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# Digestion and chewing behaviour of young sambar and red deer consuming a low quality roughage

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## SUMMARY

Low quality chaffed meadow hay, containing 10·5 g N/kg dry matter (DM), was fed to four artificially reared sambar (tropical) deer (*Cervus unicolor*) and four red (temperate) deer (*Cervus elaphus*) confined indoors in metabolism crates at Palmerston North, New Zealand, during March and April 1994. Measurements were made of DM intake (DMI), apparent digestibility, nitrogen (N) retention and the time spent eating and ruminating. Voluntary food intake (VFI), measured over days 7–11, was substantially greater for red deer than for sambar deer (67 *v.* 36 gDM/kgW$^{0.75}$/day). Dry matter intake of red deer was then restricted, so that apparent digestibility could be better compared between the two species. Eating and ruminating time/gDMI and chews during eating/gDMI were all greater for sambar deer than for red deer. Apparent digestibility of DM, organic matter (OM) and energy were low (*c.* 0·42) and not different between deer species. Apparent digestibility of neutral detergent fibre (NDF) and cellulose were highest for red deer, but lignin apparent digestibility was highest for sambar deer. Both deer species lost weight and were in negative N balance. However, despite their lower N intake, sambar deer lost significantly less N and liveweight per day (−5·6 g and −118 g) than red deer (−12·2 g and −258 g). It was concluded that red deer responded to a diet of low quality roughage by increasing VFI and cellulose digestion, whilst sambar deer responded with a lower VFI but greater chewing activity, improved lignin digestion and better N conservation. Rumen mean retention time should be measured in future experiments with sambar deer and red deer fed on low quality forage diets.

## INTRODUCTION

Studies investigating the domestication of tropical sambar deer (*Cervus unicolor*) in New Zealand (NZ) have shown that relative to temperate red deer (*Cervus elaphus*), sambar deer selected a diet higher in lignin and condensed tannin (Semiadi *et al.* 1995*a*). Sambar and red deer digested a medium quality chaffed lucerne hay with similar efficiency (*c.* 60% OMD), but sambar deer spent more time ruminating/g DM intake (DMI) (Semiadi *et al.* 1994*a*). These authors hypothesised that sambar deer may have evolved a chewing strategy to digest tropical forages, which are known to contain higher concentrations of lignin and to be of lower digestibility than temperate forages (Minson 1981), and that the increased rumination time of sambar deer may result in this species being able to digest low quality forage more efficiently than temperate red deer. The present experiment was designed to test this hypothesis.

## MATERIALS AND METHODS

### *Experimental design*

An indoor trial was conducted with artificially reared young sambar deer and red deer fed low quality chaffed meadow hay during March and April 1994 at Massey University, NZ. Voluntary food intake (VFI), apparent digestibility, nitrogen (N) excretion and jaw activity were measured. Time spent eating and ruminating, frequency of chewing and bolus formation during rumination were calculated from the records of jaw activity.

### *Animals and housing*

Three artificially reared hinds and one stag of each species were confined in specially designed deer

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Table 1. *Mean age (± S.E.) and body weight (± S.E.) of the sambar deer and red deer used in the digestion and jaw activity experiments (mean values for four sambar deer and four red deer)*

| | Sambar deer | Red deer |
|---|---|---|
| Age (days) | 369 (52·1) | 457 (6·7) |
| Body weight (kg) | | |
| Initial | 86·4 (1·21) | 75·0 (1·85) |
| Final | 82·5 (1·19) | 66·5 (1·74) |
| Liveweight gain (g/day) | −118 (3·8) | −258 (13·7) |

metabolism crates (Milne *et al.* 1978). The mean age and body weights of the deer at the start of the experiment are shown in Table 1. The sambar deer were *c.* 3 months younger than the red deer because of the later calving time of sambar deer (Semiadi *et al.* 1994*b*). The sambar were *c.* 11 kg heavier than the red deer at the start of the experiment. The crates were positioned in a well ventilated building with artificial light set at 14 h light and 10 h dark (prevailing photoperiod). One side of the cage was movable and could be used to adjust the floor area, for restriction of the deer during the jaw recording experiment.

### *Diet*

Low quality chaffed meadow hay (2–6 cm long), from one batch, was used as the sole diet. Deer were fed once daily at 08.00 h, after feed residue was removed and weighed. The deer were fed *ad libitum* for the first 11 days, with feed offered each day being 1·15 of the amount consumed the previous day. Because the red deer were eating much more than sambar deer, the feed offered to red deer was restricted to 1350 gDM/day from day 12 onwards, whilst the sambar continued *ad libitum* (1100 gDM/day offered), so that digestibility could be better compared between the two deer species. Water was available *ad libitum* and animals had access to a multi-mineral salt block (Summit Multimineral Salt Block, Dominion Salt, NZ) placed in each feed bin.

### *Digestion trial*

Apparent digestibility was measured over a 7-day period (days 15–22) following the adjustment period, with feed on offer, feed refusals, undercrate residues, urine and faeces being collected and weighed daily.

Duplicate 200 g samples of the feed on offer were taken daily, pooled and stored at −20 °C. Approximately 50 g of feed residue for each animal was collected daily and pooled per animal during the digestion period. All undercrate residues were collected daily and pooled per animal. Faecal samples (500 g) were taken daily per animal and stored at −20 °C. At the end of the trial, the faecal samples were thawed and pooled per animal, mixed thoroughly and subsampled. Urine was collected in buckets containing sufficient $H_2SO_4$ (25% v/v) to maintain pH below 3·5. Approximately 200 ml urine samples were collected daily, stored at −20 °C, and pooled per animal over the trial period.

### *Jaw recording*

Jaw harnesses, which held an air bag under the lower jaw, were fitted to the deer at the conclusion of the digestion trial (day 23). The crate floor area was reduced by means of the movable wall to stop deer from turning around within the crate. The degree of restriction was such that while the animals could not turn around, they could stand or lie down and eat or drink without hindrance. A 3-day adjustment period allowed the deer to become accustomed to the harnesses and to the reduced crate size. Jaw activity was recorded over days 26–31.

The recording system was similar to that described previously (Stafford *et al.* 1993; Hoskin *et al.* 1995). Two, four-channel chart recorders (Graphtec Linearecorder WR3701-4H*1, Japan) allowed simultaneous recording of jaw activity of the eight animals. Jaw movements were sensed as pressure changes in a partially inflated rubber bag held under the jaw by a halter. The bag, a section of bicycle inner tube, closed off at one end, filled with foam and with the other end sealed and cemented over a flexible nylon pipe (3·5 mm i.d.) was joined to a 0·8 m section of coiled rubber infusion tubing (CenVet, Australia) which accommodated animal movement. Nylon tubing connected the rubber tubing to an electronic pressure transducer (Statham, ADCG, Hong Kong) mounted outside the cage. The transducer was connected to the recorder via a pre-amplifier.

### *Time spent eating and ruminating*

Four complete 24-h periods of jaw activity starting at 08.00 h each day were recorded for each of the eight deer. The animals and recordings were inspected frequently during each 24-h period. A chart recording speed of 25 mm/min was used to record time spent eating and ruminating. Feed offered and feed refusals were also recorded during the jaw recording measurement period.

Information from the chart paper was read and tabulated, so that the time spent eating, ruminating or idling (min/24 h), number of boli during rumination (boli/bout), number of eating and ruminating bouts and the time spent eating or ruminating per bout could be calculated.

### *Efficiency of chewing during eating and rumination*

Chart recording speed was increased to 50 mm/min for a period of 6 h, on day 29, to enable the number

of chews during eating and ruminating to be calculated. The number of chews during eating was measured from ten randomly chosen, 4-min eating periods and expressed as number of chews/min eating and as chews/gDM eaten. The number of chews during rumination was measured by randomly taking 25 boli/deer and counting the number of chews in each of these boli. Data were then expressed as the number of chews/boli ruminated, chews/min ruminating, time spent chewing/bolus (s) and time elapsed between each rumination bolus (s).

### *Record interpretation*

The records were analysed for periods of eating, ruminating or idling using the following conventions (Hoskin *et al.* 1995). Eating bouts were considered to be a minimum of 5 min duration and continuous unless interrupted for more than 10 min by a bout of rumination or idling. Rumination bouts were defined as involving a minimum of three boli regurgitated and chewed, with bouts separated by a minimum of 5 min idling or feeding. Pseudo-rumination was defined as attempts at rumination, consisting of rumination bouts of less than three boli, and/or erratic rumination with inconsistent and infrequent chewing. Idling bouts were periods of no jaw movements or movements associated with drinking or head rubbing.

### *Sample processing and chemical analysis*

Samples of feed on offer, feed refusals, and undercrate residue samples from the digestion experiment were freeze-dried in duplicate, with faeces being freeze-dried in triplicate and the dry matter (DM) content determined. Samples were then ground to pass a 1 mm sieve (Willey Mill, USA) and analysed for organic matter (OM), total nitrogen (N), neutral detergent fibre (NDF), acid detergent fibre (ADF), lignin and heat of combustion. Organic matter content was measured by ashing the samples in a furnace at 500 °C for 16 h and total N (including urine) was determined by the Kjeldahl procedure. Neutral detergent fibre, ADF 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 calorimeter (Gallenkamp Autobomb, Watson Victor Ltd, UK). The sample was pelleted (0·5–0·8 g DM, 12 mm diameter) prior to combustion. Samples of feed on offer were also analysed for condensed tannins, following the procedure of Terrill *et al.* (1992).

### *Statistical analysis*

Tests for significance of differences between the two deer species were carried out by one-way analysis of variance using the Statistical Analysis System package (SAS 1987). Mean values and standard errors are presented.

## RESULTS

The diet offered contained a high concentration of total fibre (712 g/kg DM) and a low concentration of total N (10·5 g/kg DM; Table 2), confirming its classification as a low quality roughage. The diet also contained small amounts of condensed tannins, mainly bound to protein and fibre.

Voluntary feed intake stabilized by day 7 in sambar deer and by day 6 in red deer (Fig. 1). Voluntary feed

Table 2. *Chemical composition (g/kgDM) of the low quality chaffed meadow hay fed to sambar deer and red deer*

| | Contents |
|---|---|
| Organic matter | 935 |
| Heat of combustion (kJ/DM) | 18·35 |
| Total nitrogen | 10·5 |
| Neutral detergent fibre | 712 |
| Acid detergent fibre | 391 |
| Cellulose | 347 |
| Hemicellulose | 321 |
| Lignin | 44 |
| Condensed tannins | |
| Free (extractable) | 0·11 |
| Protein-bound | 1·07 |
| Fibre-bound | 0·43 |
| Total | 1·61 |

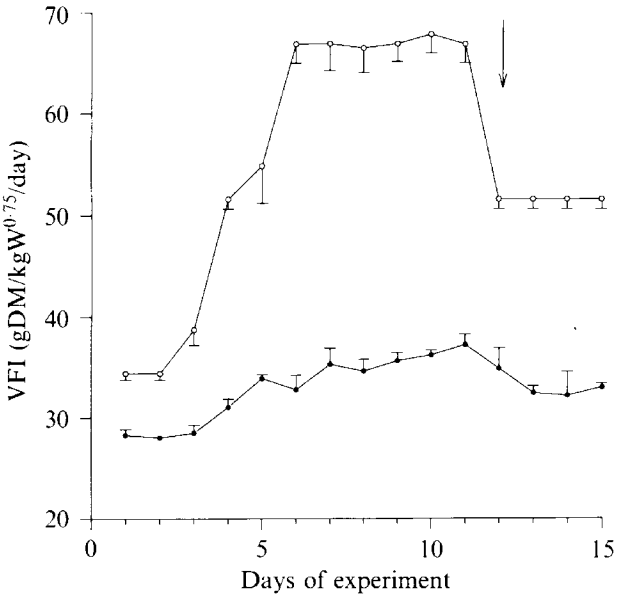


Fig. 1. Voluntary feed intake (gDM/kgW$^{0.75}$/day) of young sambar deer (●) and young red deer (○) when offered low quality meadow hay *ad libitum*. Vertical bars represent S.E. ↓ indicates intake of red deer restricted.

Table 3. *Time spent eating and ruminating in young sambar deer and red deer fed low quality chaffed meadow hay (mean values with their standard errors for four deer of each species)*

| | Sambar deer | Red deer | S.E. |
|---|---|---|---|
| DM intake | | | |
| g/day | 978 | 1313 | 34·8 |
| g/kgW$^{0.75}$/day | 35·7 | 56·4 | 1·01 |
| Eating time | | | |
| min/24 h | 511 | 400 | 20·2 |
| min/gDMI | 0·54 | 0·30 | 0·057 |
| Chews/min eating | 86 | 73 | 1·5 |
| Chews/gDMI | 46 | 22 | 4·4 |
| Eating bouts (number/24 h) | 9·1 | 6·4 | 0·63 |
| Duration eating bouts (min) | 62·5 | 71·6 | 7·62 |
| Rumination time | | | |
| min/24 h | 528 | 524 | 23·3 |
| min/gDMI | 0·55 | 0·40 | 0·017 |
| Chews/min ruminating | 81 | 78 | 6·0 |
| Boli/h | 23·7 | 21·4 | 2·13 |
| Chews/boli ruminated | 75 | 81 | 1·8 |
| Chewing time/boli ruminated (s) | 56 | 62 | 3·2 |
| Rumination bouts (number/24 h) | 11·9 | 11·8 | 0·56 |
| Boli/bout ruminated | 48·9 | 43·7 | 3·09 |
| Duration ruminating bouts (min) | 44·6 | 44·5 | 2·59 |
| Idling time | | | |
| min/24 h | 400 | 515 | 22·5 |

Table 4. *Apparent digestibility of low quality chaffed meadow hay by sambar deer and red deer (mean values with their standard errors for four deer of each species)*

| | Sambar deer | Red deer | S.E. |
|---|---|---|---|
| DM intake | | | |
| g/day | 981 | 1303 | 20·3 |
| g/kgW$^{0.75}$/day | 35·5 | 54·1 | 0·97 |
| Apparent digestibility | | | |
| Dry matter | 0·392 | 0·406 | 0·0128 |
| Organic matter | 0·409 | 0·431 | 0·0110 |
| Energy | 0·382 | 0·406 | 0·0099 |
| Neutral detergent fibre | 0·403 | 0·457 | 0·0164 |
| Acid detergent fibre | 0·377 | 0·398 | 0·0143 |
| Cellulose | 0·411 | 0·507 | 0·0168 |
| Hemicellulose | 0·411 | 0·483 | 0·0175 |
| Lignin | 0·057 | −0·138 | 0·0198 |

intake, measured over days 7–11, was significantly higher for red deer than for sambar deer ($P < 0·001$; 67·0 *v.* 35·8 g DM/kgW$^{0.75}$/day). Even with the DMI of the red deer restricted, the DMI of sambar deer was still lower ($P < 0·001$) than that of red deer, during both the digestibility (days 15–22) and jaw recording (days 23–31) periods (Tables 3 and 4). Both groups of animals lost weight (Table 1), but weight loss was significantly less ($P < 0·001$) in sambar deer than in red deer.

Total eating time (min), eating time/gDMI and frequency of chewing during eating were all greater ($P < 0·001$) for sambar deer than for red deer. The number of chews/gDMI and the number of eating bouts/day were also consistently greater ($P < 0·05$) for sambar deer than for red deer, with no significant difference between the two species in length of the eating bouts (min).

There was no significant difference between species for time spent ruminating, but ruminating time/gDMI

Table 5. *Nitrogen (N) excretion and retention in sambar deer and red deer fed on low quality chaffed meadow hay (mean values and their standard errors for four deer of each species)*

| | Sambar deer | Red deer | S.E. |
|---|---|---|---|
| N intake (g/day) | 9·9 | 13·8 | 0·25 |
| Faeces N (g/day) | 7·2 | 11·9 | 0·59 |
| Urine N (g/day) | 8·3 | 14·1 | 1·86 |
| N retention (g/day) | −5·6 | −12·2 | 1·17 |
| Faeces N (% intake) | 71·8 | 86·1 | 4·18 |
| Urine N (% intake) | 84·5 | 102·6 | 15·33 |

was significantly greater ($P < 0{\cdot}001$) for sambar deer than for red deer. The number of chews/boli ruminated was significantly less ($P < 0{\cdot}05$) for sambar deer than for red deer. All other aspects of rumination behaviour were similar for sambar and red deer.

Idling time (min/24 h) for sambar deer was consistently less ($P < 0{\cdot}01$) than for red deer. Pseudo-rumination time was very small (1 min/24 h) for both deer species.

Apparent digestibility of DM, organic matter (OM), energy, ADF and hemicellulose were not significantly different between deer species (Table 4). Apparent digestibility of NDF ($P < 0{\cdot}10$) and cellulose ($P < 0{\cdot}05$) were lower for sambar deer than for red deer. Lignin digestibility was very low for both species, but was greater for sambar deer than for red deer ($P < 0{\cdot}001$), with the negative values for red deer indicating excretion of artefact lignin in the faeces.

Nitrogen intake (g/day) for the sambar deer was considerably lower ($P < 0{\cdot}01$) than for the red deer (Table 5). Both groups of deer were in negative nitrogen balance, but young sambar deer lost approximately half as much N per day as young red deer ($P < 0{\cdot}10$), due to reduced excretion (% intake) in both faeces and urine.

## DISCUSSION

The low apparent digestibility of OM and energy, the high NDF content and the low N content (7% protein) show that the chaffed meadow hay used was indeed a low quality roughage, and this was confirmed by the loss in liveweight and negative N balance for both deer species. Tropical grasses are known to be higher in lignin content and lower in total N content and apparent digestibility than temperate grasses (Minson 1981). The meadow hay used in the present study would therefore be comparable with low quality standing tropical grasses at the end of the dry season.

Voluntary feed intake of the low quality roughage (*c.* 42% OMD) was lower for sambar deer than for red deer, as also found by Semiadi *et al.* (1995*b*) for a high quality pelleted concentrate diet (*c.* 83% OMD; 63 *v.* 86 gDM/kgW$^{0{\cdot}75}$/day). This shows that the VFI of sambar deer is naturally lower than that of red deer, regardless of digestibility of the diet. Milne *et al.* (1978) also found that red deer responded to very low digestibility Scottish hill pastures by increasing VFI, with VFI of red deer being double that of sheep, which is approximately the same difference as found between red deer and sambar deer in the present study.

Eating and ruminating time/g DMI of the low quality roughage was higher for sambar deer than for red deer. Semiadi *et al.* (1994*a*) also found more jaw activity for sambar deer than for red deer fed a medium quality diet of chaffed lucerne hay (60% OMD), with the main difference being increased ruminating activity. However, with the low quality roughage, the biggest difference was found in chewing during eating. Two processes affect the breakdown of particulate DM in ruminants, namely initial chewing during eating and further chewing during rumination (Ulyatt *et al.* 1986). The greater jaw activity during both eating and ruminating shown by sambar deer should therefore result in the breakdown of particles to a smaller size than for red deer.

Increased chewing time/g DMI by sambar deer was associated with higher apparent digestibility of lignin. Domingue *et al.* (1991*a*, *b*) found similar results in goat *v.* sheep comparisons for a low quality roughage high in lignin, where goals had more chews/g DM eaten than sheep, and this was associated with higher apparent digestibility of lignin. More chewing would be expected to reduce particle size, increase particle surface area, and hence increase access for rumen micro-organisms, thus explaining the increased lignin digestion. A greater proportion of small particles in the rumen would provide a larger surface area of particles for microbial attachment and colonization (Hungate 1966; Akin 1976, 1979; Cheng *et al.* 1977; Elliott *et al.* 1985). However, apart from lignin, no other component of the diet was digested better by sambar deer than by red deer, and in fact total fibre (NDF) and its principal constituent (cellulose) were digested less efficiently by sambar deer than by red deer.

Approximately 90% of the digestible cellulose and 82% of digestible hemicellulose is digested in the rumen (Ulyatt & MacRae 1974), and is a function of rumen fractional degradation rate (FDR) and rumen fractional outflow rate (FOR). It may be that rumen mean retention time (MRT = 1/FOR) is different for sambar deer than for red deer, and a lower cellulose digestion in sambar deer could be explained by a shorter rumen MRT for particulate matter, allowing less time for microbial attack. Rumen MRT of liquid and particulate matter needs to be measured in future experiments with sambar deer and red deer.

The negative N balance shows the low quality diet was not able to meet the N needs of each deer species.

Despite lower N intake, there was less loss of both N and liveweight in sambar deer than in red deer, showing better N conservation under conditions of negative N balance, due to proportionately lower losses of urine N and faeces N. Semiadi *et al.* (1985*b*) also found that sambar deer had a better efficiency of food conversion (kg DMI/kg LWG) than red deer when both species were fed a high quality pelleted diet, demonstrating that tropical sambar deer have a more efficient utilization of digested nutrients than the temperate red deer, when fed both above and below maintenance.

It can be concluded from the present study that sambar deer and red deer responded to a diet of low quality roughage in very different ways. The temperate red deer responded with a larger VFI and better cellulose digestion than the tropical sambar deer. The increased cellulose digestion may be due to the increase in rumen particulate MRT which occurs in red deer at peak VFI (Domingue *et al.* 1991*c*; Freudenberger *et al.* 1994), thus allowing more time for microbial fermentation. Sambar deer responded with more time spent chewing during eating and ruminating, associated with increased lignin digestion, and by better conservation of N. These differences may be the result of adaptation to the temperate and tropical climates in which their ancestors evolved.

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