# Dietary preferences of sambar (*Cervus unicolor*) and red deer (*Cervus elaphus*) offered browse, forage legume and grass species

G. SEMIADI<sup>1,2\*</sup>, T. N. BARRY<sup>1†</sup>, P. D. MUIR<sup>2</sup> AND J. HODGSON<sup>3</sup>

Departments of <sup>1</sup> Animal Science and <sup>3</sup> Plant Science, Massey University, Palmerston North, New Zealand <sup>2</sup> AgResearch, Flock House, Private Bag, Bulls, New Zealand

(Revised MS received 10 October 1994)

#### SUMMARY

Grazing sambar and red deer in New Zealand were offered a free choice of seven different plant species (forage legumes, browse and grasses) in 1992 and 1993 and dietary preference rankings were determined. Nutritive value of plants on offer and diet selected, plant height, plant species purity and stem diameter selected (browse only) were also determined. Total nitrogen (N) and organic matter digestibility (OMD) were highest for red clover, lowest for grasses and intermediate for browse species (willow, poplar and lupin). Top dietary preference ranking was willow for sambar and red clover for red deer in both years, with Yorkshire fog and prairie grass being lowly preference ranked with both deer species. Sambar selected willow stems up to 38 mm in diameter and poplar stems up to 54 mm in diameter. When the plants were grouped into browse, grass and forage legume categories, both deer species showed a similar preference ranking for grasses. Relative to grasses, sambar showed a strong preference for browse and a low preference for forage legumes, whilst red deer showed a strong preference for forage legumes of high nutritive value and a very low preference for browse. It was calculated that sambar selected a total diet higher in condensed tannins and lignin but lower in nitrogen than that selected by red deer, with similar values for total fibre and OMD. Differences in dietary preference between the two deer species may be linked with the greater ability of sambar deer to neutralize some plant secondary compounds and their more efficient rumination pattern compared with red deer. Both sambar and red deer can be classified as intermediate feeders, having a similar preference for grasses, but differing preferences for forage legumes and browse.

# INTRODUCTION

Wild red deer (Cervus elaphus) are intermediate feeders which can adapt well to browse and to forage grazing (Kay et al. 1980; Hoffman 1985). In the wild, red deer are noted for selecting plants more in relation to their abundance than to specific plant species (Kay & Staines 1981). However, wild red hinds select feed higher in total N than stags do (Kay & Staines 1981). Domesticated red deer prefer legumes to grasses and herbs, and have a high preference for red clover (Hunt & Hay 1990).

In spite of a substantial number of studies on wild sambar deer (*Cervus unicolor*), data on their dietary preferences are contradictory. Burke (1982) categorized sambar as a browser for most of the year, whilst Dinnerstein (1983) categorized sambar as a grazer. The latter view is supported by Nair & Jayson (1988), while Ngampongsai's (1987) study suggests that sambar could be categorized as an intermediate feeder. Ngampongsai (1987) in Thailand, and Kelton (1981) in New Zealand (NZ), found that wild sambar deer selected plants in proportion to their availability. The objectives of the present study were to determine the dietary preferences of sambar and red deer given free access to a range of forage legume, browse and grass species.

# MATERIALS AND METHODS

Experimental design

Dietary preferences of sambar and red deer were determined in two grazing experiments in 1992 and 1993, by offering a free choice of seven different plant species (forage legumes, browse and grasses) and

<sup>\*</sup> Present address: Puslitbang Biologi–LIPI, Jl. H. Juanda 18, Bogor 16151, Indonesia.

<sup>†</sup> To whom correspondence should be addressed.

recording the number of grazing observations on each species. Both experiments were conducted on the deer farm of AgResearch at Flock House, Bulls, NZ. Nutritive quality of plants on offer and diet selected, plant height, plant species purity, plant preference by grazing deer, and stem diameter selected were subsequently determined. Preference ranking was defined as the listing, in descending order, of the number of grazing observations recorded for each deer species on each plant species (1 = high preference ranking; 9 = low preference ranking).

#### Animals

Sambar deer comprising one adult stag and six adult hinds, and a similar number of age-matched domesticated red deer were used in the study. Both deer species were accustomed to movement between paddocks and to the presence of an observer.

## Plant species

The plant species in Expt 1 comprised two legumes (red clover, *Trifolium pratense* cv. Colenso, and lotus, *Lotus corniculatus* cv. Grasslands Goldie), two browse shrubs (lupin, *Lupinus arboreus*, and willow, *Salix matsudana* × *alba* cv. NZ 1040 Tangoio) and three grasses (Yorkshire fog, *Holcus lanatus* cv. Massey Bassyn, prairie grass, *Bromus willdenowii*, and perennial ryegrass, *Lolium perenne* cv. Grasslands Nui, with three levels of endophyte; low, medium and high). Sowing rate for prairie grass was 28 kg/ha, Yorkshire fog 7 kg/ha, lotus 8 kg/ha, lupin 120 kg/ha, red clover 7 kg/ha and perennial ryegrass 20 kg/ha. Willow stems (30 cm long) were planted at 1 m intervals.

In Expt 2, poplar (*Populus euramericana* cv. PN 870 Veronese) replaced lupin as a browse species and lotus was excluded from the study. Poplar stems (30 cm long) were planted at 1 m intervals. All other species used were as described in Expt 1.

#### Paddock management

The experimental paddock consisted of four replicated blocks, with two replicated blocks in each of two adjacent experimental areas. Each block contained six main plots,  $20 \times 2$  m per plot, for the six main plant species, with perennial ryegrass sown in the spaces between plots  $(20 \times 0.6 \text{ m})$ . The two areas (A and B) were separated by a 2 m high deer fence, but there was no fence between the two blocks in each area.

During Expt 1, before cultivation, the experimental paddock was sprayed with glyphosate (Roundup; Monsanto, NZ) at the rate of 12 litres/ha. All species, except willow, were sown 3 months later, on 2 May 1991. Willow stems were planted on 15 June 1991. Reactive superphosphate was applied at 150 kg/ha on 2 May and 4 October 1991. Nitrogen was applied

as urea 1 month after sowing, and then regularly every 2 months, at the rate of 25 kg N/ha. On 27 July 1991, legume and lupin plots were sprayed with propyzamide (Kerb Flo; Rohm and Hass Ltd, NZ) at a rate of 3 litres/ha, to remove the non-legume plants. Grass plots were sprayed with a mixture of MCPA and mecoprop (Turfix; Yates, NZ) at the rate of 12 litres/ha, to remove any legumes and broadleaved weeds. On 6 September 1991, willow plots were sprayed with a diuron and linuron mixture (Cohort; Ciba Geigy Ltd. NZ) at a rate of 4 litres/ha, to eliminate weeds. Three to four weeks before each grazing observation was conducted, grass and legume plots were cut and the herbage removed, to maintain the plants in a vegetative state. In the willow and lupin plots, any remaining weeds were cut using a sickle.

During Expt 2, on 5 June 1992, lupin areas were sprayed with glyphosate (Roundup; Monsanto, NZ) at the rate of 12 litres/ha and replaced by poplar. Poplar stems were planted on 10 July 1992. The application of nitrogen, as urea, was applied to the whole area regularly every 2 months, from October 1992 until April 1993, at the rate of 25 kg N/ha.

## Data collection

Grazing observations were conducted during weekends in December 1991, February and April 1992 (Expt 1) and in February and April 1993 (Expt 2), when other activities on the farm were minimal. Sambar and red deer groups were selected at random to go to area A first and were replaced by the second group the following day. The following weekend, the second experimental area (B) was grazed and the order of introducing the deer species was reversed.

Observations commenced 30 min after animals were introduced, to allow them to adapt to the area. Observations commenced between 08.30 and 09.00 h and recorded the number of animals grazing specific plots at 1-min intervals until 300 recordings over the two blocks had been made. Observations were made using binoculars (Nikon, Japan;  $10 \times 50$  magnification) or a telescope (Bisley Delux, Japan; D = 40 mm, 10-40 magnification) from a hide sited 50 m from the experimental paddock.

In Expt 1, data for the second and third grazing observations on lotus and the third grazing observation on lupin were excluded from the analysis, because these areas had been invaded by other plant species.

## Plant sampling and chemical analysis

The pre-grazing height of plants, other than willow, lupin and poplar, was measured using a rising plate meter (Ashborn; Palmerston North, NZ), using 30 counts per plot. Willow, lupin and poplar were measured with a conventional wooden 2-meter ruler.

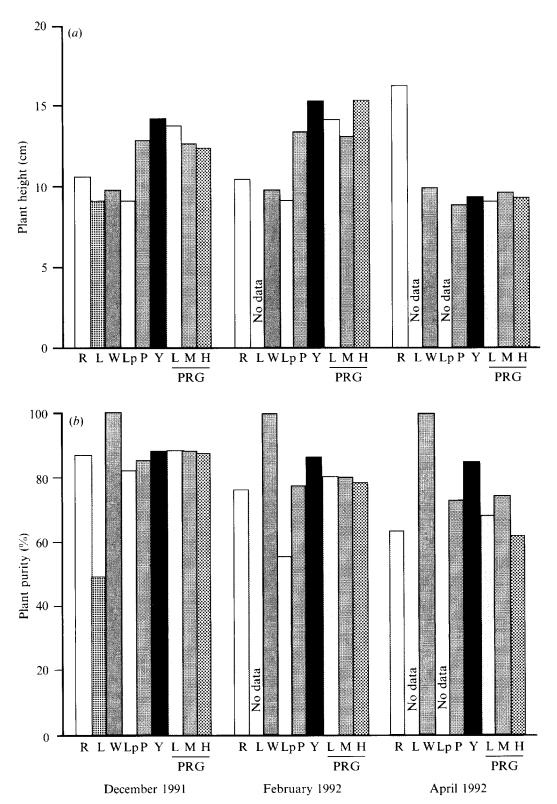
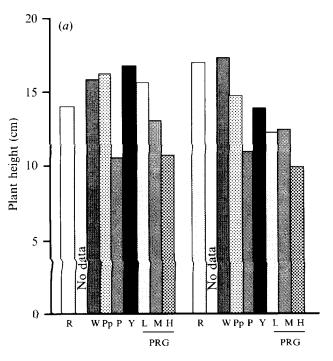


Fig. 1. Experiment 1 (a) Mean herbage height (cm, grasses and legumes; cm ÷ 10, willow and lupin) and (b) plant purity (%) of plants on offer, prior to the introduction of animals during December 1991, February and April 1992. R = red clover; L = lotus; W = willow; Lp = lupin; P = prairie grass; Y = Yorkshire fog; PRG-L = low endophyte perennial ryegrass, PRG-M = medium endophyte perennial ryegrass, PRG-H = high endophyte perennial ryegrass.



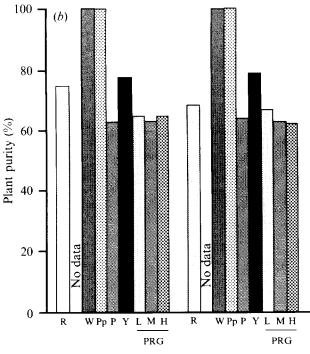


Fig. 2. Experiment 2 (a) Mean herbage height (cm, grasses and legumes; cm ÷ 10, willow and poplar) and (b) plant purity (%) of plants on offer, prior to the introduction of animals during February and April 1993. R = red clover; W = willow; Pp = poplar; P = prairie grass; Y = Yorkshire fog; PRG-L = low endophyte perennial ryegrass; PRG-M = medium endophyte perennial ryegrass, PRG-H = high endophyte perennial ryegrass.

February 1993

**April** 1993

Plant species purity was measured using point-analysis (50 counts per plot). Representative samples of plants on offer, other than willow, lupin and poplar, were cut from each plot in each block to ground level and retained for measurements of nutritive quality. Feed on offer for willow, lupin and poplar was cut from the tip area, at approximate browsing height. Willow and lupin stem diameter were measured using microcallipers. After the determination of dietary preference ranking, representative samples of the plants as selected by the animals were also collected from each plot of each block and retained for nutritive quality analysis. All samples were stored at -20 °C, freezedried and ground to pass a 1 mm sieve.

For feed on offer in Expt 1, samples were pooled between blocks within each experimental area (n = 2)at each grazing period (n = 3), giving six samples overall for each plant species. For feed on offer in Expt 2, samples were pooled between blocks over both experimental areas at each grazing period (n =2), giving two samples overall for each plant species. Samples of diet selected were analysed only from Expt 2. Samples from individual plant species of grasses and forage legumes were pooled for the two periods of observation and samples from browse plant species samples were pooled for each month of observation. Samples of forages were analysed for dry matter (DM), total N, in vitro digestibility, total fibre (NDF), lignin and condensed tannins (CT). Total fibre and lignin contents were analysed following the detergent procedures of Goering & Van Soest (1970). In vitro digestability analysis followed the method described by Roughan & Holland (1977). Condensed tannins were determined using the butanol/HCl procedure described by Terrill et al. (1992), which measures extractable, protein-bound and fibre-bound CT. Because extractable CT and protein-bound CT would be solubilized in the initial in vitro neutral detergent extraction steps, but are known to be indigestible in vivo (Terrill et al. 1994), extractable and proteinbound CT (% OM) values were deducted from all in vitro OMD determinations.

## Statistical analysis

Plant height, plant species purity, nutritive value, and number of animals grazing particular plots (which reflected dietary preference) were analysed using sas (1987). A generalized linear model was used, with variables used being deer species, plant species and month of observation. Analysis of dietary preference was also conducted by grouping the plant species into browse, legume and grass categories. Nutritional values for diet selected are presented for Expt 2 only, due to insufficient sample sizes being collected in some instances in Expt 1.

#### RESULTS

## Plant height and species purity

There was no interaction between plant species and month of observation for plant height and no significant effect of time in either year (Figs 1a and 2a). The interaction between plant species purity and month of observation was significant in Expt 1 (P < 0.001) but not in Expt 2 (Figs 1b and 2b). A decline in purity with time in some species was due mainly to competition from native grasses and weed species.

## Dietary preference

The interaction between plant species and animal species was significant in both experiments (P < 0.001; Table 1). In both years, willow was the species most preferred by sambar and red clover was the species most preferred by red deer, with the difference between the two deer species for the number of grazing observations being significant both for willow

(P < 0.001) and for red clover (P < 0.01). Prairie grass and Yorkshire fog had a low preference ranking for both deer species in both experiments.

When the plant species were grouped into browse, legume and grass categories, the interaction between plant group × animal species × time and the interaction between time and animal species were not significant in either experiment (P > 0.05). However, the interaction between plant group and animal species was significant in both years (P < 0.001); Table 2). In both experiments, sambar had more grazing observations than red deer on browse and less grazing observations on forage legumes (P < 0.01). The two deer species had similar grazing observations on grass in Expt 1, but sambar had less grazing observations than red deer on grass in Expt 2 (P < 0.05).

#### Stem diameter

Visual observations from Expt 1 indicated a large difference between the two deer species in selecting browse. Sambar selected both willow leaves and stems

Table 1. Mean number of observations for sambar and red deer grazing a range of plants in December 1991, February and April 1992 (Expt 1) and in February and April 1993 (Expt 2) in New Zealand

	Sambar deer		Red d		
Plant species	Observation*	Preference ranking	Observation*	Preference ranking	S.E. (23 d.f.)
Expt 1	***				
Willow	44.0 (25.8)	1	7.4 (4.2)	9	5.66
Lupin	17.0 (9.9)	6	20.5 (11.6)	4	5.17
Red clover	20.3 (11.9)	5	49.8 (28.4)	1	6.74
Lotus	20.6 (12.0)	4	26.4 (15.0)	2	4.17
Yorkshire fog	8.5 (5.0)	8	8.0 (4.5)	8	2.70
Prairie grass	5.0 (2.9)	9	9.4 (5.3)	7	2.08
Perennial ryegrass:	` ,		, ,		
Low endophyte	21.3 (12.4)	3	21.5 (12.2)	3	4.59
Medium endophyte	10.5 (6.1)	7	17.5 (9.9)	5	2.59
High endophyte	24.0 (14.0)	2	15.7 (8.9)	6	3.34
S.E. (95 D.F.)	1.92		1.86		
					S.E.
E 2					(15 d.f.)
Expt 2				_	
Willow	65.4 (43.6)	1	4.3 (2.9)	7	11.52
Poplar	22.0 (14.7)	2	0.5 (0.3)	8	2.40
Red clover	17.4 (11.6)	3	57.9 (38.6)	1	9.93
Yorkshire fog	6.6 (4.4)	7	11.6 (7.7)	5	2.04
Prairie grass	5.0 (3.3)	8	8.0 (5.3)	6	2.31
Perennial ryegrass:	0.0 ((.0)	<i>-</i>	24.0 (16.6)	2	3.05
Low endophyte	9.9 (6.6)	5	24.9 (16.6)	3	2.85
Medium endophyte	8.1 (5.4)	6	25.0 (16.7)	2	5.31
High endophyte	15.6 (10.4)	4	17.8 (11.9)	4	4.62
s.e. (63 d.f.)	3.21		2.86		

<sup>\*</sup> Percentage of total observations in parentheses.

104 G. SEMIADI ET AL.

Table 2. Mean number of observations\* for sambar and red deer grazing browse, forage legumes and grasses in December 1991, February and April 1992 (Expt 1) and in February and April 1993 (Expt 2) in New Zealand

S.E. Sambar deer Red deer (23 D.E.) Expt 1 20.2 (13.5) Browse 54.4 (36.3) 7.29 Grass 69.3 (46.2) 72.1 (48.0) 6.57 Legume 26.3 (17.5) 57.8 (38.5) 6.56 4.99 S.E. (35 D.F.) 5.20 S.E. (15 D.F.)Expt 2 Browse 87.4 (58.3) 4.8(3.2)13.47 45.2 (30.1) 87.3 (58.2) Grass 12.78Legume 17.4 (11.6) 57.9 (38.6) 9.93 S.E. (15 D.F.) 9.51 9.29

up to 36 mm diameter from near the tip, whereas red deer mainly chose willow leaves only. With lupin, there was no noticeable difference in stem selection, with sambar selecting stems up to 29 mm diameter, and red deer selecting stems up to 27 mm. However, red deer selected slightly more lupin leaves than sambar deer did.

As the preference ranking for willow and popular by red deer was negligible in Expt 2, no measurements of stem diameter were made. Sambar selected willow stems with a diameter up to 38 mm in February and up to 29 mm in April 1993, and popular stems with a diameter up to 54 mm in February and up to 41 mm in April 1993. Sambar tended to strip bark from willow stems more than from popular stems.

#### Nutritive value

#### Plants on offer

In both experiments, total N and OMD did not differ with month of observation but there were differences between plant species (P < 0.001; Table 3). Legumes were significantly higher in total N and OMD (P < 0.05) than grasses, with browse being intermediate. Condensed tannin concentrations were high in willow, intermediate in lotus and poplar, and present in trace amounts in the grass species and in red clover.

#### Plants selected

Red clover was consistently of higher nutritive value than the grasses (Table 4), being higher in total N and OMD and lower in fibre (NDF). The two browse species (willow and poplar) again tended to be

Table 3. Mean contents of total nitrogen (N) and condensed tannins (% DM) and organic matter digestibility (OMD; % OM) of plants on offer in December 1991, February and April 1992 (Expt 1) and in February and April 1993 (Expt 2) in New Zealand

Plant species	Total N	Total condensed tannins*	OMD
Expt 1			
Browse			
Willow†	2.4	6.84	76.3
Lupin†	2.4	ND	79.6
Legumes			
Red clover	3.6	0.04	82.3
Lotus	2.8	2.06	78.0
Grasses			
Yorkshire fog	2.6	< 0.01	72.7
Prairie grass	2.2	0.05	74.5
Perennial ryegrass:			
Low endophyte	2.2	0.11	75.5
Medium endophyte	2.1	0.12	73.7
High endophyte	2.1	< 0.01	76.7
s.e. (44 d.f.)	0.40	_	2.70
Expt 2			
Browse			
Willow†	2.7	5.65	75.8
Poplar†	3.2	2.38	83.5
Legumes Red clover	3.5	0.41	75.7
	3.3	0.41	13.1
Grasses	2.2	0.46	<i>(</i> 1.0
Yorkshire fog	2.3	0.46	61.9
Prairie grass	2·1	ND	70.1
Perennial ryegrass:	2.1	0.47	(( )
Low endophyte	2·1 2·0	0·47 0·29	66·2 67·3
Medium endophyte	2·0 2·0	0·29 0·21	69·9
High endophyte		0.71	
s.e. (14 d.f.)	0.15		1.82

<sup>\*</sup> In Expt 1 values apply for December 1991 sampling only. Sum of extractable, protein-bound and fibre-bound fractions.

ND = Not determined.

intermediate for total N, OMD and fibre, but had higher contents of lignin and CT than either red clover or the grasses. All grasses and red clover contained trace amounts of CT.

#### Condensed tannin distribution

Averaged over feed on offer and diet selected, extractable, protein-bound and fibre-bound CT represented 68, 27 and 5% of total CT for willow and 37, 59 and 4% of total CT for poplar.

<sup>\*</sup> Percentage of total observations in parentheses.

 $<sup>\</sup>dagger$  Plant parts sampled c. 20 cm from the tips, at a maximum of 1 m above ground level.

Table 4. Nutritive value of components of plant species selected by sambar and red deer in February and April 1993 (Expt 2) in New Zealand

Plant species	Total N (%DM)	NDF (% DM)	Lignin (% DM)	Total condensed tannin (%DM)*	OMD (%)
Willow					
Sambar deer	2.6	27.4	6.6	5.72	76.0
Red deer	2.6	22-9	6.4	5.69	78.8
Poplar					
Sambar deer	2.7	26.8	5.68	2.97	78.9
Red deer†	ND	ND	ND	ND	ND
Red clover					
Sambar deer	4.5	21.4	1.7	0.58	83.1
Red deer	4.5	21.4	1.8	0.65	82.7
Yorkshire fog					
Sambar deer	2.8	49.0	1.6	0.31	64.2
Red deer	3.1	42.2	1.3	0.21	73.2
Prairie grass					
Sambar deer	2.3	48.3	1.8	0.45	68.4
Red deer	3.2	38.4	1.6	0.19	70.1
PRG, LE‡					
Sambar deer	3.3	43.5	1.3	0.39	70.3
Red deer	2.8	48·1	1.6	0.28	64.7
PRG, ME‡					
Sambar	3.3	44.1	1.4	0.28	72.3
Red deer	2.8	45.2	1.9	0.36	71.5
PRG, HE‡					
Sambar	2.5	42.9	1.8	0.32	7 <b>4</b> ·5
Red deer	3.3	41.5	1.5	0.33	74.1

<sup>\*</sup> Sum of extractable, protein-bound and fibre-found fractions.

# DISCUSSION

The results of the selective grazing observation summarized in Table 1 are taken to be indicative of preferential behaviour, because of marked contrasts in the physical structure of individual plant species, the results are not adjusted for variation in the mass of vegetation contributed by each species (Hodgson 1979). The present study indicates that both deer species had a similar preference ranking for grass and that in addition sambar had a high preference for browse and a low preference for forage legumes, whilst red deer had a high preference for red clover and a low preference for browse. Wild sambar in

Florida, USA, selected browse as the first choice in all seasons, followed by forbs and grasses (Shea *et al.* 1990). Forbs and grasses are considered as an important diet for wild sambar, accounting for as much as 33% of their total diet during summer, spring and autumn, and 12% in winter (Shea *et al.* 1990). It is reported from Thailand that wild sambar have 21 preferred species of forest plants and seven preferred species of grassland plants (Ngampongsai 1987). However, the present study conflicts with the findings of Kelton & Skipworth (1987), where wild sambar in NZ selected 79% of their diet as coarse grasses of low nutrient quality. This may have been due to the very limited grass available for selection. In

Table 5. Composition of total diet selected by sambar and red deer in Expt 2 (1993 in New Zealand)

Animal species	Total N (%DM)	NDF (% DM)	Lignin (% DM)	Condensed tannin (% DM)	OMD (%OM)
Sambar deer	2.9	31.8	4.4	3·1	75.6
Red deer	3.6	34.7	1.8	0.6	75.7

<sup>†</sup> Not determined due to negligible selection by red deer.

<sup>‡</sup> PRG = Perennial ryegrass; LE = low endophyte, ME = medium endophyte, HE = high endophyte.

106

NZ, wild sambar populations are concentrated around areas of flax swamp (*Phormium tenax*), but are also found in both poplar (*Populus* sp.) and willow plantation areas (Kelton 1981). Sambar can occupy a range of habitat types and regional differences may therefore account for the differences in their observed feeding habits (Riney 1957; Schaller 1967; Kelton 1981; Dinnerstein 1983; Ngampongsai 1987; Shea *et al.* 1990).

The preference of red deer for red clover supports the findings of Hunt & Hay (1990). Selection of legumes by red deer also supports the findings of Bootsma *et al.* (1991), in which domesticated red deer tended to select more legume (white clover) in the diet than was present in the feed on offer. Clutton-Brock & Albon (1989) also found that wild red deer avoid diets with high fibre, high lignin and low digestibility. This was confirmed in the present study, where domesticated red deer selected plants high in nutrient value, such as legumes (red clover).

An estimate of the concentration of specific chemical components in the total diet selected by each deer species can be made as the summation of the proportion of animal grazing observations on a particular plant, multiplied by the composition of diet selected for that plant, as follows:

# Composition of total diet selected

=  $\Sigma$ [% of total grazing observations on plant X × concentration of nutrient in plant X selected] + [% of total grazing observations on plant Y × concentration of nutrient in plant Y selected] + ... (1)

This has been done for Expt 2 (Table 5) and shows that sambar deer tended to select a total diet lower in total N and higher in lignin and CT than that selected by red deer, with similar values for NDF and OMD. The figures, however, should be taken as a general guide only, as the calculation used (Eqn 1) assumes

intake to be proportional to the time spent feeding on each plant species.

Studies of jaw activity show that sambar ruminate for longer periods than red deer, have more rumination boli/h than red deer and spend more time ruminating per g dry matter eaten than red deer (Semiadi et al. 1994). Tropical forages are known to be higher in lignin and lower in total N than temperate forages (Minson 1981) and the rumination behaviour of sambar may be an evolutionary adaptation to reduce particle size more efficiently and recycle N to the rumen when sambar are consuming high lignin/low N tropical diets.

Differences in dietary preference ranking between the two animal species may also have evolved through the differing ability of the animals to neutralize secondary compounds present in plant species, such as CT. Condensed tannins present in plants are thought to have evolved as a defence against attack by pathogenic bacteria, fungi, insects and grazing herbivores (Barry 1989). An inability to neutralize high intakes of ingested CT would result in depressions in rumen carbohydrate digestion and in volatile fatty acids (VFI) (Barry & Duncan 1984; Barry et al. 1986). Recent studies have shown that herbivores adapted to consume tanniferous forage may cope with the presence of such secondary compounds by producing salivary proteins that bind tannins in a highly specific manner (Robbins et al. 1987). The presence of such proteins has been confirmed in the saliva of several deer species (browsers), but is absent in cattle and sheep (grazers) (Austin et al. 1989). Indeed, a recent study indicated that the ability of browsers to counteract tannins is correlated with their feeding habit, with salivary tannin-binding proteins being produced to bind the specific types of tannin that are consumed in the preferred diet (Hagermann & Robbins 1993). Initial studies showed the presence of CT-binding proteins in the saliva of both sambar and red deer used in the present studies, but the CTbinding capacity was very much greater in saliva from sambar than from red deer (A. E. Hagermann, personal communication). These results help to explain the greater dietary preference of sambar for browse species.

From the present study, it seems that both sambar and red deer can be classified as intermediate feeders, selecting a mixture of grasses, forage legumes and browse. Whilst both deer species showed a similar preference ranking for grasses, red deer showed a strong preference for selecting legumes of high nutritive value, whilst sambar showed a strong preference for browse species. Sambar may have evolved rumination and salivary protein strategies to efficiently counteract the anti-nutritional secondary compounds present in browse, such as lignin and CT.

L. and P. Rowe are thanked for providing sambar deer for research. We thank AgResearch (formerly MAF Tech) and the New Zealand Society of Animal Production for the provision of financial assistance. L. Gosling, W. Steifel and E. Sorensen are thanked for assistance with forage establishment and management. G. Semiadi received scholarship support from the Government of Indonesia and from the New Zealand Ministry of Foreign Affairs and Trade.

#### REFERENCES

- AUSTIN, P. J., SUCHAR, L. A., ROBBINS, C. T. & HAGERMAN, A. E. (1989). Tannin-binding proteins in saliva of deer and their absence in saliva of sheep and cattle. *Journal of Chemical Ecology* 15, 1335–1347.
- BARRY, T. N. (1989). Condensed tannins: their role in ruminant protein and carbohydrate digestion and possible effects upon the rumen ecosystem. In *The Roles of Protozoa and Fungi in Ruminant Digestion* (Eds J. V. Nolan, R. A. Leng & D. I. Demeyer), pp. 153–169. Armidale, Australia: Penambul Books.
- Barry, T. N. & Duncan, S. J. (1984). The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 1. Voluntary intake. *British Journal of Nutrition* 51, 485–491.
- Barry, T. N., Manley, T. R. & Duncan, S. J. (1986). The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 4. Sites of carbohydrate and protein digestion as influenced by dietary reactive tannin concentration. *British Journal of Nutrition* 55, 123–137.
- BOOTSMA, A., ATAJA, A. M. & HODGSON, J. (1991). Diet selection by young deer grazing mixed ryegrass/white clover pasture. *Proceedings of the New Zealand Grassland Association* 51, 187-190.
- BURKE, P. (1982). Food plants utilized by sambar. *Australian Deer* 17, 7-12.
- CLUTTON-BROCK, T. H. & ALBON, S. D. (1989). Red Deer in the Highlands. Melbourne: BSP Professional Books.
- DINNERSTEIN, E. (1987). Deer, plant phenology and succession in the lowland forests of Nepal. In *Biology and Management of the Cervidae* (Ed. C. M. Wemmer). Washington DC: Smithsonian Institute Press.
- GOERING, H. K. & VAN SOEST, P. J. (1970). Forage Fiber Analysis. USDA Agriculture Research Service No. 379.
- HAGERMAN, A. E. & ROBBINS, C. T. (1993). Specificity of tannin-binding salivary proteins relative to diet selection by mammals. *Canadian Journal of Zoology* 71, 628–633.
- Hodgson, J. (1979). Nomenclature and definitions in grazing studies. *Grass and Forage Science* **34**, 11–18.
- HOFFMAN, R. R. (1985). Digestive physiology of the deer—their morphophysiological specialisation and adaptation.
  In *Biology of Deer Production* (Eds P. F. Fennessy & K. R. Drew), pp. 393–407. The Royal Society of New Zealand Bulletin 22.
- HUNT, W. F. & HAY, R. J. M. (1990). A photographic technique for assessing the pasture species performance of grazing animals. *Proceedings of the New Zealand Grassland Association* 51, 191-196.
- KAY, R. N. B. & STAINES, B. W. (1981). The nutrition of the red deer (*Cervus elaphus*). Nutrition Abstracts and Reviews, Series B 51, 601–622.
- KAY, R. N. B., ENGELHARDT, W. V. & WHITE, R. G. (1980). The digestive physiology of wild ruminants. In *Digestive Physiology and Metabolism in Ruminants* (Eds. Y. Ruckebusch & P. Thivend), pp. 743–761. Lancaster: MTP Press.

- KELTON, S. D. (1981). Biology of sambar deer (Cervus unicolor Kerr. 1792) in New Zealand with particular preference to diet in a Manawatu flax swamp. MSc thesis, Massey University, New Zealand.
- Kelton, S. D. & Skipworth, J. P. (1987). Food of sambar deer (*Cervus unicolor*) in a Manawatu (New Zealand) flax swamp. *New Zealand Journal of Ecology* 10, 149–152.
- Minson, D. J. (1981). Nutritional differences between tropical and temperate pastures. In *World Animal Science* (Ed. F. H. W. Morley), pp. 143–157. Netherlands: Elsevier.
- NAIR, P. V. & JAYSON, J. A. (1988). Habitat utilization by large mammals in teak plantations and natural forests. Kerala Forest Research Institute. Research Report No. 56. Kerala, India.
- NGAMPONGSAI, C. (1987). Habitat use by the sambar (*Cervus unicolor*) in Thailand: a case study for Khao-Tai National Park. In *Biology and Management of the Cervidae* (Ed. C. M. Wemmer). Washington DC: Smithsonian Institute Press.
- RINEY, T. (1957). Sambar (*Cervus unicolor*) in sand hill country. *Proceedings of the New Zealand Ecology Society* 5, 26–27.
- ROBBINS, C. T., Mole, S., Hagerman, A. E. & Hanley, T. A. (1987). Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology* **68**, 1606–1615.
- ROUGHAN, P. G. & HOLLAND, R. (1977). Predicting in-vivo digestibilities of herbages by exhaustive enzymic hydrolysis of cell walls. *Journal of the Science of Food and Agriculture* **28**, 1057–1064.
- Schaller, G. B. (1967). The Deer and the Tiger. Chicago: The University of Chicago Press.
- Semiadi, G., Barry, T. N., Stafford, K. J., Muir, P. D. & Reid, C. S. W. (1994). Comparison of digestive and chewing efficiency and time spent eating and ruminating in sambar deer (*Cervus unicolor*) and red deer (*Cervus elaphus*). Journal of Agricultural Science, Cambridge 123, 89–97.
- SHEA, S. M., FLYNN, L. B., MARCHINTON, R. L. & LEWIS, J. E. (1990). Part II. Social behaviour, movement ecology and food habits. In *Ecology of Sambar Deer on St Vincent National Wildlife Refuge, Florida, Bulletin No. 25*, pp. 13–62. Tallahassee, Florida: Tall Timbers Research Station.
- STATISTICAL ANALYSIS SYSTEM (1987). SAS/STAT Guide for Personal Computers. Version 6. Cary, NC: SAS Institute.
- TERRILL, T. H., ROWAN, A. M., DOUGLAS, G. B. & BARRY, T. N. (1992). Determination of extractable and bound condensed tannin concentrations in forage plants, protein concentrate meals and cereal grains. *Journal of the Science of Food and Agriculture* 58, 321–329.
- TERRILL. T. H., WAGHORN, G. C., WOOLLEY, D. J., MCNABB, W. C. & BARRY, T. N. (1994). Assay and digestion of <sup>14</sup>C-labelled condensed tannins in the gastrointestinal tract of sheep. *British Journal of Nutrition* **72**, 467–477.