.6	0.96
(%)	W	47.4	52.7	46.6	1.11
Rumen pool [$]	S	5.55	5.28	4.58	0.30
(g/Kg $W^{0.75}$)	W	3.55	3.67	4.06	0.22
FDPR [$]	S	3.71	4.26	3.63	0.18
(%/h)	W	5.20	4.92	4.52	0.20
"Apparent" FDR [!$]	S	1.05	0.73	0.66	0.10
(%/h)	W	1.73	1.70	1.24	0.12

[@] Animals fed "ad-lib".

[$] Animals fed at 90% "ad-lib".

[!] FDPR (hemicellulose) - FOR (lignin).

S = summer.

W = winter.

Table 4.12. Voluntary intake of lignin, rumen pool (g/Kg $W^{0.75}$), fractional disappearance rate (FDPR, %/h) and fractional degradation rate (FDR, %/h) of lignin by deer, goats and sheep fed on lucerne hay in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Voluntary intake [@] (g/Kg $W^{0.75}$/d)	S	6.87	7.21	5.47	0.364
	W	5.14	6.15	5.86	0.343
Digestibility [@] (%)	S	18.7	18.9	14.6	0.77
	W	15.8	21.9	9.4	0.76
Rumen pool [$] (g/Kg $W^{0.75}$)	S	8.16	7.08	5.76	0.409
	W	5.70	5.95	6.12	0.324
FDPR [$] (%/h)	S	3.53	4.43	4.04	0.184
	W	4.37	4.15	3.69	0.234
FDR [$] (%/h)	S	0.86	0.80	0.72	0.086
	W	0.90	0.93	0.66	0.100

[@] Animals fed "ad-lib".

[$] Animals fed at 90% "ad-lib".

S = summer.

W = winter.

hemicellulose ($P<0.1$) and lignin ($P<0.001$). There were no differences, however, in the "apparent" FDR (%/h) of cellulose, hemicellulose and in the FDR (%/h) of lignin between the two seasons.

Compared to sheep, deer also showed an increase ($P=0.16$) in the apparent digestibility of total fibre from winter to summer, despite the increase in voluntary feed intake (g/Kg $W^{0.75}$/d). The apparent digestibilities of cellulose ($P=0.14$), hemicellulose ($P>0.1$) and lignin ($P>0.1$) increased in summer. In contrast to sheep, the rumen "apparent" FDR (%/h) of cellulose ($P<0.01$), hemicellulose ($P<0.05$) and the FDR (%/h) of lignin ($P>0.1$), were slower in deer in summer than in winter.

Goats tended to have a lower apparent digestibility of total fibre in summer ($P=0.14$) than in winter, which was associated with an increase in the summer voluntary DMI (g/Kg $W^{0.75}$/d). This was reflected in lower apparent digestibilities of cellulose ($P>0.1$), hemicellulose ($P>0.1$) and lignin ($P=0.11$) in summer. Goats had slower rumen "apparent" FDR (%/h) of cellulose ($P<0.01$), hemicellulose ($P<0.01$), and FDR (%/h) of lignin ($P>0.1$) in summer, compared to winter.

4.3.6.2 Species Effects

In winter, deer digested the total fibre of the feed better than sheep ($P=0.13$), but the difference attained significance ($P<0.01$) only for the least digestible component of the fibre, lignin. In summer, deer digested the total fibre of the feed better ($P=0.09$) than sheep, despite the superior summer voluntary DMI (g/Kg $W^{0.75}$/d) in deer, compared to sheep. Hence, the apparent digestibilities of cellulose ($P<0.05$), hemicellulose ($P>0.1$) and lignin ($P=0.07$) were all greater in deer than in sheep in summer. There were no differences ($P>0.1$) between deer and sheep in the FDR (%/h) of all the three components of fibre. Deer, compared to sheep, appeared to digest fibre more efficiently both in winter, when the voluntary DMI (g/Kg $W^{0.75}$/d) was lower than in sheep, and in summer, when the voluntary DMI (g/Kg $W^{0.75}$/d) was greater than in sheep.

Goats digested the total fibre of the feed more efficiently ($P<0.001$) than sheep in winter, when the voluntary DMI (g/Kg $W^{0.75}$/d) was similar between the two species. This was reflected in greater apparent digestibilities of cellulose ($P<0.01$), hemicellulose ($P<0.05$), and especially lignin ($P<0.001$) by goats, compared to sheep. Goats digested lignin better than sheep by 12.5 units, when fed in winter on the medium quality forage used in the present study. In summer, when the goats achieved superior ($P<0.05$) voluntary DMI (g/Kg $W^{0.75}$) than sheep, there were no differences ($P>0.1$) in the apparent digestibility of total fibre between the two species. Hence, there were no significant ($P>0.1$) differences in summer between goats and sheep, in the apparent digestibilities of cellulose and hemicellulose. However, goats digested the least digestible component of fibre, lignin, better than sheep ($P<0.05$) by 4.3 units, despite their higher voluntary DMI (g/Kg $W^{0.75}$/d) than sheep.

4.3.7 Rumen Water Transactions

4.3.7.1 Seasonal Effects

There were no significant ($P>0.1$) seasonal differences in the drinking water or in the total water intakes (g/g DMI/d or g/Kg $W^{1.0}$/d) in all three species (Table 4.13).

Sheep did not show a significant seasonal trend ($P>0.1$) in the net rumen water balance or rumen water outflow (g/Kg $W^{1.0}$/d). In contrast, deer and goats showed a significant ($P<0.05$) increase in the net rumen water balance (g/Kg $W^{1.0}$/d), in summer compared to winter. The magnitude of the increase was greater in deer (74%), than in goats (42%). It appears that both deer and goats have a greater internal recycling of water in summer, compared to winter, and this is not due to seasonal differences in total water intakes (g/Kg $W^{1.0}$/d). Rumen water outflow (g/Kg $W^{1.0}$/d) showed a significant increase in summer compared to winter both in deer ($P<0.05$), and in goats ($P<0.05$).

When expressed as g/g DMI/d, the increases in summer of the net rumen water balance and rumen water outflow in deer and goats were of

Table 4.13. Water flows into and out of the rumen: 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 90% "ad-lib" intake, in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Drinking water:					
g/Kg $W^{1.0}$/d	S	55.7	64.7	52.7	3.15
	W	55.2	60.9	54.1	3.89
g/g DMI/d	S	2.56	2.63	3.06	0.201
	W	3.25	2.42	2.62	0.126
Total water intake: !					
g/Kg $W^{1.0}$/d	S	58.9	68.7	55.3	3.1
	W	58.7	66.1	58.1	4.2
g/g DMI/d	S	2.70	2.78	3.21	0.202
	W	3.46	2.63	2.83	0.125
Water outflow: @					
g/Kg $W^{1.0}$/d	S	293	288	204	16.9
	W	194	220	237	9.8
g/g DMI/d	S	13.7	11.4	11.5	0.94
	W	11.4	9.0	11.7	0.40
Net rumen water balance $					
g/Kg $W^{1.0}$/d	S	235	219	149	15.7
	W	135	154	179	7.6
g/g DMI/d	S	11.0	8.7	8.3	0.83
	W	8.0	6.3	8.9	0.36

! Drinking water + water in feed.

@ Rumen liquid pool x FOR (/d) of Cr-EDTA.

$ Rumen outflow - total water intake = salivary secretion + net inflow of water across rumen wall.

S = summer; W = winter.

smaller magnitude than when expressed as g/Kg $W^{1.0}$/d, but were in the same direction.

4.3.7.2 Species Effects

When compared to sheep in winter, deer showed significantly ($P<0.05$) lower net rumen water balance (g/Kg $W^{1.0}$/d), and rumen water outflow (g/Kg $W^{1.0}$/d) ($P=0.11$). However, in summer, the net rumen water balance ($P=0.06$), and rumen water outflow ($P=0.07$) were greater in deer than in sheep. Goats, compared to sheep, had a greater ($P=0.07$) net rumen water balance in summer (g/Kg $W^{1.0}$/d). In winter, there were no significant ($P>0.1$) differences between the two species.

There were no significant differences ($P>0.1$) in the drinking water intake (g/g DMI/d) between goats and sheep, both in summer and in winter.

4.3.8 Rumen Fermentation Patterns

4.3.8.1 Seasonal Effects

There were no significant seasonal trends ($P>0.1$) in sheep in the molar proportions of acetate, propionate, butyrate (iso- and n-), iso-valerate and the ratio of acetate/propionate (Ac/Pr) (Table 4.14). The molar proportions of n-valerate showed a significant ($P<0.01$) decrease in summer.

In contrast to sheep, deer showed seasonal cycles of rumen fermentation, with increases in summer in the molar proportions of acetate ($P<0.1$), iso-butyrate ($P<0.1$) and n-valerate ($P<0.01$). The molar proportions of propionate showed a significant decrease in summer ($P<0.01$), and hence the Ac/Pr ratio was increased significantly ($P<0.05$) in summer.

Goats also showed seasonal cycles of rumen fermentation, with increases in summer of the molar proportions of acetate and iso-butyrate ($P<0.05$), and decreases in the molar proportions of propionate ($P<0.1$) and n-valerate ($P<0.01$). Hence, the Ac/Pr ratio was significantly increased ($P<0.01$) in summer in goats.

Table 4.14. Total VFA (mmol/L), and molar concentrations of acetate, propionate, butyrate (n- and iso-) and valerate (n- and iso-) (moles %) in the rumen of deer, goats and sheep fed on lucerne hay at "ad-lib" intake, in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Total VFA (mmol/L)	S	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
iso-butyrate	S	1.75	1.79	1.67	0.058
	W	1.44	1.55	1.59	0.070
n-valerate	S	1.17	1.58	1.66	0.043
	W	1.62	2.23	2.01	0.060
iso-valerate	S	1.54	1.13	0.94	0.055
	W	1.24	1.28	0.95	0.062
Acetate/propionate ratio	S	4.20	3.76	4.01	0.085
	W	3.62	3.37	3.76	0.061

S = summer; W = winter.

4.3.8.2 Species Effects

In summer, the Ac/Pr ratio was greater in deer than in sheep ($P>0.1$) and goats ($P<0.1$), with deer>sheep>goats. In winter, there were no significant differences ($P>0.1$) in the Ac/Pr, between the 3 species.

4.3.9 Seasonality in Nitrogen Retention

There was a significant ($P=0.08$) increase of 88% in N retention (mg/100 g DMI/d) in sheep in summer, compared to winter (Table 4.15). The apparent digestibility of N was greater ($P=0.08$) in summer compared to winter and urinary N excretion (% of total N digested) was lower ($P=0.07$) in summer compared to winter.

Deer also showed a seasonal trend in N balance, with a 100% significant ($P<0.05$) increase in the N retained (mg/100 g DMI) in summer, compared to winter. This was associated with an increase in summer in the apparent digestibility of N ($P<0.1$), and a decrease ($P<0.05$) in urinary N excretion (% of total N digested).

Goats, in contrast to sheep and deer, showed no seasonal trends in N retention (mg/100 g DMI/d), or in the apparent digestibility of N or in the urinary N excretion (% of the total N digested).

4.3.10 Ammonia Kinetics in the Rumen

Ammonia kinetic data for deer, goats and sheep in winter are summarised in Table 4.16. Summer data for NH_3-N concentration (mg N/L), rumen pool size of NH_3-N (mg N/g N intake) and outflow of NH_3-N in water leaving the rumen (mg N/g N intake/d) are also given. Enrichment with ^{15}N of rumen NH_3-N, bacterial-N, and digesta-NAN for deer, goats and sheep are shown in Figure 4.3.

Table 4.15. Nitrogen (N) intake, faecal N and urinary N excretion, N balance, and apparent N digestibility by deer, goats and sheep fed on lucerne hay at "ad-lib" intake, in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Intake (mg/Kg $W^{0.75}$/d)	S	1715	1995	1556	84.0
	W	1450	1749	1710	92.9
Faecal excretion	S	549	593	480	24.1
(mg/Kg $W^{0.75}$/d)	W	532	490	572	34.8
Urinary excretion	S	889	1156	852	82.3
(mg/Kg $W^{0.75}$/d)	W	833	888	1002	46.9
Nitrogen balance:					
mg N/Kg $W^{0.75}$/d	S	27.8	35.5	22.5	3.66
	W	10.7	37.1	13.9	2.06
mg N/100 g DMI	S	42.6	51.4	43.7	5.99
	W	21.3	63.8	23.2	3.06
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
Urine N (percentage intake)	S	52.2	57.0	55.3	2.57
	W	57.3	50.6	59.5	1.26

S = summer

W = winter.

Table 4.16. Kinetics of ammonia (NH_3-N) production in the rumen of deer, goats and sheep fed on lucerne hay at 90% "ad-lib" intake in winter, together with the rumen NH_3-N concentration (mg N/L), rumen NH_3-N pool (mg N/g N intake) and NH_3-N outflow (mg N/g N intake/d) from rumen, in summer and in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Total N intake (NI) (g/Kg $W^{0.75}$/d)	S	1.90	1.95	1.43	0.076
	W	1.63	1.63	1.61	0.095
Rumen NH_3-N kinetics:					
NH_3-N concentration (mg N/L)	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 water (mg N/g NI/d)	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/d)	W	535	692	607	35.9
IRL - NH_3-N outflow in water (mg N/g NI/d)	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

S = summer.
W = winter.

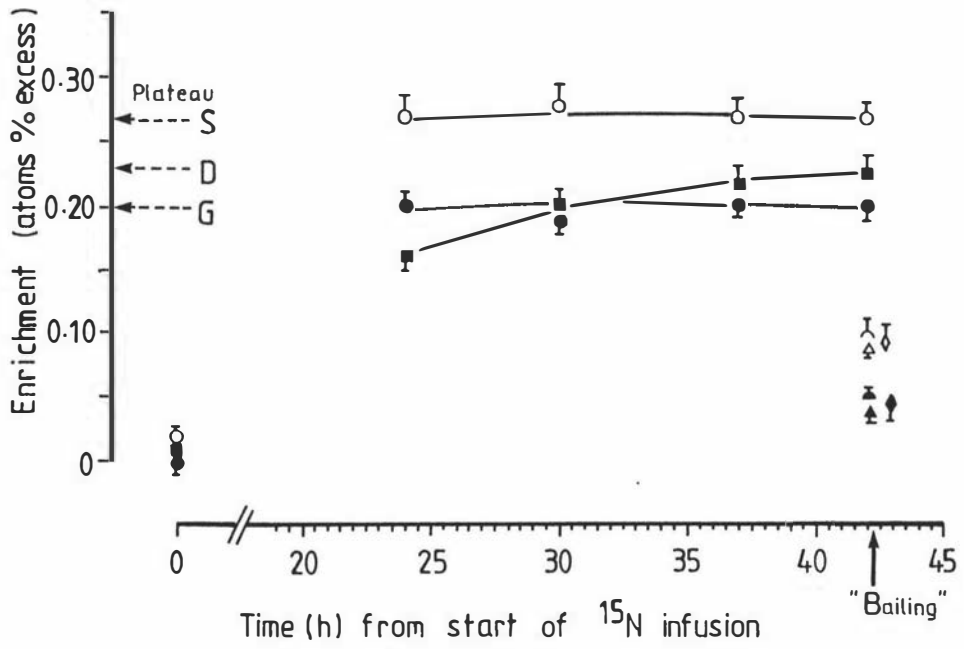

Figure 4.3. Enrichment with ^{15}N (atoms % excess) of rumen fluid NH_3-N, (deer ■, goats •, sheep o), bacterial-N (deer ◊, goats △, sheep ⌒) and rumen digesta-NAN samples (deer ♦, goats ▲, sheep ⬬) (± SEM).

4.3.10.1 Rumen Ammonia Concentration, Rumen Ammonia Pool and Rumen Ammonia Outflow from the Rumen

4.3.10.1.1 Seasonal Effects

Both sheep and goats showed no significant ($P>0.1$) differences in the rumen NH_3-N concentration (mg N/L), rumen NH_3-N pool (mg N/g N intake) or NH_3-N outflow (mg N/g N intake/d) from the rumen, between summer and winter. In contrast to sheep and goats, deer showed a significant increase of 56% in the rumen NH_3-N concentration ($P<0.01$), rumen NH_3-N pool ($P<0.01$), and in the NH_3-N outflow from the rumen ($P<0.05$), from winter to summer. There were no seasonal significant ($P>0.1$) differences in the rumen pH in the three species.

4.3.10.1.2 Species Effects

When compared to the sheep in winter, the deer showed a significantly ($P<0.01$) lower concentration (mg N/L) of NH_3-N in the rumen, a lower ($P<0.01$) rumen NH_3-N pool size (mg N/g N intake), and a lower ($P<0.01$) outflow of NH_3-N in the water leaving the rumen (mg N/g N intake/d). In summer, however, there were no significant differences ($P>0.1$) in the rumen NH_3-N concentration, rumen NH_3-N pool size or in the rumen outflow of NH_3-N, between deer and sheep.

Goats, compared to sheep, showed no significant ($P>0.1$) differences in the rumen NH_3-N concentration (mg N/L) both in summer and in winter. The NH_3-N outflow from the rumen (mg N/g N intake/d) and the rumen NH_3-N pool (mg N/g N intake) were not significantly different ($P>0.1$) to sheep in summer. In winter, however, both the NH_3-N pool and the outflow of NH_3-N in the water leaving the rumen, were significantly lower ($P<0.05$) in goats, than in sheep.

4.3.10.2 Ammonia Production Rate in the Rumen

NH_3-N production in the rumen was measured in deer, goats and sheep in winter. There were no significant differences ($P>0.1$) in the N intake (g/Kg $W^{0.75}$/d) between deer, goats and sheep.

The IRL of NH_3-N (mgN/gN intake/d), tended to be higher in goats than in sheep ($P>0.1$), and deer ($P=0.14$). There were no significant differences ($P>0.1$) between sheep and deer. IRL minus the rumen NH_3-N outflow rate (mg N/g N intake/d), which represents the combined values for NH_3-N incorporated into microbial-N and total NH_3-N absorbed through the rumen epithelium, was higher in goats than in sheep and deer ($P<0.05$). There were no significant differences ($P>0.1$) between sheep and deer.

The proportion of rumen bacterial-N derived from rumen NH_3-N tended to be greater in goats than in sheep ($P=0.12$), and deer ($P<0.1$). Both sheep and deer showed no significant differences ($P>0.1$) in the proportion of rumen NH_3-N incorporated in the bacterial cells.

4.4 DISCUSSION

4.4.1 Seasonal Cycles in Nutrient Supply in Deer, Goats and Sheep

The results of the present experiment have indicated that the domestic sheep showed a seasonal cycle of fibre digestion and N retention, with maximum values in summer and minimum values in winter, but showed no seasonality in VFI (g/Kg $W^{0.75}$/d).

In contrast to sheep, the deer which has recently been farmed (last two decades) showed marked seasonal cycles of (i) voluntary DMI, (ii) DDMI and MEI, (iii) apparent fibre digestibility, (iv) rumen NH_3-N concentration, (v) VFA molar proportions and Ac/Pr ratio, (vi) N retention, (vii) internal recycling of water to the rumen and (viii) rumen pool size of DM + liquid. The results of the present experiment indicated that all the seasonal cycles listed above showed a peak in summer and a trough in winter, with no evidence of a decrease in the MRT (h) of digesta in summer when the VFI showed a significant increase.

The goats appeared to occupy an intermediary position, with seasonal cycles of (i) VFI, (ii) rumen pool size of DM + liquid, (iii) VFA molar proportions and Ac/Pr ratio and (iv) internal recycling of water to the rumen, which all showed an increase in summer compared to

winter in the present experiment. However the seasonal cycles observed in goats were not as extensive and marked as those observed in deer. The summer increase in the VFI of goats occurred at the expense of a decrease in the DMD, and in the apparent digestibility and FDR (%/h) of all fibre components (cellulose, hemicellulose and lignin), with no effects on the MRT of rumen digesta. The net effect was no seasonal change in MEI (MJ/Kg $W^{0.75}$/d) and DDMI (g/Kg $W^{0.75}$/d).

The seasonal cycles of VFI in deer can be considered as a consequence of their seasonal cycle of body growth, and of protein and energy metabolism (Silver et al., 1969; Mitchell, McCowan and Nicholson, 1976; Moen, 1978, 1985; Barry et al., 1989). In addition to VFI, the present experiment has shown that there are seasonal effects upon a number of other digestive criteria in sheep, deer and goats, and it is suggested that these all occur as a consequence of the seasonal rhythms of metabolism and growth (including body growth and wool growth). The secondary effects can be listed as:

1. Rumen effects (MRT, rumen pool size, rumen fermentation including NH_3-N concentration, VFA proportions and Ac/Pr ratio, internal recycling of water to the rumen).

2. Post-rumen effects (MRT and microbial fermentation).

3. Use of absorbed nutrients (N retention).

To present a compact discussion concerning a large amount of data on the reasons for the observed seasonal cycles in nutrient supply in sheep, goats and deer, the rest of the Section will concentrate on two main factors, namely:

1. VFI and N retention, and

2. Digestive efficiency.

The two factors will be discussed in relation to, (i) seasonal effects upon nutrient supply, and (ii) species differences (sheep v/s deer and sheep v/s goat) in nutrient supply.

4.4.2 Seasonal Effects upon Nutrient Supply

4.4.2.1 Voluntary Feed Intake and Nitrogen Retention

The increase in N retention in sheep during summer can be associated to the photoperiodic rhythm of wool growth which is greater in summer (Nagorcka, 1979; Robards, 1979; McLelland, Wickham and Blair, 1987). Wool growth requires a supply of essential sulphur amino-acids, and has been associated with increased N retention in sheep (Wynn and Wallace, 1979). Milne et al. (1978), have also reported an increased N retention in the domestic sheep in summer, when fed both on low and high/medium quality forages.

The factors which will contribute to an increase in VFI are:

1. Rumen pool size, and

2. MRT of digesta in the rumen.

The results of the present experiment on deer are in agreement with previous reports which show a marked decrease in appetite in castrated deer in winter, and an increase in VFI in summer (Pollock, 1975; Milne et al., 1978; Suttie and Simpson, 1985). The increased DMI in summer, in the present experiment, is associated with the ability of the rumen to accommodate a greater (+ 51%) digesta load (rumen pool size of DM + liquid). No measurement was made of the rumen capacity (measured as the rumen water-filled capacity), to determine if there were any increases in summer of the ratio of rumen digesta load/rumen capacity, and of the rumen capacity itself. These two factors are possible components which, together with an increase in the digesta load, might have also contributed to an increase in VFI in summer.

Whilst there was no change in the rumen MRT of Cr-EDTA and Ru-Phen with the increase in VFI (+ 34%) in summer, the rumen MRT of lignin (and hence particulate matter) actually increased by 26%. The combined effects of a greater rumen pool size, with an increase in particulate matter MRT in the rumen, probably explains the mechanism

of how the deer were able to increase their VFI in summer, whilst also increasing fibre digestibility.

The study of Milne et al. (1978), together with the present experiment, appear to be the only published experimental work on seasonal cycles of VFI, digestibility and rumen MRT of digesta in deer. The results of Milne et al. (1978), confirm the present findings of an increase in N retention, VFI and DDMI in summer in deer when fed both on low and high quality diets. Milne et al. (1978), found that the increase in VFI was associated with an increase (when fed on low quality forage), or with no change (when fed on high-quality pelleted grass diet) in the rumen MRT of Ru-Phen. Milne et al. (1978) and Milne (1980), therefore, postulated that the deer could possibly show a compensatory enlargement of the rumen in summer to allow for the increase in DMI, DDMI and MRT of digesta in summer. It appears that the results of the present experiment are the first direct evidence that deer show an increase in the rumen digesta load (and VFI) in summer, compared to winter.

The increased N retention observed in deer during summer can be explained as part of the increase in the whole protein deposition, which is known to occur in spring/summer in deer (Drew, 1976; Mitchell et al., 1976; Hamilton and Blaxter, 1981; Hofmann, 1985). The seasonal cycles of growth in deer are associated with changes in the hormone status of IGF-I, growth hormone and prolactin (Ryg and Jacobsen, 1982b; Suttie et al., 1989; Barry et al., 1989). Prolactin infusion has been associated with increased N retention in lambs kept in continuous darkness (Brinklow and Forbes, 1982), but its association with N retention in deer is not known.

Although goats showed an increase in VFI in summer compared to winter, the ability of the rumen to accommodate an increase in digesta load (+27%), was more restricted in goats than in deer (+51%). The increase in VFI in goats was not associated with any changes in the MRT of Cr-EDTA, Ru-Phen and lignin, but was associated with a marked reduction in DMD and in the FDR of all the fibre components, with the effects being greater than in sheep and deer. The results tend to suggest that the size of the rumen of goats (rumen digesta load), restricts the apparent digestibilities of DM and fibre in summer,

although the rumen MRT of digesta is unchanged. Hence, the rumen digestive capacity (as shown by a reduction in the FDR or digestive/rumen capacity in summer) tends to fall in summer with the increase in VFI and rumen digesta load. Thus unlike deer, goats seem unable to keep the rumen fermentation rate as the rumen enlarges in summer. There is no other published data on the seasonality of nutrient supply in goats. It is known that goats enter a period of growth stasis in late autumn/winter (McCall et al., 1989), and the seasonal cycles of feed intake in goats may be linked to the metabolic demand of growth in the same way as they are in deer.

4.4.2.2 Digestive Efficiency

Rumen digestive efficiency can be affected by the following factors, namely:

1. Rumen NH_3-N concentration,
2. IRL of NH_3-N in the rumen,
3. Rumen pool size,
4. MRT of digesta in the rumen,
5. Proportions of particle size in the rumen, and surface area of particles,
6. Rumen FDR (i.e digestive rate/rumen capacity),
7. Internal recycling of water to the rumen.

The increased apparent fibre digestibility of sheep in summer, was not associated with any seasonal changes in rumen MRT of Ru-Phen, Cr-EDTA and lignin, or in the rumen NH_3-N concentration. As the summer increase in apparent fibre digestibility cannot be explained by events within the rumen, it is possible that it represents increased post-ruminal digestion, perhaps including increased MRT in this region of the digestive system. This has not been measured in the present

experiment, and should be included in further experiments of seasonal VFI in sheep.

The increased apparent fibre digestibility of deer in summer can be associated with the longer rumen MRT of lignin, which would thus allow for a longer time of exposure of the feed particles to microbial attack. Lignin, as an internal dietary marker is part of all the particle sizes present in the rumen (Faichney, 1984). Hence, it is assumed that the "apparent" rumen FOR of particles in deer is slower in summer than in winter. Other reasons might be that as the rumen enlarges in summer, there are associated increases in other factors that could affect the rate of rumen digestion, namely:

1. Increase in the internal recycling of water to the rumen, of which saliva appears to be a main component, since there was no increase in the voluntary water intake in summer in deer.

2. Increase in the rumen NH_3-N concentration.

The combined factors listed above may have contributed to keep up the rumen digestive rate and apparent fibre digestibility in deer, as the rumen digesta load and VFI increased in summer.

Although the winter rumen NH_3-N concentration in deer was above the threshold of 50 mg of NH_3-N/L, below which microbial crude protein production is claimed to be suppressed (Satter and Slyter, 1974), the low concentration might have limited the rate of rumen carbohydrate fermentation (Mehrez et al., 1977). This might have been a contributing factor to the reduced digestive efficiency of deer in winter, and hence a contributing factor to the low winter VFI.

The decrease in apparent fibre digestibility in summer in goats can be associated with a lower rate of digestive capacity, as indicated by the lower "apparent" FDR of fibre in summer, including cellulose, hemicellulose and the FDR of lignin. The increase in VFI (+17%) in summer was not associated with large increases in the following factors to the same extent as they occurred in deer, namely:

1. The internal recycling of water to the rumen, which might have limited the rate of rumen digestion,

2. The rumen NH_3-N concentration which did not show any changes in summer.

The 2 factors listed above could possibly explain the decrease in the rumen digestive rate and lowered apparent fibre digestibility in summer, despite no changes in the seasonal rumen MRT of digesta.

4.4.3 Species Differences in Nutrient Supply

4.4.3.1 Voluntary Feed Intake and Nitrogen Retention

The lower DMI (g/Kg $W^{0.75}$/d) of deer in winter, compared to sheep, was associated with a smaller rumen digesta load in the deer, with no differences between the 2 species in the MRT of Ru-Phen and lignin. In summer the deer achieved a greater VFI than sheep, although there were no differences between the 2 species in the rumen digesta load.It is possible that deer have a greater rumen capacity (water-filled rumen capacity, g/Kg $W^{0.75}$) in summer than sheep, thus allowing for a greater VFI in deer in summer.

In both deer and sheep, the increased N retention in summer, is possibly associated with an increase in the metabolic demand for growth, wool growth for sheep and body growth for deer.

The greater DMI (g/Kg $W^{0.75}$/d) of goats in summer, compared to sheep, was associated with a greater rumen digesta load in goats (+24%), than in sheep, with no associated changes in the rumen MRT of digesta.

4.4.3.2 Digestive Efficiency

The greater apparent digestibility of fibre in deer than sheep during summer was associated with a longer MRT of particulate matter, as measured with lignin, and a larger recycling rate of water to the rumen, but with no differences in the rumen digesta load (per Kg $W^{0.75}$). The results of the present experiment appear to conflict with

the data of Milne et al. (1978), who reported that sheep digested fibre more efficiently than deer, and was associated with a longer rumen MRT of Ru-Phen in sheep. Our data support the findings of Fennessy et al. (1980) with New Zealand deer, who showed that deer digest fibre better than sheep.

The greater superiority of goats in digesting fibre than sheep, especially lignin, which is the least digestible component of fibre, was observed both in summer and in winter

Two principal reasons can be advanced for the superior apparent fibre digestibility of goats, namely:

1. The greater proportion of small particles in the rumen contents of goats, and consequently a larger surface area for the attachment of microorganisms, and microbial attack. Goats possibly chew better the medium quality forage diet used in the present experiment, and break it down to finer particles than do sheep.

2. The greater IRL of NH_3-N in the rumen of goats in winter. Although the rumen NH_3-N concentration was not different between the two species, the IRL (mg N/g N intake/d) tended to be greater in goats than in sheep.It is possible that when fed on the medium quality forage diet used in the present experiment, the recycling of N into the rumen, either by salivary N secretion or diffusion across the rumen, is greater in goats than in sheep.

4.4.4 Marker and Tracer Methodology

4.4.4.1 Marker Methodology

The ratio of FOR lignin/FOR particles <1.0 mm, gives an indication of how good lignin is to being an "ideal" marker for the particulate phase of rumen digesta. The ratio should "ideally" be unity, since lignin is a component of all particles (Faichney, 1984), and the concentration of lignin increases in the particles as they are reduced in size to <1.0 mm (Uden et al., 1974; Van Soest, 1975). Hence, the FOR (%/h) of lignin should "ideally" be close to the rate of outflow of particles <1.0 mm from the rumen. The results (Table 4.17) of the

Table 4.17. Ratios of FOR (%/h) of lignin/FOR of particles <1.0 mm, FOR of Cr-EDTA/FOR of particles <1.0 mm and FOR of Cr-EDTA/FOR of lignin in deer, goats and sheep fed on lucerne hay, at 90% "ad-lib" intake.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Ratio:					
FOR lignin/FOR particles <1.0 mm	W	0.83	1.05	0.94	0.046
FOR Cr-EDTA/FOR particles <1.0 mm	W	3.58	3.01	2.98	0.139
FOR Cr-EDTA/FOR lignin	S	5.97	3.07	3.24	0.308
	W	4.77	2.82	3.12	0.110

S = summer.
W = winter.

present experiment showed that the ratio was close to unity for goats and sheep, indicating that lignin is a good overall particulate phase marker for goats and sheep, when fed the lucerne chaff. The ratio for deer was slightly lower than unity and was lower than that of goats ($P=0.07$).

The ratio obtained for the 3 species is in the order of the fineness of particles (0.25-<0.25 mm) in the rumen contents (Table 4.7), with goats having greater proportions of small particles than sheep and deer (goats>sheep>deer). Previous ruminant work has shown that the lignin consumed is sometimes converted to a soluble lignin carbohydrate-complex in the rumen, precipitated in the abomasum and recovered as solid matter in the faeces (Gaillard and Richards, 1975; Neilson and Richards, 1978; Fahey and Jung, 1983). It may be that lignin solubility in the rumen is related to the particle size of rumen digesta, and is in the order goats>sheep>deer, and thus contributes to the ratio FOR lignin/FOR particles <1.0 mm, being in the same direction.

The ratio of rumen FOR Cr-EDTA/FOR particles <1.0 mm, indicates that liquid leaves the rumen about three times faster than particles <1.0 mm, both for goats and sheep. The ratio for deer was slightly higher, showing that in this species in winter, water leaves the rumen faster in relation to particulate matter, than is the case for sheep ($P=0.11$) and goats ($P>0.1$). The ratio of rumen FOR Cr-EDTA/FOR lignin was much faster in deer than in sheep and goats ($P<0.001$), both in summer and in winter, confirming that water leaves the rumen of deer proportionally faster than particles. The deer tended ($P=0.13$) to show a seasonal trend in the ratio, with an increase in summer of the FOR Cr-EDTA/FOR lignin, indicating a faster movement of water out of the rumen in relation to particulate matter in summer.

4.4.4.2 Tracer Methodology

The interpretation of isotope kinetic data require that the N pools and the N transactions in the pools are under steady-state conditions (Nolan and Leng, 1972; Nolan, 1975).

This was achieved during the present experiment by feeding at 1h-intervals, with the animals fed at 90% "ad-lib" intake. Coefficients of variation (CV) for feed intake (g/Kg $W^{0.75}$ /d) were: for sheep (range = 0.30%-12.0%; mean = 4.75%); for deer (range = 0.93%-5.27%; mean = 2.88%); for goats (range = 3.96%-10.7%; mean = 6.70%).

Figure 4.3 shows that the enrichment at "plateau" of rumen NH_3-N with ^{15}N was reached after a longer time of ^{15}N infusion in deer (35 h), than in sheep and goats (24 h).It is assumed that the faster rumen FOR (%/h) of liquid in deer might have delayed the attainment of the enrichment at "plateau" of rumen NH_3-N fluid with ^{15}N.

4.4.5 Estimation of Nitrogen Outflow from the Rumen

The calculated estimates of microbial NAN and total NAN outflow to the abomasum (Table 4.18), were based on the same assumptions and equations as reported in Chapter 3.

The calculated microbial NAN and total NAN outflow to the abomasum (g/g N intake/d), indicated that there were unlikely to be major differences between the three species, when fed on the medium quality forage used in the present experiment.

Previous ruminant work (Harrison, Beever, Thomson and Osbourn, 1975), indicated that as the dilution rate of water from the rumen increases, there are associated increases in the molar proportions of acetate and decreases in the molar proportions of propionate, and increases in the rates of microbial protein outflow to the abomasum (Isaacson, Hinds, Bryant and Owens, 1975; Thomson, Beever, Mundell, Elderfield and Harrisson, 1975).

The results of the present study indicated that the seasonal trends in the ratio of FOR Cr-EDTA/FOR lignin, were associated with similar seasonal trends to that of Ac/Pr. As the FOR Cr-EDTA/FOR lignin increased in summer in deer, the Ac/Pr also showed a significant increase ($P<0.05$). Goats also showed a seasonal trend of an increase in summer in both ratios, whilst sheep did not show evidence of any seasonal effects on either ratio. In summer, the ratio FOR Cr-

Table 4.18. Calculated microbial-NAN (g) and calculated nonmicrobial-NAN (g) rumen pool sizes, together with the calculated abomasal flows (g/d) in deer, goats and sheep fed on lucerne hay at 90% "ad-lib" in winter.

(Mean values for five deer, seven goats and eight sheep, with the standard error of means (SEM).)

		Deer	Goats	Sheep	SEM
Rumen pool size:					
Microbial-NAN	g	15.1	8.0	12.0	0.93
	g/g NI [@]	0.30	0.32	0.36	0.025
Nonmicrobial NAN	g	8.6	7.5	7.7	0.45
	g/g NI	0.17	0.29	0.23	0.008
Total-NAN	g	23.7	15.5	19.7	1.09
	g/g NI	0.47	0.61	0.59	0.024
NAN flow to the abomasum:					
Microbial-NAN	g/d [!]	26.9	13.0	19.3	1.12
	g/g NI/d	0.54	0.52	0.59	0.032
Nonmicrobial-NAN [#]	g/d	7.5	6.1	6.2	0.43
	g/g NI/d	0.15	0.24	0.18	0.011
Total-NAN	g/d	34.4	19.1	25.5	1.18
	g/g NI/d	0.69	0.75	0.77	0.034
Proportion of microbial-NAN/total-NAN		0.78	0.68	0.75	0.016

[@] NI = dietary N intake.

[!] Microbial-NAN (g) x FOR (/d) of Ru-Phen.

[#] Nonmicrobial-NAN (g) x FOR (/d) of lignin.

EDTA/FOR lignin and Ac/Pr, was significantly greater in deer than in sheep and goats.

It can be concluded that the net effects of a greater rumen outflow of water to that of the particulate phase in deer affects significantly the Ac/Pr, more so in summer.In winter, the calculated NAN outflow to the abomasum in deer was not significantly different ($P>0.1$), to that of goats and sheep, but the calculated proportions of microbial NAN/total NAN outflow to the abomasum, tended to be greater in deer than in sheep ($P>0.1$) and goats ($P<0.05$). This may be associated with the greater FOR Cr-EDTA/FOR lignin of deer, than sheep and goats. The greater Ac/Pr ratio in summer in deer, may possibly contribute to a greater microbial output to the abomasum in summer, compared to goats and sheep.

4.5 CONCLUSIONS

4.5.1 Sheep did not show any evidence ($P>0.1$), of seasonal cycles (summer vs winter) in DMI, DOMI (g/g $W^{0.75}$/d), MEI (MJ/Kg $W^{0.75}$/d), or MRT of rumen digesta (h) and rumen pool size of DM + liquid (g/Kg $W^{0.75}$). However, apparent fibre digestibility ($P<0.001$) and N retention ($P=0.08$) were greater in summer than in winter.

4.5.2 Deer showed marked seasonal cycles of increased VFI and DDMI (+30%; $P<0.1$), MEI (+25%; $P<0.1$), rumen pool size of DM + liquid (+51%; $P<0.01$), N retention ($P<0.05$), apparent fibre digestibility ($P=0.16$), Ac/Pr ratio ($P<0.05$), rumen NH_3-N concentration (+56%; $P<0.01$), and internal recycling of water to the rumen (+74%; $P<0.05$), in summer compared to winter. Rumen MRT of lignin in deer increased in summer (+26%; $P=0.16$), despite the greater VFI in summer. The MRT of Cr-EDTA and Ru-Phen showed no changes with season ($P>0.1$).

4.5.3 There were no associated depressions in the DMD and OMD of the feed offfered by deer in summer, despite the increase in VFI.

4.5.4 Goats showed evidence of seasonal cycles of VFI (+ 17%; $P>0.1$) and rumen pool size of DM + liquid (+ 27%; $P<0.01$), in summer which was associated with a decrease in DMD ($P<0.01$), FDR ($P<0.01$) and apparent total fibre digestibility ($P=0.14$). The net effects resulted

in no seasonal differences in the DDMI and MEI between summer and winter (P>0.1).

4.5.5 Deer digested total fibre better than sheep in summer (P=0.09), and this was associated with a longer rumen MRT of lignin, greater rumen NH_3-N concentration and an increase in the internal recycling of water to the rumen in summer, compared to winter.

4.5.6 Goats digested fibre better than sheep, both at greater intakes (g/Kg $W^{0.75}$/d) in summer (P>0.1), and at similar intakes in winter (P<0.001), with the superiority being greatest for lignin, the least digestible component of fibre. The contributing factors to a greater apparent digestibility of fibre by goats than sheep may be the greater proportions (+15%; P<0.01) of small particles (<1.0 mm) in the rumen digesta of goats, providing a larger surface area for microbial attachment and attack, and the tendency for a greater IRL of NH_3-N (mg N/g N intake/d), in the rumen of goats than in sheep, in winter.

4.5.7 The deer could maintain a greater DMI, DOMI and an increase in apparent fibre digestibility and rumen digesta load in summer than in winter, whereas goats achieved a greater DMI in summer at the expense of a lowered OMD and apparent fibre digestibility. The deer, in contrast to goats, appear to keep the digestive capacity in summer as the VFI increases, by increasing (i) the rumen digesta load, (ii) the rumen NH_3-N concentration and (iii) the internal recycling of water to the rumen, which all do not increase as significantly in goats as in deer.

4.5.8 Both deer and sheep selected for a feed lower in fibre and greater in N.In contrast, goats showed no evidence of selection.

4.5.9 The threshold to passage of particle size through the reticulo-omasal orifice was 1.0 mm for sheep, deer and goats.

4.5.10 The deer had a faster rumen FOR of water (15.6%/h), than sheep (10.4%/h) and goats (10.0%/h), both in summer and in winter. The FOR of small particles (<1.0 mm) was greater in deer, than in sheep and in goats (deer>sheep>goats). The ratio of FOR Cr-EDTA/FOR lignin was greater in deer than in sheep and goats (P<0.001), both in

summer and in winter. The deer tended ($P=0.13$), to show a seasonal trend of an increased FOR Cr-EDTA/FOR lignin, in summer than in winter, with both goats and sheep showing no evidence of a seasonal trend ($P>0.1$).

4.5.11 The ratio of rumen FOR lignin/particles <1.0 mm, indicated that the value was close to unity for goats and sheep, and was slightly less than unity for deer. This indicates that lignin was a good particulate-phase marker, when the animals were fed on the lucerne chaff.

4.5.12 There were no differences ($P>0.1$), between sheep, deer and goats, in the calculated NAN outflows to the abomasum, when fed on the medium-quality forage used in the present experiment.

4.5.13 Deer tended to have a greater calculated proportion of microbial NAN/total NAN flowing to the abomasum than sheep ($P>0.1$), and goats ($P<0.05$).

4.5.14 Deer tended to show ($P=0.13$), an increase in summer in the ratio of FOR Cr-EDTA/FOR lignin. This was associated with an increase ($P<0.05$) in Ac/Pr in summer, compared to winter. The goats showed a significant increase ($P<0.01$) in Ac/Pr in summer, and sheep showed no evidence of a seasonal trend ($P>0.1$). The ratio FOR Cr-EDTA/FOR lignin, increased slightly in goats and sheep in summer, but the differences did not attain significance. The Ac/Pr ratio was best related to the FOR Cr-EDTA/FOR lignin.

CHAPTER 5. TIME SPENT EATING AND RUMINATING IN GOATS AND SHEEP DURING A 24-H PERIOD, AND THE EFFICIENCY OF CHEWING DURING EATING AND RUMINATING UPON THE BREAKDOWN OF FEED PARTICLES.

5.1 INTRODUCTION

The breakdown of particulate dry matter (DM) in the rumen affects the clearance of digesta from the rumen, and hence voluntary feed intake (Ulyatt et al., 1986). Feed particles cannot leave the rumen until they have been reduced to <1.0 mm, which is the critical threshold size to passage through the reticulo-omasal orifice, both for sheep (Reid et al., 1979; Poppi et al., 1980; Chapters 3 and 4), for goats (Chapters 3 and 4) and for deer (Chapter 4).

Two processes affect the breakdown of particulate DM in ruminants (Ulyatt et al., 1986), namely:

1. Initial chewing during eating, and

2. Further chewing during rumination.

Microbial digestion "per se" does not contribute to particle size reduction (Ulyatt, 1983), but assists in weakening plant cell-wall material in the rumen and facilitates particle size breakdown during rumination (Evans, Burnett and Bines, 1974; Chai, Kennedy and Milligan, 1984; Ulyatt et al., 1986).

Data in Chapters 3 and 4 indicated that the proportion of small particles (<1.0 mm) in the rumen digesta of goats, was larger than in sheep, when fed both on low and medium quality forages. It was concluded that goats were more efficient "chewers" than sheep. However, it was not possible to discriminate between effects due to the amount of time spent chewing per 24 h, either eating or ruminating in the two species, or between the effects of chewing during eating and/or ruminating upon the breakdown of feed particles. There are no published data on the efficiencies of chewing during eating and ruminating upon the breakdown of feed particles in the rumen of goats. Data have been reported for sheep (Dulphy, Remond and Theriez, 1980; Ulyatt et al., 1986), and for cattle (Gill, Campling and Westgarth, 1966;

Kennedy, Lirette, Chai and Milligan, 1986), when fed both on fresh forages and dried feeds.

The objectives of the present study were to determine the total amounts of time spent eating and ruminating per 24-h in a comparison study between goats and sheep, when fed on a medium quality forage. One limited study by Geoffroy (1974) indicated that goats spent less time ruminating than sheep, and slightly more time eating than sheep. A further objective of the study was to determine the efficiency of chewing upon particle size breakdown of feed by goats and sheep during eating. The rate of eating (g DM/min), number of chews/min spent eating, number of chews/g DMI, and the particle size distribution of the boli that had been chewed once (% of particles in the DM), were determined. The efficiency of chewing during rumination upon particle size breakdown by goats and sheep was also studied. The number of chews/min spent ruminating and the contributions of rumination to breakdown of feed particles in the rumen (% of particles in the DM) were investigated.

5.2 EXPERIMENTAL

5.2.1 Diet

Lucerne hay *(Medicago sativa)*, containing 903 g OM/Kg DM and 25.9 g N/Kg DM, was fed to the animals, who were allowed free access to a multimineral salt block (50 g), placed in the feed bin (Appendix A). The hay was chaffed into 50-80 mm lengths.

5.2.2 Animals

Five Border-Leicester/Romney cross wethers aged 3½ years and weighing 66.8 Kg LWT (SD 4.39), and five castrated Angora-NZ feral goats, aged 3½ years and weighing 44.6 Kg LWT (SD 3.08), were used in the present experiment. They were all fistulated in the rumen, and fitted with permanent rubber cannulae (63 mm ID). They were housed individually in conventional metabolic crates.

5.2.3 Experimental Design

The experimental design is shown schematically in Figure 5.1.

The present experiment was carried out in June-July 1988. The preliminary period was of 12 days' duration (d1-d12), when the animals were fed "ad-lib". The lucerne chaff was placed upon belt-feeders which delivered the day's ration in 24 feeds, at 1h-intervals. Jaw harnesses were fitted on the animals on d-5 of the preliminary period, and left on for increasing periods of time, until the animals got used to the harnesses. The experiment was divided into three parts, and the following investigated: time spent chewing during eating and ruminating per 24-h, efficiency of chewing during eating and efficiency of chewing during ruminating upon reducing particle size.

During d13-d27, the animals were restricted to 90% of "ad-lib" feed intake. Continuous jaw recordings were taken for four consecutive days during d15-d18, and time spent eating, ruminating and idling (neither eating nor ruminating) were recorded. The efficiencies of chewing during eating and rumination were measured during d19-d22 and d25-d27, respectively.

5.2.4 Methodology

5.2.4.1 Determination of Time Spent Eating and Ruminating per 24-h

5.2.4.1.1 Method: Four goats and four sheep were taken from those described in Section 5.2.2. They were fitted with jaw harnesses, adapted to record automatically the time spent chewing during eating, rumination and resting. Jaw activity was obtained by sensing (with a hearing aid device) the compression of a balloon held under the jaw by the harness, and connected to a pressure transducer (Biocom Type 1010 C), mounted away from the animals. Two pressure transducers were used, each one fitted with four recording channels. Records of the jaw activity were made on multi-channel heat sensitive chart paper, with a chart drive of 2.5 mm/min. Recordings were made continuously for four consecutive days on all animals.

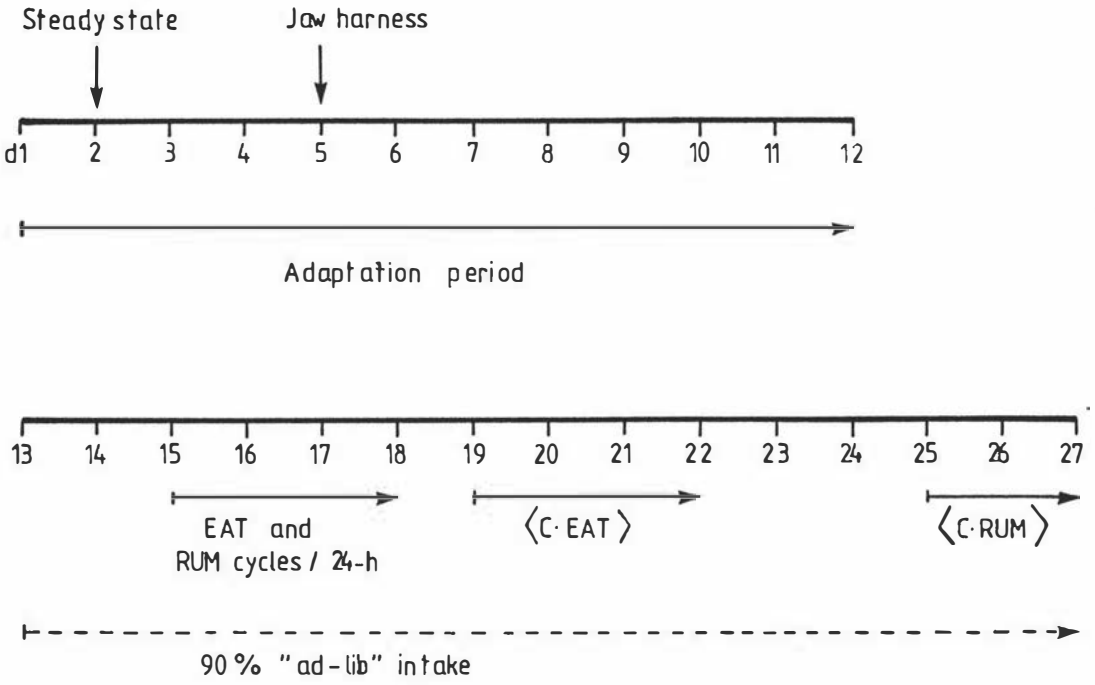

Figure 5.1. Schematic representation of the experimental design (Experiment 3).

5.2.4.1.2 Calculations: Examples of the traces showing the chewing behaviour during eating and rumination for goats and sheep are given in Figures 5.2 and 5.3. Each of the 4-days' recording periods was divided into twelve 2-hour periods (6-8 a.m, 8-10 a.m, ..., 2-4 a.m, 4-6 a.m), and the time spent eating, ruminating and resting counted for each period, per day, and per animal. Mean values of four days were then calculated for each animal, and a 24-h rumination and eating cycle for goats (n=4) and sheep (n=4) determined.

5.2.4.2 Efficiency of Chewing During Eating

5.2.4.2.1 Method: Five goats and five sheep (all those described in Section 5.2.2.), were used during the experiment, with the measurements being recorded on one goat and one sheep per day. The animals were fitted with jaw harnesses one day prior to the start of the measurements. The animals were "bailed" at 9.00 hours, and the rumen digesta kept warm over a bucket of hot water (temp=70 C). The drinking water and salt block were removed. The animals were then offered a "test-meal" of 200 g DM for the goats and 250 g DM for the sheep, for 30 mins. Continuous jaw movements were recorded during the 30 mins-eating period, with the heat sensitive chart paper travelling at 1 mm/sec. This allowed a counting of the actual number of chews/min spent eating. Examples of the traces obtained are given in Figures 5.4-5.5.

At the end of the 30-mins eating period, any feed residues were removed, weighed, and the DMI (g) recorded. The animals were then "bailed" again, and the total pool of boli present in the rumen, which had been chewed during eating only and swallowed once, was collected through the rumen fistula and weighed. Subsamples were taken for, (i) triplicate determinations of DM by freeze-drying, (ii) particle size analysis, (iii) total N (as % DM and % OM). The previously warmed rumen digesta was then returned back to the animals.

5.2.4.2.2 Calculations

(i) The number of chews/min were counted for each animal for 10 periods of 60 sec (representing 600 mm on the chart paper). Mean

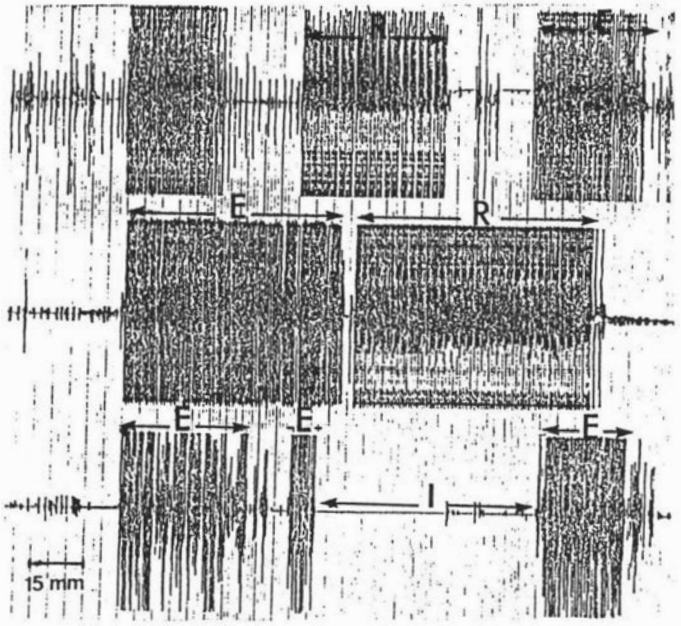

Figure 5.2. Trace of rumination (R) and eating (E) cycles by goats (I - idling).

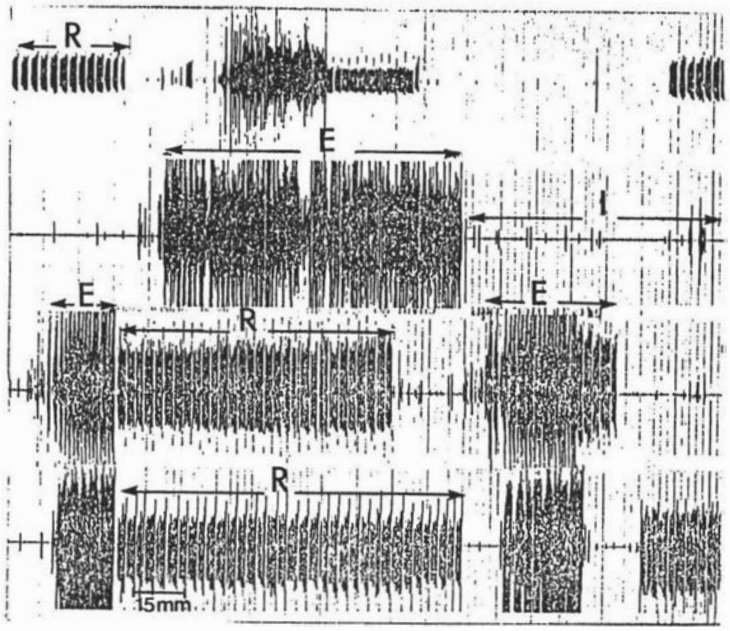

Figure 5.3. Trace of rumination (R) and eating (E) cycles by sheep (I - idling).

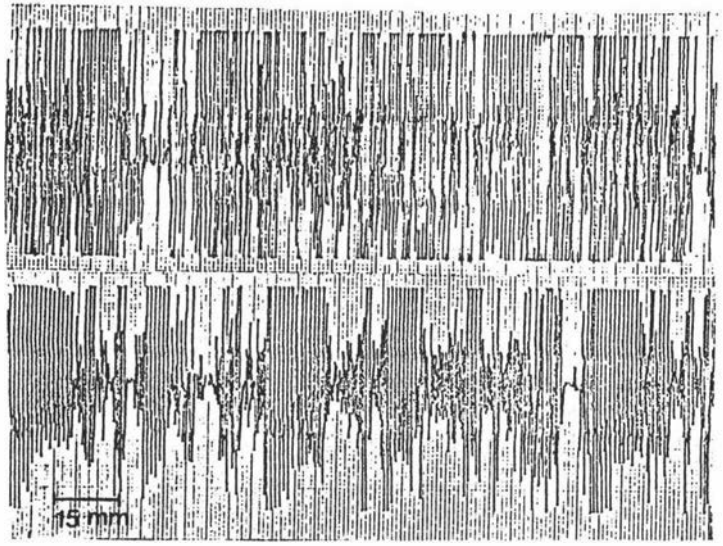

Figure 5.4. Trace showing number of chews during eating by goats.

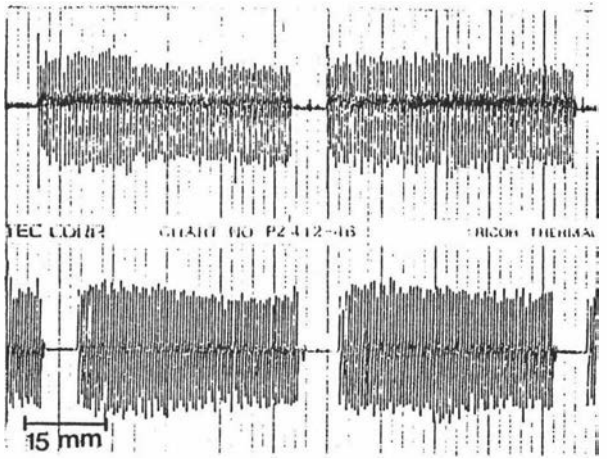

Figure 5.5. Trace showing number of chews during eating by sheep.

values for the number of chews/min spent eating and the number of chews/g DMI, were then calculated for each goat and sheep.

(ii) An index of efficiency of chewing during eating (<C.EAT>) in reducing particle size to <1.0 mm was calculated (Equation 1).

$$<C.EAT> = \frac{\text{(g DM <1.0 mm in boli - g DM consumed <1.0 mm)}}{\text{(g DM of feed consumed >1.0mm)}} \quad (1)$$

(iii) <C.EAT> was also expressed as <C.EAT> per number of chews/g DMI.

(iv) The "apparent" salivary secretion (g/g DMI and g/g OMI) was calculated (Equations 2 and 3).

"Apparent" salivary secretion (g/g DMI) = (2)
Total pool (g) of boli (DM + H_2O) - Feed (g) intake (DM + H_2O)/g DMI

"Apparent" salivary secretion (g/g OMI) = (3)
Total pool (g) of boli (OM + H_2O) - Feed (g) intake (OM + H_2O)/g OMI

The "apparent" salivary secretion represents the combined values for saliva secreted during the 30-mins eating period, and water flows into and out of the rumen during the course of the measurement period.

(v) The "apparent" salivary N secretion rate (mg N/g OMI) was calculated (Equation 4).

"Apparent" salivary N secretion rate (mg N/g OMI) =

$$\frac{\text{Total N in rumen boli (mg) - Total N in feed consumed (mg)}}{\text{g OMI}} \quad (4)$$

(vi) The total N content in the "apparent" saliva (mg N/g saliva OM) was calculated (Equation 5).

N in "apparent" saliva (mg N/g OM in saliva) =

$$\frac{\text{mg N in "apparent" saliva (mg)}}{\text{g saliva OM}} \qquad (5)$$

5.2.4.3 Efficiency of Chewing During Rumination

5.2.4.3.1 Method: Five goats and five sheep (described in Section 5.2.2.) were used during the experiment, with the measurements being recorded on two goats and two sheep per day. The animals were fitted with the jaw harnesses one day prior to the measurement period. The animals were offered a "test-meal" at 8.00 hours, for 3 h, 500 g DM for goats and 600 g DM for sheep. At 11.00 hours, the feed refusals from the "test-meal" were removed, weighed and the DMI (g) determined. Drinking water and the salt block were removed. Continuous jaw movements were recorded from 11.00 hours to 19.00 hours, with the jaw movements being due to rumination only. The heat sensitive chart paper was travelling at 1 mm/sec. This allowed the counting of actual number of chews/min spent ruminating. Examples of the traces obtained are given in Figures 5.6 and 5.7.

The animals were "bailed" at 14.00 and 19.00 hours. At each "bailing", the rumen digesta was weighed, mixed thoroughly, subsampled and returned back to the animal. Subsamples of rumen digesta were taken for: (i) triplicate DM determinations, and (ii) particle size analysis. The efficiency of chewing during rumination in breaking down feed particles in the rumen between 14.00 and 19.00 hours was then determined.

5.2.4.3.2 Calculations

(i) The number of chews/min were counted for each animal for 15 periods of 60 sec (3 periods of 60 sec/h, from 14.00 to 19.00 hours), during the measurement period. Mean values of the number of chews/min during ruminating were then obtained for each animal over this period.

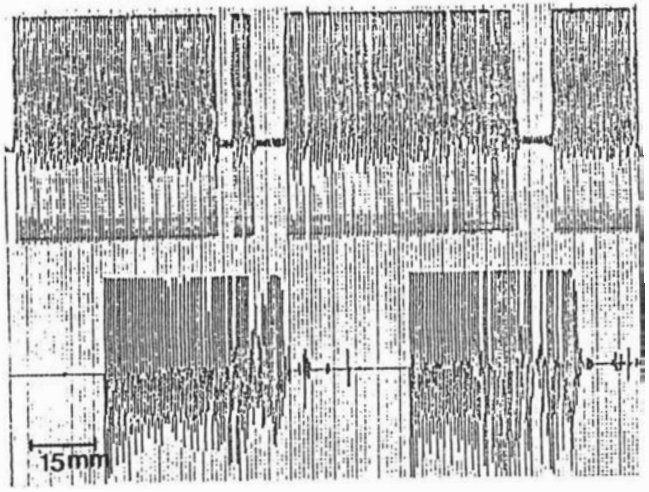

Figure 5.6. Trace showing number of chews during rumination by goats.

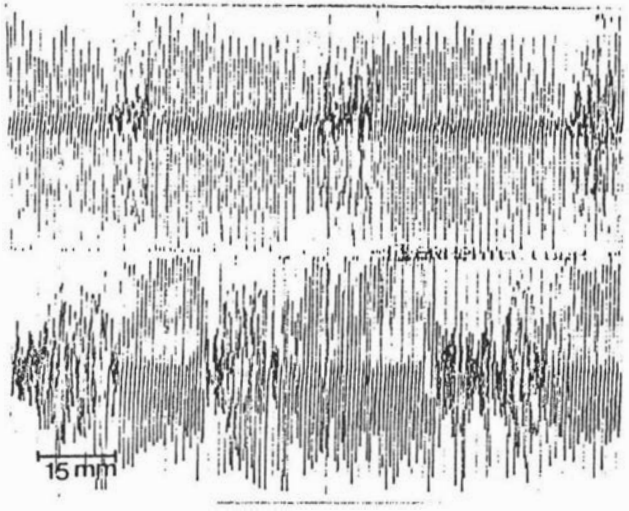

Figure 5.7. Trace showing number of chews during rumination by sheep.

(ii) The total time spent ruminating (h) was determined for each animal during the 5-h measurement period, and the total number of chews calculated (Equation 6).

$$\text{Total number of chews during Rum (14.00 - 19.00 hours)} = \text{Total time Rum (mins)} \times \text{Number of chews per min Rum} \quad (6)$$

(iii) The proportion of particles >1.0 mm in the rumen digesta was determined at 14.00 and at 19.00 hours. An index of efficiency, for chewing during rumination (<C.RUM>) in breaking down feed particles >1.0 mm during that period of 5 h (14.00-19.00 hours), was calculated (Equation 7).

$$\langle C.RUM \rangle = \frac{\text{(Pool size >1.0 mm (A) (14.00 hours)} - \text{Pool size >1.0 mm (B) (19.00 hours))}}{\text{Pool size >1.0 mm (14.00 hours)}} \quad (7)$$

(Pool size (A) was determined after subsampling of rumen digesta for particle size analysis, and was material actually returned to the rumen. Pool (B) represented material actually removed from the rumen).

The calculation (7) was based on the assumption that feed particles >1.0 mm cannot leave the rumen (Grenet, 1970; Poppi et al., 1980). Hence it was assumed that the reduction in the rumen pool size of particles >1.0 mm during the period of 14.00-19.00 hours was due only to rumination, without any loss of particles >1.0 mm flowing out of the rumen.

(iv) <C.RUM> was also expressed as <C.RUM> per total number of chews spent ruminating during the 5-h measurement period.

5.2.5 Chemical Analysis

Chemical analysis was carried out using the methods described in Section 2.9. The following analyses were performed. Samples of feed

offered and boli were analysed for OM, total N (% DM and % OM) and particle size. The DM of the rumen digesta samples was determined by freeze-drying for five days, until constant loss in weight (FD 57 freeze-dryer; WGG Cuddon (NZ) Ltd.).

5.2.6 Statistical Design and Analysis

A complete randomised design was used, with comparisons between goats and sheep being made using one-way analysis of variance. Mean values with the standard error of the difference (SED) are presented.

5.3 RESULTS

5.3.1 Time Spent Chewing During Eating and Ruminating by Goats and Sheep, During 24 h

There were no significant differences in the DMI (g/Kg $W^{0.75}$/d), between goats and sheep when fed on lucerne hay in winter.

Figure 5.8 and Table 5.1 show that, over a period of 24 h, goats spent more time (3.1 h; +85%; $P<0.01$) chewing during eating than sheep. This comprised 2 h more during the day and 1 h more during the night.

The total amount of time spent ruminating per 24 h by goats was significantly lower (2.2 h; -35%; $P<0.05$) than in sheep, comprising 1 h less during both the day and night periods. There were no differences ($P>0.1$) between the two species in the total amount of time spent chewing, per 24 h.

5.3.2 Efficiency of Chewing During Eating Upon the Breakdown of Feed Particles

The rate of eating (g DMI/min) was faster ($P=0.07$) in sheep (+62%), than in goats (Table 5.2), but when the rate of eating was expressed as g DMI/Kg $W^{0.75}$/min, the differences between goats and sheep disappeared ($P>0.1$). The frequency of chewing during eating (number of chews/min) was significantly greater ($P<0.01$) in goats than in sheep. Hence, the number of chews per gDMI during eating in goats

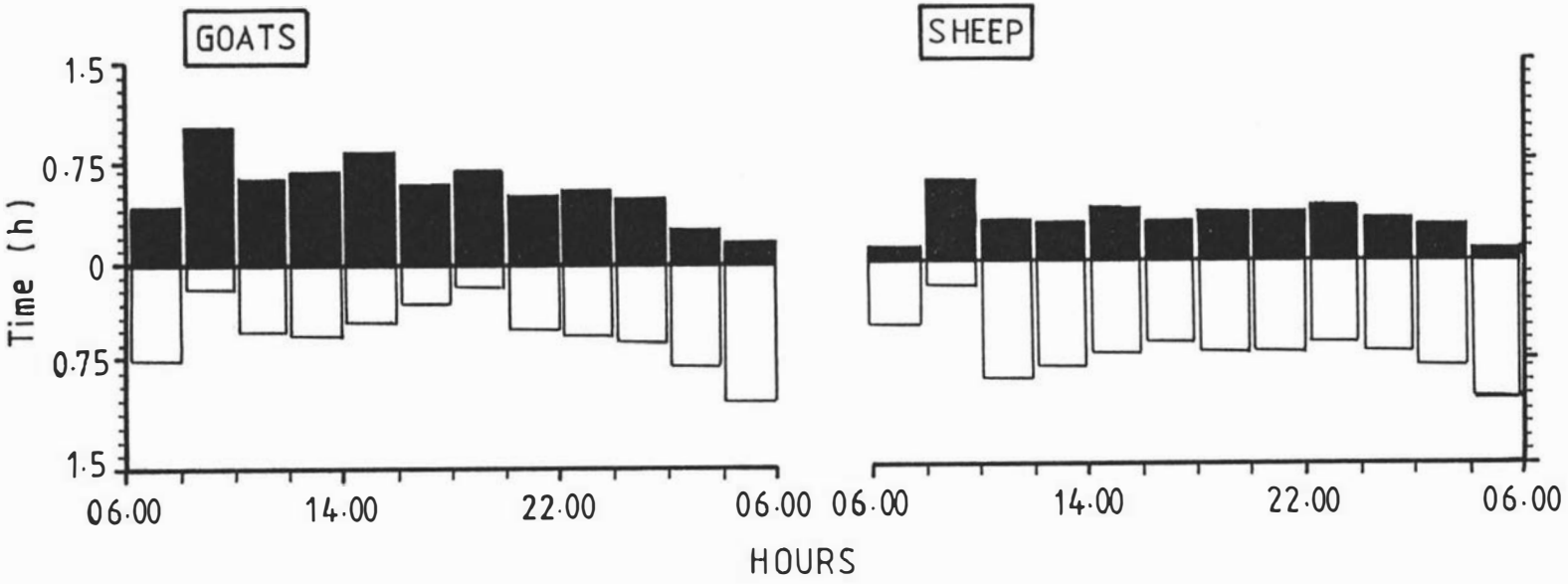

Figure 5.8. Time (h) spent chewing during eating (■) and ruminating (□) over a 24-h period, by goats and sheep, fed on lucerne hay at 90% "ad-lib" intake.

Table 5.1. Time (h) spent chewing during eating and ruminating per 24 h in goats and sheep, fed on lucerne hay, at 90% "ad-lib" intake.

(Mean values with their standard error of difference (SED) for four goats and four sheep.)

Time	Chewing behaviour (h)	Goats	Sheep	SED	
24-h period:	RUM	6.1	8.3	0.69	*
	EAT	6.8	3.7	0.57	**
	(RUM + EAT)	12.9	12.0	0.37	NS
	RUM/EAT ratio	0.92	2.29	0.276	**
Day:	RUM	2.7	3.7	0.35	*
(6 am - 6 pm)	EAT	4.3	2.0	0.35	***
	(RUM + EAT)	7.0	5.7	0.16	**
Night:	RUM	3.5	4.6	0.44	(*)
(6 pm - 6 am)	EAT	2.6	1.7	0.33	*
	(RUM + EAT)	6.1	6.3	0.27	NS
Dry matter intake (g/Kg $W^{0.75}$/d)		56.2	52.4	3.94	NS

RUM = Time spent chewing during rumination.

EAT = Time spent chewing during eating.

(RUM + EAT) = Total time spent chewing (eating + ruminating).

*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1; NS Non-significant

Table 5.2. Efficiency of chewing during eating upon the breakdown of feed particles by goats and sheep, fed on lucerne hay.
(Mean values with their standard error of the difference (SED) for five goats and five sheep.)

	Goats	Sheep	SED	
Feeding behaviour:				
Intake rate (g DM/min)[@]	3.71	6.02	1.08	(*)
(g DM/Kg $W^{0.75}$/min)[@]	0.20	0.24	0.024	NS
Number of chews/min eating[@]	154	128	3.7	**
Number of chews/g DMI	44	21	9.8	(*)
Particle size reduction:[@] (% dietary DM retained on sieve)				
> 4.0 mm	5.4	19.3	1.90	***
2.0 mm	4.7	7.2	1.06	*
1.0 mm	11.3	12.9	4.32	NS
0.5 mm	15.7	10.3	1.20	**
0.25 mm	24.9	20.1	1.62	*
< 0.25 mm	38.0	30.3	5.46	NS
< 1.0 mm	78.6	60.6	6.08	*
> 1.0 mm	21.4	39.4	6.08	*
Index of efficiency of chewing during eating (<C.EAT>)	0.85	0.48	0.068	**
<C.EAT> / number of chews. g DMI^{-1}	0.021	0.024	0.0050	NS
"Apparent" salivary secretion:[!]				
g/g DMI	7.8	5.8	0.97	(*)
g/g OMI	8.7	6.5	1.08	(*)
"Apparent" salivary N secretion rate (mg/g OMI)	13.0	3.3	3.65	*
N in "apparent" saliva secretion (mg/g)	1.48	0.50	0.42	(*)

[@] Feed particle size >1.0 mm for lucerne chaff fed was 95.2%.
[!] Test meal offered for 30 mins.
(Salivary secretion + water flows into rumen.)
*** P<0.001; ** P<0.01; * P<0.05; (*) P<0.1; NS Non-significant

was 109% greater than in sheep, with the difference attaining significance at P=0.08.

The calculated index of efficiency during eating (<C.EAT>) showed the greater effectiveness of goats (+77%) in reducing the feed particles to below the threshold (1.0 mm) to passage, than sheep (P<0.01). When <C.EAT> was corrected for the number of chews/gDMI, there were no significant differences between goats and sheep (P>0.1). Table 5.2 shows that the boli which were chewed during eating only and swallowed once, contained significantly greater proportions (% of dietary DM retained on sieves) of small particles (1.0-0.5 mm, 0.5-0.25 mm and <0.25 mm), and smaller proportions of large particles (>4.0 mm and 4.0-2.0 mm) for goats than for sheep.

The calculated "apparent" salivary secretion (g/g DMI and g/g OMI) was greater during eating in goats than in sheep (P=0.08). The calculated "apparent" salivary N secretion rate (mg N/g OMI) (P<0.05), and the calculated N in "apparent" saliva (mg N/g OM saliva) (P=0.06), were also greater in goats than in sheep.

5.3.3 Efficiency of Chewing During Ruminating Upon the Breakdown of Feed Particles

The frequency of chews per min spent ruminating was significantly lower (P<0.001) in goats than in sheep (Table 5.3). Both goats and sheep spent 32-33% of the 5-h measurement period ruminating (P>0.1).

The calculated efficiency of chewing during ruminating (<C.RUM>), indicated that sheep tended to be more effective (+23%) in breaking down the rumen pool of large particles (>1.0 mm) to particles <1.0 mm during ruminating than goats (P>0.1). When corrected for the total number of chews per minute ruminating during the 5h-measurement period, the differences between goats and sheep disappeared.

Table 5.3. Efficiency of chewing during ruminating (RUM) by goats and sheep, upon the breakdown of feed particles >1 mm during a 5-h period (14.00 - 19.00 hours).

(Mean values with their standard error of the difference (SED) for five goats and five sheep.)

	Goats	Sheep	SED	
Total number of chews (14.00-19.00 h)	7631	9878	1261	NS
Time (h) spent RUM (14.00-19.00 h)	1.62	1.64	0.216	NS
Number of chews/min RUM	79	100	2.03	***
Index of efficiency of chewing.RUM (<C.RUM>)	0.48	0.59	0.139	NS
<C.RUM> / number of chews. min^{-1} RUM	0.006	0.006	0.0015	NS

*** P<0.001; NS Non-significant.

5.4 DISCUSSION

The results of the present experiment showed that goats spent more time eating (+ 3.1 h; $P<0.01$), and less time ruminating (-2.2 h; $P<0.05$), per 24 h, than sheep when fed a chaffed lucerne hay diet. Geoffroy (1974), also reported that goats spent more time eating (+0.67 h/24 h; $P>0.1$), and less time ruminating (-1.5 h/24 h; $P<0.01$) than sheep, when fed on chopped ryegrass hay, with the differences between the 2 species thus being of smaller magnitude than observed in the present study, especially in the time spent eating.

The calculated index of efficiency of chewing during eating (<C.EAT>), indicated that goats were 85% efficient at breaking down large particles to <1.0 mm during eating, compared to 48% for sheep. Ulyatt et al. (1986), reported a mean <C.EAT> index of 43.5% for sheep fed on fresh and dried forages (range: 34.6-51.6%), which is much below that reported for goats in the present study.

The greater efficiency of chewing during eating can be due to 3 main factors (Ulyatt et al., 1986), namely:

1. Number of chews per min spent eating.

2. The grinding surface area of the teeth ($mm^2/Kg\ W^{0.75}$).

3. The articular surfaces of the skull and jawbones, which determine the forces applied during eating.

When corrected for the number of chews/min spent eating, the significant differences ($P<0.01$) in <C.EAT> between goats and sheep disappeared. It is therefore concluded that the greater number of chews/min spent eating in goats is a major component explaining their greater <C.EAT> values, compared to sheep. Factors 2 and 3 were not measured in the present experiment, and are possible components which together with factor 1 could all have influenced the process of a more efficient particle size reduction during eating in goats.

A greater proportion of small particles in the rumen provides a larger surface area of particles which is available for microbial

attachment and colonisation (Hungate, 1966; Akin, 1976; Cheng et al., 1977; Akin, 1979; Elliott et al., 1985). Thus, the presence of a greater proportion of small particles (<1.0 mm), in the rumen of goats than sheep for a longer period of time may have contributed to the greater apparent fibre digestibility by goats compared to sheep, as observed in Chapters 3 and 4.

Because of the longer time they spent chewing, and their greater effectiveness of chewing during eating, it seems that goats do not require to ruminate for as long as sheep. The process of rumination serves to reduce further the refractory size of particles which have not been broken down to <1.0 mm during eating (Pearce and Moir, 1964; Reid et al., 1979; Ulyatt, 1983; Chai et al., 1984; Ulyatt et al., 1986).

Data in Table 5.2 indicated that there was a greater proportion (+ 84%), of particles >1.0 mm in the boli swallowed after eating by sheep, compared to goats. Rumination in sheep appears to play a major role in breaking down the feed particles which are >1.0 mm in the rumen, and is not as important in goats. The greater efficiency of chewing during rumination (<C.RUM>) by sheep than goats (59% vs 48%), in breaking down the feed particles to <1.0 mm can be accounted for by the greater number of chews per min during rumination in sheep than in goats. Ulyatt et al. (1986), reported that the mean <C.RUM> obtained with sheep fed on fresh forage and dried diets was 53.6% (range 39.0-53.6%), a value close to the one obtained for sheep in the present experiment.

Both the apparent rate of "salivary secretion" and of "salivary N secretion" during eating, appeared to be greater in goats than in sheep, in the present experiment. This, together with the greater amount of time the goats spent eating, imply that goats have a greater N recycling capacity into the rumen through "salivary secretion" than sheep, thus explaining the greater rumen IRL of NH_3-N (mg N/g N intake/d), observed in goats when fed the lucerne chaff diet (Chapter 4).

Seth et al. (1976) have also reported greater rates of both parotid salivary secretion (+ 40%; $P<0.01$), and total salivary N secretion in goats during eating of a fresh forage diet than in sheep.

The greater "salivary secretion" rate in goats could also assist in a greater solubilisation of the dry diet used in the present study, as the forage is ground between the molars in the presence of saliva. This could be another factor in releasing the cell-contents during eating (Kay, 1966; Ulyatt, 1983), and explain a greater apparent fibre digestibility by goats compared to sheep .

5.5 CONCLUSIONS

5.5.1 Goats spent more time eating (+ 3.1 h; $P<0.01$), and less time ruminating (- 2.2 h; $P<0.05$) per 24 h, than sheep when fed a lucerne chaff diet.

5.5.2 The efficiency of chewing during eating (<C.EAT>) in breaking down feed particles to <1.0 mm was greater in goats (85%; $P<0.01$) than sheep (48%).

5.5.3 The process of rumination in sheep served to reduce the feed particles which were >1.0 mm in the rumen to <1.0 mm. Sheep tended to be more efficient in this process than goats (59% vs 48%), with the difference not attaining significance ($P>0.1$).

5.5.4 Because of the longer time goats spent eating, and the greater effectiveness of their eating in reducing particle size, goats did not require to ruminate for as long a period of time as sheep.

5.5.5 Chewing during eating was the more important component in breaking down feed particles to <1.0 mm in goats, whereas chewing during rumination was the more important component in sheep. The greater frequency of chews (number of chews/min) during eating in goats, or during ruminating in sheep, was the major component of efficiency in both the eating and rumination processes.

5.5.6 Goats had greater apparent "salivary secretion" rates during eating ($P<0.1$), and greater apparent "salivary N secretion" rates during eating ($P<0.05$) than sheep. This, together with the greater amount of time spent eating, helps explain the greater IRL of NH_3-N in the rumen of goats than sheep, when fed the same diet (Chapter 4).

CHAPTER SIX. EFFECTS OF SUBCUTANEOUS MELATONIN IMPLANTS DURING LONG DAYLENGTH ON VOLUNTARY FEED INTAKE, RUMEN CAPACITY AND HEART RATE OF DEER FED A MEDIUM QUALITY FORAGE.

6.1 INTRODUCTION

The seasonal rhythm of voluntary feed intake in deer is controlled by changes in daylength (Simpson et al., 1984; Suttie, Corson and Fennessy, 1984; Suttie and Simpson, 1985). Increasing daylength (spring/summer) is associated with high feed intake and decreasing daylength (autumn/winter) is associated with low feed intake (Milne et al., 1978; Suttie et al., 1984; Chapter 4). Metabolic rate (heat production), heart rate and activity are greater in summer and lower in winter in the white-tailed deer (Silver et al., 1969; Moen, 1978).

Periods of darkness are associated with a rise in the plasma concentration of the hormone melatonin (Me), much above that of daytime levels (Arendt, 1979; Asher et al., 1988). As the length of night-time increases from summer to winter, the length of time Me is secreted is longer in winter than in summer (Wurtman and Anton-Tay, 1969; Plotka et al., 1981; Bittman et al., 1983). Decreasing daylength and elevated plasma Me concentration have been associated with a decrease in feed intake in deer in winter (Simpson et al., 1984; Suttie et al., 1984).

Currently, it is known that deer which have been treated with exogenous Me in late spring/early summer, show a phase-shift in their reproductive physiology, with an advancement in sexual behaviour and mating in both males and females (Bubenik, 1983; Webster and Barrell, 1985; Asher, Barrell, Adam and Staples, 1988; Fisher, Fennessy and Milne, 1988). These results indicate that the constant administration of Me from a subcutaneous (s.c.) implant interferes with the normal photoperiodic regulation of reproductive physiology in deer. Melatonin acts to block the effects of long-days, and functions physiologically to entrain the seasonal reproductive rhythms to photoperiod, but there is no direct evidence that the appetite rhythm in deer is synchronised to the photoperiod by Me. As voluntary feed intake (VFI), metabolic rate and reproductive rhythms are closely linked in deer (Suttie and Kay, 1985; Curlewis, Loudon and Coleman,

1988; Barry et al., 1989), it is possible that the effects of day-length on the seasonal VFI are synchronised by Me.

Objectives of the present experiment were to investigate the effects of constant release s.c. implants of Me on VFI, rumen capacity, rumen digesta load and heart rate (an index of metabolic rate) in castrated male Red Deer, during periods of increasing day-length (spring/ summer). This was done to see if the seasonal changes in digestive function observed in deer in Chapter 4, could be altered by exogenous Me administration. The Me-Treated animals were exposed to a constant exogenous Me concentration in spring for 2 months. Measurements of DMI, rumen capacity, rumen digesta load and heart rate were carried out 2½ months (t1; early summer), 6 months (t2; late summer), 8½ months (t3; late autumn) and 10½ months (t4; late winter) respectively, after the first Me implant.

High concentration of plasma prolactin (P) has been associated with long daylength, high food intake and rapid weight gain in the Red Deer (Suttie and Kay, 1985), reindeer (Ryg and Jacobsen, 1982b), and in the sheep (Forbes, Driver, Brown, Scanes and Hart, 1979). Exogenous Me during long daylength depresses the plasma concentration of P to base-line levels in deer (Webster and Barrell, 1985) and in sheep (Kennaway, Dunstan, Gilmore and Seamark, 1983; Lincoln and Ebling, 1985; Poulton, English, Symons and Arendt, 1986, 1987). The effect of s.c. implants of Me on plasma P concentration was also measured during the present experiment and the results will be reported elsewhere.

6.2 EXPERIMENTAL

6.2.1 Experimental Design

The experimental design is shown schematically in Figure 6.1.

The first melatonin implants were inserted on 15 September 1988 (d1), and thereafter every 21 days for a period of 63 days (d21, d42, d63). The last implants were administered on 18 November 1988. The Me administration period was then followed by 4-week measurement periods (indoor trials) of VFI, rumen capacity, rumen digesta load and heart rate, to determine the immediate, short-term and long-term post-

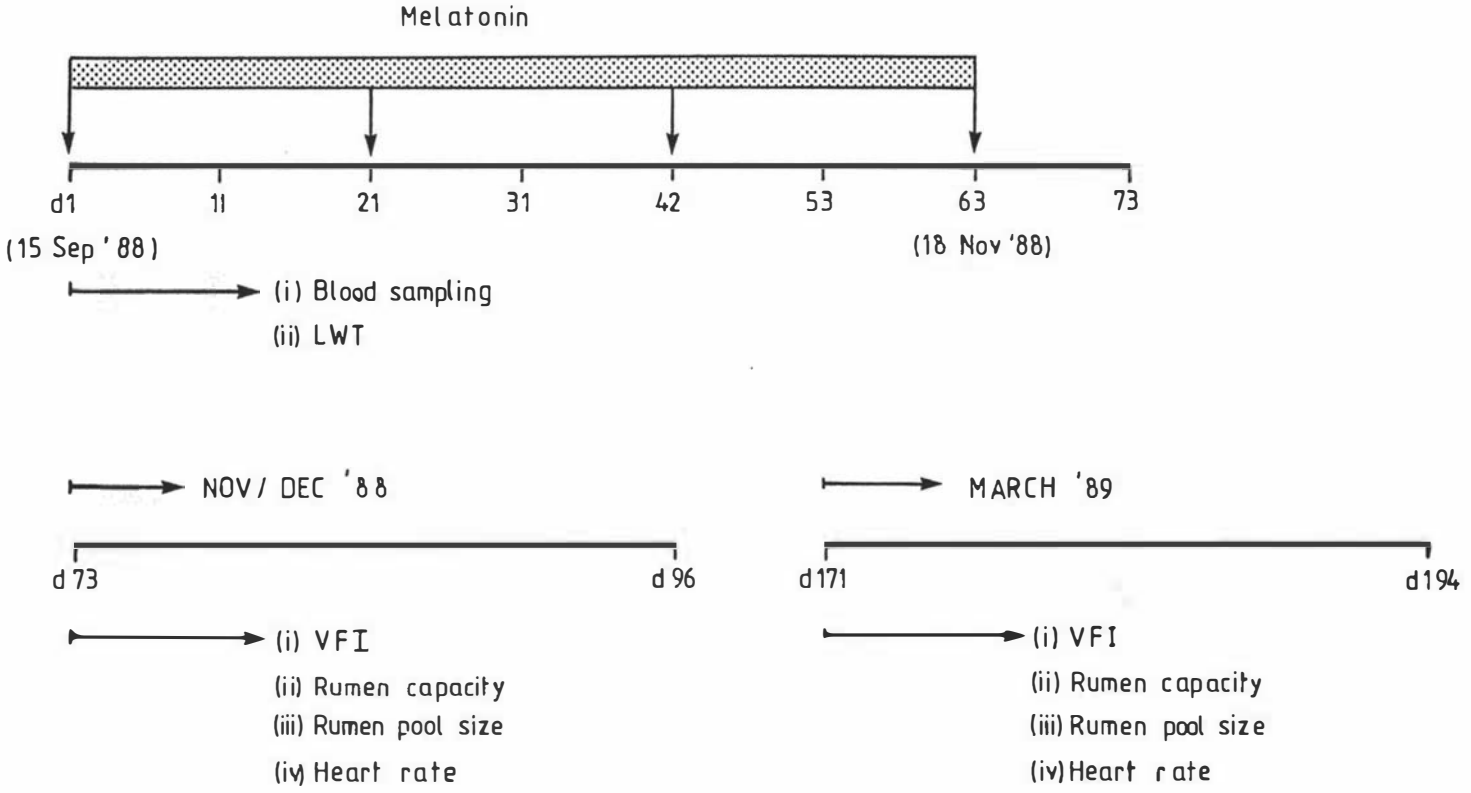

Figure 6.1. Schematic representation of the Experimental design (Experiment 4).

treatment effects of Me, namely in late November-December (t1), March (t2), May (t3) and August (t4).

This Chapter is concerned with the first two periods (t1 and t2) only. Results of periods t3 and t4 will be reported elsewhere.

6.2.2 Animals and Management

Thirteen castrated hand-reared Red Deer, aged 4 years, were used, including 7 deer fistulated in the rumen and fitted with permanent rubber cannulae (83 mm ID), and 6 non-fistulated deer. The fistulated and non-fistulated deer were balanced for LWT at the start of the experiment (15 September 1988), and allocated to 2 groups, Control (3 fistulated, 3 non-fistulated) and Me-Treated (4 fistulated, 3 non-fistulated). The Control group weighed 95.9 Kg LWT (SD 16.7), and the Me-Treated group weighed 95.7 Kg LWT (SD 14.0), at the start of the experiment.

In between the indoor trials, the Control and Treated groups were allowed to graze together on a mixed ryegrass/clover pasture. When housed indoors, the animals were kept under natural ambient light regimens.

6.2.3 Melatonin Treatment

Two implants, each containing 18 mg melatonin (M) (Regulin Batch 1000695-1; Regulin Ltd., Melbourne, Australia) were inserted sub-cutaneously at the base of the ear using a 8 mm gauge stainless steel trocar. The animals were restrained during the operation in a deer-crush.

6.2.4 Blood Sampling

Blood samples were taken from the jugular vein of Control and Treated groups, at 10-d intervals (11.00 hours), from 15 September to 18 November 1987 (d1, d11, d21, d31, d42, d53, d63, d73), and again on 5 April 1989 (d-205). Blood was taken by venipuncture of the jugular vein (2 x10 ml, heparinised Vacutainers). Blood sampling was carried

out before Me implantation, with the animals restrained in a deer-crush.

6.2.5 Liveweight Recording

The animals were weighed at 10-d intervals as from 15 September 1987 (Figure 6.1.).At the beginning and completion of each indoor feeding trial, the LWT of the animals was again recorded.

6.2.6 Diet

When kept indoors, the animals were fed on lucerne hay *(Medicago sativa)*, containing 896 g OM/Kg DM and 29.8 g N/Kg DM, and allowed free access to a multimineral salt block (50 g) (Appendix A). The hay was chaffed into 50-80 mm lengths before feeding.

6.2.7 Determination of Voluntary Feed Intake

Voluntary feed intake (VFI) of lucerne chaff (g/Kg $W^{0.75}$/d) was measured with the animals kept indoors during the periods t1 and t2. The fistulated animals were kept in metabolic crates (Section 2.3), and the non-fistulated animals were kept in individual pens with sawdust provided as bedding.

During each of the 2 experimental periods (t1 and t2), the animals were allowed an adaptation period of 12 days. VFI was measured for 8 days (t1=d85-d92; t2=d183-d190). The animals were fed "ad-lib", with that offered being 15% greater than the previous day's consumption. The non-fistulated animals were fed twice daily, and the fistulated ones were fed continuously from automatic belt-feeders at hourly intervals. Samples of feed offered were collected daily, pooled over the 8-day measurement period, and stored for chemical analysis. A daily duplicate oven dry-matter determination (Section 2.5) was done on the feed refusals of each animal, and the feed offered.

6.2.8 Rumen Capacity and Rumen Pool Size

Rumen capacity and rumen pool size (total DM + liquid, DM and liquid pools) were determined (g/Kg $W^{0.75}$) during the periods t1 and t2, using 3 Control and 4 Me-Treated fistulated animals.

At the completion of the VFI determination, the animals were restricted to 90% "ad-lib" intake for 4 days (t1 = d93-d96; t2 = d191-d194). The animals were "bailed" over d97-d99 (t1) and again over d195-d197 (t2), with 2 animals (1 Me-Treated and 1 Control) being used per day. Prior to bailing, the animals were sedated with 1 ml of 2% Rompun (xylazine; Haverlockhart, Bayvet (USA) Division). The rumen digesta was removed from the fistula (ID 83 mm), weighed, subsampled for triplicate DM determinations, and then kept warm over a bucket of warm water (temp 70 C). To determine the rumen water-filled capacity, a soft deflated rubber meteorological balloon (air capacity: 100g; Totex Corporation (Japan)), was then placed inside the empty rumen, and filled with water (temp 24 C) from a tared water-tank, through a rubber tubing (5mm ID) placed in the neck of the balloon (Figure 6.2).

The balloon was estimated to be full when the balloon + water had accommodated all parts of the rumen. The rumen water-filled capacity was calculated as the loss in weight of the water tank (g) after filling the balloon. The water from the balloon was then siphoned out until it could be removed by hand and drained. The warmed rumen digesta was returned back to the animal. The whole process lasted for a period of about 1 h.

6.2.9 Heart Rate

Heart rate was measured during t1 (d100-d102), and t2 (d198-d200), using 1 Control and 1 Me-Treated animal per day. Pre-gelled adhesive silver-chloride electrodes with press-studs (39 mm diameter; Medicotest (Denmark)), were glued to the closely-clipped skin of the animals on the dorso-lumbar and axillary regions (one per location). A portable electrocardiograph (ECG) (Cardisuny 501 A; Fukuda M-E (Medical Electronics); Kogyo Co. (Ltd.) Japan) was used to detect and record cardiopotentials from the body of the animals. The electrodes were connected to the ECG by standard electrical cables. Recording

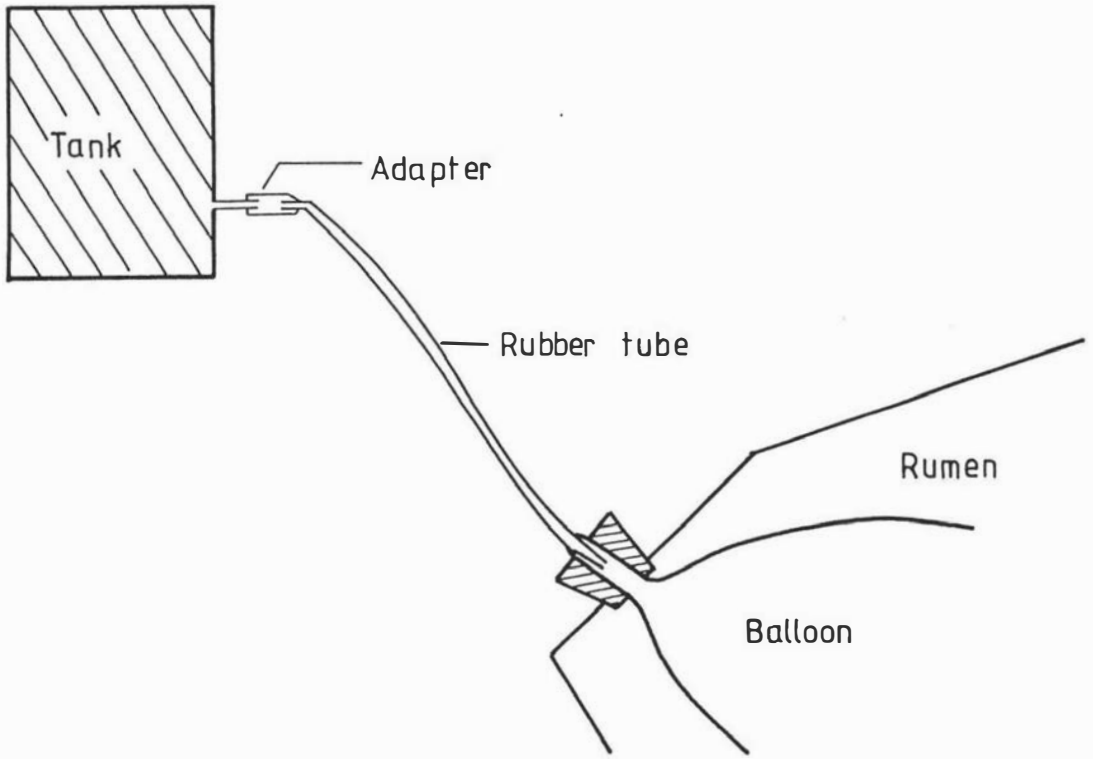

Figure 6.2. Measurement of rumen water-filled capacity in the deer.

was done automatically on high-sensitivity chart paper (Z-fold type; Fukuda M-E (Medical Electronics); Kogyo Co. (Ltd.) Japan), with a chart drive of 25 mm/sec and the calibration signal being 1 mv square wave.

Recording was done with the animals standing, under resting conditions, at periodic intervals over a period of 15 mins. Examples of the traces obtained from 1 Control and 1 Me-Treated animal are shown in Figures 6.3 and 6.4.

6.2.10 Radioimmunoassay of Melatonin

Plasma Me concentrations were determined by direct radioimmunoassay (RIA) as described by Fraser, Cowen and Franklin (1983). Duplicate samples of plasma (0.5 ml) were used. The antiserum (704/8483 Guildhary Antisera, University of Surrey, Guildford (U.K)) was raised in a sheep against N-acetyl-5-methoxytryptophan-bovine thyroglobulin and used at a final dilution of 1:8000. Low, medium and high melatonin control samples were included at frequent intervals in each assay. The inter-assay coefficients of variation were 27.5% for the low control (n = 30; mean = 21.4 pg/ml), 17.2% for the medium control (n = 30; mean = 121 pg/ml) and 15.8% for the high control samples (n = 29; mean = 510 pg/ml). The intra-assay coefficients of variation were 21.0%, 10.7% and 10.1% respectively for the three control samples. Sensitivity was 10 pg/ml.

6.2.11 Chemical Analysis

Chemical analysis was carried out using the methods described in Section 2.9. The following analyses were performed. Samples of feed offered were analysed for OM and total N (% DM). The DM of the rumen digesta samples was determined by freeze-drying for five days, until constant loss in weight (FD 57 freeze-dryer; WGG Cuddon (NZ) Ltd.).

6.2.12 Calculations

The heart rate (beats/10 sec) was measured on 10 occasions for each animal over the measurement period. The mean heart rate (beats/min), per animal was then calculated.

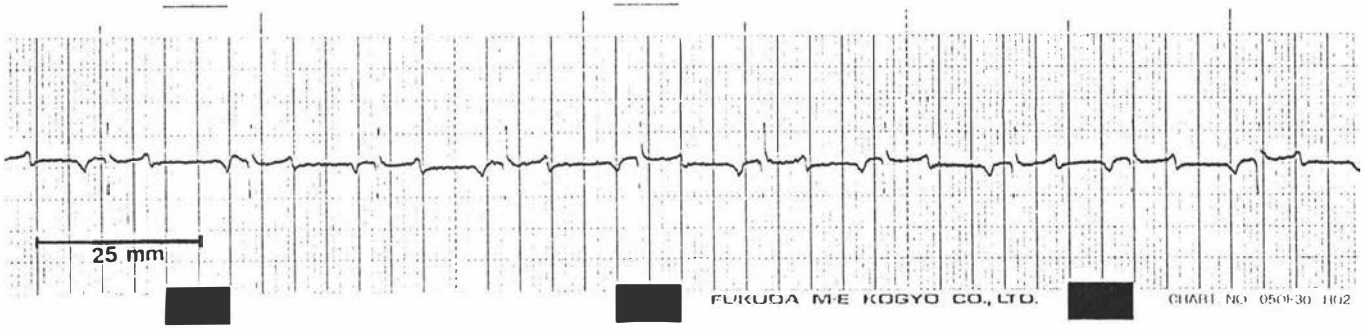

Figure 6.3. Trace showing number of heart beats by the Control deer.

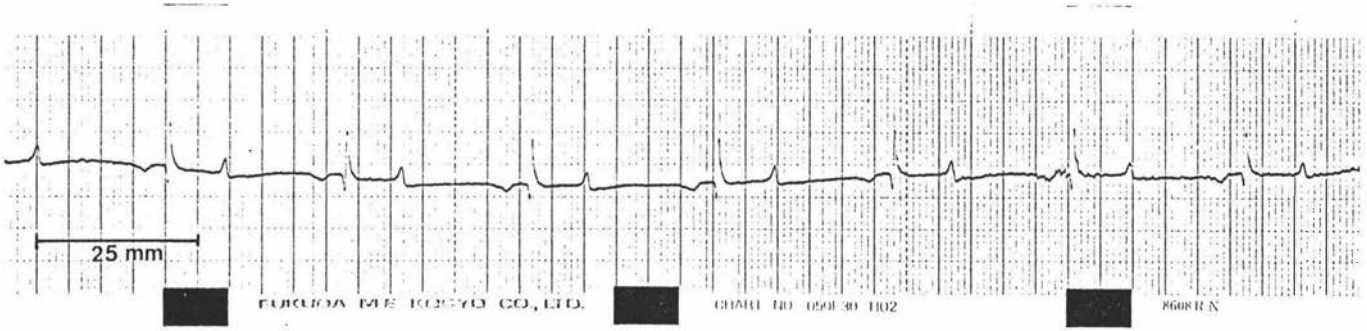

Figure 6.4. Trace showing number of heart beats by the melatonin-Treated deer.

6.2.13 Statistical Analysis

A split-plot design was used, with treatment as main plot (x2), and time (x2) as sub-plots (early summer and late summer). The differences between treatment and time effects, and treatment x time interactions, were determined by analysis of variance procedures.

6.3 RESULTS

6.3.1 Effects of Melatonin Treatment on Liveweight

Figure 6.5 shows that treatment with s.c. implants of Me did not affect the liveweight (LWT) profile of the Me-Treated group, which showed no significant differences from the Control group, either during or following the period of implantation.

6.3.2 Effects of s.c. Melatonin Implants on Day-time Plasma Melatonin Concentrations

By 11 days after the first s.c. Me implants (36 mg Me), the mean day-time Me concentration increased dramatically from 4 pg/ml to 154 pg/ml (Figure 6.6). By 21 days from implantation, the mean day-time Me concentration had declined to 116 pg/ml, and steadily decreased to a mean of 60 pg/ml by d-42 of Me treatment. This was followed by an increase in the day-time plasma Me concentration, which averaged 140 pg/ml between d53-d73. The Control group showed almost non-detectable day-time plasma Me concentrations during the sampling period. On d-205 (5 April 1989), the mean daytime plasma Me concentration was 31 pg/ml for the Me-Treated group, and 4 pg/ml for the Control group.

6.3.3 Effects of Melatonin Treatment on Voluntary Feed Intake, Rumen Pool Capacity and Rumen Pool Size

Treatment with Me in early spring tended to depress VFI (g/Kg $W^{0.75}$/d), rumen water-filled capacity and rumen pool size (g/Kg $W^{0.75}$), with effects generally failing to attain significance ($P>0.1$) in t1 (d73-d102), but attaining significance (VFI and rumen capacity, $P<0.05$; rumen pool size, $P<0.1$), during t2 (d171-200) (Table 6.1). There were no significant treatment x time interactions ($P>0.1$), and

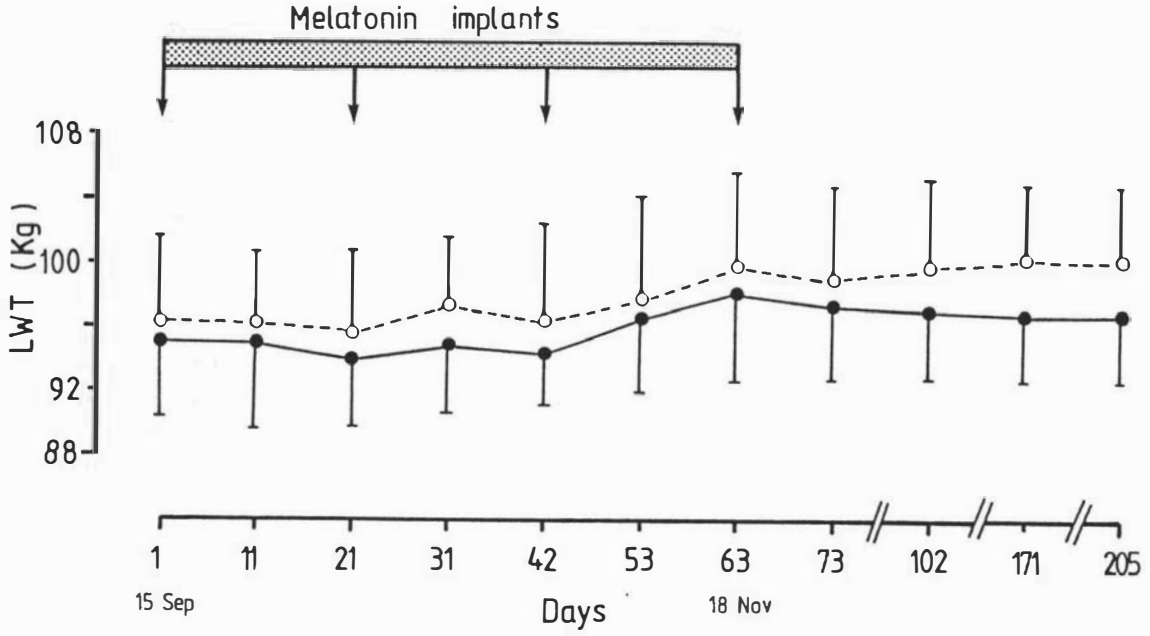

Figure 6.5. Profiles of mean liveweight (± SEM) for Control (o) and melatonin-Treated (•) Red Deer castrates.

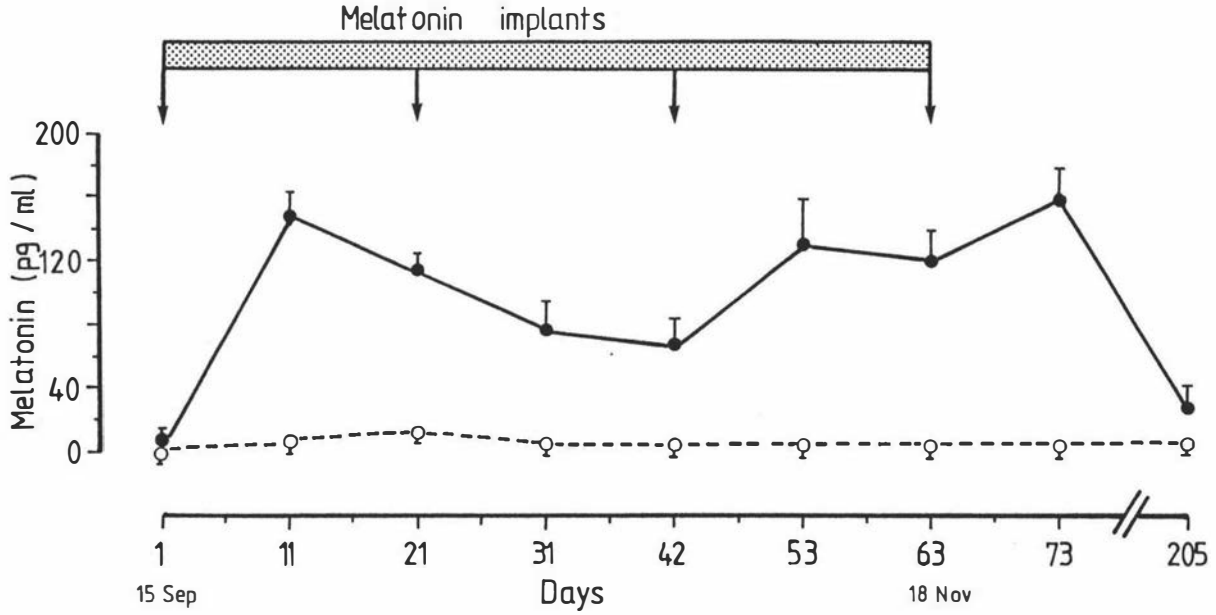

Figure 6.6. Profile of mean daytime (± SEM) plasma melatonin concentrations (pg/ml) of Control (o) and melatonin-Treated (•) Red Deer castrates in spring/summer.

Table 6.1. Voluntary dry matter intake (DMI, g/Kg $W^{0.75}$/d), rumen capacity, rumen pool size of dry matter (DM) + liquid, rumen pool size of DM, rumen pool size of liquid (g/Kg $W^{0.75}$), and heart rate (beats/min) of control (C) and melatonin-treated (Me-T) Red Deer castrates at d88-d106 (t1) and d191-d210 (t2), after the first subcutaneous implants of melatonin.

(Mean values with their standard error of difference (SED) are shown.)

		Control	Me-treated	SED	
Voluntary DM intake !	t1	77.5	70.0	6.58	NS
(g/Kg $W^{0.75}$/d)	t2	83.0	70.3	4.89	*
Rumen capacity @	t1	451	444	55.2	NS
(g/Kg $W^{0.75}$)	t2	529	479	15.6	*
Rumen pool size: @ (g/Kg $W^{0.75}$)					
DM + liquid	t1	353	306	34.7	NS
	t2	365	296	33.2	(*)
DM	t1	46.9	40.6	6.27	NS
	t2	54.2	41.5	6.50	(*)
Liquid	t1	306	266	28.5	NS
	t2	311	255	27.5	(*)
Ratio of rumen (DM + liquid pool)/rumen capacity @	t1	0.79	0.70	0.072	NS
	t2	0.69	0.62	0.070	NS
Heart rate (beats/min) @	t1	65.0	51.5	6.04	(*)
	t2	66.3	51.0	6.17	(*)

All treatment x time are NS (P>0.1).

! C: n = 12; T: n = 13.

@ C: n = 3; T: n = 4.

* P<0.05; (*) P<0.1; NS Non-significant.

no significant (P>0.1) time effects (t1 vs t2), for either the Control or Me-Treated groups.

6.3.4 Effects of Melatonin Treatment on Heart Rate

Melatonin implants significantly (P<0.1) reduced heart rate (beats/min), in the Me-Treated group compared to the Control group, during both measurement periods t1 and t2, 101 d and 199 d after the initiation of Me treatment (Table 6.1).

6.4 DISCUSSION

Chapter 4 showed that deer had marked seasonal cycles of nutrient supply, including VFI and rumen digesta load. The cycles showed a peak in summer and a trough in winter.Objectives of the present experiment were to determine if Me administration would interrupt these seasonal cycles in deer, and looked at the immediate (t1) and short-term post-treatment effects (t2), of exogenous Me given in spring, when the normal endogenous Me level is low in the seasonal secretion profile.

Exogenous constant-release Me implants increased day-time plasma Me concentration significantly, and this was kept at high levels during the treatment period of 63 days. The progressive decline in day-time plasma levels (observed between d21-d42), indicates that exogenous Me may have been metabolised rapidly by the deer over this time period, but the progressive increase over d42-d63, suggests that this was a transitory phase. At d205, the day-time Me plasma concentration of Me-treated animals showed a marked decline, but had not yet reached the normal (Control group) day-time concentrations of Me, indicating that the implants were not yet completely exhausted, 140 days after the last Me implants. Asher *et al.* (1988), reported that declining plasma Me concentrations after the last implant were apparent for about 60 days, after which normal low day-time Me concentrations were recorded, and it appears that the exhaustion of the Me implants occurred earlier than that obtained in the present experiment.

The results of the present experiment showed that Me induced changes in the normal cycles of (i) VFI, (ii) rumen water-filled capacity, (iii) rumen digesta load and (iv) heart rate in the deer, thus interrupting the normal cycles of an increase in summer of the above parameters. The Me-Treated group showed a lower VFI, associated with a smaller rumen water-filled capacity and rumen digesta load, and a slower heart rate than the Control group, both at t1 and t2, with the differences being significant at t2 only.

There were no immediate (t1) and short-term post-treatment effects (t2) of Me on LWT, despite the lower appetite of the Me-treated group. This may be associated with a decrease in heat production (as indicated by the lower heart rate), in the Me-Treated group, which together with low appetite would negate any effects on LWT.

The results of the present experiment indicate that exogenous Me implants acted to block the effects of long days, and are consistent with the general view (Barry et al., 1989), that Me is the hormone which entrains the seasonal cycles in deer to photoperiod, and that exogenous Me interferes with this process. As Me-Treated animals experienced reduced VFI, rumen capacity, rumen digesta load and heart rate in summer, it is possible that Me administration has "re-set" the circannual rhythms of these criteria. It is possible that exogenous Me administration during long daylength initiates changes in the endocrine system, similar to those induced by exposure to short-days, including possible changes in the secretion of prolactin (P) and thyroid hormones. Plasma P secretion has been shown to decrease to base-line levels, following Me implantation in deer (Webster and Barrell, 1985), and in sheep (Kennaway et al., 1983; Lincoln and Ebling, 1985). However, the neurohormonal pathways by which Me influences seasonal cycles of VFI and associated rumen cycles, are as yet unknown.

The medium (t3) and long-term (t4) post-treatment effects of Me administration on VFI, rumen water-filled capacity, rumen digesta load and heart rate, will be measured in folllow-up studies. Two possible effects may possibly occur as the deer go through a normal climatic Southern hemisphere winter (May-August), namely:

1. The Me-Treated deer may experience a third successive "true" winter, when the normal endogenous plasma Me concentration increases in autumn/early winter, and relays the signal of short daylength to the animals, with a resulting depression in VFI and rumen digestion. This would suggest that Me administration in spring has "re-set" the circannual rhythm in deer for a period of 6 months.

2. The Me-Treated deer may experience an "artificial" spring/summer, with increased VFI and rumen digestion. This would suggest that Me administration in spring has "re-set" the circannual rhythm in deer for an annual cycle of 12 months.

The results of the present experiment tend to confirm that exogenous Me administration acts to relay the effects of changing daylength, and advances the seasonal physiology of deer, namely: (i) VFI (present experiment), (ii) coat growth (Bubenik, 1983; Fisher et al., 1988), (iii) rutting activity and early oestrus (Webster and Barrell, 1985; Asher et al., 1988; Fisher et al., 1988), (iv) antler growth (Bubenik, 1983), (v) plasma P secretion (Webster and Barrell, 1985).

Since Me is the hormone entraining the seasonal cycle of VFI (and associated rumen cycles), to photoperiod, it seems probable that deer which are successfully immunised against Me (resulting in high anti-Me antibody titres), may biologically lose the timing of seasonal events. Hence, the winter depressions in VFI and LWT, associated with short daylength and high plasma Me concentrations, could possibly be reduced in magnitude. However, previous work (Ataja et al., 1989; Duckworth and Barrell, 1989), indicates that a successful immunisation against Me in deer, depends on 3 critical factors, namely:

1. Time (age), at which immunisation is initiated, and

2. Use of powerful adjuvants to increase the production of Me-binding antibody proteins by the immune system.

3. It appears that there is a 5-month delay period, between the time of the primary immunisation against Me and the establishment of a high anti-Me antibody titre (Ataja, unpl. data). The lag period has to be taken into account, to

coincide peak antibody titres with the decrease in VFI in deer during the autumn/winter period.

It appears that immunisation is best done at birth, when the calves have not yet developed their endogenous circannual rhythms (Duckworth and Barrell, 1989). Preliminary results suggest that immunisation of Red Deer against Me at birth, can modify the seasonal pattern of LWT changes in yearling stags, which become about 8.5 Kg heavier than the Control group in spring by 11 months of age (Duckworth and Barrell, 1989). This may indicate an increase in the VFI (g/Kg $W^{0.75}$/d), and perhaps an improved rumen digestion, of the immunised deer in winter, compared to the Control group. There are no data as yet, on the effects of immunisation against Me on the VFI, rumen capacity and rumen digesta load of deer in winter. Obtaining such data is an important area for research into nutrient utilisation by farmed Red Deer.

6.5 CONCLUSIONS

6.5.1 Melatonin implantation of castrated Red Deer in spring depressed VFI (g/Kg $W^{0.75}$/d), rumen water-filled capacity and rumen digesta load (g/Kg $W^{0.75}$) and heart rate (beats/min), with the post-treatment effects being more pronounced in t2 (d171-d200), than t1 (d73-d102).

6.5.2 There were no effects on LWT changes, and this was probably associated with compensatory effects of a low heart rate (and metabolic heat production), and low VFI in the Me-Treated group, and a fast heart rate and greater VFI (g/Kg $W^{0.75}$/d) in the Control group.

6.5.3 As Me administration in spring induced winter-associated cycles of low VFI, smaller rumen capacity and rumen digesta load, and slower heart rate in the deer, with maximum effects being found at t2, it is possible that Me is a factor in entraining the seasonal cycles of intake and digestion in Red Deer to photoperiod.

6.5.4 Successful immunisation against Me (resulting in high anti-Me antibody titres), constitutes a potential method of binding high plasma Me concentrations during autumn/winter and of reducing the winter depressions in VFI and body growth in Red Deer.

6.5.5 Work is required on the effects of immunisation against Me on the control of VFI during winter in seasonal deer, and the neuro-hormonal pathways by which Me influences the seasonal cycles of VFI, rumen digestion and growth in deer.

CHAPTER 7. GENERAL DISCUSSION.

The following themes which have been developed throughout the study, will be discussed, namely:

1. Seasonal cycles of nutrient supply in deer, goats and sheep.

2. Comparative VFI and rumen digestion in goats and sheep.

3. Comparative VFI and rumen digestion in deer and sheep.

4. Potential control of winter VFI in deer.

5. Rumen outflow rates and marker methodology, and

7. Conclusions.

7.1 SEASONAL CYCLES OF NUTRIENT SUPPLY IN DEER, GOATS AND SHEEP

The marked seasonality of nutrient supply in deer, with an increase in DMI and DMD in summer and a trough in winter, was associated with seasonal changes in a number of rumen digestive criteria in the same direction. Table 7.1 shows that the increased DMI (g/Kg $W^{0.75}$/d) in summer in deer was associated with concurrent increases in the rumen fermentation capacity, as shown by the increase in the rumen NH_3-N concentration, internal recycling of water to the rumen, rumen digesta load (DM + liquid), apparent fibre digestibility, MRT of lignin and Ac/Pr ratio.

Goats also showed a seasonal increase in VFI (g/Kg $W^{0.75}$/d) in summer. Table 7.1 shows that whilst goats also increased rumen digesta load, internal recycling of water to the rumen and a number of other rumen digestive characteristics in summer, the extent of the increases was not as marked as for deer. Hence, unlike deer, the increased VFI in summer in goats occurred at the expense of a reduced DMD and apparent fibre digestibility.

It is known that the proportion of DM digestion that occurs in the rumen tends to decrease as VFI increases (Rode and Satter, 1986a),

Table 7.1. Seasonal cycles of dry matter intake (DMI) and associated cycles of rumen digestive function (as % increase or decrease from winter to summer), in deer, goats and sheep.

	Deer	Goats	Sheep
Dry matter intake ($g/Kg\ W^{0.75}/d$)	+33.8	+19.7	-4.7
Digestible dry matter intake ($g/Kg\ W^{0.75}/d$)	+29.9	+4.6	-10.8
Apparent dry matter digestibility (%)	+3.7	-9.8	-3.0
Apparent digestibility of total Fibre (%)	+11.2	-5.8	+12.8
Mean rumen retention time of lignin (h)	+25.8	-4.8	0
Rumen pool size of (DM + liquid) ($g/Kg\ W^{0.75}$)	+51.3	+26.9	-10.4
Rumen NH_3-N (mg N/L)	+56.4	-4.2	+5.2
Internal recycling of water to rumen ($g/Kg\ W^{1.0}/d$)	+74.1	+42.2	-16.8
FOR Cr-EDTA/FOR lignin	+27.3	+8.1	+2.2
Ac/Pr ratio	+16.0	+11.6	+6.6

and is regarded as a biological constraint to ruminant production (Rode, Coulter, Mears and Lawson, 1986b). However, unlike goats, deer were able to increase the extent of rumen digestion during summer, when VFI increased, thus ensuring no decrease in apparent energy digestibility.

The deer have shown a faster FOR of liquid relative to that of lignin from the rumen, compared to goats and sheep, with the magnitude being greater in summer. A possible consequence of a fast turnover of liquid relative to lignin in the rumen of deer compared to sheep and goats may be an associated decrease in the molar proportions of propionate in the rumen, and an increased microbial-NAN outflow to the abomasum, especially in summer. Work is required to study the effects of the faster turnover of liquid relative to lignin (and particulate matter) in the rumen of deer, and microbial-NAN outflow to the abomasum, compared to sheep.

Both deer and goats have shown seasonal cycles of VFI compared to the domesticated sheep, which showed no evidence of seasonal cycles of VFI in the present study. Feral breeds of sheep (like the Soay), still show marked seasonal cycles of VFI, with low intakes in winter and high intakes in summer (Kay, 1979; Kay and Suttie, 1981; Argo and Smith, 1983). It seems that the length of time that deer have been subjected to domestication and controlled feeding (20 years) is not long enough to have altered the seasonal VFI patterns. The cycles have been related to an adaptation of the animals with the normal seasonal cycles of feed availability in the wild state (Suttie, Goodall, Pennie and Kay, 1983). In contrast, the domesticated sheep which has been selected and fed by man for 6000 years, appears to have lost the seasonal VFI patterns.

It is concluded that the current farming of seasonal breeds of deer, like the Red Deer, is faced with the problem of an inherent reduced appetite in winter leading to reduced rates of body growth during this period. Possible methods for increasing winter VFI in seasonal breeds of deer have to be studied (Section 7.4), to optimise returns from a deer farming industry in New Zealand, and elsewhere.

7.2 COMPARATIVE VOLUNTARY FEED INTAKE AND RUMEN DIGESTION BY GOATS AND SHEEP

The present study has shown the following differences between goats and sheep in the utilisation of forage diets (both low quality and medium quality diets), namely:

1. Superior apparent fibre digestibility by goats, compared to sheep, with the difference between the two species being greater for the least digestible component, lignin.

2. Greater DMI (g/Kg $W^{0.75}$/d), and DMD of a low quality feed by goats, compared to sheep.

3. Seasonality in nutrient supply of goats, with a greater VFI in summer, and no such evidence for sheep.

4. The threshold to passage of particles through the reticulo-omasal orifice was 1.0 mm for both goats and sheep when fed on low and medium quality forage diets.

The superior apparent digestibility of fibre by goats compared to sheep has been associated in the present study with two consistent factors, namely (i) greater proportions of small particles (<1.0 mm), and lower proportions of large particles (>4.0 mm) in the rumen digesta of goats, compared to sheep, and (ii) greater absolute values for the production rate (IRL) of NH_3-N (g/d or g/Kg $W^{0.75}$/d) in the rumen of goats, compared to sheep (Table 7.2).

The results showed that goats had a greater IRL of NH_3-N (g/Kg $W^{0.75}$/d) from the rumen than sheep, both on low (+71%) and medium (+16%) quality diets. However, it appears that the scaler (g/g dietary N intake/d) used to express the results of IRL, might create artifact values. This occurred especially on the low quality diet (Chapter 3) when the N intake (g/d) by goats was much greater than in sheep.

Goats appear to have a mechanism for concentrating NH_3-N in the rumen when fed on low quality forages. This was associated with a

Table 7.2. Comparative study between goats and sheep of the irreversible loss rate (IRL) of NH_3-N and particle size breakdown of feed in the rumen.

	Medium quality diet[@]		Low quality diet[†]	
	Goats	Sheep	Goats	Sheep
Dietary N intake:				
g N/d	27.1	33.6	10.9	8.7
g N/Kg $W^{0.75}$/d	1.63	1.61	0.67	0.40
Rumen NH_3-N (mg N/L)	165	172	115	80
IRL of rumen NH_3-N:				
g/d	18.8	20.4	13.6	10.7
g/Kg $W^{0.75}$/d	1.13	0.98	0.84	0.49
g/g N intake/d	0.69	0.61	1.26	1.25
Small particles (<1.0 mm) in rumen digesta (DM) (%)	84.9	74.0	83.9	80.6
Large particles (>4.0 mm) in rumen digesta (DM) (%)	2.9	8.5	5.1	9.6

[@] Lucerne chaff (28.2 g N/Kg DM)

[†] Threshed prairie grass straw (13.6 g N/Kg DM).

slower rumen water inflow and outflow (g/g DMI/d) from the rumen of goats than sheep. It appears that the significantly lower water intake (g/g DMI/d) by goats than sheep, is an important component contributing to the concentrating effect of NH_3-N in the rumen of goats. A greater rate of NH_3-N production in the rumen of goats suggests the availability of a greater amount of NH_3-N available for the resident microbial population, and hence for a potential increase in apparent fibre digestibility, compared to sheep.

The longer eating time and greater salivary N secretion rate during eating by goats compared to sheep (Chapter 5), suggest that goats may have a greater salivary contribution to the recycling of urea-N to the rumen than sheep, when fed on the medium quality forage diet. Previous ruminant work suggests that, when fed on low quality roughage diets, the major route of urea-N entry into the rumen is through salivary secretion (Norton, Murray, Entwistle, Nolan, Ball and Leng, 1978; Norton, Moran and Nolan, 1979; Norton, 1984). It is possible than when fed on the low quality diet used in Chapter 3, goats showed a greater capacity than sheep to conserve urea at the kidney, and recycle more urea-N back to the rumen for re-utilisation by the microbial population. This would maintain greater concentrations of NH_3-N in the rumen of goats, and contribute to a greater apparent fibre digestibility by goats than sheep

The greater proportions of small particles (<1.0 mm) and smaller proportions of large particles (>4.0 mm) in the rumen of goats (Chapter 3 and 4) than sheep, were associated with differences in (i) the greater frequency of chewing during eating by goats than sheep, and (ii) the more efficient <C.EAT> of goats than sheep. We assume that the differences observed on the medium quality diet (Chapter 5) would be maintained on the low quality diet. The significance of a greater efficiency by goats than sheep in breaking down feed particles to <1.0 mm during eating may have the following consequences, namely:

1. Rumen contents of goats have a larger surface area provided by the small particles (<1.0 mm) for microbial attachment and colonisation, essential to microbial attack, as described by Akin (1976; 1979), and Elliott and Norton (1985).

It is considered that one of the processes limiting the rate of fibre digestion is the initial rate of bacterial attachment (Rode et al., 1986b), and bacterial adhesion is accelerated by plant tissue damage (Latham, 1980). It is possible that the greater <C.EAT> by goats than sheep conveyed an advantage of a greater initial breakdown and bacterial adhesion of feed particles during eating, and hence contributed to a greater apparent fibre digestibility, especially of lignin, by goats than sheep.

2. Goats do not have to ruminate for such long periods as sheep, since their efficiency of chewing during eating is greater. It is possible that there is a lag period, imposed by the rumination of a greater pool of particles >4.0 mm in the rumen of sheep than goats, and breakdown to smaller particles (<1.0 mm) prior to microbial adhesion and attack.

The rumen environment of goats, with (i) greater molar proportions of n-butyrate and n-valerate, (ii) pH of 6.73 and (iii) greater concentration of NH_3-N, possibly favoured the growth of cellulolytic bacteria, and hence increased apparent fibre digestibility in goats compared to sheep, when fed on the low quality diet.

The superior VFI (g/Kg $W^{0.75}$/d) of low quality forage diets by goats than sheep (+65%) were associated with two factors, namely:

(i) a larger rumen pool size (g/Kg $W^{0.75}$) of (DM + liquid) in goats than sheep, and

(ii) larger proportions of small particles (<1.0 mm) in the rumen of goats, and possibly a more efficient <C.EAT> by goats than sheep when fed on the low quality forage diets.

Goats had a larger rumen pool size of (DM + liquid) than sheep when compared on a Kg $W^{0.75}$ scaler. A larger rumen pool size per Kg $W^{0.75}$ would allow a larger VFI (g/Kg $W^{0.75}$) by goats than sheep. Small particles (<1.0 mm) pack more densely in the rumen (Martz and Belyea, 1986), and may have contributed to a greater VFI (g/Kg $W^{0.75}$/d) by goats than sheep fed on the low quality forage diets.

It is concluded that the greater production rates of NH_3-N in the rumen and a greater <C.EAT> by goats and sheep, are possible factors contributing to a greater apparent fibre digestibility by goats compared to sheep, both on low- and medium-quality diets. Optimum conditions in the rumen environment, possibly favouring the growth of cellulolytic bacteria, may have been an additional contributing factor to the greater apparent fibre digestibility by goats than sheep, when fed on the low-quality forage diets. A larger rumen pool size (g/Kg $W^{0.75}$) of (DM + liquid) in goats than sheep was associated with a superior VFI (g/Kg $W^{0.75}$/d) by goats when fed on a low quality forage diet.

7.3 COMPARATIVE VOLUNTARY FEED INTAKE AND DIGESTIVE EFFICIENCY BY DEER AND SHEEP

The greater VFI (g/Kg $W^{0.75}$/d) by deer than sheep, at the peak of the seasonal intake cycle in summer, may be associated with a larger (Chapter 4) rumen digesta load (g/Kg $W^{0.75}$) and possibly a larger (Chapter 5) rumen capacity (g/Kg $W^{0.75}$) in the deer.

The results of the present study showed that deer in New Zealand digested fibre more efficiently than sheep, both in summer and in winter, at the peak and trough of the VFI cycle. Our data are supported by previous deer vs sheep studies, made in New Zealand by Fennessy *et al.* (1980). The results obtained, contrast with the general trend of work in Scotland, where deer digested fibre less efficiently than sheep, and this was associated with a shorter MRT of particulate DM in the rumen. The data obtained in the present study showed that the rumen MRT of lignin (as an internal marker for particulate DM) was longer for deer than in sheep in summer, and contrast with the findings of Milne *et al.* (1978) in Scotland.

It is possible that the difference in the rumen MRT of particulate DM between deer and sheep is a factor in explaining the differences in fibre digestive efficiency between the two species obtained in the Northern and Southern hemispheres.

7.4 POTENTIAL CONTROL OF WINTER VFI IN DEER

Figure 7.1 suggests a possible role for the hormone melatonin (Me) in the control of VFI in seasonal deer, in spring/summer (initiation of pathway 1), and in autumn/winter (initiation of pathway 2). The seasonal VFI in deer may be entrained to photoperiod by Me, by the onset of the following cycles, namely:

1. High concentration of plasma Me in autumn/winter (pathway 2) is associated with the onset of the reproductive cycle, and the release of LHRH, LH (luteinising hormone) and testosterone (T) (Lincoln et al., 1972; Lincoln et al., 1984; Suttie and Kay, 1985).

It is hypothesised that a decline in VFI in winter is associated with the production of LHRH, LH and T. The rutting period has been associated with a marked decline in VFI in deer (Suttie et al., 1983) and also in the feral Soay breed of sheep (Argo and Smith, 1983). High plasma Me concentrations may also influence other neuroendocrine events, unknown at the present, leading to lower winter VFI in seasonal breeds of deer.

2. It is assumed that low plasma concentrations of Me in spring/summer (pathway 1) shut off the release of LHRH and consequent production of T, and initiate the release of (i) Prolactin (P) (Suttie, 1980; Ryg and Jacobsen, 1982b), (ii) Thyroid Hormones (TH) (Rindberg et al., 1978), (iii) Growth Hormone (GH) (Suttie et al., 1989) and (iv) Insulin-like Growth Factor I (IGF-I) (Suttie et al., 1989). These hormones have been associated with an increase in appetite and growth in spring/summer in the seasonal deer.

The results of the present study have shown that exogenous administration of Me in spring disrupts the normal summer-associated cycles of an increase in VFI, rumen capacity, rumen digesta load and heart rate in castrated seasonal Red Deer. High concentrations of plasma Me in spring/summer by exogenous Me implants relay a signal of short daylength in seasonal deer, possibly by shutting off pathway 1 and initiating pathway 2 and other neuro-hormonal pathways not known at present. Hence, the Me-treated deer "re-sets" its circannual

REFERENCES USED TO PREPARE FIGURE 7.1.

1. Lincoln (1971; 1985).
2. Lincoln et al. (1972).
3. Mirachi et al. (1978).
4. Rindberg et al. (1978).
5. Schultze, Seal, Plotka, Letellier, Verme, Ozaga and Parsons (1981).
6. Ryg and Jacobsen (1982a; b).
7. Lincoln et al. (1984).
8. Barrell et al. (1985).
9. Fennessy and Suttie (1985).
10. Fennessy, Suttie and Fisher (1985).
11. Asher et al. (1988).
12. Fisher, Fennessy and Milne (1988).
13. Suttie et al. (1989).
14. Chapter 6 (present thesis).

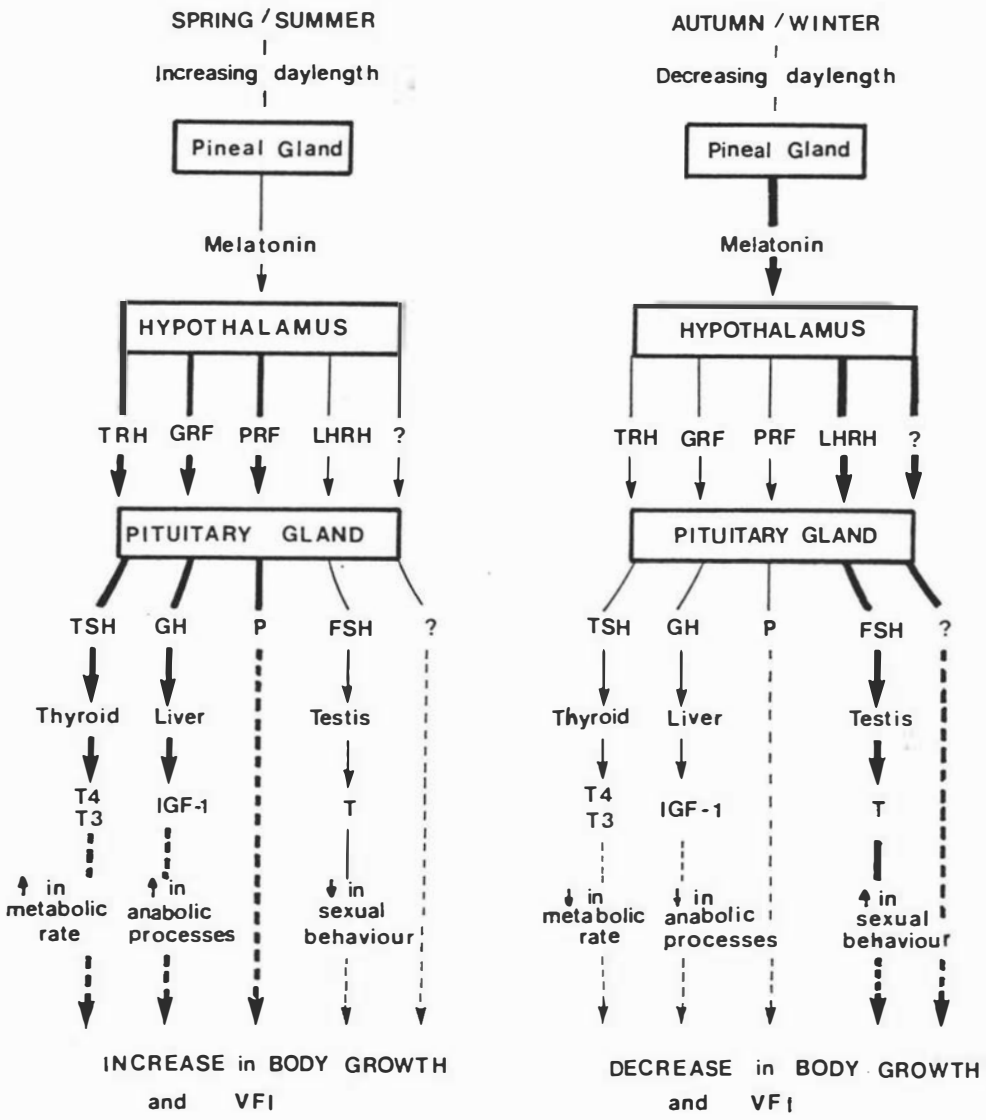

Figure 7.1. Control of voluntary feed intake in seasonal breeds of deer: a working hypothesis

rhythm and experiences an "artificial" winter. The question of the effects of a low Me plasma concentration in winter can then be raised.

Figure 7.1 indicates that the autumn/winter and spring/summer associated cycles of VFI are inherent to the seasonal breeds of deer and are hormonally linked. Manipulation of the seasonal cycle of VFI to reduce the winter trough in VFI in seasonal breeds of deer may be possible by reducing the concentration of plasma Me in autumn/winter and the Me-associated pathway 2 associated with a high concentration of Me, namely by:

1. Immunisation against Me of seasonal breeds of deer calves at birth, and
2. Immunisation against LHRH in yearling stags.

Successful immunisation against Me with high concentrations of anti-Me antibody titres in autumn/winter may prevent the initiation of pathway 2, and favour the continuation of pathway 1. Work is required to study the effects of immunisation against Me on the following factors, namely:

1. Hormonal status of the deer during an annual cycle (profiles of P, GH, IGF-I and TH);
2. Effects on VFI during autumn/winter, measured outdoors and using indigestible markers;
3. Effects on body growth. Preliminary studies have suggested good prospects for immunisation of Red Deer calves at birth against Me, for sustained body growth throughout autumn/winter (Duckworth and Barrell, 1989).

Immunisation against LHRH in yearling stags, to coincide high anti-LHRH antibody titres with late summer/autumn, may possibly block the surge in plasma testosterone in autumn/winter. Hence, rutting may be prevented, as well as the testosterone (rutting)-associated effects of a decrease in VFI in winter.

It is concluded that the potential for increasing winter VFI in deer is associated with reducing high autumn/winter plasma Me concentrations in seasonal deer. Immunisation against plasma Me appears to

provide good prospects. More work is required to study the effects of immunisation against Me on (i) the changes in neurohormonal pathways, and (ii) the effects on winter VFI in seasonal breeds of deer. At present our knowledge is fragmentary and very minimal.

7.5 RUMEN OUTFLOW RATES AND MARKER METHODOLOGY

Table 7.3 summarises the rumen Fractional Outflow Rates (FOR, %/h) of Cr-EDTA, lignin and the "apparent" FOR of particles <1.0 mm observed for deer, goats and sheep in the present studies. Cr-EDTA labels the liquid phase of the digesta. Lignin is an internal dietary marker for particulate dry matter, and is a component of the particles. The "apparent" FOR of particles <1.0 mm represents the "apparent" outflow of particles which are below the critical threshold size to passage through the reticulo-omasal orifice.

The rumen FOR (%/h) of markers, and hence the phase which they label, was defined (Section 2.10.1.1) as the proportion of the outflow of the marker (g/h) from the rumen (under steady state and in equilibrium), to the rumen pool size (g) of the marker in the rumen dry matter.

$$\text{FOR of marker (\%/h)} = \frac{\text{Rumen Outflow of marker (mg/h)} \times 100}{\text{Rumen pool size of marker (mg)}}$$

The FOR (%/h) of lignin (L) was defined as the proportion of the faecal lignin output to the total rumen lignin pool size.

$$\text{FOR of L (\%/h)} = \frac{\text{Faecal L output (mg/h)} \times 100}{\text{Rumen L pool size (mg)}}$$

The following conclusions are made from data in Table 7.3, namely:

(i) There were small differences between goats and sheep in the FOR (%/h) of all three markers, when fed on both low and medium

Table 7.3. Rumen marker outflow rates (FOR, %/h) and marker methodology for deer, goats and sheep fed on a low† and a medium@ quality forage diet.

	Diet	Deer	Goats	Sheep
FOR Cr-EDTA	Low	ND	8.0	8.7
	Medium	16.3	9.6	10.3
FOR Ru-Phen	Low	ND	6.7	6.9
	Medium	7.6	6.8	6.9
FOR lignin	Low	ND	2.6	3.3
	Medium	3.5	3.5	3.3
FOR particles <1.0 mm	Low	ND	3.5	3.7
	Medium	4.4	3.3	3.6
FOR Cr-EDTA/FOR of particles <1.0 mm	Low	ND	2.41	2.56
	Medium	3.58	3.01	2.98
FOR lignin/FOR of particles <1.0 mm	Low	ND	0.75	0.86
	Medium	0.83	1.05	0.94
FOR Cr-EDTA/FOR lignin	Low	ND	3.24	2.92
	Medium	4.77	2.82	3.12

† Summer data; @ Winter data

ND = not determined.

quality forage diets, with the values being slightly lower for goats, especially when fed on the low quality forage diet.

(ii) Deer showed a faster FOR of Cr-EDTA and of particles <1.0 mm from the rumen than both goats and sheep.

(iii) Water (Cr-EDTA) leaves the rumen in the same ratio to particles (<1.0 mm) for both goats and sheep; approximately 2.5 times faster for the low quality forage and approximately 3.0 times faster for the medium quality forage diet.

(iv) Water leaves the rumen of deer at a faster rate in relation to particulate matter than for sheep and goats, and this is substantiated by a faster ratio of FOR Cr-EDTA/FOR lignin in deer, than in sheep and goats.

(v) The ratio of FOR lignin/FOR particles <1.0 mm should ideally be 1.0, since lignin is a component of all particles. A ratio of >1.0 mm may indicate solubility of lignin in the rumen, and a faster outflow of soluble lignin leaving the rumen in water than the particles. A ratio of <1.0 mm may indicate the digestion of lignin posterior to the rumen.

Data in Table 7.3 indicate that the ratio was constant for sheep both on low and medium quality diets, and support the use of lignin as a marker for particulate dry matter in sheep (Faichney, 1984). Lignin was a good marker to study the seasonal effects within species, fed on the same diet (summer vs winter) for deer, goats and sheep. The results of the present experiment indicate that the use of lignin as a particulate marker poses some problems when looking at (i) inter-species comparisons (Chapter 3: goats vs sheep; Chapter 4: deer vs goats vs sheep), when large differences between species are noted for the ratio of FOR lignin/FOR particles <1.0 mm, and (ii) within-species comparison studies, especially for goats, when fed on different diets (low quality forage diet (Chapter 3) and medium quality forage diet (Chapter 4)). It appears that the differences are associated with the different proportions of particle sizes in the rumen of the three species, and the difference in the "apparent" FOR (%/h) of particles 1.0 - 0.5 mm from the rumen.

7.6 CONCLUSIONS

We conclude from the present study that goats utilise low quality forage diets better than sheep, and maintain a higher DMI and DDMI (g/Kg $W^{0.75}$/d) than sheep. Goats digest the fibre components of both low and medium quality forages, especially lignin (the least digestible component) more efficiently than sheep. These two advantages of goats over sheep will be best exploited when goats are grazed on the lower quality pastures, and sheep allowed to graze on medium and better quality pastures where they will perform better.

The present study has shown that the Red Deer have an inherent seasonal cycle of VFI and associated cycles of rumen digestion. The seasonal cycles have been associated with an adaptation to the environmental changes in feed availability in the wild. It is concluded that if under farming conditions this strategy is suitable for hinds, it hinders venison production which is aimed at a target slaughter weight of 95 Kg liveweight in late spring/early summer, to suit the export market requirements. This requires high growth rates in all seasons. More research is required on the control of winter VFI in the seasonal breeds of deer, and in the suitability of crossing Red Deer with the tropical breeds of deer to see if the hybrid shows reduced seasonality under New Zealand conditions.

APPENDIX A: Multimineral Salt Block

Dominion Salt (NZ) Ltd.

Flavour boosted multimineral salt block.

Contains zinc, copper and cobalt sulphates, potassium iodate, molasses and 3 ppm selenium.

APPENDIX B: Formulation for mineral pre-mix.

Formulation by Pfizer Laboratories (NZ) Ltd.

Ingredients	Amounts Rounded	Percent as Fed
Salt	370.61	37.061
Dicalcium phosphate	285.78	28.578
Potassium carbonate	181.72	18.172
Potassium chloride	120.00	12.000
Magnesium oxide	34.15	3.415
Ferrous sulphate	2.89	0.289
Selenium (conc 1%)	2.40	0.240
Copper sulphate	0.95	0.095
Zinc oxide	0.92	0.092
Manganous oxide	0.43	0.043
Sodium molybdate	0.12	0.012
Cobalt carbonate	0.02	0.002
Calcium iodate	0.01	0.001

Total weight 1000.00

Nutrient amounts in 1.2500 units are shown below

		Amounts	
		Min	Actual
		1.2500	1.2500
Sodium	grams	137.61	182.06
Chloride	grams	281.20	281.20
Calcium	%	16.48	17.66
Phosphorus	%	6.43	6.43
Potassium	grams	75.00	75.00
Magnesium	grams	23.05	23.05
Iron	grams	1.12	1.12
Copper	grams	0.30	0.30
Manganese	grams	0.33	0.33
Zinc	grams	0.92	0.92
Molybdenum	grams	0.06	0.06
Selenium	grams	0.03	0.03
Cobalt	grams	0.01	0.01
Iodine	grams	0.01	0.01
Potassium carbonate	grams	0.00	227.15
Salt	grams		463.26

APPENDIX C: Formulation for Liquid Vitamin Supplement

Hydrovit® liquid vitamin supplement

May and Baker (NZ) Ltd, Animal Health Products

Vitamin A	=	100,000 IU/g
Vitamin D3	=	20,000 IU/g
Vitamin E	=	40 mg/g

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