New Zealand Journal of Zoology, 2005, Vol. 32: 117–126
0301–4223/05/3202–0117

The diets of introduced rusa deer (*Cervus timorensis russa*) in a native sclerophyll forest and a native rainforest of New Caledonia

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Abstract New Caledonia has an exceptionally diverse and unique flora, and there is growing concern about the impacts of introduced wild rusa deer on native forests. The diets of free-ranging rusa deer from two native forest sites were studied using rumen content analysis. Samples ($n = 61$) from a sclerophyll forest site consisted principally of graminoids ($64.6 \pm 4.4\%$ dry weight), mainly native grass, but the proportion of woody species increased during the dry season. In the rumen samples from the rainforest site ($n = 56$), woody species were the predominant plants ($61.9 \pm 3.7\%$ dry weight), and the composition of the diet was more constant across seasons. Most of the food items found could not be identified to species level, but it is estimated that native plants represent 40–60% of rusa deer diet. Although more work is needed to assess diet preferences and impacts of rusa deer, we suggest that they represent a potentially important threat to some native plant species in New Caledonia.

Keywords biodiversity conservation; Cervidae; *Cervus timorensis russa*; diet; herbivore impacts; introduced ungulates; native plants

Z04027; Online publication date 13 May 2005
Received 23 July 2004; accepted 19 January 2005

INTRODUCTION

Ungulates have major impacts on the species composition of plant communities (e.g., Augustine & McNaughton 1998), especially on insular endemic plants that evolved in the absence of large mammalian herbivores (Wardle et al. 2001). There is a widespread perception that insular endemic floras are especially vulnerable to ungulates because they lack effective defences against herbivores (Marquis 1991; Paulay 1994). This paradigm has been questioned by Forsyth et al. (2002), who argued that plants do not need to evolve in the presence of herbivores to have properties that confer resistance to herbivory, and listed many native plants of New Zealand avoided by introduced ungulates. Nevertheless, several studies have demonstrated that introduced wild and domestic ungulates can have strong impacts on insular plant species composition, including New Zealand (Allen et al. 1984; Nugent et al. 2001b), Hawaii (Snowcroft & Giffin 1983; Cabin et al. 2000), and the Micronesian Islands (Wiles et al. 1999). It has been suggested that plant consumption and trampling by introduced ungulates represent a major threat to sclerophyll forests of New Caledonia (Bouchet et al. 1995). This archipelago is considered one of the world's hotspots for biodiversity conservation (Mittermeier et al. 1998; Myers et al. 2000), because its unique flora and fauna with high endemic ratios are threatened by human activities and invasive introduced species (Mittermeier et al. 1996).

New Caledonia is of particular interest for research on plant-herbivore interactions. The native flora is very diverse and unique, with more than 3250 species of vascular plants described, of which more than 75% are endemic (Jaffré et al. 2001). Rainforest habitats have the most diverse flora (2011 vascular species, 82% endemic) and cover approximately 400 000 ha (Jaffré et al. 1998), i.e., 24% of the total surface of the main island of "Grande Terre". The sclerophyll forest has a total of 409 native phanerogams species, of which 233 are endemic and 53 are restricted to this vegetation type (Jaffré et al. 1994). The coverage of this habitat has been greatly reduced by land clearance, fire, and the action of introduced ungulates, and now probably occupies less than 100 km^2, about 2% of its probable original extension (Bouchet et al. 1995). Most remnants of sclerophyll forests are adjacent to grazed savannas or grasslands, which have a low plant diversity (129 species) and very few endemic species (Jaffré et al. 1994). Approximately 1600 plant species have been introduced in New Caledonia (MacKee 1994). Several species, intentionally introduced to improve cattle pastures, are now widespread and dominant in savannas, secondary shrubland and ruderal habitats.

Until the arrival of humans, about 3500 years ago, New Caledonia's largest herbivores and frugivores were birds and bats, respectively. It was only in the late 18th and 19th centuries that the first large herbivores, including wild pigs *Sus scrofa*, goats *Capra hircus*, cattle *Bos Taurus*, and rusa deer *Cervus timorensis russa*, were introduced to the island. The deer were imported from Java during the 1870s, and the population reached an estimated 220 000 animals before the Second World War, and is currently thought to number about 110 000 (Chardonnet 1988). Today, rusa deer are widespread in the "Grande Terre" of New Caledonia, where they represent an important food resource for both Melanesian and European people, but also a potential threat for the conservation of its biodiversity. There are very few published papers on the diet of rusa deer (Fraser-Stewart 1981; Nugent 1993; de Garine-Wichatitsky et al. 2003). Rusa deer are thought to have a negative effect on the abundance of endemic plants in New Caledonian sclerophyll forests (Bouchet et al. 1995) and rainforests (Le Bel et al. 2001). However, this impact has not been documented in detail and there is no published information on the diet of wild rusa deer, even though this information is crucial for effective management of their impact (Forsyth et al. 2002). This paper presents the results of a study on the diets of free-ranging wild rusa deer in a sclerophyll forest and a rainforest in New Caledonia using rumen-contents analysis.

MATERIAL AND METHODS

Study sites

This work was conducted in New Caledonia (South Pacific), where three major seasons prevail (ORSTOM 1981): hot wet season (mid November–mid May; mid April–mid May is a transition period); cool dry season (mid May–mid September); and hot dry season (mid September–mid November).

Two study sites (Fig. 1) with contrasting vegetation were selected, approximately 20 km apart, both with large deer populations. The first site ("Mépouiri", Poya district) is a privately owned ranch, located on the western coast of "Grande Terre" (altitude 0–100 m), where Limousin cattle (*Bos taurus*) are farmed extensively, and deer are farmed inside an enclosure. The total area of the ranch is 3700 ha, and density estimates for free-ranging rusa deer (using nocturnal line-transect sight counts) ranged between 0.75 and 1.60 deer/ha according to the site and season in 1998 (Le Bel, Brescia & Barré unpubl. manuscript). The vegetation consists of savanna, dominated by *Acacia farnesiana*, *Bothriochloa pertusa*, and *Heteropogon contortus*, and remnants of native sclerophyll forest (Chalaye unpubl. manuscript; Jaffré, Rigault & Dagostini unpubl. manuscript). The second site ("Forêt Plate", Pouembout district) was located in the central chain of mountains (altitude between 300 and 700 m), and comprised approximately 3000 ha. The vegetation was a mosaic of rainforest and tree savannas dominated by *Melaleuca quinquenervia*.

The estimated current coverage of sclerophyll forests and rainforests on Grande Terre is illustrated in Fig. 1. The map is based on data from aerial photographs and ground truthing for sclerophyll forests (Boyeau 2004), and has been redrawn with permission from Jaffré et al. (1998) for rainforests.

Sample collection

Hunters provided a total of 117 samples of rumen contents from rusa deer (64 males and 53 females) shot on the study sites. Samples from Forêt Plate (n = 56) were collected during the cool dry season (July–August 2001; n = 26) and during the hot wet season (March–April 2002; n = 30). Samples from Mépouiri (n = 61) were collected on a monthly basis

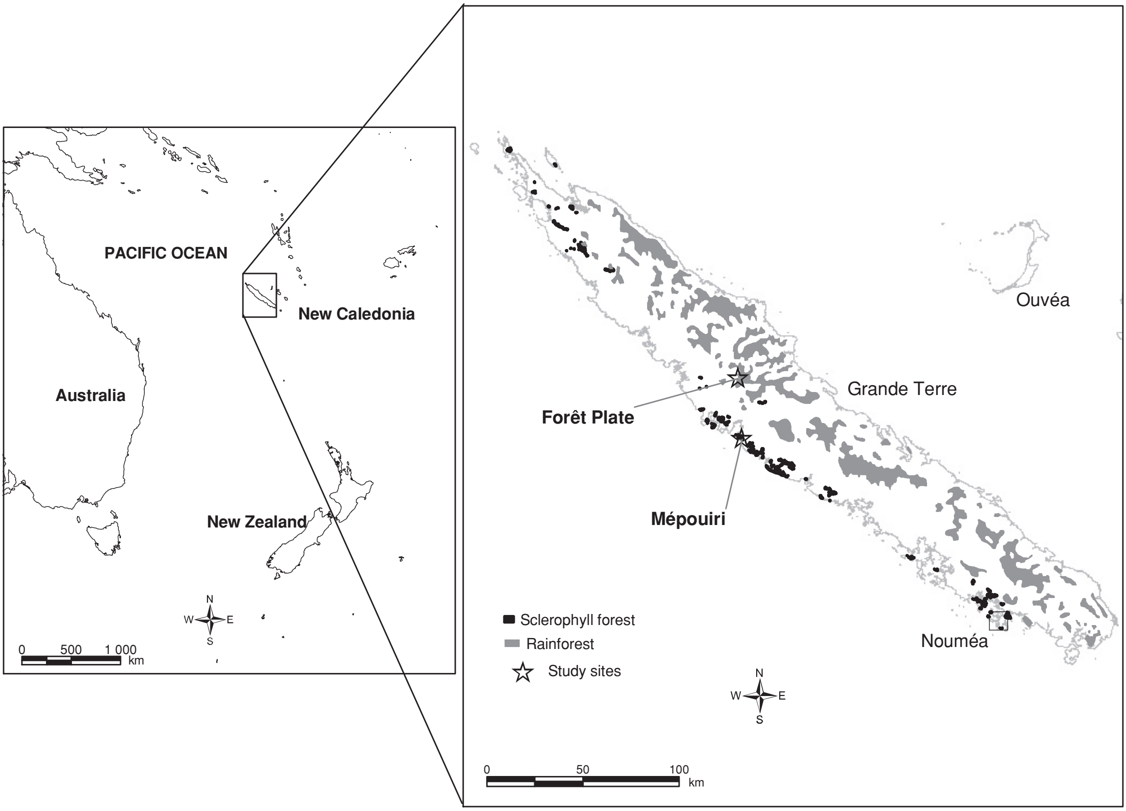

Fig. 1 Location of New Caledonia, study sites (Mépouiri, Forêt Plate), and present surface areas of sclerophyll forests on "Grande Terre" (after Boyeau 2004) and rainforests (redrawn with kind permission of Springer Science and Business Media, from Jaffré et al. 1998, fig. 1).

from May to November 1998 (except in September 1998), and also in March–May 2002 (hot wet season). All rumen samples were collected within 1 h of the deer being shot, and the rumen contents were thoroughly mixed before a sample was taken (minimum of 100 g). Samples were stored frozen until analysed at the laboratory of the Institut Agronomique néo-Calédonien (Païta, New Caledonia).

Rumen content analysis

We followed the procedure of Chamrad & Box (1964). Rumen samples were thawed and washed over a 5.0 mm sieve positioned on top of another 2.0 mm sieve. The retained material on each sieve was sorted macroscopically, and each food item was assigned to one of five categories: graminoids (Gramineae and Cyperaceae), herbs (dicotyledonous herbaceous), ferns (ferns and tree ferns), woody species, and miscellaneous (unidentified fibres or other items). Items were identified to genus or species macroscopically or microscopically by comparison with a reference collection of epidermis of plants consumed by ungulates on the study sites (based on the results of browse-surveys made at both sites; de Garine-Wichatitsky unpubl. data). Plant names and status (native/introduced) follow Jaffré et al. (2001) for indigenous species and MacKee (1994) for introduced species. Plant parts (stem, leaf, flower, pod, fruit, and seed) were differentiated. The sorted materials were oven-dried and weighed (60°C until constant weight of samples). The results were pooled for 2.0 and 5.0 mm sieves to calculate the percentage of total food items identified and the percentage of total dry matter (% DM) represented by each plant type in each rumen content. After checking the normality (Kolmogorov-Smirnof test) and the homogeneity of variances (Levene test), the numbers of food items in the rumen samples were compared between sites using student's *t*-test, and between seasons using an ANOVA (Sokal & Rohlf 1998) followed by pair-wise comparisons using the Scheffé test (Day & Quinn 1989).

RESULTS

Between-sites variations

The percentage of food items found in each plant category differed markedly between the two study sites for both the frequency of occurrence (% of samples) and the contribution to the dry weight (%DM) of rumen contents (Tables 1 and 2). Graminoids had the highest frequency of occurrence, and were found in almost all rumen samples from both sites (100% for Mépouiri and 93% for Forêt Plate). However, while graminoids represented 64.6% DM (±4.4) of the Mépouiri samples, their contribution to the Forêt Plate samples was only 28.4% DM (±3.3). Woody species were also frequently observed in both Mépouiri (70%) and Forêt Plate (100%), but their contribution to the dry weight of rumen contents in Forêt Plate (61.9 ± 3.7% DM) was much higher than those from Mépouiri (19.2 ± 3.5% DM). Ferns were frequently found in the rumen samples from Forêt Plate (73%), although they only accounted for a minor proportion of the total dry matter (4.7 ± 1.1% DM), but they were never encountered in the rumen samples from Mépouiri. Herbs were frequently observed in the rumen samples from Mépouiri (74%), and to a lesser extent in the rumen samples from Forêt Plate (55%), but their contribution to the dry weight of rumen contents was limited (16.2 ± 3.9% DM for Mépouiri and 4.6 ± 1.5% DM for Forêt Plate).

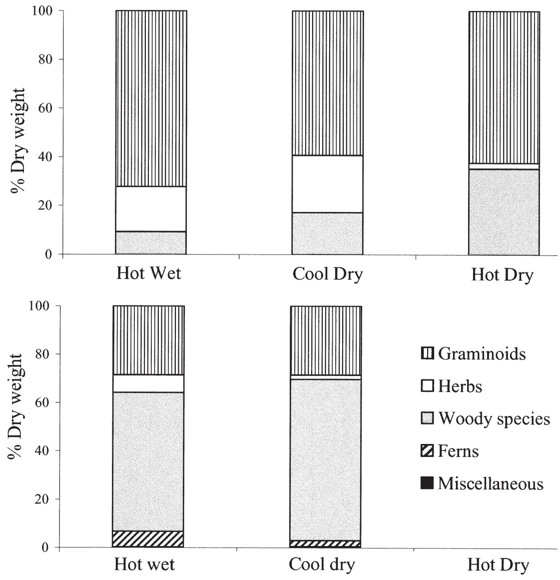

Fig. 2 Seasonal variations in the proportions of plant types in the rumen (% dry weight) of rusa deer from Mépouiri (hot wet season: Mar–May 2001 and May 2002, *n* = 21; cool dry season: Jun–Aug 1998, *n* = 24; hot dry season: Oct–Nov 1998, *n* = 16), and from Forêt Plate (hot wet season: Mar–Apr 2002, *n* = 30; cool dry season: Jul–Aug 2001, *n* = 26; no data for hot dry season).

Seasonal variations

The influence of season on the contribution of each plant category in the rumen samples (%DM) was also very different in Forêt Plate compared with Mépouiri (Fig. 2). At Mépouiri, there was a marked increase of the proportions of woody species between the hot wet and the dry seasons (maximum of 35.1% DM during the hot dry season), whereas the proportion of graminoids decreased during the same period (maximum of 72.2% DM during the hot wet season), and herbs were encountered only during the hot wet season and the cool dry season (18.5% DM and 23.5% DM, respectively). At Forêt Plate, there was little variation in the proportion of each plant category (%DM) between the hot wet season and the cool dry season (no data were collected in the hot dry season). A slight increase of proportion of woody species (maximum 68.0% DM during the cool dry season), corresponded to a slight decrease in both ferns and herbs, whereas the proportion of graminoids remained constant between seasons (27.6% DM and 29.3% DM, respectively, for the hot wet and the cool dry seasons).

The average number of food items found in the rumen samples from Forêt Plate was significantly higher (*t*-test; $t = 2.043$, 115 d.f., $P < 0.05$) than in those from Mépouiri (Table 3). There was no significant difference in the number of food items found in rumen samples from Forêt Plate between the hot wet season and the cool dry season (*t*-test; $t = -0.756$, 54 d.f., $P > 0.05$). However, season had a significant effect (ANOVA; $F = 15.906$, 2 d.f., $P < 0.001$) on the number of food items found in the rumen samples from Mépouiri (Table 3), which increased significantly from an average 6.95 (±0.44) during the hot wet season to 8.92 (±0.43) during the cool dry season (Scheffé test; mean difference = –1.7708, $P < 0.01$), and from 8.92 (±0.43) during the cool dry season to a maximum of 10.69 (±0.47) during the hot dry season (Scheffé test; mean difference = –1.964, $P < 0.05$).

Table 1 Food items found in rumen samples from rusa deer (n = 61) from Mépouiri (sclerophyll forest/savanna vegetation). Status (MacKee 1994; Jaffré et al. 2001): N = native species; I = introduced naturalised species; – = status unknown.

Plant species	Status	Samples (%)	Total dry weight (%)
Graminoids		**100**	**64.6**
Unidentified Gramineae*	–	100	36.7
*Heteropogon contortus**	N	46	11.7
*Stenotaphrum dimidiatum**	I	30	4.5
*Bothriochloa pertusa**	I	34	3.3
Brachiaria spp.*	N	52	2.3
*Chrysopogon aciculatus**	N	39	2.1
*Dichantium aristatum**	I	62	1.3
*Dactyloctenium aegyptium**	I	20	1.0
*Paspalum orbiculare**	N	7	0.7
Axonopus compressus	I	8	0.3
Cynodon dactylon	N	8	0.3
Unidentified Cyperaceae*	–	7	0.3
Axonopus affinis	I	5	0.2
Chloris divaricata	N	1	<0.1
Eragrostis tenella	N	2	<0.1
Herbs		**74**	**16.2**
*Stachytarpheta urticaefolia**	I	16	7.7
*Mimosa pudica**	I	16	5.8
*Desmodium triflorum**	I	54	1.4
Unidentified herbs*	–	31	1.2
Achyrantes aspera	N	2	<0.1
Ageratum conyzoides	I	1	<0.1
Crotalaria striata	I	2	<0.1
Desmanthus virgatus	I	1	<0.1
Euphorbia hirta	I	2	<0.1
Spermacoce assurgens	N	3	<0.1
Vernonia cinera	N	1	<0.1
Woody species		**70**	**19.2**
Unidentified woody stems and leaves*	–	51	8.9
*Acacia farnesiana**	I	34	3.8
*Sida retusa**	I	5	1.8
Sida spp.*	I	11	1.6
*Casuarina collina**	N	11	1.1
*Psidium guajava**	I	3	1.1
Carissa ovata	N	8	0.4
Jasminum dydinum	N	3	0.3
Croton insularis	N	2	<0.1
Malvastrum spp.	I	1	<0.1
Vitex trifolia	I	2	<0.1
Unidentified fruit and seeds	–	2	<0.1

*Comprised >10% of total dry weight in at least one rumen-content sample.

Table 2 Food items found in rumen material from rusa deer (n = 56) from Forêt Plate (rainforest/savanna vegetation). Status (MacKee 1994; Jaffré et al. 2001): N = native species; I = introduced naturalised species; – = status unknown.

	Status	Samples (%)	Total dry weight (%)
Graminoids		**93**	**28.4**
Unidentified Gramineae*	–	93	16.5
*Axonopus affinis**	I	29	3.6
Imperata spp.*	N	21	2.2
Carex spp.*	N	23	1.2
Paspalum spp.*	I	9	1.2
Costularia spp.*	N	4	1.1
Unidentified Cyperaceae*	–	30	1.0
*Themeda quadrivalis**	I	9	0.8
Killinga spp.*	N	16	0.5
Oplismenus spp.	N	14	0.2
Sacciolepis indica	N	2	0.1
Cyperus spp.	–	5	<0.1
Cyrtococcum oxyphyllum	N	4	<0.1
Herbs		**55**	**4.6**
*Stachytarpheta urticaefolia**	I	16	2.3
Unidentified herbs*	–	39	1.0
*Mimosa pudica**	I	5	0.8
Desmodium triflorum	I	25	0.4
Ageratum conyzoides	I	4	0.2
Euphorbia hirta	I	2	0.1
Ferns and tree ferns		**73**	**4.7**
*Lygodium reticulatum**	N	21	2.1
Unidentified ferns*	–	48	1.3
*Orthiopteris firma**	N	13	0.6
Blechnum spp. *	N	7	0.3
Adiantum spp.	N	5	0.1
Davallia spp.	N	4	0.1
Pellea spp.	N	2	0.1
Lycopodium spp.	N	4	<0.1
Woody species		**100**	**61.9**
Unidentified woody stems and leaves*	–	95	50.2
Unidentified fruit and seeds*	–	30	5.7
Schefflera spp.*	N	32	3.4
*Lantana camara**	I	16	1.5
Indigofera spp.*	I	4	0.5
Cassia spp.*	I	7	0.4
Smilax spp.	N	5	0.2
Casuarina collina	N	2	<0.1
Sida spp.	I	2	<0.1
Miscellaneous		**9**	**0.4**
Unidentified fibre	–	7	0.4
Unidentified type	–	2	<0.1

*Comprised >10% of total dry weight in at least one rumen-content sample.

Status of food items

A total of 57 plants were identified to genus or species. Only seven species were found in the rumen samples from both sites, and these were all introduced (*Ageratum conyzoides*, *Axonopus affinis*, *Desmodium triflorum*, *Euphorbia hirta*, *Mimosa pudica*, *Stachytarpheta urticaefolia*) except for the widespread endemic species *Casuarina collina*.

A total of 33 species/taxa were identified in the rumen samples from Mépouiri (13 graminoids, 10 herbs, and 10 woody species), of which 19 were introduced species and 14 native species (Table 1). The most frequently observed plant types (>30% samples) were introduced grass (*Bothriochloa pertusa*, *Dichantium aristatum*, *Stenotaphrum dimidiatum*), native grass (*Brachiaria* spp., *Chrysopogon aciculatus*, *Heteropogon contortus*), one introduced herb (*Desmodium triflorum*), and one introduced shrub (*Acacia farnesiana*). The contribution of native species to the total dry weight of rumen contents from Mépouiri was low (19.0% DM), with *Heteropogon contortus* being the only native species with a significant contribution (11.7% DM), whereas several introduced species (*Acacia farnesiana*, *Bothriochloa pertusa*, *Mimosa pudica*, *Stachytarpheta urticaefolia*, *Stenotaphrum dimidiatum*) had a contribution of >3% DM. Overall, introduced species comprised 33.9% of the total dry weight (Fig. 3). Nearly half (47.1%) of the total dry weight was made of food items that could not be identified to species level, and thus their status (introduced or native) could not be determined. Unidentified items were mainly graminoids (37.0% DM), with few woody stems and leaves (8.9% DM), and herbs (1.2% DM).

A total of 30 species/taxa were identified in the rumen samples of Forêt Plate (11 graminoids, 5 herbs, 7 ferns, and 7 woody species), of which 12 were introduced species and 17 native species (Table 2; the status of one graminoid species was unknown). The most frequently observed plant types (>20% of samples) were the fruits of a native tree (*Schefflera* sp.), two native graminoids (*Carex* spp. and *Imperata* spp.), one native fern (*Lygodium reticulatum*), one introduced grass (*Axonopus affinis*), and one introduced herb (*Desmodium triflorum*). The contribution of native species to the total dry weight of rumen contents from Forêt Plate (12.2%) was similar to the contribution of introduced species (11.8%), but a large proportion of food items (representing 76.1% DM) could not be identified to species level (Fig. 3). The majority of unidentified items were woody species (55.9% DM), with several graminoids (17.5% DM), and few ferns (1.3% DM), and herbs (1.0% DM).

Site	Unidentified	Introduced	Native
Mépouiri	47.11	33.86	18.96
Forêt Plate	76.12	11.81	12.23

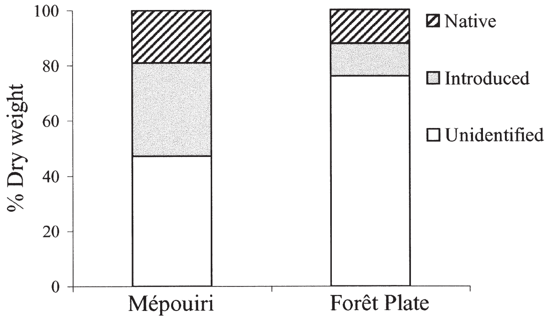

Fig. 3 Proportions (% dry weight) of introduced, native, and unidentified plants in the rumen contents of rusa deer samples from Mépouiri (n = 61) and from Forêt Plate (n = 56).

Table 3 Number of food items found in rumen samples (mean ± SE) from rusa deer from Mépouiri and Forêt Plate, New Caledonia (n is the number of rumens sampled).

Site	Season	n	No. of food items
Mépouiri	All seasons	61	8.70 ± 0.31
	Hot wet	21	6.95 ± 0.44
	Cool dry	24	8.92 ± 0.43
	Hot dry	16	10.69 ± 0.47
Forêt Plate	All seasons	56	9.68 ± 0.36
	Hot wet	30	9.93 ± 0.49
	Cool dry	26	9.38 ± 0.53

DISCUSSION

Between-sites and seasonal variations

The rumen contents analysed in this study, collected from two sites with contrasting native vegetation (sclerophyll forest and rainforest) and adjacent savanna habitat, show that free-ranging rusa deer have variable diets in New Caledonia. They are mixed-feeders, and the proportion of graze/browse in their diets is highly variable between sites and seasons. The diet of deer from the sclerophyll forest/savanna habitat (Mépouiri) consisted principally of grass (including native and introduced pasture species), but the proportion of woody species in the diet increased from the hot wet season to the cool dry season, and reached a maximum during the hot dry season. This seasonal increase of the woody components corresponds to a decrease in the biomass available and in the nutritional quality (especially nitrogen content) of most pasture grasses in New Caledonia (CIRAD-EMVT/DAF 1994), both of which reach a minimum during the hot dry season. In contrast, woody plants dominated the diet of rusa deer in the rainforest/savanna habitat (61.9% DM), as in similar habitat occupied in New Zealand by rusa deer (Nugent 1993). Although no data were available for the hot dry season at the rainforest site, it seems that the proportions of grass/browse are relatively constant across seasons.

Diversity of food items

The diversity of plant types (Gramineae and Cyperaceae, dicotyledonous herbs, ferns and tree ferns, shrubs and trees), plant parts (leaves, stems, twigs, fruits, and seeds) and plant species consumed by rusa deer is large. Rumen contents from both sites had an unusually large number of moderately important foods (<5% DM) compared with other ruminants, as found by Nugent et al. (2001a) for rusa deer in New Zealand. A total of 57 species was identified to genus or species, but only seven species (six of them being introduced species widespread in savanna and secondary scrublands; MacKee 1994) were recorded in the rumen contents from both sites. The mean number of food items found in rumen contents from our sites (9.17 ± 0.24) was slightly higher than was found by Stafford (1997) during a study carried out on sambar deer in New Zealand with similar methods. However, the number of food items in rumen contents was higher in the samples from the rainforest site, where the vegetation is more diverse and structurally complex, compared with the sclerophyll forest/savanna site, which has been already highly modified by deer and cattle.

Status of food items

Most of the food items in the rumen contents analysed during this study could not be identified to genus or species, and thus their status (native/introduced) was unknown. This problem was more acute for the samples from the rainforest site, presumably because of the diversity and the complexity of the vegetation there. An approximate estimate of the proportions of native species in the diet of rusa deer from each site can be made if it is assumed that all plant parts from introduced species were identified. This assumption is probably realistic because the few introduced woody plants living in this rainforest/savanna habitat (e.g., *Lantana camara*) almost certainly would have been identified, and there are apparently no introduced ferns or tree ferns in Forêt Plate. Unidentified woody plant parts and ferns found in the rumen samples from Forêt Plate are thus probably native plants. The same is probably true for the woody plant parts and some of the graminoids found in the rumen contents from Mépouiri. If these figures were representative, native plants would represent >40% dry weight for the rumen contents from Mépouiri, and >60% of dry weight for the rumen contents from Forêt Plate.

Significance of rusa deer as a threat

Nugent et al. (2001a) concluded that rusa deer are not a significant threat to forest or shrubland ecosystems in New Zealand, because their limited area of distribution corresponds to habitats already highly modified. In contrast, we believe that rusa deer represent a potentially major threat to native habitats in New Caledonia, because they are widespread in all the terrestrial habitats of "Grande Terre", with the exception of most maquis areas. In addition, there is currently no management plan of rusa deer populations at a significant level, besides several marginal local initiatives. The major concern is the conservation of endemic species restricted to sclerophyll forests (Jaffré et al. 1998), because most remnants of this highly fragmented habitat, some of which contain unique populations of rare endemic species (Bouchet et al. 1995; Jaffré et al. 1998), are currently subject to the actions of uncontrolled rusa deer populations. Rainforests cover a much bigger area than sclerophyll forests (Jaffré et al. 1998), but rusa deer populations rarely enter this habitat. Although deer densities are usually lower in rainforest than in sclerophyll forests or savannas, there are several reports by local inhabitants and field technicians concerning recent increases in rusa deer populations in rainforest/savanna areas, with perceived impacts on the composition and the structure of the vegetation.

Because rusa deer are mixed feeders and incorporate many different plant species in their diet, they are likely to consume a large number of native species, and could potentially lead to the local extinction of populations of rare endemic plants. However, this study does not provide information on the diet preferences of rusa deer, which require an estimation of the ratio of the proportion of the species ingested relative to their availability (Manly et al. 2002). More research is needed to determine which species are preferred by rusa deer, in order to improve the management of their impacts (consequences of their feeding and trampling) on the native plant communities of New Caledonia.

ACKNOWLEDGMENTS

We are grateful to Marcel and Claude Metzdorf for permission to carry out this study on their estate, and to the DDEE of Province Nord and the Mairie de Pouembout for the permission to work in Forêt Plate. We also thank the villagers of Ouaté Tribe, P. Bertoni, the hunters of the Association des Chasseurs de Pouembout, and the staff of the DDEE of Province Nord for their field assistance. Fabrice Brescia, Nicolas Barré, Delphine Pouget, and Laurent Chardonnet (IAC) also helped in data collection. Many thanks to Bernard Suprin (DRN Province Sud) and Tanguy Jaffré (IRD Nouméa) for their assistance in the identification of plant reference samples or plant fragments. Fig. 1 was drawn by Sylvain Dauré (IAC), and we thank the Programme de Conservation des Forêts Sèches de Nouvelle-Calédonie and the SMAI (Gouvernement de Nouvelle-Calédonie) for providing data on the estimated coverage of sclerophyll forests, and Tanguy Jaffré and Springer Science and Business Media for permission to reproduce the map of rainforest coverage (adapted from fig. 1, Jaffré et al. 1998). This work was funded by IAC/CIRAD, the French Ministry of Environment (Projet Ecofor no. 2000.08) and the Programme de Conservation des Forêts Sèches de Nouvelle-Calédonie (Volet 1. Action 10).

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