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Rumino-reticular motility in red deer (*Cervus elaphus*) fed chaffed lucerne hay during winter and summer

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Abstract Rumino-reticular contractions and jaw activity were monitored in four castrated red deer fed chaffed lucerne hay *(Medicago sativa)* ad libitum during winter (WW) and summer (SS), and when fed the winter voluntary food intake level during summer (SW). Each recording session lasted for 7 days. The mean dry matter intake (DMI) was significantly greater ($P < 0.05$) during SS (2977 g/day) than WW (2406 g/day) or SW (2230 g/day). The mean daily eating time was significantly greater ($P < 0.05$) during SS (465 min/day) than during WW (409 min/day) or SW (404 min/day) but eating time per unit DMI was similar for all three recording sessions. The mean daily rumination time was significantly greater ($P < 0.05$) during SS (378 min/day) and SW (403 min/day) than during WW (332 min/day). The frequencies of AS and BS contractions of the rumino-reticulum were not significantly different during the three recording sessions. The significant increase in voluntary food intake reported in red deer stags during the summer was accompanied by a significant increase in eating and rumination time but not a significant increase in forestomach motility. The number of AS and BS contractions/day in red deer was 1797 and 498 respectively.

Keywords red deer; *Cervus elaphus*; rumino-reticular movements; season; chewing

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INTRODUCTION

Since 1969, when deer farming formally began in New Zealand, red deer (*Cervus elaphus*) have become an important farm animal. The primary source of these animals was the extensive feral deer population, built up by successive liberations between 1861 and 1923 (Challies 1985). The ongoing domestication of this species has allowed research of a recently wild ungulate to be undertaken in order to better understand their nutrition and physiology.

The voluntary food intake (VFI) of red deer, especially stags and castrated stags, differs from sheep and cattle in that VFI is significantly greater in summer than in winter (Kay 1979; Domingue 1991a). Domingue (1991a) found that the increase in VFI during summer was accompanied by an increase in rumino-reticulum pool volume, a longer mean retention time of digesta in the rumino-reticulum, and a greater recycling of water to the rumino-reticulum than in winter, but that the actual volume of digesta flowing from the rumino-reticulum was greater in the summer. Barry et al. (1991) have reviewed the control of VFI in red deer.

An increase in VFI in sheep will increase the workload of the mechanisms responsible for outflow of digesta from the rumino-reticulum to the omasum.

It is generally agreed that outflow to the omasum occurs primarily in association with the A sequence (AS) of rumino-reticular contractions. The regular occurrence of an outflow at the time of the second reticular contraction of the AS was observed by Wester (1926) and by Schalk & Amadon (1928), and has been confirmed by many investigators using a range of methods including flow measurement probes (Stevens et al. 1960; Ehrlein & Hill 1969; Bueno 1975), and direct observation by endoscopy (Ehrlein & Lebzien 1976; MacBride et al. 1984). Increased rumino-reticular motility has been associated with increased voluntary food intake in cattle (Freer et al. 1962; Freer & Campling 1965; van Bruchem et al. 1991) and sheep (Malbert & Baumont 1989). However, from the observations of Freer & Campling (1965) in cattle and of Ulyatt et al. (1984) in sheep, it appears that increase in digesta outflow rate associated with increased voluntary food intake is more likely to be achieved by increasing the amount of digesta passed per AS contraction, rather than by increasing the frequency of these contractions.

The aim of this investigation was to determine whether the increased VFI by deer during the summer as compared with winter, was accompanied by significant changes in eating, rumination, and/or in the frequency of A sequence rumino-reticular contractions.

MATERIALS AND METHODS

Design

Four adult castrated deer were fed indoors on chaffed lucerne (*Medicago sativa*) hay for three observation periods during winter (WW) and summer (SS). During WW, and for one SS period, the animals were fed ad libitum, and during the second summer period (SW) they were fed at the level of the winter VFI. Food intake, eating time, rumination time, rumino-reticular motility, and body weight were measured during these observation periods.

Animals and animal care

The castrated stags used in the trial were hand-reared and had been fitted with 83 mm diameter rumen cannula under general anaesthesia 3 years earlier. The animals were accustomed to handling and to being held in specially designed deer metabolism cages. When not indoors, the animals grazed ryegrass/white clover pastures adjacent to the animal house.

Cages

Deer metabolism cages similar to those described by Milne et al. (1978) were used. Each cage had a floor space of 1.8 × 1.2 m and was 1.57 m high. The lower 1 m of the walls was solid (12 mm plywood) and the upper 0.57 m was "open" (7.5 cm square steel mesh). The roof was also 7.5 cm steel mesh. The floor was made of heavy steel mesh and had suspended beneath it a system for collecting faeces and urine. A detachable food trough was fastened to the front of the cage and a water bucket fastened to one side. One side wall of the cage was movable and could be used to adjust the floor area. Small doors in both sides of the cage allowed access to the animal. The cage floor was 0.77 m above the ground and the cages were located in a purpose-designed deer shed.

Diet

The animals were fed on the same batch of lucerne *(Medicago sativa)* hay throughout the trial. The hay was chaffed into 50–80 mm lengths 2–3 days before being fed and was held in the deer shed until used.

The deer were fed once daily at 1000 h. In WW and SS, the amounts of chaffed hay offered each day was 25% more than the individual VFI over the previous 24 h. In SW, the chaff offered was the mean daily VFI during the WW period of individual animals. The feed remaining in the feed bin of each animal was collected and weighed each morning and the VFI calculated on a wet basis. Grab samples were taken from the feed offered and that rejected for dry matter analysis and calculation of the dry matter intake (DMI). Water was replenished several times during each 24-h period and a salt block (Dominion Salt, New Zealand) was available at all times.

Recording apparatus

The recording system was similar to that described by Stafford et al. (1992) for measuring jaw activity and rumino-reticular motility in deer. An individual 4-channel chart recorder (Gould 240.OS recorder or Harvard Universal Oscilloscope or Graphtec WR3701–4 h × 1) was assigned to each animal, allowing simultaneous recording of jaw activity and rumino-reticular motility.

Jaw movements were sensed as pressure changes in a partially inflated rubber bag held under the jaw by a halter. The bag was a section of bicycle inner tube, closed off at one end. The other end was sealed and cemented over a flexible nylon pipe (3.5 mm i.d.) which was joined to a 0.8 m section of coiled rubber infusion tubing (Expandite IV tubing, CenVet, Australia) which accommodated animal movement. Nylon piping connected this rubber tubing to an electronic transducer (Biocom type or Statham ADCG, Hong Kong) mounted outside the cage. The transducer was connected via a pre-amplifier to the pen recorder.

Rumino-reticular motility was detected by recording the pressure changes in partially inflated balloons, containing 10–20 ml of air, tied to lengths of copper tubing appropriately bent to position the balloons in the reticulum or the dorsal or ventral sacs of the rumen. The copper tubing, which was sheathed with PVC to avoid contact between the stomach contents and the metal, was bent at 90° as it emerged from the cannula so that the tubing ran close to and parallel to the flank of the animal; this external bend was in the same plane as the internal bend immediately inside the cannula, allowing a visual check of the position of the balloons. The copper tubing was wedged in the cannula by a tightly fitting cork grooved down its sides to accommodate the tubing. Additional anchorage was provided by placing over the array of emerging tubes a piece of rigid PVC plumbing pipe (12 cm i.d., 2 mm wall), one end of which had slots cut into it to engage individual tubes and so prevent their rotation; the PVC anchor was then tied to the cannula. Each of the copper tubes was connected by a 1 m length of coiled infusion tubing to a nylon pipe leading to a pressure transducer (Statham ADCG, Hong Kong) connected in turn to a pre-amplifier the output of which was displayed by a pen-recorder.

Restraint of animals

To prevent the deer from turning around during recording sessions and so tangling the recording lines, the width of the cages was reduced by means of the movable wall. The degree of restriction was such that although the animals could not turn around, they could stand or lie down and eat or drink without hindrance.

Initially deer had to be sedated with a low dose of xylazine (20 mg/animal; Rompun 2% solution, Bayer AG Germany) and to be squeezed by the movable wall to allow opening of the cannula, the insertion of the balloons, closure of the cannula, and securing of the tubing and anchor. However, after this procedure had been carried out several times the deer allowed balloon replacement when simply pushed against the cage wall, and xylazine was rarely used. Yohimbine (20 mg/animal; Reversine, Parnell Laboratories, NZ) was used to counter the effect of xylazine when the balloons had been positioned. This also reversed the inhibitory effect of xylazine on rumino-reticular motility (Stafford & Reid unpubl. data). The positioning of the balloons was checked by inspection of the chart records obtained.

Recording sessions

The four deer were placed in individual cages 2 weeks before recording started, to allow them time to become accustomed to the cage, the diet, and the personnel attending them. Recording was carried out during winter (May) and summer (November/December) of 1991. A recording session lasted for seven 24-h periods, each period starting at 1000 h and continuing to 1000 h next day. Both animals and recordings were inspected frequently during each 24-h period, animal identification and the time of inspection being entered on each record. Recordings from the previous 24 h were removed each morning at 1000 h.

For each animal, four 24 h records from the seven made during each recording sessions were chosen for analysis based on their completeness and clarity. The DMI of each animal during these four 24-h periods were used in the analysis.

Record interpretation

The pattern of events taken as indicating the occurrence of an A sequence of contractions (AS) commenced with a biphasic positive pressure wave in the reticulum, followed by a monophasic positive pressure wave in the dorsal rumen sac and one (usually) or more positive pressure waves in the ventral rumen sac (Fig. 1).

The pattern of events taken as indicating the occurrence of a B sequence of contractions (BS) was a positive pressure wave in the dorsal rumen sac followed by one (usually) or more positive pressure waves in the ventral rumen sac. This sequence was not obviously associated with any significant co-ordinated pressure changes in the reticulum (Fig. 1).

Commonly, BS contractions were accompanied by eructation, which caused a brief, sharp positive pressure spike in some reticular pressure tracings (Fig. 1B,bc).

The pattern of events observed during rumination commenced with a pressure change in the reticulum. This was taken to indicate the additional ("extra") reticular contraction of rumination associated with

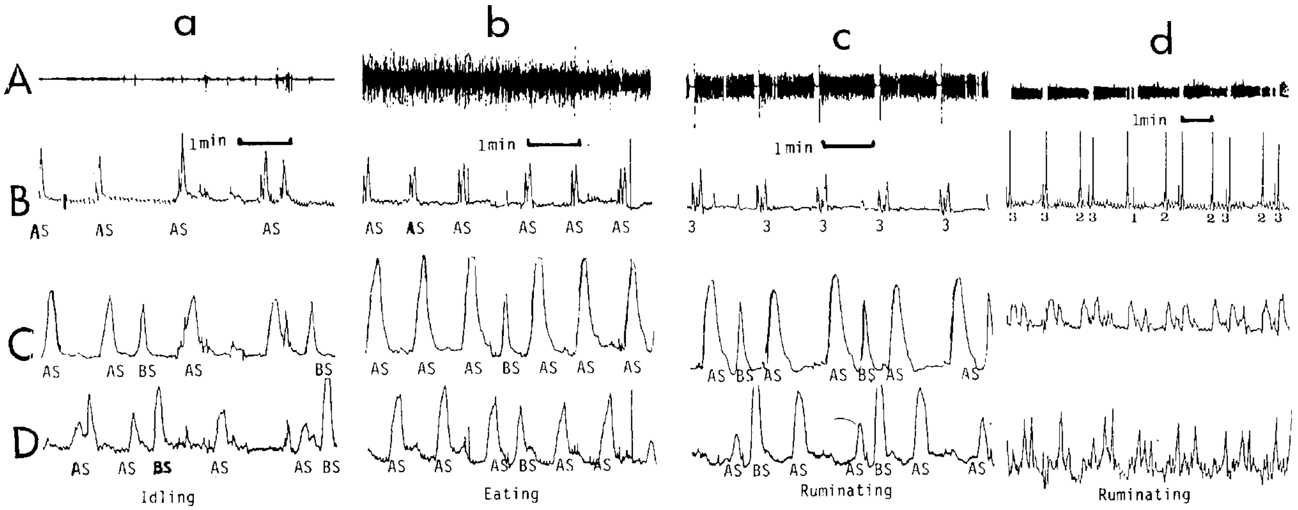

Fig. 1 Recordings of jaw movements (A) and pressure changes in the reticulum (B) and in the dorsal (C) and ventral (D) rumen sacs of red deer during idling (a), eating (b), and ruminating (c) (d). 1, monophasic reticular contraction associated with regurgitation; 2, biphasic reticular contraction of AS; 3, triphasic reticular contraction of rumination; AS, an A sequence contraction; BS, a B sequence contraction.

regurgitation of the rumination bolus. The extra reticular contraction was then followed by the pressure changes in the reticulum, and dorsal and ventral rumen sacs associated with a normal AS contraction (Fig. 1c,BCD). Variations in this pattern were observed in the present study (Fig. 1d,B) and AS contractions were classified 1, 2, and 3 according to the number of phases of contractions of the reticulum.

Identification of AS and BS contractions was usually easy (Fig. 1); occasional difficulty occurred when animals were restless or were snorting during eating.

The characteristic pattern of rumination (consistent amplitude of jaw record) was readily identified in the record of jaw activity (Fig. 1cA,dA). Intensive eating was also readily identified, but periods of erratic eating, grooming, and restlessness required careful assessment. The records were analysed in terms of periods of eating, ruminating, or idling using the following conventions. Eating bouts (which sometimes lasted several hours) were considered to be continuous unless interrupted for more than 10 min by a bout of rumination or idling. This convention was adopted because whereas eating was vigorous immediately after the fresh ration of chaffed hay was offered at 1000 h, it gradually became desultory, with more time being spent turning feed over in the bin. Rumination bouts were defined as involving a minimum of three boluses regurgitated and chewed. Idling bouts were periods during which there were no jaw movements, or (by direct observation or from recognised patterns in the record) the animal was grooming, rubbing its cage, licking, or drinking.

Statistical analysis

For each animal, the mean values for DMI (g DM/day), the eating time (ET), rumination time (RT), the numbers of AS and BS contractions, the number of rumination bouts and the number of regurgitated boluses, and the time spent eating and ruminating per g DMI were calculated for a 4 × 24-h period selected for each animal for each of the three recording sessions WW, SS, and SW.

The data were analysed by one-way analysis of variance in which the treatment (session) was the main effect. When a session affected in a significant way a given parameter, the means of that parameter were separated using a LSD test (SAS 1988).

RESULTS

Food intake

The mean DMI of the four animals during each recording session (4 × 24-h periods) are shown in Table 1. The DMI was significantly ($P < 0.05$) greater during SS than either during WW or during SW recording sessions. Overall, the SS DMI was 24 and 33% greater than the WW and SW DMI respectively.

Alimentary behaviour

The mean daily ET was significantly ($P < 0.05$) greater during the SS session than during the WW or SW sessions (Table 1). However, there was no significant difference in the time (min) spent eating per g DMI (Table 1). The mean daily RT was significantly ($P < 0.05$) greater during the SS and SW than the WW session (Table 1). The time spent ruminating per g DMI was significantly greater ($P < 0.05$) during SW than during SS or WW (Table 1).

The daily pattern of feeding and rumination was similar in all recording sessions. There was a bout of feeding after the animals were fed at 1000 h and further bouts of feeding around 1800 and 0700 h (Fig. 2). More time was spent feeding between 2400 and 0700 h during the summer than the winter. Rumination occurred at any time over the 24-h period but there was a greater incidence around 1200 and 0400 h. The overall daily mean number of boli regurgitated for rumination was significantly greater ($P < 0.05$) during SS than during WW but there was no significant difference between SW and SS or SW and WW (Table 1). The number of bouts of rumination/day was significantly greater ($P < 0.05$) during SW than during SS or WW (Table 1).

Rumino-reticular motility

There were no significant differences between the mean daily number of AS or BS contractions during the three recording sessions (Table 1). The frequency of AS contractions was greater during feeding than during either ruminating or idling (Table 1). The hourly frequencies of both AS and BS contractions were lowest during the early morning hours (Fig. 2), the nadir being between 0300 and 0500 h. The frequency of AS contractions increased markedly with feeding. The ratio of AS to BS contractions during the WW, SS, and SW recording sessions was 3.6:1, 3.6:1, and 3.7:1 respectively. The ratio of AS to BS contractions during feeding, ruminating, and idling (means of all animals and all recording sessions) was 3.5:1, 3.4:1, and 4.8:1 respectively.

The rumino-reticular contractions associated with rumination sometimes demonstrated unusual features (Fig. 1dB) including the occurrence of an

Table 1 Mean voluntary food (DM) intake, liveweight, daily eating and ruminating time, A sequence and B sequence contraction frequencies, and number of rumination bouts and regurgitated boluses per day in red deer fed chaffed lucerne hay. Hay was fed ad libitum during winter and summer and restricted to the winter VFI during the summer/winter session. Data (mean ± standard error) are from 4 × 24-h recording periods for all four deer for each of the recording sessions.

	Winter	Summer	Summer/Winter
Liveweight (kg)	105 ± 4.1	112 ± 4.0	112 ± 4.0
DMI (g DM/day)	2406 ± 100	2977 ± 210	2230 ± 100
Daily eating time (min)	409 ± 18	465 ± 26	404 ± 19
Daily ruminating time (min)	332 ± 9	378 ± 10	403 ± 13
Bouts of rumination/day	13 ± 1.0	14 ± 0.08	17 ± 1.2
Rumination boli/day	296 ± 11.8	348 ± 15.4	329 ± 15.1
Time (min)/bolus	1.1 ± 0.06	1.1 ± 0.05	1.2 ± 0.05
ET/g DMI (min)	0.17 ± 0.0006	0.16 ± 0.006	0.18 ± 0.009
RT/g DMI (min)	0.14 ± 0.007	0.13 ± 0.010	0.18 ± 0.010
AS (contractions/day)	1783 ± 26	1827 ± 64	1781 ± 23
BS (contractions/day)	500 ± 42	514 ± 33	481 ± 31
AS (contractions/min)			
Eating	1.5 ± 0.04	1.5 ± 0.08	1.5 ± 0.06
Ruminating #	1.1 ± 0.05	1.2 ± 0.07	1.1 ± 0.08
Idling	1.2 ± 0.02	1.2 ± 0.08	1.1 ± 0.05
BS (contractions/min)			
Eating	0.5 ± 0.07	0.4 ± 0.05	0.4 ± 0.05
Ruminating	0.3 ± 0.05	0.4 ± 0.05	0.3 ± 0.04
Idling	0.3 ± 0.04	0.3 ± 0.03	0.3 ± 0.04

Includes all AS contractions recorded during rumination.

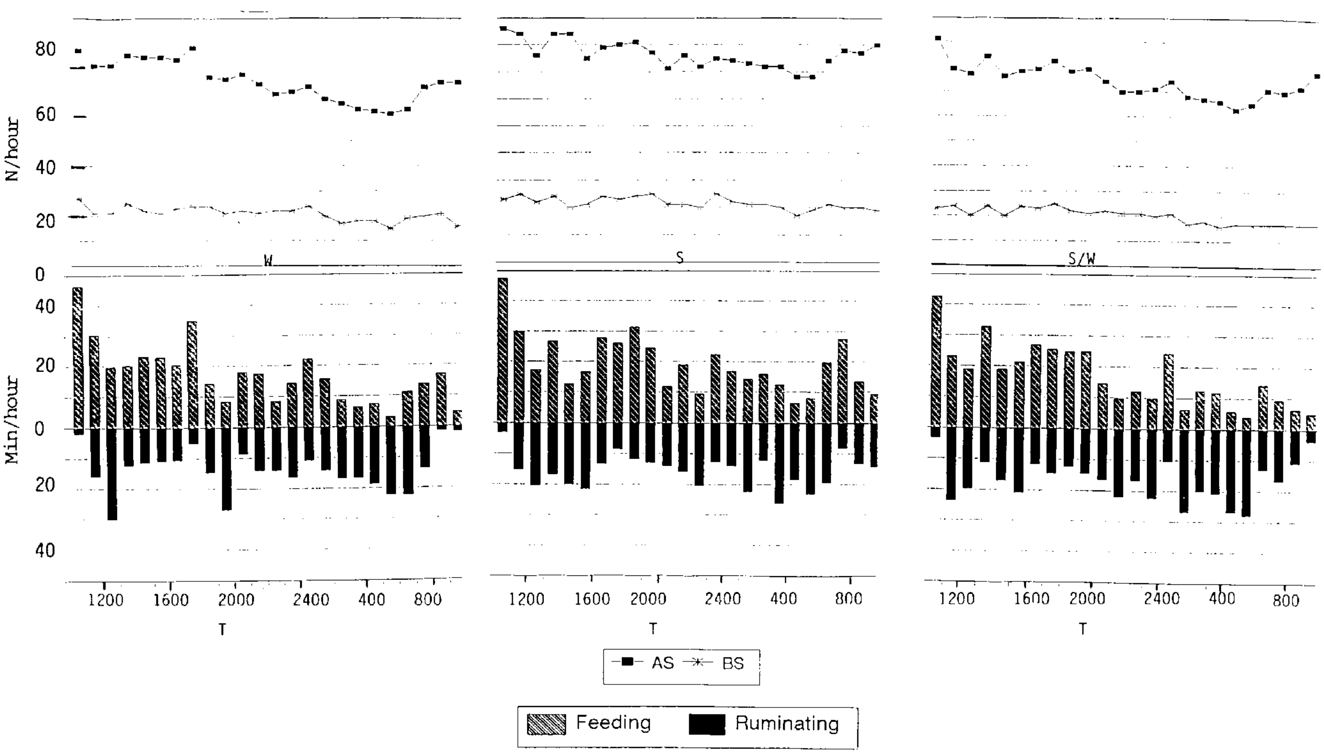

Fig. 2 Circadian pattern of time spent eating and ruminating and of AS and BS contractions recorded from red deer during winter, summer, and summer/winter.

apparently normal AS (2, Fig. 1d,B) during chewing of a regurgitated bolus, and the occurrence of a single reticular contraction (1, Fig. 1d,B) associated with regurgitation which was independent of diphasic reticular contractions. These features were observed in all the animals.

DISCUSSION

The daily DMI and ET were significantly greater during the SS than during the WW or SW recording sessions; however, the time spent feeding per g DMI was similar in all three recording sessions. The overall mean eating time of 426 min/day is similar to that observed by Semiadi et al. (1993) throughout the year in a mob of mixed-age male and female red deer grazing a mixed unimproved sward (444 min/day) The ET of yearling stags fed chaffed lucerne hay while in cages (330 min/day; Semiadi et al. 1992) was much lower, but the total chewing time of those animals (eating 330 min, rumination 528 min) was 858 min/day. This total chewing time was greater than for deer in this study i.e. 797 min/day (eating 426 min, rumination 371 min). The younger deer used by Semiadi et al. (1992a) may have been more nervous than the deer used in this study. This nervousness may have been reflected in a more rapid eating time compensated for by a longer rumination time. By contrast, the ETs of cattle and sheep fed chaffed lucerne hay were 231 and 207 min respectively (Waghorn & Reid 1983), much shorter than the ET of red deer. However, the intake level of the cows and sheep (52 and 53 g DM/kg $BW^{0.75}$) was substantially lower that of the deer (73.6 g DM/kg $BW^{0.75}$). An additional factor contributing to the difference in ET between species could be a difference in bite weight and the rate of intake; Mitchell et al. (1992) found that bite weight and rate of intake scaled to metabolic weight was much larger in sheep than in red deer.

The daily rumination time was significantly greater during the SS session than the WW session, probably reflecting the higher summer intake. The overall mean RT of 371 min/day was much lower than that found in the study by Semiadi et al. (1992), when caged deer having a DMI of 1894 g of chaffed lucerne hay ruminated for 528 min. The latter were young deer of both sexes about 13 months of age compared with the mature 6-year-old animals used in the present study. The mean RT of cattle fed chaffed lucerne hay (349 min/day) was similar to that of the deer in this study, but sheep ruminated for a far longer period (516 min/day) (Waghorn & Reid 1983). The basis of these differences and similarities is not clear. It is not simply a reflection of feed intake levels, since the cattle and sheep ate closely similar amounts per kg BW $^{0.75}$. It is also not clear why RT in the SW session was significantly longer than in the WW session despite a lower DMI. One possibility is that under the condition of feeding in the SW session, dietary selection was reduced. The amount of feed offered was restricted to the winter intake, but the animals had a summer appetite, driving them to eat nearly everything offered to them, including material that they would normally reject. If the proportion of coarser material in the diet is thus increased, RT per g DMI might be expected to increase. Other factors may be involved. It could be speculated that there is a seasonal cycle to rumination which is independent of DMI or that the limited activity possible in the caged situation during the longer days of summer leads to "boredom", which is reduced by rumination.

The number of AS contractions per day was greater in red deer than in cattle and sheep fed a similar diet or wapiti fed brome grass but lower than in the white-tailed deer (Table 2). In the latter species fed alfalfa hay and whole kernel corn, AS contractions occurred at a rate of about 2/min, or about 2880 AS/day (calculated from Dziuk et al. 1963). However, the number of BS contractions was lower in red deer than in white-tailed deer (640 BS/day calculated from Dziuk et al. 1963), cattle, and sheep (Table 2). The reasons for the lower frequency of BS contractions in red deer is unclear. Possibilities are that red deer eructate more efficiently than the other species, expelling more gas per BS, or that gases are more efficiently absorbed through the fore-stomach wall. The liquid fractional outflow rate from the rumen to the intestines is 60% faster in red deer than in sheep or goats during winter and summer (Domingue et al. 1991b) and as gas, especially CO_2 as bicarbonate, will be dissolved in this fluid the outflow from the rumen may be sufficient to reduce the requirement for eructation. A simple hypothesis would be that there is more severe selection pressure on wild than on domesticated ruminants to reduce the odour released and the waste of nutrients involved during eructation and that mechanisms have evolved to reduce these. The rate of gas production would not seem to be a significant factor —the rates of gas production from sheep and deer rumen contents measured in vitro are similar (Waghorn & Stafford 1993). Leakage of gas through or around the rumen cannula did not appear substantial in the present study. The animals were examined frequently but escaping gas was seldom heard.

The increase in the frequency of rumen contractions following feeding seen in cattle and sheep (Waghorn & Reid 1983) was less obvious in red deer (Fig. 2). The ratio of AS to BS contractions in the red deer in this study (3.6:1) was greater than in cattle (1.9:1) or sheep 1.7:1) (Waghorn & Reid 1963), but similar to the ratio in white-tailed deer (Dziuk et al. 1963) which was between 3:1 and 6:1.

The variations in the pattern of motility associated with rumination were unexpected. Rumino-reticular walls and structures are known to house sensory nerve endings capable of being stimulated by a variety of factors arising from the digesta. Applied stimuli such as rubbing which occurs during the placement of balloons, can evoke regurgitation, rumination, changes in the frequency and detail of AS, and be excitatory or inhibitory (Ash & Kay 1959; Reid 1962; Leek & Harding 1975; Nicholson & Belkhiri 1990). A further study is being carried

Table 2 Frequency of A sequence and B sequence contractions in domesticated and tamed animals.

	White-tailed deer (1)	Red deer (4)	Red deer (3)	Wapiti (3)	Cattle (2)	Sheep (2)	Goats (5)
AS/day	2880	1797	2009	1661	1670	1454	1437
BS/day	640	498	–	–	878	835	904
AS:BS	4.5:1	3.6:1	–	–	1.9:1	1.7:1	1.6:1

(1) Calculated from Dziuk et al. (1963)
(2) Waghorn & Reid (1983)
(3) Calculated from Kay (1987) assuming that 33% of time spent eating, ruminating, and idling.
(4) Present study. Mean of all animals, all recording sessions, and all activities.
(5) McSweeney & Kennedy (1992)

out with red deer using alternative methods of recording to determine whether the variations seen here are a normal phenomenon in this species. Even if the variations prove to be an artefact produced by the recording system, the fact that disruption of temporal relationships occurs is of considerable interest.

It is possible that the frequency of AS contractions or the ratio of AS to BS contractions could be used as an additional parameter to differentiate between browsers (concentrate), intermediate feeders, and grazers (roughage) as defined by Hofmann (1985). Grazers such as cattle and sheep have a lower frequency of AS contractions than red deer. The food eaten by browsing animals (concentrate feeders) such as white-tailed deer is rapidly fermented and the structural anatomy of the forestomach facilitates a faster passage rate of ingesta than in grazers (Hofmann 1989). This faster passage may be facilitated by the more frequent AS contractions seen in white-tailed deer (Dziuk et al. 1963). The forestomach of intermediate feeders such as red deer is structurally intermediate between browsers and grazers (Hofmann 1989) and it is possible that the frequency of rumino-reticular motility may also be intermediate. However, goats, which are classified as browsers, fed chopped wheaten had AS and BS contraction (Table 2) frequencies similar to those of sheep (McSweeney & Kennedy 1992).

Although there were significant differences between the winter and the summer DMI, ET, and RT, the frequency of AS and BS contractions was not significantly different between these sessions or the summer/winter (SW) session. This indicates that in red deer the increased digesta throughput during the summer is not dependent upon an increase in the number of AS contractions but rather on an increase in digesta throughput per contraction, and reflects the findings of Ulyatt et al. (1984) and Malbert & Baumont (1989) in sheep and Freer & Campling (1965) in cattle fed different levels of VFI. If correct, this conclusion implies a nett increase in the amount of digesta passing through the reticulo-omasal orifice during each AS contraction. There remains no convincing evidence for passage out at any other time in the contraction cycle.

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