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A comparison of the voluntary intake and digestion of a range of forages at different times of the year by the sheep and the red deer (*Cervus elaphus*)

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1. Comparisons were made between castrated male Scottish Blackface sheep and red deer (*Cervus elaphus*) of voluntary forage intake (VFI), digestibility and the mean retention time (MRT) of a particulate-phase marker (^{103}Ru-phenanthroline) in the alimentary tract, when a range of forages: dried-grass pellets, chopped dried grass, fresh-frozen *Agrostis–Festuca* spp. and heather (*Calluna vulgaris*, L. Hull) were given at different times of the year.

2. On both the dried-grass-pellet and chopped dried-grass diets the red deer and sheep ate similar quantities. Both species had a higher VFI of dried-grass pellets in July than in November. The sheep digested the dried-grass-pellet diet better than the red deer and this was associated with a longer MRT of the particulate-phase marker in the alimentary tract.

3. The VFI of *Agrostis–Festuca* spp. and heather by the red deer was twice that of the sheep. The VFI of heather by the sheep increased by 32 % between January and April, and the VFI of both the *Agrostis–Festuca* spp. and heather diets by the red deer increased by 65–70 %. The sheep digested the *Agrostis–Festuca* spp. better than the red deer but the red deer digested the heather slightly better than the sheep. MRT of the particulate-phase marker was greater for the sheep than for the red deer on both diets. The digestibility and MRT of both diets in the red deer did not decrease with the seasonal increase in VFI, suggesting a possible hypertrophy of the alimentary tract.

Domesticated sheep and feral red deer (*Cervus elaphus*) are the principal producers of food for human consumption from a large proportion of the rough grazings of Scotland. In any study of land use or resource management it is necessary to know whether there are differences between the two species in the biological efficiency with which they use the resource. These can be brought about by differences between the species in their grazing behaviour, ability to consume more of a diet and digest it better, in their efficiency of utilization of the end-products of digestion and in their nutrient requirements. It is the second aspect which is examined in this paper.

Sheep and red deer eat many similar plant species which range from highly digestible grasses in summer to poorly digested grasses and heather (*Calluna vulgaris*, L. Hull) in winter (Hobson, 1969), but seasonal fluctuations in voluntary intake by red deer (Simpson, 1976) and other *Cervidae* (Long, Cowan, Strawn, Wetzel & Miller, 1966; McEwan & Whitehead, 1970) would appear to be greater than those found with sheep (Gordon, 1964). Preliminary results of Kay & Goodall (1976) have indicated that with good-quality roughage diets there were only small differences between sheep and red deer in voluntary intake (VFI), digestibility and mean retention time of undigested residues in the gut. However, comparisons using poor quality roughages have not been made.

The present experiments were designed to examine the differences between the sheep and the red deer in VFI, digestibility and mean retention time of a particulate-phase marker (MRT) when low-quality *Agrostis–Festuca* spp. and heather were given in the winter and spring and good-quality chopped or pelleted dried grass were given in summer and autumn. A preliminary report of this study has already been given (Milne, MacRae, Spence & Wilson, 1976).

Table 1. *Chemical composition (g/kg dry matter) of diets offered to red deer* (Cervus elaphus) *and sheep*

	Dry matter (g/kg)	Ash	N	Neutral-detergent fibre*	Acid-detergent fibre†	Acid-detergent lignin†
			Experiment no. 1			
Dried-grass pellets						
November	915	85	28·3	503	274	33
July–August	877	89	23·5	569	300	37
Chopped dried grass						
July	875	87	25·3	580	320	42
August	882	95	17·8	631	329	39
			Experiment no. 2			
Agrostis–Festuca						
December	481	84	11·8	622	357	43
January	482	69	12·7	621	377	44
April	414	87	14·5	620	342	41
Heather						
December	448	33	10·1	442	377	208
January	444	40	10·4	454	351	189
April	436	32	10·5	434	362	191

* Van Soest & Wine, 1967. † Van Soest, 1965.

EXPERIMENTAL

Animals

Twelve red deer calves were weaned from hill grazings at 5 months of age in November, 1974, off hinds which had been gathered as newly born calves from sites throughout Scotland and hand-reared at the Hill Farming Research Organisation–Rowett Research Institute Experimental Red Deer Farm at Glensaugh, Kincardineshire, Scotland. After weaning, the calves were loose-housed for 10 months, fed on a diet of hay and barley concentrate and accustomed to regular handling. They were castrated in March, 1975, at the age of 9 months.

Twelve Scottish Blackface castrated male sheep were weaned from hill grazings at 5 months of age in the same year as the red deer. They were kept at pasture throughout the winter, when they were given supplementary concentrate feeding, and during the following summer.

From September 1975 the deer and the sheep were managed similarly. Between experimental periods the animals were loose-housed and fed on a diet of hay and barley-based concentrate to meet their estimated maintenance requirements.

During the experimental periods the red deer (mean (±SE) live weight 74·5±2·14 kg) were housed in individual pens (dimensions 1·2 m × 1·7 m × 1·6 m) which had an expanded-metal floor and wooden side panels (see Plate 1). During each balance period the adjustable side panels were moved to produce metabolism pens (dimensions 0·8 m × 1·7 m × 1·6 m). During the experimental periods the sheep (mean (±SE) live weight 51·4±1·12 kg) were also housed in individual metabolism pens of a standard design. Live weights were recorded at the beginning and end of each experimental period. Continuous artificial lighting was provided, but daylight was not excluded.

Diets

Dried-grass pellets. Herbage from a predominantly perennial ryegrass sward, harvested in July 1975, was dried in a low-temperature drier, ground through a 1·0 mm screen and pelleted (approximate dimensions 15 mm × 10 mm).

Dried grass. The chopped dried grass was harvested in June and July 1976 from predominantly perennial ryegrass swards and dried in a low-temperature drier. Mean staple length was approximately 50 mm.

Agrostis–Festuca. The herbage was harvested in August 1975 with a flail harvester from a site at House o' Muir Research Farm, Midlothian, Scotland, and stored at −20° until offered to the animals.

Heather. Current season's shoots of heather were harvested with a modified small flail harvester in early September 1975 from a site at Glensaugh Research Station, Kincardineshire, Scotland, and stored at −20° until offered to the animals. The heather offered to the sheep contained 860 g dry matter/kg current season's shoots.

The chemical compositions of the diets are given in Table 1.

Experimental design

Expt 1. Dried-grass pellets were offered to twelve deer and twelve sheep in November and to six deer and six sheep in July–August. The six animals from each species allocated to the dried-grass-pellet diet in July were selected such that their mean intake in November was similar to the mean intake of the twelve animals in November. Chopped dried grass was offered to the remaining animals in July–August. VFI and digestibility determinations were made when the diets were offered *ad lib.* Mean retention time of a particulate-phase marker was measured at restricted intakes (80 % of VFI in November; 70–90 % of VFI in August).

Expt 2. *Agrostis–Festuca* spp. and heather were each offered *ad lib.* to six deer and six sheep in December, January and April. Random allocation of animals to the different diets was made after ranking the deer and the sheep in pairs according to their VFI of the dried-grass-pellet diet in November (Expt 1). Each animal received the same diet throughout the three measurement periods.

Experimental procedures and analyses

VFI and digestibility measurements. In each experimental period the animals were accustomed to their diets for 2–3 weeks before the start of the balance period. Balance periods were of 10 d duration when voluntary intakes were being measured and of 7 d duration at restricted levels of intake in Expt 1. The animals were fed twice daily at 08.30 hours and 16.30 hours. A refusal margin of 30 % was allowed with the dried-grass diets and 40 % with the *Agrostis–Festuca* spp. and heather diets. Quantitative collections of faeces and urine were made using standard procedures.

Samples of food and food refusal for dried grass and dried-grass pellets were oven-dried at 90°; corresponding samples of *Agrostis–Festuca* spp. and heather and all faeces samples were freeze-dried. Urine samples were preserved with 1 M-sulphuric acid and stored at −20°. Bulked samples of food, faeces and refusals were analysed for ash content by heating at 550° for 2 h; nitrogen content of all samples was determined by a micro-Kjeldahl method. Neutral-detergent fibre (NDF) content was determined by the method of Van Soest & Wine (1967) and acid-detergent fibre and lignin contents by the methods of Van Soest (1965). In vitro organic matter (OM) digestibility of samples of food refusal

Table 2. *Expt* 1. *Mean voluntary intakes of organic matter (OMI) and nitrogen, mean apparent digestibility coefficients of organic matter (OM), neutral-detergent fibre (NDF) and N and N balance results for red deer and sheep offered dried-grass pellets* ad lib.

	OMI			Apparent digestibility			
	g/d	g/kg $W^{0.75}$ per d	N intake (g/d)	OM	NDF	N	N balance (g/d)
			November 1975				
Red deer	1457	57·3	43·4	0·627	0·569	0·609	+8·4
Sheep	1377	71·3	41·4	0·665	0·607	0·656	+6·6
			July 1976				
Red deer	2246	82·3	58·0	0·573	0·565	0·589	+17·7
Sheep	1960	88·2	50·3	0·585	0·593	0·604	+11·2
SEM	116·4	4·83	3·42	0·0096	0·0135	0·0117	1·38

for the *Agrostis–Festuca* spp. and heather diets were determined by the method of Tilley & Terry (1963), as modified by Alexander & McGowan (1966).

MRT measurements. MRT of the particulate-phase marker ^{103}Ru-phenanthroline (Tan, Weston & Hogan, 1971) was measured after a single oral dose of the marker (14 μCi/animal administered in gelatin capsules). Faecal collections were then made hourly for 36 h in Expt 1 and for 48 h in Expt 2. Thereafter collections were made at regular intervals and with decreasing frequency until at least 7 d after administration of the marker.

Each faecal sample was weighed and a representative sample of approximately 12 g taken for counting. These 12 g samples were dried, weighed to determine their dry matter (DM) content and counted for 10 min using a scintillation spectrometer (NE 8312; Nuclear Enterprise Ltd, Sighthill, Edinburgh).

MRT of the ^{103}Ru-phenanthroline for the total alimentary tract was calculated by the method of Faichney (1975). Values for the compartmental MRT of the marker in the digestive tract were obtained by an iterative curve-fitting technique similar to that described by Grovum & Williams (1973) using a computer program for linear compartmental modelling (K. W. Davies, personal communication). Where the relationship between the faecal ^{103}Ru-phenanthroline concentration and period after dosing was best described by two exponential equations, the rate-constants of these equations were considered to represent values for MRT in the rumen, and caecum and proximal colon (hereafter referred to as caecum) (Grovum & Williams, 1973). The transit time of the marker was taken as the calculated interval before first appearance of the marker in the faeces (Grovum & Williams, 1973). Values designated as 'fitted' total values for MRT for the whole gut were obtained by adding the estimated values for MRT in the different compartments and the transit time (see Table 6).

Statistical analysis

An examination of the effects of season, species of animal and type of diet and their interactions was carried out by analysis of variance (EDEX statistical programme; Hunter, Patterson & Talbot, 1973).

RESULTS

Expt 1

The mean voluntary intake of organic matter (OMI) and N and digestibilities of OM, NDF and N, together with N balance results for red deer and sheep offered the dried-grass-pellet diet are given in Table 2. There was no significant difference between the

Table 3. *Expt* 1. *Mean intakes of organic matter (OMI), mean digestibility coefficients of organic matter (OM) and neutral detergent fibre (NDF), whole-gut mean retention times (MRT), compartmental MRT (considered to represent rumen and caecal MRT) and transit times of* ^{103}*Ru-phenanthroline in red deer and sheep offered dried-grass pellets at* 80 % *of voluntary intake*

	OMI		Digestibility		MRT (h)			Transit time (h)
	g/d	g/kg $W^{0.75}$ per d	OM	NDF	Total	Rumen	Caecal	
			November 1975					
Red deer	1183	46·6	0·608	0·516	22·6	13·0	3·4	7·3
Sheep	980	51·0	0·672	0·625	36·4	19·1	7·0	9·4
			August 1976					
Red deer	1764	64·5	0·584	0·569	21·1	12·0	3·2	6·2
Sheep	1612	72·6	0·607	0·597	26·3	12·9	5·1	8·3
SE of mean	76·62	3·16	0·0089	0·0124	2·28	1·99	0·855	0·393

Table 4. *Expt* 1. *Mean voluntary intakes of organic matter (OMI), mean apparent digestibility coefficients of organic matter (OM), neutral detergent fibre (NDF) and nitrogen of chopped dried grass offered to red deer and sheep* ad lib., *and mean OMI and digestibility coefficients, whole-gut mean retention time (MRT), compartmental MRT (considered to represent rumen and caecal MRT) and transit times of* ^{103}*Ru-phenanthroline in red deer and sheep offered chopped dried grass at 70–90 % of voluntary intake*

	OMI		Apparent digestibility		
	g/d	g/kg $W^{0.75}$ per d	OM	NDF	N
		Voluntary intake: July 1976			
Red deer	1444	53·2	0·708	0·743	0·674
Sheep	1332	62·6	0·718	0·755	0·694
SEM	111·5	4·27	0·0099	0·0120	0·0138

	OMI		Digestibility	MRT (h)			Transit time (h)
	g/d	g/kg $W^{0.75}$ per d	OM	Total	Rumen	Caecal	
			Restricted intake: August 1976				
Red deer	1070	39·5	0·629	41·1	25·1	5·3	9·6
Sheep	918	42·8	0·636	43·2	18·3	14·2	10·8
SEM	76·85	3·24	0·0065	2·85	1·68	1·69	0·52

OMI by the deer and sheep, although the sheep ate more ($P < 0·05$) when OMI was expressed per kg metabolic live weight ($W^{0.75}$). Both species had higher ($P < 0·05$) OMI in July compared with November; those of the deer increased by 54 % and those of the sheep by 42 %. The digestibilities of OM and NDF were lower ($P < 0·001$) in July than in November, but at both times they were higher ($P < 0·05$) in the sheep than in the deer. There was no significant difference between the intakes of N by the deer and the sheep. The deer were in a greater ($P < 0·01$) positive N balance than the sheep, even though the sheep had a higher apparent N digestibility ($P < 0·01$).

When the intakes of OM by the deer and sheep were restricted to approximately 80 %

Table 5. *Expt 2. Mean voluntary intakes of organic matter (OMI) and nitrogen, mean apparent digestibility coefficients of organic matter (OM), neutral-detergent fibre (NDF) and N and N balance for red deer and sheep offered* Agrostis–Festuca *spp. and heather* ad lib.

	OMI			Apparent digestibility			
	g/d	g/kg $W^{0.75}$ per d	N intake (g/d)	OM	NDF	N	N balance (g/d)
			December 1975				
Red deer							
Agrostis–Festuca spp.	945	38·3	11·6	0·405	0·362	0·201	−2·6
Heather	846	34·1	8·7	0·467	0·298	0·116	−3·7
Sheep							
Agrostis–Festuca spp.	363	20·2	3·9	0·475	0·429	0·165	−2·4
Heather	310	17·0	2·9	0·405	0·167	0·0284	−2·8
			January 1976				
Red deer							
Agrostis–Festuca spp.	1130	46·3	15·3	0·433	0·362	0·382	ND
Heather	811	29·5	8·7	0·460	0·301	0·184	ND
Sheep							
Agrostis–Festuca spp.	413	23·1	5·2	0·524	0·458	0·425	ND
Heather	322	17·8	3·3	0·462	0·240	−0·218	ND
			April 1976				
Red deer							
Agrostis–Festuca spp.	1864	70·0	29·0	0·460	0·419	0·390	2·3
Heather	1405	54·9	15·0	0·469	0·297	0·269	2·5
Sheep							
Agrostis–Festuca spp.	443	24·6	6·6	0·520	0·491	0·432	−1·0
Heather	443	23·8	4·7	0·441	0·196	−0·087	−3·6
SEM	67·5	2·99	1·11	0·0178	0·0187	0·0482	0·36

ND, not determined.

of their VFI values in November and August, differences between the deer and sheep in digestibility of OM and NDF were maintained. The values for MRT of ^{103}Ru-phenanthroline in the whole gut, rumen and caecum and the transit times were all shorter ($P < 0.01$) for the deer than the sheep when they were fed on the dried-grass-pellet diet (see Table 3). For both species the transit times and whole-gut MRT of the marker were shorter ($P < 0.05$) in August than in November.

The chopped dried grass fed at restricted intake in August was of a different quality to that fed *ad lib.* in July (see Table 1). There was no significant difference between the two species in voluntary intake per d or per kg $W^{0.75}$ per d in July or digestibility in July and August (see Table 4). There was also no significant difference between the values for whole-gut MRT in August, although the marker stayed longer ($P < 0.05$) in the rumen and for a shorter ($P < 0.01$) time in the caecum of the deer than in that of the sheep.

Expt 2

Mean values for OMI and N intakes, mean digestibilities of OM, NDF and N and mean N balance results for *Agrostis–Festuca* spp. and heather offered to the red deer and sheep are given in Table 5.

On both diets and at the different times of year, the values for OMI by the deer were greater ($P < 0.05$) than those by the sheep, both on an absolute and on a per kg $W^{0.75}$

Table 6. *Expt. 2. Whole-gut mean retention time (MRT), compartmental MRT (considered to represent rumen and caecal MRT, with a third compartment found in sheep offered heather) transit times and 'fitted' total MRT of* ¹⁰³*Ru-phenanthroline in red deer and sheep offered diets of* Agrostis–Festuca *spp. and heather ad lib.*

	MRT (h)				Transit time (h)	'Fitted' total MRT (h)
	Total	Rumen	Caecal	Third compartment		
			January 1976			
Red deer						
Agrostis–Festuca spp.	27·4	17·0	2·8	—	9·0	28·7
Heather	37·7	21·3	5·2	—	11·7	38·1
Sheep						
Agrostis–Festuca spp.	56·1	25·2	12·4	—	16·0	53·6
Heather	66·6	24·1	13·5	7·5	19·2	64·6
			April 1976			
Red deer						
Agrostis–Festuca spp.	32·5	23·4	2·1	—	6·9	32·4
Heather	40·9	28·2	4·7	—	10·7	43·5
Sheep						
Agrostis–Festuca spp.	53·4	28·0	12·4	—	14·9	55·2
Heather	54·9	23·1	13·8	7·0	15·2	59·1
SEM	3·09	2·41	1·66	2·40	0·86	2·97

basis. The values for OMI of the *Agrostis–Festuca* spp. diet by the deer were greater ($P < 0·01$) than those of heather. Values for OMI of the two diets by the sheep were not significantly different. The sheep had greater ($P < 0·05$) (32 %) OMI for heather in April compared to December and January while the OMI for both diets by the deer were greater ($P < 0·001$) (65–70 %) in April.

The digestibilities of OM and NDF of *Agrostis–Festuca* spp. were lower ($P < 0·05$) for the deer than for the sheep. However, the digestibility of NDF of the heather was higher ($P < 0·05$) for the deer. The differences in digestibility of OM and NDF of these diets by the two species are unlikely to be attributable to different extents of diet selection, since in vitro OM digestibility of food refusals from the deer and the sheep were not significantly different. The digestibility of OM and NDF of heather by the deer was not significantly different between periods whereas the digestibility of OM and NDF of *Agrostis–Festuca* spp. was higher ($P < 0·05$) in April than December. The digestibility of OM and NDF of heather and *Agrostis–Festuca* spp. by the sheep was lower ($P < 0·05$) in December than January or April.

Because of the higher VFI values, N intakes were higher ($P < 0·001$) for the deer than for the sheep on both diets in December and in April. The apparent digestibility of N of heather was higher ($P < 0·001$) in the deer than in the sheep in all three periods, but on *Agrostis–Festuca* spp. there was no difference between the species. In December there was no significant difference between the N balance of the deer and the sheep on either diet. In April, however, on both diets the deer were in a higher ($P < 0·05$) positive N balance than the sheep.

The values for whole-gut and compartmental MRT, transit times and 'fitted' total MRT of ^{103}Ru-phenanthroline in deer and sheep on diets of *Agrostis–Festuca* spp. and heather are given in Table 6. In both January and April the differences between the sheep and deer on either diet in rumen MRT were small compared with the significant ($P < 0·001$) differences in caecal MRT and transit times. With sheep offered heather, a third compartment was found. The MRT of the third compartment were smaller than those considered to represent caecal MRT. Whole-gut MRT were shorter ($P < 0.001$) in the deer than the sheep on both diets and at all times of year.

DISCUSSION

Although the red deer and sheep in this experiment were of similar age and physiological condition the deer were on average 23 kg heavier than the sheep. It is generally considered that VFI is proportional to $W^{0.75}$ of different mature species (see Taylor & Young, 1968) but although the animals used were immature, it has been assumed that valid comparisons can be made on a $W^{0.75}$ basis.

The fact that there were only small differences in the VFI of the sheep and the deer with ground, pelleted and chopped dried grass of moderate to high digestibility (Expt 1) substantiates the earlier observations of Kay & Goodall (1976). However, with roughages of low digestibility, i.e. *Agrostis–Festuca* spp. and heather (Expt 2), the VFI by the deer were twice those of the sheep. Even though the VFI by the sheep on both the *Agrostis–Festuca* spp. and heather diets were as much as 20% lower than those by similar sheep on such diets found in other experiments conducted at the same time of year in this laboratory (J. A. Milne, A. Tait & A. J. F. Russel, unpublished results; C. S. Lamb, J. C. MacRae and A. J. F. Russel, unpublished results), the VFI of the poor-quality roughages by the deer were still considerably higher than those normally found with sheep. In experiments in which the voluntary intakes by cattle and sheep were compared, sheep have tended to eat less food on a $W^{0.75}$ basis than have cattle (Buchman & Hemken, 1964; Blaxter, Wainman & Davidson, 1966; Demarquilly & Weiss, 1971); these differences being less with ground forages (Buchman & Hemken, 1964) and greater with long roughages of poorer quality (Demarquilly & Weiss, 1971). Thus in this respect red deer appear to be more analogous to cattle than sheep.

Both species showed differences in VFI when given the same diets in different months of the year. There were small differences in chemical composition between batches of the same diet (see Table 1), but it is unlikely that these differences could have caused the differences in VFI. Thus with the dried-grass-pellet diet the lower VFI values were associated with higher N and lower NDF contents, whilst with the *Agrostis–Festuca* spp. diets, although the higher VFI were associated with higher N and lower NDF contents, similar responses in VFI were obtained with heather which did not differ in chemical composition when offered at the same times. It is more likely that variations in dietary pretreatment or real seasonal differences were responsible.

In Expt 1 the animals were given the same diet (hay and concentrate) for similar lengths of time before being given the dried-grass-pellet diet in November and July. Thus the differences in VFI in Expt 1 would not appear to be attributable to dietary pretreatment. In Expt 2 there were differences in dietary pretreatment, in that dried-grass pellets were given to the animals for 7 weeks before the December period whilst a hay and concentrate diet was given before the April period. Greenhalgh & Reid (1974) showed that sheep offered a dried-grass-pellet diet for 18 weeks had developed smaller rumens than those fed on the same dried grass chopped. Thus the low VFI in December may have been due in part to a reduction in rumen size. However, it is probable that the effects of any dietary pretreatment would have been considerably reduced before the January measurements were made. Further evidence to support this contention is that when four of the same group of deer were offered the same *Agrostis–Festuca* spp. diet in January 1977, after a dietary pretreatment of hay and concentrate, the voluntary intakes of the animals were similar (41.6 ± 2.2 g OM/kg $W^{0.75}$ per d) to those reported in Expt 2. Thus the differences in intake of *Agrostis–Festuca* spp. and heather between January and April are probably attributable to a real seasonal effect.

Pronounced seasonal effects on VFI of other *Cervidae* have been reported (Long *et al.* 1966; McEwan & Whitehead, 1970; Simpson, 1976) and with sheep, Gordon (1964) noted small seasonal differences in VFI of hay of a similar pattern to those found here. Simpson (1976) also showed the importance of day-length in the stimulation of seasonal cycles in VFI by red deer. In the present experiment the animals were given artificial light continuously but day-light was not excluded. Although the differences in the light intensity between day and night were small they would have been sufficient for the animals to perceive changes in day-length.

It is a generally accepted hypothesis that with medium-quality long-roughage diets, the control of VFI is related mainly to the filling effect in the digestive tract, particularly in the rumen, and to the rate of removal of undigested residues from that organ (Campling, 1970). This implies a close relationship between VFI, digestibility and MRT such that valid comparisons between species of digestibility and the MRT of a particulate-phase marker can only be made at similar levels of intake. At equal intakes of the dried-grass-pellet diet (Expt 1) the digestibilities of OM and NDF were greater and the marker MRT was longer for the sheep than the deer. However, when the two species ate similar amounts of the chopped-dried-grass diet there were no differences in digestibility or MRT. These results do not support the findings of Kay & Goodall (1976), which indicated slightly poorer digestion and shorter MRT of hay and dried grass by red deer than by sheep. Comparisons between the species of digestibility and marker MRT with the poor-quality-roughage diets (Expt 2) are not possible because the range of intakes of the two species was different.

^{103}Ru-phenanthroline was used as the particulate-phase marker to obtain estimates of compartmental and total MRT. Oral administration of ^{103}Ru-phenanthroline is unlikely to fulfil the requirements of a valid particulate-phase marker (i.e. that the marker should be uniformly distributed throughout the particulate-phase of the digesta, irrespective of particle size, and should remain attached to those particles which were initially labelled) and indeed this latter criterion appears not to be met (Spence & Milne, unpublished results). However, ^{103}Ru-phenanthroline is still considered a useful means of obtaining comparative estimates of particulate-phase retention times between different species of animals on the same diet. The relationship between faecal ^{103}Ru-phenanthroline concentration and time was in most instances best fitted by two exponential equations. The rate-constants of these equations are considered to represent MRT in the rumen and caecum of sheep (Grovum & Williams, 1973). In eight out of the eleven sheep offered heather, the relationship between faecal ^{103}Ru-phenanthroline concentration and time was best fitted by three exponential equations and these animals had the longer total MRT. It is not known which section of the digestive tract the third compartment may represent.

It has been suggested that to avoid errors in the interpretation of these MRT wherever compartmental analyses are used, total MRT should also be calculated (Faichney, 1975). In this experiment (see Table 6) there was good agreement between the sum of the two and three compartmental MRT and transit times and the total MRT of marker, suggesting that some confidence can be placed in these compartmental MRT.

On the dried-grass-pellet and *Agrostis–Festuca* spp. diets, marker MRT in the rumen were shorter for the deer than the sheep and were associated with lower digestibilities and higher absolute intakes. These results are in accord with previously established relationships between intake, digestibility and MRT, with the rumen being considered the most important organ of the digestive tract where these relationships might develop. The seasonal changes in intake, digestibility and marker MRT in the rumen with the dried-grass-pellet diet for both species and with heather for the sheep can be considered similarly.

The increases in VFI by the deer of the *Agrostis–Festuca* spp. and heather diets of 70% between January and April, however, were not accompanied by any changes in digestibility and were associated with small increases in rumen marker MRT. The hypothesis that the voluntary intake of long roughages is controlled by the filling effect in the digestive tract, particularly the rumen, can only hold for the deer at both times of the year if the volume, weight or length of the digestive tract, or at least some part of it, has increased. Tulloh & Hughes (1965) and Tulloh (1966) found that the VFI, rumen volume, weight of digesta DM and the dimensions of the digestive tract were greater for lactating than for dry cows. It is suggested that the increase in VFI observed with the deer may be associated with a hypertrophy of the digestive tract, which could arise from endocrine changes associated with changes in day-length.

Although the digestible OMI by red deer and sheep given dried grass in summer were similar, the red deer ate at least twice as much digestible OM as the sheep on poor-quality roughages in the winter. There is little comparative information on grazing behaviour, on how sheep and red deer utilize the end-products of digestion or indeed on the relative maintenance requirements of the two species at various times of the year. Fasting heat production per kg $W^{0.75}$ has been found to be higher for the red deer than the sheep, but there is some doubt as to whether this finding may have been the result of the red deer being less accustomed to the measurement procedures (see Knox, Wesley, Crownover & Nagy, 1974). Without this information it is not possible to say whether red deer would be better adapted than sheep to utilizing land resources, but these experiments have demonstrated higher digestible OMI of hill vegetation by red deer in winter and spring.

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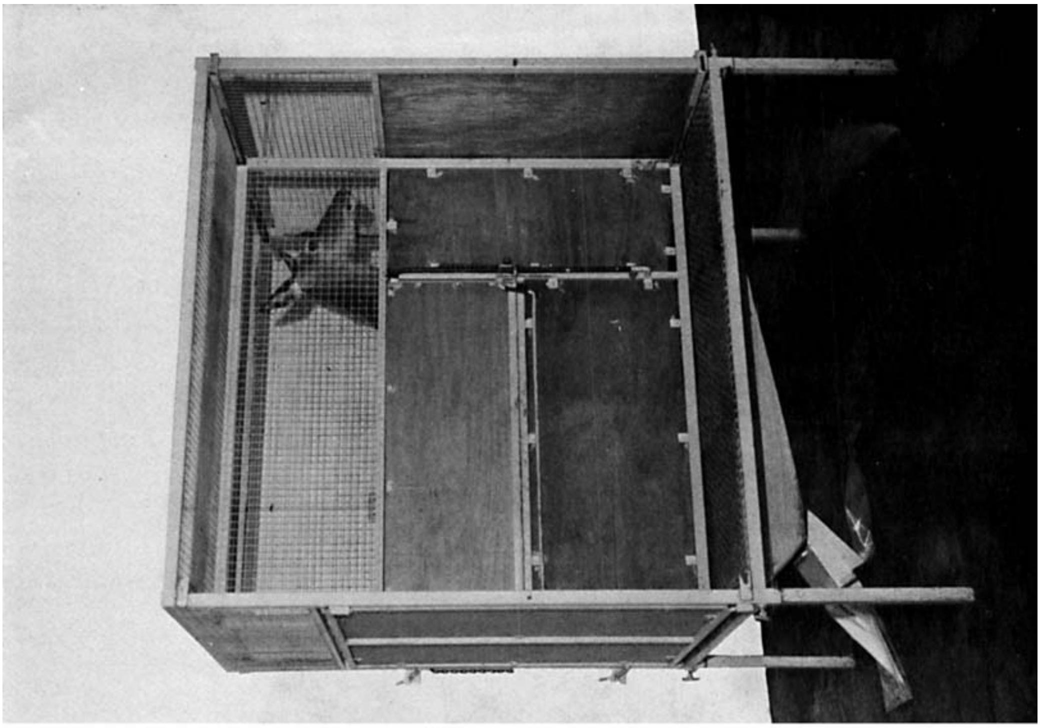

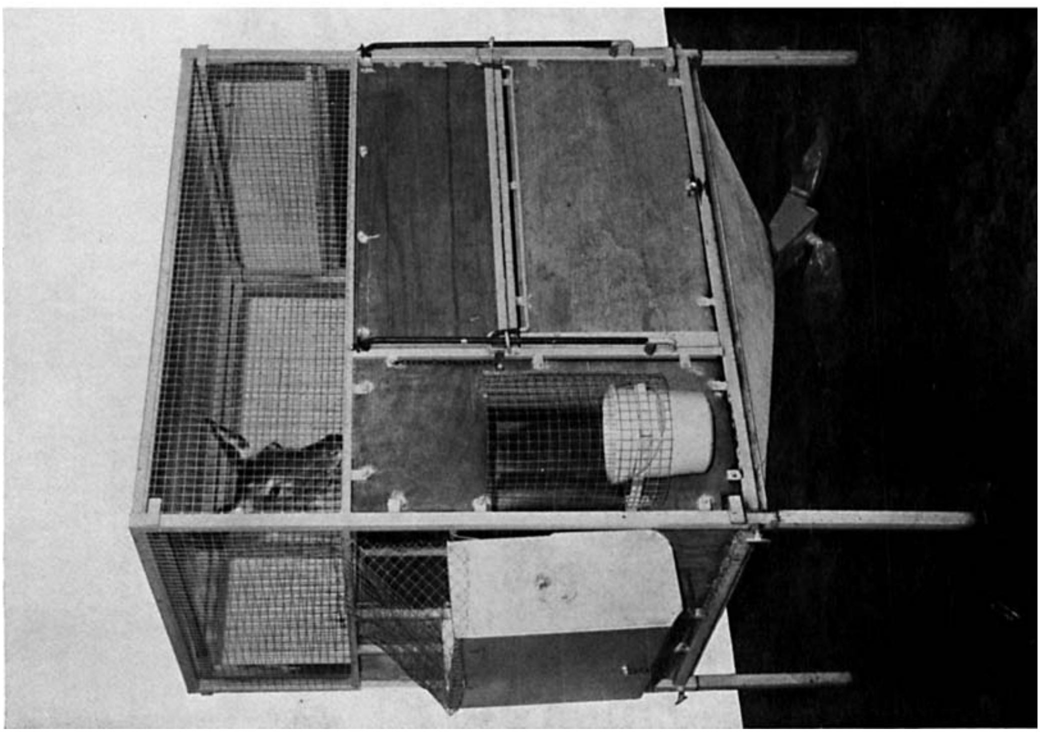

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EXPLANATION OF PLATE

Adjustable pen used for digestive and metabolic studies with red deer. Left-hand side of plate shows use as pen for long-term housing and right-hand side shows movable side wall adjusted to facilitate metabolic studies.

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