Comparison of digestive and chewing efficiency and time spent eating and ruminating in sambar deer (*Cervus unicolor*) and red deer (*Cervus elaphus*)

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SUMMARY

Artificially reared sambar (tropical) deer and red (temperate) deer were confined indoors in metabolism cages and fed chaffed lucerne hay *ad libitum* for 4-week periods during summer and winter at Flock House Agricultural Centre, New Zealand, during 1992. Measurements were made of voluntary feed intake (VFI), apparent digestibility, faeces particle size distribution, eating and ruminating time and the rate of chewing during eating and ruminating. Red deer reduced VFI (kg DMI/day) markedly from summer to winter, associated with a reduction in the duration of each eating bout. Sambar deer slightly increased VFI over this time, associated with an increase in chewing frequency. Digestive efficiency was similar in both species, and the critical particle size for leaving the rumen was passage through a 1 mm sieve for both species. Time spent eating/g DMI was greater for sambar deer than for red deer during summer, but there was no difference during winter. Relative to red deer, sambar deer consistently spent more time ruminating/g DMI, and spent a greater proportion of total ruminating time as daytime ruminating and had more daytime ruminating bouts. Duration of each ruminating bout (min) was similar for the two deer species, but sambar deer had less chews/bolus ruminated but more rumination boli/h than red deer. Differences between sambar deer and red deer were more pronounced in ruminating than in eating behaviour, and sambar deer may have evolved a different rumination pattern to break down low-quality tropical forages more effectively.

INTRODUCTION

The voluntary feed intake (VFI) pattern in red deer is marked by seasonal fluctuations, being high in summer and low in winter (Suttie *et al.* 1983; Barry *et al.* 1991). Other distinctive seasonal changes in red deer from winter to summer are increases in rumen pool size of both dry matter and liquid, due to a slowing of fractional outflow rate (FOR), and an increase in the rate of ammonia production (Freudenberger *et al.* 1994). The digestive efficiency of red deer does not change between winter and summer, even though there is a marked increase in feed intake from winter to summer (Milne *et al.* 1978; Sibbald & Milne 1993; Freudenberger *et al.* 1994).

To have a high probability of leaving the rumen, particles must be reduced to below a critical size (Reid *et al.* 1977), identified as passage through a 1 mm sieve for sheep (Ulyatt *et al.* 1986). Reduction to this size occurs through chewing during both eating and ruminating (Ulyatt *et al.* 1986). Because no further particle reduction occurs after leaving the rumen (Poppi *et al.* 1980), faeces particle size can be used as an index of particle size of material leaving the rumen.

In field studies, sambar deer showed a tendency to be nocturnal grazers, whereas red deer grazed mainly during morning and evening (Semiadi *et al.* 1993*a*). However, it was not possible to record the actual time sambar deer spent ruminating in the paddock. Thus, eating and ruminating activities were recorded under controlled conditions, using automated jaw recording, in the present study.

Objectives of the present study were to compare the feed intake, digestive and chewing efficiency, eating and ruminating time (h/24 h), and feed and faecal particle distributions of sambar deer and red deer in two seasons, during summer and winter.

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Table 1. *Mean age* (s.d.) *and body weight* (s.d.) *of sambar deer and red deer used in the digestion and chewing efficiency trials, during both summer and winter 1992 (mean values and their standard deviation for five red deer and four sambar deer)*

	Summer		Winter	
	Sambar deer	Red deer	Sambar deer	Red deer
Age (days)	249 (84·8)	393 (11·2)	397 (90·8)	545 (5·1)
Body weight (kg)	66·7 (13·40)	96·1 (7·83)	101·8 (11·24)	111·2 (13·80)

MATERIALS AND METHODS

Experimental design

Measurements of VFI, apparent digestibility, faeces particle size and eating and ruminating times were made during summer (S: January–February 1992) and winter (W: July–August 1992), with sambar deer and red deer fed chaffed lucerne hay from the same batch. All animals were artificially reared and kept indoors in metabolism cages. Within each season, experiments were also conducted on time spent eating and ruminating, efficiency of chewing during eating and efficiency of chewing during rumination.

Location

The study was carried out at Flock House Agricultural Centre, AgResearch Grasslands, Bulls, Manawatu, located on the west coast of the North Island, New Zealand (40° 14′ S, 175° 16′ E). Average annual rainfall is 875 mm with a dry period from January to March (summer), and strong westerly winds during October and November (spring). The mean monthly temperature ranges from 9 to 20 °C.

Animals

Initially, five stags and one hind of each deer species were artificially reared (Semiadi *et al.* 1993*b*), to make them tame and easily manageable under experimental conditions. However, as the study progressed, two sambar deer were lost, one from a neck injury and one from malignant catarrhal fever (MCF). Animals were selected for experimental measurements based upon temperament, and whether they would settle in the metabolism cages. This was particularly true for sambar deer, which were rather nervous even after being artificially reared.

Apparent digestibility, voluntary feed intake (VFI), and faeces particle size distribution were determined using five red deer (four stags and one hind) and four sambar deer (three stags and one hind). These same animals were used in both the summer and winter periods.

All jaw recording measurements were made with four red deer stags in summer and three red deer stags in winter, two of which were the same animals in both seasons. Three sambar deer stags were used in both seasons, two of which were the same animals in both seasons.

Mean age and body weight of the deer during each season is shown in Table 1. The sambar deer were *c.* 6 months younger than the red deer in both experiments, because of the different times of calving between the two deer species (Semiadi *et al.* 1994). All deer were kept in metabolic cages, similar to those described by Milne *et al.* (1978), under natural daylength and ambient temperature.

Diet

Throughout the digestion and jaw recording periods, all animals were fed chaffed lucerne hay (2–6 cm long), which came from the same batch. Water and a small multimineral salt block (Summit Multimineral Salt Block, Dominion Salt, NZ) was available at all times.

Adjustment to the chaffed lucerne hay diet commenced 1 week before placing the animals in the metabolic cages. At this time, the animals allocated to jaw recording were also fitted with leather jaw harnesses. Once in the metabolic cages, a further 7-day period of adjustment occurred, with feed offered being 15% greater than the previous day's consumption.

Digestion trial

Digestibility and VFI were measured over a 7-day period following the adjustment period, with feed on offer, feed refusals and under-crate residues being weighed daily. Animals were fed once daily, between 08.00 and 09.00 h, at 15% greater than the previous day's consumption. Water containers were refilled twice daily.

Duplicate samples of feed on offer were taken daily. For each digestion period samples of feed on offer were pooled. Approximately 10% of feed residual for each animal was collected daily and pooled per animal for each digestion period. All under-crate residues were collected daily and pooled per animal. Faecal samples were collected and weighed daily per animal and stored at −20 °C. At the end of the trial,

Table 2. *Chemical composition (g/kg dry matter (DM))*
of chaffed lucerne hay (Medicago sativa) *fed to sambar*
deer and red deer during digestibility trials conducted in
summer and winter

	Summer	Winter
Organic matter	916	908
Heat of combustion (KJ/kg DM)	18·5	18·7
Total nitrogen (N)	28·8	27·8
Cellulose	257	246
Hemicellulose	163	177
Lignin	78	80
Total fibre*	501	503

* Cellulose + hemicellulose + lignin.

the faecal samples were thawed and pooled per animal, mixed thoroughly, and subsampled. A sample of 200 g of the mixed faeces from each animal was taken for particle size analysis. All samples were stored at − 20 °C until required for analysis.

Jaw recording

At the end of each digestion period, the animals selected for jaw recording were retained in the cages. One side of the cage wall was adjusted so that the animals could only make movements backward or forward, but could not turn around, thus minimizing damage to the jaw recording equipment. The period of adjustment under such conditions lasted for 2 days before chewing activities were recorded.

Each animal was fitted with a jaw harness with a balloon attached under the lower jaw. Jaw movement was obtained by sensing the compression of the balloon connected to a pressure transducer. Records of jaw activity were made on multi-channel heat sensitive chart paper, as described by Domingue *et al.* (1991*a*). Three experiments were conducted during jaw recording, as follows:

Time spent eating and ruminating

During this period the paper chart drive speed was set at 25 mm/min and records were made for 4 consecutive days with each animal. Animals were fed once per day, *ad libitum*, at 08.00–09.00 h, with free access to drinking water. Feed on offer, feed refusals and under-crate residues were collected and recorded daily, as described for the digestion trials.

Information from the chart paper was read and tabulated during the 4 day recording, so that the time spent eating or ruminating, number of boluses during rumination, number of eating and ruminating bouts and the time spent per bout eating or ruminating could be measured. A 'bout' is defined as having at least three boluses regurgitated and chewed or continuous ruminating lasting 3 min or longer.

Efficiency of chewing during eating

The morning after Expt 1 was completed, all experimental animals were fasted for 3 h, from 08.00 to 11.00 h. A test meal of 30 min duration, using

Table 3. *Voluntary feed intake and apparent digestibilities of sambar deer and red deer fed* ad libitum *on chaffed lucerne hay in summer and winter (mean values with their standard error for five red deer and four sambar deer)*

		Sambar deer	Red deer	S.E.
Voluntary DM intake				
g/day	Summer	1244	1898	199·2
	Winter	1404	1345	275·2
g/kg $W^{0.75}$ per day	Summer	53·5	61·7	5·94
	Winter	43·9	40·0	8·84
Apparent digestibility				
Dry matter	Summer	0·581	0·596	0·0076
	Winter	0·581	0·575	0·0167
Organic matter	Summer	0·589	0·609	0·0077
	Winter	0·593	0·589	0·0166
Total fibre	Summer	0·468	0·500	0·0092
	Winter	0·484	0·486	0·0255
Cellulose	Summer	0·524	0·549	0·0071
	Winter	0·538	0·556	0·0336
Hemicellulose	Summer	0·567	0·604	0·0168
	Winter	0·563	0·572	0·0242
Lignin	Summer	0·074	0·089	0·0126
	Winter	0·087	0·078	0·0150

Table 4. *Distribution of particle size (% DM retained on each sieve) of feed on offer and faeces in sambar and red deer fed* ad libitum *on chaffed lucerne hay, during summer and winter (mean values with their standard error for five red deer and four sambar deer)*

	Summer			Winter		
Sieve size (mm)	Sambar deer	Red deer	S.E.	Sambar deer	Red deer	S.E.
Feed on offer*						
5·6	34·6			29·8		
4·0	20·6			24·2		
2·0	22·6			21·8		
1·0	13·5			14·1		
0·5	6·3			7·0		
< 0·5	2·3			3·1		
Faeces						
2·0	0·47	0·46	0·07	0·24	0·34	0·08
1·18	0·12	0·42	0·17	0·52	0·61	0·21
1·0	0·74	0·67	0·03	0·67	0·55	0·08
0·5	27·3	26·7	0·92	25·5	26·2	1·53
0·25	37·6	38·3	2·02	38·9	36·4	1·45
< 0·25	33·8	33·3	1·66	34·2	35·9	2·76
< 1·0	98·68	98·46	0·20	98·58	98·50	0·23

* Feed offered to both species.

1·1 kg of chaffed lucerne hay, was then given and jaw movements during eating were recorded. During this period, the paper chart drive speed was set at 60 mm/min to enable the number of chews during eating to be calculated. At the end of recording, the feed remaining was weighed. Data were then expressed as the number of chews/min and number of chews/ g DM eaten. The procedure was repeated at 21.00 h, where fasting took place from 18.00 to 21.00 h. Between repeat trials, the animals were fed with 0·5 kg chaffed lucerne hay. Mean values were then calculated from both morning and evening trials.

Efficiency of chewing during ruminating

The morning after Expt 2 was completed, the animals were fed for 3 h (08.00–11.00 h) with 1·5 kg of chaffed lucerne hay as a test meal. Feed and water were then removed, and ruminating activity was recorded for 5 h, with chart drive speed set at 60 mm/min. Feed on offer and feed residues were recorded. Data were then expressed as the number of chews during ruminating/ bolus, number of chews during ruminating/min, time spent chewing per bolus ruminated (sec) and time elapsed between each rumination bolus (sec).

Sample processing and chemical analysis

All feed and residue samples from the digestion and jaw recording experiments were freeze-dried in dupli- cate, with faeces being freeze-dried in triplicate and the dry matter (DM) content determined. Samples were then ground to pass a 1 mm sieve (Wiley Mill,

USA), and analysed for organic matter, total nitrogen (N), hemicellulose, cellulose, lignin and energy con- tents. Organic matter content was measured by ashing the samples in a furnace at 500 °C for 16 h and total N was determined by the Kjeldahl procedure. Hemi- cellulose, cellulose and lignin contents were analysed following the detergent procedures of Goering & Van Soest (1970). Gross energy was determined through heat of combustion using an adiabatic bomb calor- imeter (Gallenkamp Autobomb, Watson Victor Ltd, UK). The sample was pelleted (0·5–0·8 g DM, 12 mm diameter) prior to combustion.

Pelleted faecal samples prepared for particle frac- tion analysis were thawed in water for 12 h before being wet-sieved to pass five different sieve sizes (4, 3, 2, 1 and < 1 mm) (Domingue et al. 1991b). Particle size distribution of samples of feed on offer and refusals was determined using the dry sieving tech- nique, to pass five different sizes of sieve (5·6, 4, 2, 1, 0·5 and < 0·5 mm). Each fraction was then oven dried at 100 °C for 16 h and reweighed. Data are expressed as percentages.

Statistical analysis

Effects of season and season v. deer species inter- actions for VFI, digestibility and faeces particle size data were assessed using repeat measures analysis of variance (Gill & Hafs 1971), with summer and winter as two time periods, using the Statistical Analysis System package (SAS 1987). Due to different animals of the same species being used for summer and winter

Table 5. (*Expt 1*). *Time spent eating and ruminating* (*min*) *in sambar deer and red deer fed* ad libitum *with chaffed lucerne hay, during summer* (*sambar* n = 3; *red* n = 4) *and winter* (*sambar* n = 3; *red* n = 3) (*mean values with their standard error*)

		Sambar deer	Red deer	S.E.
Voluntary DM intake				
g/day	Summer	1373	2122	90·8
	Winter	1802	1447	220·4
g/kg $W^{0·75}$ per day	Summer	58·7	70·9	2·82
	Winter	55·9	44·8	9·53
Eating (min)				
min/g DMI*	Summer	0·28	0·16	0·016
	Winter	0·14	0·16	0·018
min/24 h*	Summer	383	332	17·4
	Winter	254	221	24·2
min/06.00–18.00 (day)	Summer	208	197	23·3
	Winter	124	113	10·8
min/18.00–06.00 (night)	Summer	175	135	19·4
	Winter	130	108	21·3
Eating ratio (night:day)	Summer	0·84	0·68	0·168
	Winter	1·05	0·96	0·193
Ruminating (min)				
min/g DMI*	Summer	0·41	0·25	0·018
	Winter	0·30	0·25	0·020
min/24 h*	Summer	554	520	37·5
	Winter	544	355	42·6
min/06.00–18.00 (day)	Summer	240	214	23·8
	Winter	238	101	19·8
min/18.00–06.00 (night)	Summer	314	306	18·4
	Winter	306	254	25·6
Ruminating (night:day) ratio	Summer	1·30	1·43	0·168
	Winter	1·28	2·56	0·187

* Refers to total time eating or ruminating/24 h.

in the jaw recording experiments, the data were analysed separately for each season using one-way analysis of variance.

RESULTS

The chemical composition (g/kg DM) of the chaffed lucerne hay used in the digestibility trials during summer and winter was relatively constant (Table 2). Voluntary DM intake (kg/day) showed a weak interaction ($P < 0·10$) between deer species and season (Table 3), with VFI of red deer decreasing markedly from summer to winter, whereas that of sambar deer increased slightly. When expressed as g/kgW$^{0·75}$ per day, VFI was significantly lower in winter than in summer ($P < 0·01$), but the species × season interaction was not significant, although it seems that the decline in VFI from summer to winter was greater for red deer (-35 %) than for sambar deer (-18 %). This difference, depending on how VFI is calculated, is due to liveweight in sambar deer increasing more from

summer to winter than for red deer (Table 1). Apparent digestibility of all components measured (Table 3) did not change between seasons and was not different between sambar deer and red deer.

The distribution of particle size in the feed on offer was similar between summer and winter. There was no significant interaction between time × animal species for the distribution of faecal particle sizes, and the distribution of faecal particle sizes showed no significant differences between species at any sieve size during both summer and winter (Table 4). The proportion of faecal particle sizes < 1·0 mm in summer for sambar and red deer was 98·7 and 98·5 %, respectively, and in winter it was 98·9 and 98·5 % respectively.

Sambar deer consistently spent a slightly longer time eating than red deer (Table 5), during both summer and winter, and during both day and night-time, but none of these effects attained significance ($P > 0·05$). However, total eating time/g DMI was greater for sambar deer than for red deer during

Table 6. (*Expt 1*). *Number of eating and ruminating bouts in sambar deer and red deer fed* ad libitum *with chaffed lucerne hay in summer* (*sambar* n = 3; *red* n = 4) *and winter* (*sambar* n = 3; *red* n = 3) (*mean values with their standard errors*)

		Sambar deer	Red deer	S.E.
Eating				
Number of eating bouts				
24 h	Summer	11·8	12·3	1·39
	Winter	10·8	12·9	1·70
06.00 18.00 (day)	Summer	6·8	7·3	0·59
	Winter	5·3	7·1	0·50
18.00–06.00 (night)	Summer	5·0	5·0	1·06
	Winter	5·4	5·8	1·25
Minute/bout eating				
06.00–18.00 (day)	Summer	32·1	28·2	4·30
	Winter	23·3	16·2	3·45
18.00–06.00 (night)	Summer	33·4	34·8	5·83
	Winter	27·0	19·4	5·04
Ruminating				
Number of ruminating bouts				
24 h	Summer	14·5	13·4	0·66
	Winter	15·9	11·6	2·71
06.00–18.00 (day)	Summer	7·8	5·9	0·72
	Winter	8·0	4·6	1·33
18.00–06.00 (night)	Summer	6·8	7·5	0·57
	Winter	7·9	6·9	1·47
Minute/bout ruminating				
06.00 18.00 (day)	Summer	33·5	37·9	1·68
	Winter	31·4	27·5	3·57
18.00 06.00 (night)	Summer	43·8	40·5	2·98
	Winter	42·0	37·8	5·45

summer ($P < 0.01$), but there was no species difference during winter. It seems that eating time/g DMI was similar for red deer in summer and in winter, whereas it declined markedly in sambar deer between the seasons.

Sambar deer also tended to spend more time ruminating than red deer (Table 5), during both summer and winter and during the day and the night, with the effects attaining significance during winter for total (24 h) time ($P < 0.01$) and for daytime ruminating ($P < 0.001$). Total time spent ruminating (min/g DMI) was greater for sambar deer than for red deer, both in summer ($P < 0.001$) and in winter ($P < 0.10$). Total time spent ruminating/g DMI seemed to be constant between seasons in red deer, but to decline in sambar deer from summer to winter.

The ratio night:daytime eating was consistently greater for sambar deer than for red deer, whilst the ratio night:daytime ruminating was consistently less for sambar than for red deer, but only the ratio for ruminating attained significance in winter ($P < 0.01$).

There was little difference between the two species in number of eating bouts (Table 6). The number of daytime ruminating bouts was greater for sambar

deer than for red deer both in summer ($P < 0.10$) and in winter ($P < 0.01$), but there was no species difference for night ruminating bouts. Ruminating time (min)/bout was similar for red deer and sambar deer, and there was no significant species difference during daytime and night-time.

Within each season there were no differences between sambar deer and red deer in short term intake rate and in the number of chews/g DMI during eating (Table 7), although chewing rate/time tended to be lower for sambar deer than for red deer in summer ($P < 0.01$), but not in winter.

Sambar deer had a lower number of chews/bolus ruminating and a lower chewing time/ruminated bolus than red deer both in summer ($P < 0.01$) and in winter ($P < 0.10$), but had more rumination boli/h than red deer ($P < 0.01$). There was no difference between species in chewing rate during rumination.

DISCUSSION

Where significant species differences were detected in this paper, interpretation is complicated by the sambar deer being on average 5 months younger than the red

Table 7. (*Expts 2 and 3*). *Chewing efficiency during eating, and chewing efficiency during ruminating in sambar and red deer fed* ad libitum *with chaffed lucerne hay in summer (red* n = 4; *sambar* n = 3) *and winter (red* n = 3; *sambar* n = 3) (*mean values with their standard error*)

		Sambar deer	Red deer	S.E.
Eating (Expt 2)				
Intake rate				
g DMI/minute	Summer	8·0	8·8	0·78
	Winter	14·3	12·5	1·32
mg DMI/kg BW$^{0.75}$ per min	Summer	12·0	11·0	0·10
	Winter	23·0	24·0	0·40
No. of chews/min eating	Summer	84·1	100·3	2·54
	Winter	104·1	100·6	7·50
Number of chews/g DMI	Summer	11·0	11·7	0·93
	Winter	7·4	8·6	1·05
Ruminating (Expt 3)				
No. of chews/bolus ruminated	Summer	59·6	94·1	6·27
	Winter	63·8	85·2	8·05
Chewing time/bolus ruminated (sec)	Summer	40·7	61·7	3·62
	Winter	42·5	59·6	5·84
Number of boli/h	Summer	68·0	48·0	3·83
	Winter	72·5	50·6	4·47
Number of chews/min ruminating	Summer	89·9	91·5	7·30
	Winter	92·2	86·9	3·63
Pause between bolus ruminating (sec)	Summer	5·2	5·1	0·29
	Winter	5·6	5·1	0·16

deer, which could not be avoided because of the inherent species differences in calving time. Such differences are, however, considered to be real, because of their repeatability 6 months later and because in the case of traits such as rumination, a large number of aspects of this differed between the two deer species regardless of season of the year. Such results suggest fundamental differences between sambar (tropical) and red (temperate) deer, but it is acknowledged that in the present investigation the two deer species could not be statistically compared at the same age at the same time.

The seasonal trend of VFI in the present red deer data confirms previous studies, being high in summer and low in winter (Suttie *et al.* 1983; Barry *et al.* 1991; Domingue *et al.* 1991*b*). This indicates that the physiological cycles of temperate deer are strongly linked to photoperiod, as concluded by Barry *et al.* (1991). The mechanism of red deer for reducing VFI from summer to winter seemed to be by reducing the time per eating bout, whilst keeping the number of eating bouts per day and the chewing rate/min relatively constant between seasons. Hence, eating time (min)/g DMI and DMI/min (6·3; Table 5) did not change in red deer between summer and winter. With sambar deer the best indicator of seasonal changes in VFI is considered to be kg DM/day, as this is not complicated by changes in liveweight.

Using this parameter, Semiadi (1993) demonstrated an endogenous cycle of VFI in growing sambar deer, with a maximum in autumn and a minimum in spring, and with the amplitude of the cycles being much less than for red deer. The VFI obtained for sambar deer in the present study supports this trend. It seems that sambar deer achieved their greater VFI in winter with an increased DMI/min eating (7·1 *v.* 3·6 g DM/min; Table 5), probably due to increased chewing frequency during eating in winter (Table 7).

The present study showed that passage through a 1 mm sieve was the critical particle size for leaving the rumen in both species of deer, as shown in sheep (Ulyatt 1983), and confirming the finding in red deer (Domingue *et al.* 1991*b*). Studies in mule deer and elk also show a similar trend, with 92 and 89%, respectively, of feed particles consumed > 2·8 mm being reduced to < 1·0 mm by rumination (Spallinger & Robbins 1992). Apart from particle size, efficiency of feed utilization by the rumen is also dependent on the shape of feed particles. The rumen of browsing animals is more inclined to pass larger cube-shaped particles, rather than long thin particles, as present in mixed feeders (Renecker & Hudson 1990). The distribution of faecal particle size from the present study did not significantly change with season, as was also found in moose (*Alces alces*) and elk (*Cervus elaphus nelsoni*) (Renecker & Hudson 1990). Chai *et*

al. (1984) concluded that the efficiency of chewing during rumination in breaking down the feed particles is greater than during eating, whilst Spallinger & Robbins (1992) found in mule deer (*Odocoileus hemionus hemionus*) and elk that the principal mechanism for breaking down feed particles is chewing during rumination rather than microbial digestion.

Although there were changes between seasons in VFI, apparent digestibility did not change between seasons in either species. Constant digestibility between seasons in red deer is due to a reduction in rumen fractional outflow rate during summer, leading to an increase in rumen pool size at this time and allowing longer time for rumen microbial fermentation (Domingue *et al.* 1991*b*; Freudenberger *et al.* 1994) and to increased ammonia production. Digestive function in sambar deer, and how this differs from red deer, requires future study.

One of the major differences between sambar deer and red deer was in rumination behaviour, with sambar deer spending more time ruminating/g DMI, having shorter time (sec) per ruminated bolus than red deer, but having more ruminating bouts and boli/h. Such differences might be expected to lead to a more efficient rate of particle breakdown during rumination in sambar deer, to a faster rate of turnover of rumen contents during rumination and to increased saliva

production (and hence rumen N recycling). If this is true, it might be expected that digestive efficiency in sambar deer could be greater than for red deer when diets high in fibre (and hence low in digestibility) are fed. This hypothesis needs to be tested experimentally; it seems logical, as tropical forages are well known to be of lower digestibility than temperate forages (Van Soest 1982), and it may well be that sambar deer have evolved a rumination pattern designed for the efficient breakdown of such forage.

Relative to red deer, it also seems in the present study that sambar deer did more of their ruminating during the daytime. This may complement their nocturnal grazing under field conditions (Semiadi *et al.* 1993*a*) and may be part of an evolutionary mechanism allowing them to ruminate whilst hiding from predators during the daytime.

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