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Comparative diet of the two forest cervids of the genus *Mazama* in French Guiana

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Abstract: The diets of the two Amazonian brocket deer (the red brocket *Mazama americana* and the grey brocket *Mazama gouazoubira*) were studied in French Guiana through the examination of stomach contents. The two species are mainly frugivore–granivores, even during the annual period of fruit scarcity (56% of the annual diet in red brockets and 68% in grey brockets). Both rely heavily on fruits and seeds, but overcome the fall in fruit availability by eating significant quantities of fibres, leaves and flowers, particularly the red brocket. Seasonal variation in quantity consumed was observed only for gravid females, which suggests that reproduction may be dependent on the fruiting season. Both species took a wide variety of plants (respectively a total of 79 and 107 species, and 8.4 and 8.9 species per stomach on average). They can be considered non-selective feeders, choosing fruits above all according to their abundance, their size, and perhaps their softness. Both species are seed eaters, destroying nearly all seeds ingested. The two species are potential competitors, but their diet competition may be reduced by their large difference in body size and somewhat different ecological niches. These deer are among the most generalized frugivores of the Guianan forest, thus reducing their food competition with other frugivores.

Key Words: food competition, frugivory, terrestrial vertebrates, tropical forest

INTRODUCTION

Two deer species occur in mainland forests of French Guiana: the red brocket (*Mazama americana*, Erxleben 1777) and the grey brocket (*M. gouazoubira*, Fischer 1814). They are important species of the large terrestrial guild of vertebrates, which have been studied in some parts of South America (Bodmer 1989, 1990 *a*, *b*, 1991*a*, *b* in Peru; Branan *et al.* 1985 in Suriname; Stallings 1984 in Paraguay), but never in French Guiana. Until now, the diets of these deer have been investigated most often for one species only, without special consideration for the other brocket species or for other terrestrial vertebrates inhabiting the same forest areas.

This paper presents a study of the diet of these two forest species, based on the examination of stomach contents. Its aim is to provide information on the deer's use of each food type, on the way each species adapts its diet to seasonal food availability, and on its role in seed predation and seed dispersal. In particular, this study will investigate how the large difference in body weight between the two species (the red brocket is 2.7 times heavier than the grey brocket) could be the cause of a reduced food competition between them, especially during the season of fruit scarcity. The study will also consider the feeding strategies of these ruminants, compared with those of other sympatric terrestrial frugivores.

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MATERIAL AND METHODS

All samples come from French Guiana (2–6°N, 52–54°W), where the mean air temperature is 26–27 °C, and annual averages of rainfall and relative humidity vary from 2000 to 4000 mm and from 80 to 100% (data Météo France). The year can be divided into three periods: a long and marked dry season from July to November, a short rainy season from December to February, and a longer and more intense rainy season from March to June (Figure 1).

The tropical forest covers more than 90% of French Guiana. From the viewpoint of floristic diversity, it is a primary evergreen forest, with 130–200 tree species (dbh > 10 cm) per ha (Prevost & Sabatier 1996). However, the flora is dominated by a few families: Caesalpiniaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae (Sabatier & Prevost 1990). The very marked variations in fruiting can be divided into three broad periods of similar length, preceding the variations of rainfall (Guillotin *et al.* 1994, Henry 1994, Sabatier 1985): (1) February–May, the

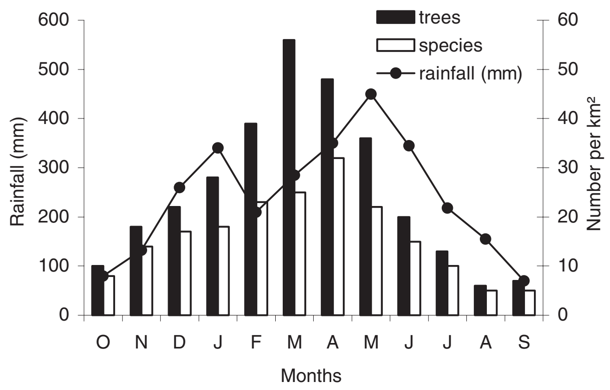

Figure 1. Annual variations of rainfall (data Météo France from 1981 to 1991) and seasons of fruiting (number of fruiting species and of fruiting trees per km^2, from Sabatier 1985 and Henry 1994), in French Guiana.

main fruiting season; (2) June–September, a period of fruit scarcity; (3) October–January, the flowering and early fruiting season (Figure 1). These strong seasonal variations occur every year throughout French Guiana (Barret 2001, Henry 1994, 1999), which leads us to consider it as typical for the whole of French Guiana and to use it in diet comparisons.

The composition of the vertebrate community of French Guiana is typical for the whole Amazonian region. Both studied cervids are wary, secretive and solitary animals. The red brocket is the larger of the two (body weight 40–48 kg vs. 15–18 kg) and is both nocturnal and diurnal, whereas the grey brocket is mostly diurnal. Red brocket deer were observed many times in open forest areas, while grey brockets seem to prefer closed vegetation (Dubost & Henry, unpubl. data; Emmons & Feer 1990). Some large terrestrial species could be competitors of the two ruminants.

Stomachs were collected at monthly intervals from specimens killed by native hunters for their own subsistence over much of the northern half of the forest area. They were fixed in 10% formalin immediately after death and preserved in hermetic tanks. The contents of rumen and reticulum, the two stomach parts storing the food before rumination, were removed, washed and filtered through sieves from 5 mm^2 to 1 mm^2. All the large particles (> 5 mm^2) were separated by major food type under a microscope (fruits-seeds, fibres, leaves, flowers, fungi and animal matter), and then for fruits and seeds by fruit parts (entire fruit, pericarp or seed). The fibres category included all vegetative parts apart from leaves, such as stems, petioles and bark. These ruminants swallow most food items whole or slightly crushed: the resulting large particles represented an average 49–52% of each stomach's contents. This allowed the estimation of the size of most fruits or fruit parts swallowed by measuring their minimum diameter, except for animals whose second molar had not erupted, an indication that they had not finished their main growth and thus were still suckling. Most flower buds were also swallowed whole allowing them to be measured. A significant part of the smaller elements in the stomach (≥ 5–10% of the total weight) was also separated by food type, in order to permit both their botanical identification and the calculation of their proportion of the whole stomach contents. Fruit and seeds were identified at specific level, sometimes under the microscope, by one of the authors (D. Sabatier), using a large fruit reference collection from French Guiana. The different food categories were dried at 80 °C for 72 h, and finally weighed.

The importance of each food type was calculated as its % of dry weight in stomach contents. Its occurrence was the % of samples containing it. An index of usage U_i of each plant species was used, where $U_i = P_{ij} \times P'_{ij}$, P_{ij} is the proportion by weight of the plant species i in all stomach contents of the cervid species j, and P'_{ij} its frequency (Dubost 1984). Changes across the three broad seasons defined above were analysed.

Diet variety was based on the mean number of plant species per stomach, and the number of all identified plant species for a given cervid species. We also studied how the total number of plant species increased according to the number of analysed stomachs, classified randomly.

Overlap indices were calculated by the Levins equation (1968):

$$\alpha_{jk} = \frac{\sum_{i=1}^{n} P_{ij} \times P_{ik}}{\sum_{i=1}^{n} (P_{ij})^2}$$

where α_{jk} gives the overlap of the diet of the deer species k on the deer species j, P_{ij} is the proportion by weight of the food category i in all stomach contents of the cervid j, and P_{ik} the proportion in the cervid species k. This index permits a quantification of the dietary overlap of deer k on j, or conversely of j on k, by using P_{ik} as denominator.

All intra- and interspecific comparisons were carried out with the non-parametric Mann–Whitney U-test, and correlations with the Spearman's rank correlation coefficient r_s. Other tests used contingency tables and χ^2 (Siegel & Castellan 1988). After angular transformation of the data, three-way ANOVA, with species, site and season as factors, was performed to assess differences between the general composition of diets, using Systat 9.0 software. Finally, Covariance Matrix PCA was used for the % of each item in stomach contents, to show the main factors of variation in diet composition, and performed with the ADE-4 program (Thioulouse *et al.* 1997).

Some sources of error exist. First, hard parts of fruits (i.e. integument) remain longer in stomachs than soft parts (pulp). Furthermore, some small items pass directly to the omasum. In addition, some plant species could not be identified; thus, some small portions remained indetermi-

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nable. Because of the small quantities concerned, these items were not considered likely to affect analyses.

RESULTS

General composition of diets

The average weight of stomach contents was 1.5 times higher in gravid females than in other adults and subadults (red brocket: $n_1 = 5$, $n_2 = 17$, $U = 12$, $P < 0.01$; grey brocket: $n_1 = 4$, $n_2 = 23$, $U = 11$, $P < 0.01$). Also, quantities of food ingested by non-gravid females were 1.3 times higher than those ingested by males (red brocket: $n_1 = 8$, $n_2 = 9$, $U = 17$, $P < 0.05$; grey brocket: $n_1 = 9$, $n_2 = 14$, $U = 32$, $P < 0.05$). This was the only significant difference found between males and females within each species.

Fruits, fibres and leaves occurred in all stomachs analysed (Table 1). Red brockets ate mostly fruits and seeds (56% dry weight). Fibres were the next in importance (24%), and leaves counted for 13%. Flowers also represented a significant part of the diet (5%), appearing in 46% of the stomachs. Fungi (0.6%) and animal matter (0.5%) were found respectively at frequencies of 32% and 68%. Grey brockets also ate mostly fruits and seeds (68% dry weight). Leaves represented 14% of the feeding, and fibres 11%. Flowers constituted 5% of the food, occurring in 50% of the stomachs. Fungi and animal matter appeared in minor amounts (less than 1% of the diet), and were respectively found in 30% and 62% of the stomachs.

The composition of the diets of the two brockets was broadly similar, considering the relative importance of each food type ($r_s = 0.98$, $n = 5$, $P < 0.05$). As shown by PCA analysis (Figure 2a), the main overall difference between them occurs in the proportions of some food types: grey brockets eat significantly more fruits–seeds and leaves than red brockets ($n_1 = 29$, $n_2 = 34$, $z = 2.22$, $P < 0.05$; Table 2), which consume more fibres ($n_1 = 29$, $n_2 = 34$, $z = 1.70$, $P < 0.05$). Nevertheless, ANOVA does not reveal any significant difference within either brocket species with respect to site or season.

Seasonal variations

In both species, the relative composition of the diets varied little through the year (correlations between seasons: $r_s \geq 0.98$, $n = 5$, $P < 0.05$). Both cervids appeared

Table 1. Proportion (mean ± SD dry weight) and % occurrence (in italics) of each food category, mean number of distinguished plant species per stomach, and proportion and % occurrence of each fruit part in the fruits–seeds category in the diet of the two ruminants over the whole year and according to the seasons. FM: February–May, main fruiting season; JS: June–September, period of fruit scarcity; OJ: October–January, flowering and early fruiting season. n = number of stomachs. Significance of differences with the following season: +++ = P < 0.001; ++ = P < 0.01; + = P < 0.05; ns = not significant.

	Red brocket							Grey brocket						
Season	Year	FM		JS		OJ		Year	FM		JS		OJ	
n	28	10		6		12		34	13		12		9	
Food category														
Fruits–seeds	56.0	69.3 ± 21.2	+	42.7 ± 30	ns	56.1 ± 21.6	ns	68.3	81.3 ± 8.3	+	66.7 ± 15.7	ns	56.8 ± 23.9	ns
	100	*100*		*100*		*100*		*100*	*100*		*100*		*100*	
Fibres	23.9	24 ± 16.2	ns	26.5 ± 16.4	ns	21.2 ± 20.3	ns	11.0	7.7 ± 6.5	+	14.5 ± 7.1	+	10.8 ± 7.1	ns
	100	*100*		*100*		*100*		*100*	*100*		*100*		*100*	
Leaves	12.6	4.4 ± 7	+	19.4 ± 24.5	ns	14.1 ± 17.4	+++	14.0	8.9 ± 6.9	+	16.6 ± 10.9	ns	16.6 ± 17.1	+++
	100	*100*		*100*		*100*		*100*	*100*		*100*		*100*	
Flowers	4.6	0.1 ± 0.2	+	8.7 ± 18.6	ns	5.1 ± 9	++	5.0	0.3 ± 0.8	ns	1 ± 2.1	+++	14 ± 17	++
	46	*30*		*50*		*58*		*53*	*31*		*50*		*78*	
Fungi	0.6	0.1 ± 0.2	ns	0.6 ± 1.4	ns	1 ± 2.3	ns	0.6	0.1 ± 0.3	ns	0.4 ± 1.3	ns	1.3 ± 3.1	ns
	32	*30*		*33*		*33*		*30*	*15*		*43*		*33*	
Animal matter	0.5	0.4 ± 0.6	ns	0.4 ± 0.5	ns	0.8 ± 1.5	ns	0.3	0.4 ± 0.9	+	0.2 ± 0.2	ns	0.2 ± 0.3	ns
	68	*70*		*67*		*67*		*62*	*46*		*83*		*56*	
Others	1.7	1.7		1.7		1.7		0.9	1.3		0.6		0.8	
Number of distinguished plant species per stomach	8.4	9.7 ± 4.3	ns	7.0 ± 3.3	ns	8.5 ± 3.4	ns	8.9	9.5 ± 3.1	ns	8.6 ± 2.2	ns	8.6 ± 3.9	ns
Fruit part														
Entire fruit	11.3	3.3	ns	16.2	ns	14.4	+	7.6	2.7	+	6.6	ns	13.4	+++
	12.5	*6.5*		*15.6*		*17.6*		*6.1*	*3.9*		*7.5*		*8.1*	
Pericarp	27.0	29.6	ns	18.1	ns	33.3	ns	34.4	33.8	ns	34.5	ns	34.8	ns
	18.8	*20.4*		*20.0*		*16.7*		*20.7*	*18.6*		*18.9*		*27.0*	
Seed	61.7	67.1	ns	65.7	ns	52.3	ns	58.0	63.5	ns	58.9	ns	51.8	ns
	68.7	*73.1*		*64.4*		*65.7*		*73.2*	*77.5*		*73.6*		*64.9*	

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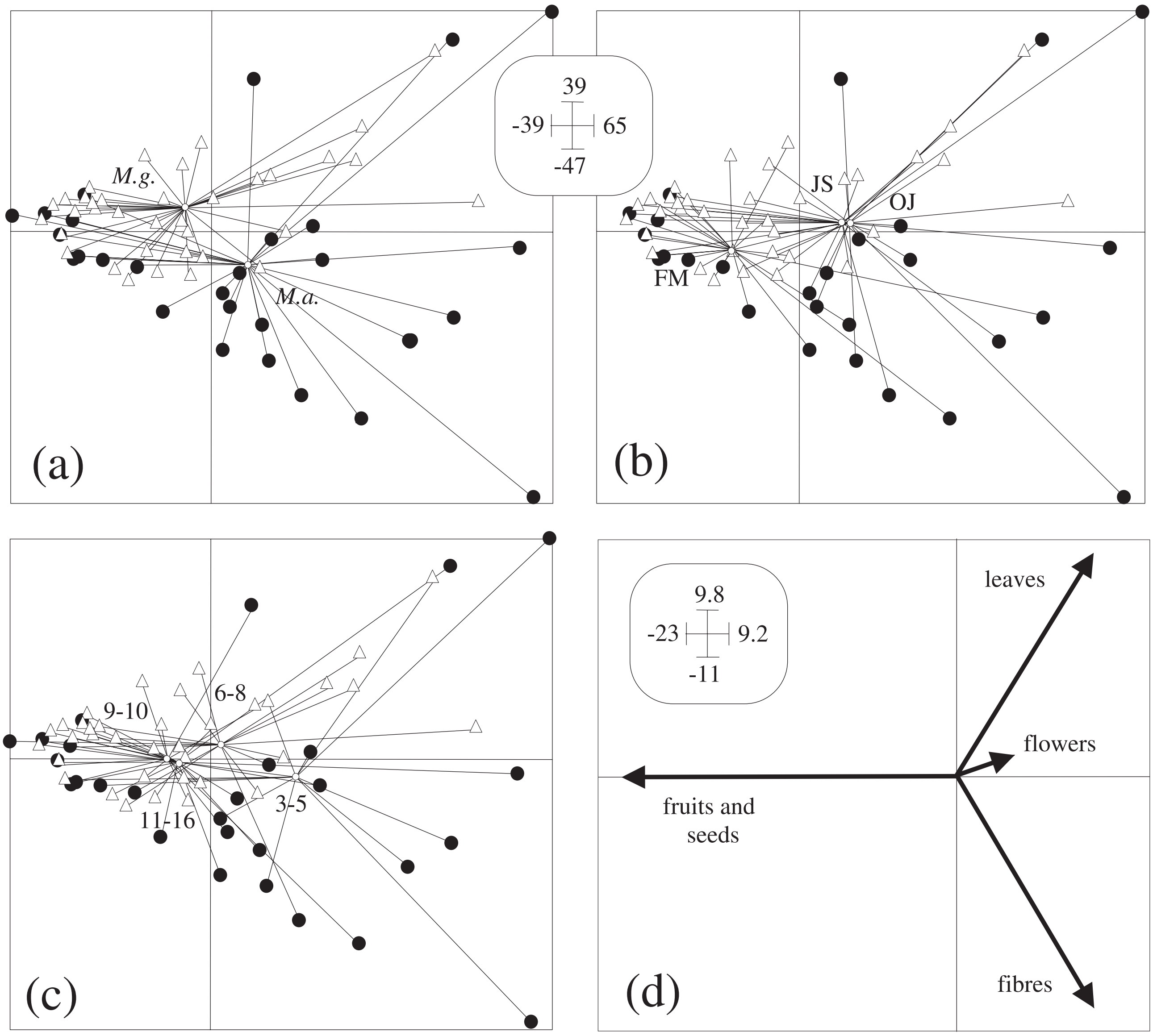

Figure 2. Selected results of the covariance matrix PCA on the percentage of food items consumed: a–c: scatter diagrams of the sampling units on the 1 × 2 components plane; (a): diagram by species (M.g. = *Mazama gouazoubria* (grey brocket), M.a. = *Mazama americana* (red brocket)); (b): by season (FM = February–May, main fruiting season; JS = June–September, period of fruit scarcity; OJ = October–January, flowering and early fruiting season); (c): by mean number of fruit and seed species per stomach. Filled circles: individuals of red brocket; triangles: individuals of grey brocket. (d): projection of main variables (food categories) on the same plane.

to focus heavily on fruits and seeds, and only they turn to fibres and leaves. Mean proportions of fruits and seeds were maximum and individual variation minimum during February–May, the main fruiting season, whereas leaves and fibres were more heavily consumed in June–September, the period of fruit scarcity (Figure 2b). Flowers were mostly eaten, sometimes in huge quantities, in October–January, the flowering and early fruiting season, when they are easiest to find (except the high proportion of flowers recorded in the diet of one red brocket shot during the period of fruit scarcity, a few days before the theoretical flowering season). The quantities of fungi eaten by both species were at a maximum in October–January, the flowering and early fruiting season, which corresponds to the beginning of the rainy season. The variation in animal matter appears very low and no seasonal tendency emerged in either cervid species.

The differences in general diet between the two species were a little more marked in both seasons of main fruiting and fruit scarcity, than during October–January, the flowering and early fruiting season (Table 2). Red brockets ate fewer fruits and seeds than grey brockets in June–September, the period of fruit scarcity. But their fibre consumption was always 2–3 times greater, accord-

Table 2. Differences in intake of main food categories between the two cervids. +++ = $P < 0.001$; + = $P < 0.05$; ns = not significant. Red = red brocket; grey = grey brocket. Other abbreviations as in Table 1.

Food category	Year	FM	JS	OJ
Fruits–seeds	+	ns	+	ns
	red < grey		red < grey	
Fibres	+	+++	+	+
	red > grey	red > grey	red > grey	red > grey
Leaves	+	+	ns	ns
	red < grey	red < grey		
Flowers	ns	ns	ns	ns
Fungi	ns	ns	ns	ns
Animal matter	ns	ns	ns	ns

ing to the season ($n_1 = 29$, $n_2 = 34$, $z = 2.08$, $P \leq 0.05$). Red brockets ate fibres in almost constant amounts during the year, unlike grey brockets which ate fewer fibres in February–May, the main fruiting season and more fibres in June–September, the period of fruit scarcity. With regard to leaves, a significant difference ($n_1 = 29$, $n_2 = 34$, $z = 2.11$, $P < 0.05$) between the two ruminants appeared only in February–May, the main fruiting season. Whether we looked at quantities or frequencies consumed, our results were the same.

Fruit and flower species eaten

The cumulative curve of plant species per stomach (Figure 3) did not level off for either species. This is also true for curves of plant species shared by the two cervids. The curve is steeper for grey brocket than for the other ruminant: we found an average of 2.8 new species per analysed stomach for red brockets vs. 3.2 for grey brockets ($n_1 = 28$, $n_2 = 34$, $z = 1.71$, $P < 0.05$). Furthermore, the average number of species distinguished per stomach was slightly lower for red brockets than for grey brockets (8.4 vs. 8.9; Table 1) and did not vary significantly between seasons or by sex. Despite this small difference, the dietary characteristics of these two ruminants are not fundamentally different (compare Figures 2b and 2c).

Identified plant species in red brockets represent 61% of the total weight of fruits, seeds and flowers, that is 42% of the total diet. A total of 79 plant species belonging to 38 families was identified (Appendix 1). Grey brocket stomachs included 107 plant species belonging to 39 families. These species constituted 38% of the total weight of fruits, seeds and flowers (28% of the total diet). For both cervids, the top identified plant families are those ranking foremost in the French Guianan flora: Sapotaceae, Lecythidaceae, Moraceae, Caesalpiniaceae, Clusiaceae, Annonaceae. However, some families, like Burseraceae and Chrysobalanaceae, are conspicuously under-represented in the diets of the brockets.

The identified species came from every habitat: from lowlands to montane forests. Nevertheless, both cervids ate mainly plants growing at low altitude, i.e. swamps, riparian or lowland forest, including many species of the mainly lowland family Lecythidaceae.

A notable difference between the two ruminants was that plant species of open-forest areas were more often eaten by red brockets than by grey brockets: eight (10% of all species recorded) were identified in red brocket contents vs. three (3%) in grey brocket. While referring to their respective indices of usage, red brockets eat seven times more of this resource than of other plant species. Two pioneer species were often consumed by them: *Cecropia obtusa* and *C. sciadophylla*. The genus *Solanum*, which mostly contains pioneer species, is less utilized, but appeared several times in red brocket stomachs (Appendix 1).

Level of consumption of fruit and flower species

Most plant species were recorded from only one stomach: 65% in the red brocket and 67% in the grey brocket. On the contrary, only a few species (two or four according to ruminant) appeared in more than 25% of the contents. These most frequent plant species were also eaten in the largest quantities. In fact, there was a correlation between the frequency of an eaten plant species and its mean quantity in a stomach. This correlation was more marked in red brockets than in grey brockets ($r_s = 0.55$, $n = 79$, $P < 0.005$ vs. $r_s = 0.22$, $n = 107$, $P < 0.05$).

Moreover, there was an overall correlation between the relative abundance of plant families in the field, according to Sabatier & Prevost (1990) and their consumption level by red brockets ($r_s = 0.54$, $n = 38$, $P < 0.001$) and by grey brockets ($r_s = 0.36$, $n = 39$, $P < 0.05$). In the grey brocket, the eight most utilized plant species (each of them with an index of usage > 2% of the sum of indices) were either very common or common, or belong to very widespread genera.

Five plant species in red brockets (*Bagassa guianensis*, *Carapa* sp., *Eperua falcata*, *Eriotheca* sp. and *Eschweilera* sp.) and four species in grey brockets (*Dicorynia guianensis*, *Eschweilera* sp., *Inga* sp. and *Virola michelii*) appeared to be particularly well used, each of them with an index of usage ≥ 5% of the sum of all indices. Such preferred species were particularly important in their diets, because, although they count together for only 6.3% of all identified species in red brocket and for 3.7% in grey brocket, they represent respectively 49.2 and 55.5% of the sum of all indices.

The index of usage also reveals some differences between the two cervids. The shared species were more heavily utilized by red brockets than exclusive ones ($n_1 = 31$, $n_2 = 48$, $z = 3.23$, $P < 0.01$). This was not true for the smaller cervid. This greater index of usage of shared plant species in red brockets is both the result of higher proportions in weight (the 31 shared species represent 55.0% of

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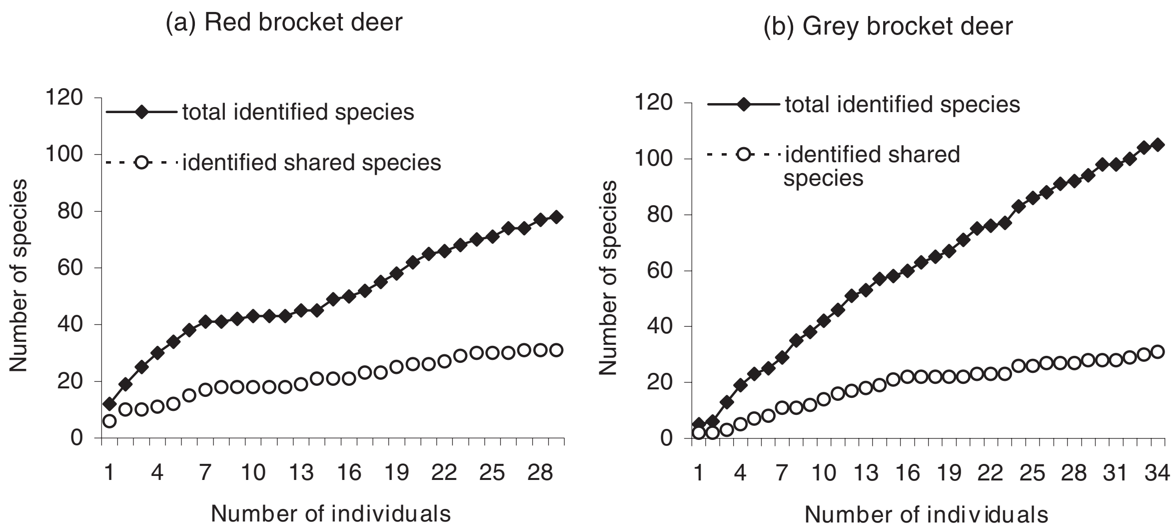

Figure 3. Curves of cumulative plant species as a function of the number of individuals analysed.

the total weight in red brockets vs. 24.2% in grey brockets: $n_1 = n_2 = 31$, $z = 3.26$, $P < 0.01$) and higher relative frequencies (respectively, 9.9% and 6.4%: $n_1 = n_2 = 31$, $z = 2.6$, $P < 0.01$). On the whole, 90% of shared species were common or very common. The plant species which were at the same time abundant and accessible to the two cervids, were shared at high rates.

Concerning the ingested parts, more than 90% of the species were found as seeds in both cervids. However, among the 10% remainder, we noticed that nearly all items of *Eperua falcata* and *Eschweilera* sp. were ingested as flowers by the two cervids. In contrast, *Bagassa guianensis*, a common species in red brocket stomachs, was consumed to 85% as entire fruits.

Fruit parts eaten

Seeds were the most significant part (around 60% of the total weight) of the fruits–seeds category in the two cervids (Table 1). For both species, pericarps constitute approximately a third, and entire fruits around a tenth. Annual differences between proportions of seeds and those of pericarps or entire fruits were significant within each species ($n_1 = n_2 = 29$, $z = 4.69$ and 5.43 respectively, $P < 0.01$ in red brockets; $n_1 = n_2 = 34$, $z = 3.68$ and 4.65 respectively, $P < 0.01$ in grey brockets). In each season, differences between proportions of each category were significant (P varying from < 0.05 to < 0.01 in red brockets, and being always < 0.01 in grey brockets), except between that of entire fruit and pericarp in June–September, the period of fruit scarcity for red brockets, and between that of pericarp and seed in October–January, the flowering and early fruiting season for grey brockets.

Besides, frequencies of various parts corresponded roughly to their respective values in terms of weight. Table 1 shows that these values were nearly constant throughout the year. However, a slight tendency appears: seeds were minimal in October–January, the flowering and early fruiting season (perhaps many immature fruits without developed seeds are eaten), and maximal in February–May, the main fruiting season. Conversely, the consumption of entire fruits was weaker in this last season, and the difference with the preceding one was significant in both species (red brocket: $n_1 = 10$, $n_2 = 12$, $U = 31$, $P < 0.05$; grey brocket: $n_1 = 9$, $n_2 = 13$, $U = 30$, $P < 0.05$). Despite these common points, the two cervids feed differently when fruits are scarce: red brockets eat more entire fruits and half as many pericarps compared with grey brockets (fruits: $n_1 = 6$, $n_2 = 12$, $U = 14$, $P < 0.05$; pericarps: $n_1 = 6$, $n_2 = 12$, $U = 10$, $P < 0.01$).

Physical characteristics of the eaten fruits and flowers

In both species, items of 1–2 cm minimum diameter were more important in terms of ingested dry weight (Figure 4). This was very striking for grey brockets (the total weight of 1–2-cm items represented 65% of the weight of all measured elements, vs. 45% for red brockets). In fact, the range of size is tighter for the smaller cervid: almost no item was bigger than 3 cm, vs. 4 cm for the red brocket. By contrast, this last cervid swallows many items measuring 2–4 cm (33% vs. 23% for the grey brocket), although it also ate almost three times more smaller elements ranging between 0.5 and 1 cm than the grey brocket (21.4% vs. 8.0%). These small elements were often seeds of *Bagassa guianensis*, *Cecropia* sp. or *Ficus* sp. All are eaten in quantity and found intact in stomach contents (e.g. 98% of seeds of *Cecropia* sp. or *Ficus* sp. in four randomly taken stomachs), in contrast to the majority of the bigger seeds which were destroyed.

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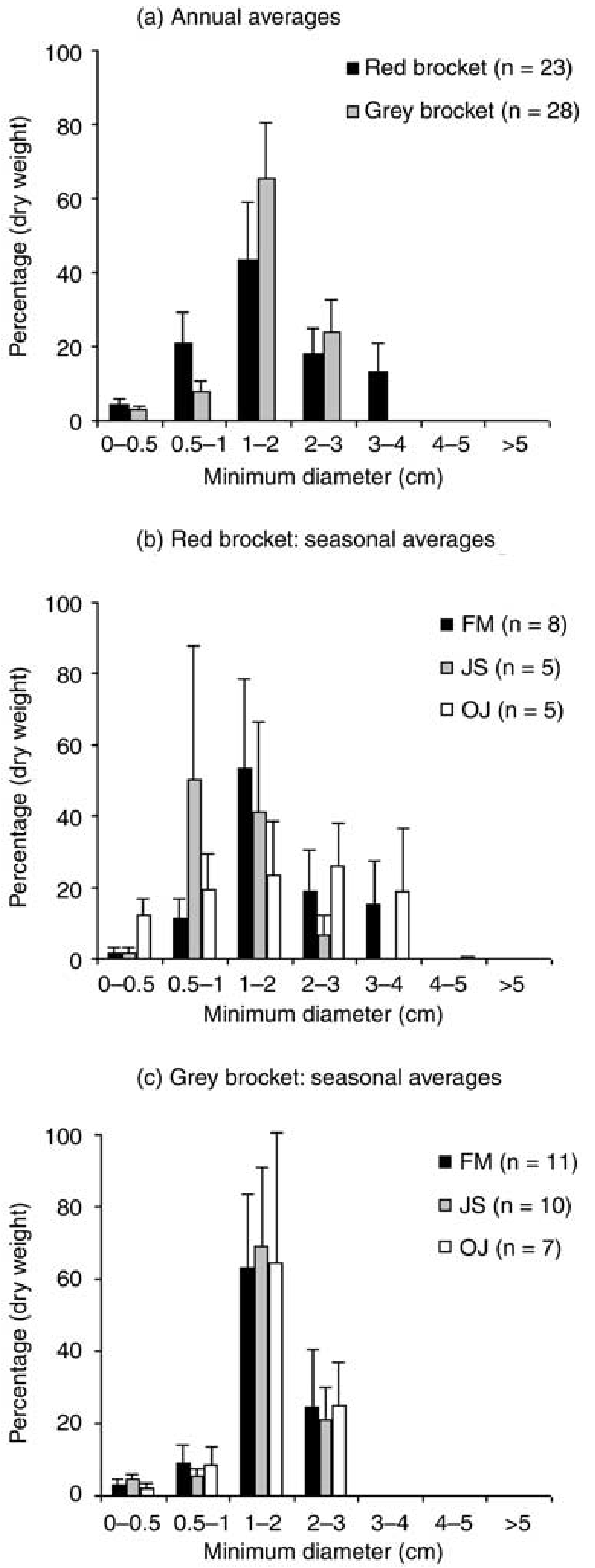

Figure 4. Dry weight % of fruit parts eaten, according to their size. FM = February–May, main fruiting season; JS = June–September, period of fruit scarcity; OJ = October–January, flowering and early fruiting season.

Table 3. Overlap indices of the diets of the two brocket species.

	Overlap index	
Criterion of overlap	Red brocket on grey brocket	Grey brocket on red brocket
Plant species	0.15	0.13
Parts eaten	1.00	0.98
Size of items	0.70	1.21

The respective importance of each fruit size in the diet of red brockets varied a lot from one season to another: red brockets consumed mostly elements measuring 0.5–1 cm in June–September, the period of fruit scarcity, when small fruits seemed the most abundant (Sabatier 1985). Conversely, the seasonal fruit sizes were very similar in grey brockets, with a constant prevalence of the 1–2-cm size category.

These cervids ate large quantities of pulpy fruits (about 60% of dry weight in red brockets and 80% in grey brockets). Pulpy fruit is the most abundant fruit type in French Guiana (Sabatier 1985), so this result is not surprising. However, more than 60% of the pulpy fruits that were eaten have a hard exocarp. This is a much higher frequency than is found in the field, indicating some selectivity for hard exocarp pulpy fruit (Sabatier, unpubl. data).

According to van Roosmalen's guide (1985), most of the identified species found in stomachs (60% in red brocket, 65% in grey brocket) produce brightly coloured fruits. This coincides well with the 60% of coloured fruits found by van Roosmalen among the 774 species he described.

Overlap of diets

Over the year, the two brockets shared 46 fruit species (Appendix 1). Thus, the percentage of fruit species exclusive to red brockets was lower (41.7%) than for grey brockets (57.0%).

The overall overlap indices by plant species eaten were weak and comparable in the two species (0.13–0.15); they were even lower, when pairwise comparisons were made per site and per season (11 out of 15 were below 0.05). By contrast, overlap indices were high in both parts and sizes of fruits eaten. The grey brocket swallows greater proportions of pericarp and medium-sized fruits than the red brocket (Table 1 and Figure 4). In the sizes of fruits eaten, the diet of the red brocket was more overlapped than overlapping (Table 3).

DISCUSSION

Overall composition of diet

No seasonal variation of food quantities was observed for either species. But, considering that gravid females eat

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higher quantities of food than other adults, reproduction may be related to seasonal variations of fruiting, as observed by Henry for agoutis and peccaries (1994, 1997*a*, *b*). The size differences between males and females (Dubost, unpubl. data) would then explain the differences in food quantities ingested between sexes.

Multivariate analyses have not revealed significant differences in diet composition of the two brockets according to site and season. Both species are frugivores–granivores across sites and throughout the year. In fact, seeds may be the major food type of these ruminants, in spite of the over-estimation of hard parts like seeds, which need to stay a longer time in stomachs for digestion. Cervids thus eat preferentially the most energy-rich parts of plants (fruits and seeds) as do other tropical forest ruminants. Owing to the fact that flowers also contain more energy than fibres and leaves, it is not surprising that they can be a seasonally preferred food. The ability to eat fibres and leaves allows cervids to overcome the shortfalls in fruit abundance. Fungi and animal matter are the least important food types; that may be due both to their low energetic value and low availability, and to the need for minimal amounts of essential amino-acids.

Terborgh (1986) supposed that palm fruits are one of the most important food resources for Amazonian terrestrial frugivores during the dry season (i.e. the period of fruit scarcity). We found that they were very rarely consumed by cervids in this period, representing less than 8% of the diet of the red brocket and 2% of the grey brocket. In fact, palm fruits can only be important for frugivores–granivores with strong breaking or gnawing capacities. With regard to other fruit species, only one (*Virola surinamensis*) is eaten by more than half of red brocket individuals in the period of fruit scarcity, but then only with a very low index of usage, and not at all during the main fruiting season. Three other species are eaten often and in great quantities during the flowering and early fruiting season (*Cecropia sciadophylla*, *Eschweilera* spp. and *Ficus* spp.). Similar patterns occur in grey brockets, where the most commonly eaten species group (*Ficus* spp.) is taken only in moderation by less than half of the individuals in the period of fruit scarcity, but eaten intensively (along with *Inga* spp.) during the main fruiting season, and largely replaced by *Eschweilera* spp. as the most favoured fruit during the flowering and early fruiting season. Thus, apparently no single fruit group in French Guiana plays the role of keystone resource for any brocket during this period of fruit scarcity.

According to Branan *et al*. (1985), the seasonal variation in fruit consumption by red brockets in Suriname is more important than in French Guiana (fruits and seeds varying from 15% to 85% of the diet, vs. 43–69%). But these authors made their estimations from volume proportions. Since their study was made out of monthly averages, while ours used 4-mo averages, one might suggest that our results underestimate the real variations of the proportions of each food type. In fact, considering the high values of standard deviations, individual differences could be the most striking characteristic of the fruit consumption in tropical forests.

With a minimal average of eight plant species per stomach and a high number of total identified species, the two forest cervids are clearly generalists. Nevertheless they do focus on a small number of very common species. The average of identified plant species per stomach is two times higher than the one obtained in red brockets in Suriname by Branan *et al*. (1985) and 11 times that of grey brockets in Paraguay (Stallings 1984). This may be due partly to both the much wider area and longer time of collection and to the more precise analysis of stomach contents in our study.

Interspecific differences

The two ruminants belong to the same family and genus; they have comparable mouth and digestive system characteristics. Consequently, their diet differences should be due above all to their weight difference, as supposed initially. From this viewpoint, the smaller cervid should have the more energetic diet, but also lower absolute quantitative needs, and then should be less dependent on the limitations of food resources. This may explain why it is really more of a frugivore–granivore than the other species, as Bodmer (1989) also suggested.

At the period of fruit scarcity, the consumption of fruits–seeds differs from the other seasons, especially in red brockets. Red brocket eats significantly larger quantities of fibres than grey brocket (twice as much), at a constant level throughout the year (from 1/4 to 1/5 of dry weight), even in the main fruiting season. In contrast, grey brockets use fibres in inverse proportion to fruits and seeds, implying that they only consume fibres when fruit and seeds are unavailable. These differences are exactly what one would expect given the difference in their body sizes: owing to their lower relative metabolism, larger ruminants can survive on lower protein resources than smaller ones.

This unequal dependence on food availabilities may oblige them to choose food in different ways. Thus, while plant species seem selected by red brockets according to their abundance, this is only the case for the 10 most eaten species selected by grey brockets. Because grey brockets pass up many common foods taken by red brockets and available to both species, they are clearly more selective.

Our results show that the selection of fruits and seeds might be based on the size of the elements. This may explain why red brockets, having a larger gape, eat larger fruits than grey brockets. Most 2–3-cm fruits can be ingested by the two cervids, but grey brockets definitely eat more 1–2-cm items in all seasons than red brockets.

In fact, the larger gape of red brockets allows them to take advantage of some abundant big fruits, like *Bagassa guianensis* or *Virola kwatae*, but they are also constrained to eat smaller fruits, when such large fruits are unavailable. So, red brockets seem more opportunist and more dependent on fruit availabilities, whereas grey brockets, thanks to both their lower needs and smaller gape, can have a diet essentially based on a high intake of 1–2-cm items. Thus, this latter species would be less dependent on seasonal variations.

Interspecific potential competition

In spite of some differences, both cervids have a rather similar diet, choosing their food chiefly according to its abundance, energetic value, size, hardness and colour. For both cervids, the top identified plant families are those ranking foremost in the French Guiana flora and the most frequent species are eaten in the largest quantities. Because the two species live in the same forest, they should thus be competitors. That is obvious, considering the high overlap index of their diet in fruit sizes and vegetable forms eaten (flowers, seeds, pericarps, entire fruits). With regard to these two categories, the red brocket diet is more overlapped than overlapping. Contrary to what could be supposed, the trophic separation of the two cervids is no more marked in the period of fruit scarcity than in other seasons. This confirms that this period is not as severe as expected for brockets in French Guiana and that each species has a fairly similar diet throughout the year.

But in fact, the real competition between the two cervids could be weaker. First, red brockets eat larger quantities of fibres (twice as much) and less fruits than grey brockets throughout the year, even in the main fruiting season. Second, the dietary overlap indices of the brockets by plant species eaten are very low over the whole of Guiana as in every given site. This is probably the result of their great difference in body weight, which may lead them to choose different fruit species. But, this can be due above all to the very high plant diversity of French Guianan forests, where the total number of phanerogam species is estimated at 4200–5200 (Cremers & Hoff 1996). Others factors, such as the respective activity cycle of each cervid species could also intervene, because nocturnal arboreal vertebrates are less numerous both in species and in individuals than diurnal ones, and thus fewer fruits and fruit species are available on the ground for nocturnal than for diurnal terrestrials: red brockets are both diurnal and nocturnal, while grey brockets are mostly diurnal (Dubost & Henry, unpubl. data; Emmons & Feer 1990). Besides, the bigger species would forage in open areas, unlike grey brockets which usually remain in closed forest, as is shown both by field observations (Dubost & Henry, unpubl. data; Emmons & Feer 1990) and by our list of eaten plant species. Thus, the two cervids may occupy different ecological niches, which could consequently reduce their competition for food.

Comparison with other frugivores

Six Guiana frugivore mammals are potential competitors of the brockets. They are the tapir *Tapirus terrestris* (Henry *et al*. 2000), the two peccaries *Tayassu pecari* and *T. tajacu* (Bodmer 1989, Fragoso 1994, Henry 1994, Judas 1999, Kiltie 1981), and three large rodents: the paca *Agouti paca* (Gallina 1981), the agouti *Dasyprocta leporina* (Henry 1999), and the acouchy *Myoprocta exilis* (Dubost 1988). The big ground-dwelling birds *Crax alector*, *Psophia crepitans*, *Tinamus major* and *Penelope marail* also eat many fruits (Erard *et al*. 1991, Thery *et al*. 1992).

Although the list of fruits eaten by these frugivores is largely incomplete, each of them consumes many fewer fruit species than either brocket. Besides, these frugivores are often specialists of certain fruit types or fruit parts, or show other feeding strategies: the tapir can swallow much larger fruits than the brockets (Henry *et al*. 2000); peccaries forage in herds, actively searching for areas rich in hard nuts (Fragoso 1994, Kiltie 1981); agoutis and acouchies scatter-hoard their food. Considered singly, none of the above terrestrial species appears a serious competitor for the brockets. However, competition could still occur if the production of 1–2-cm diameter fruits, which are preferred by most frugivores, but which are also often common and generally produced en masse, does not result in a local saturation of predators.

Role in forest regeneration

Because of their frugivore–granivore diet, cervids are directly implicated in the processes of forest regeneration, but it is hard to understand their exact role in seed dispersal. A large majority of seeds is destroyed during the rumination, as also observed by Bodmer (1989). Thus, most very common species, like *Euterpe oleracea*, *Oenocarpus bacaba* and *Virola surinamensis* are eaten in large amounts by the two cervids, but their seeds are destroyed. The same is true for other less common species, like *Carapa* cf. *guianensis*, *Dicorynia guianensis*, *Inga* spp., *Maripa scandens*, *Virola kwatae* and *V. michelii*. In contrast, small seeds belonging to genus *Cecropia* (pioneers), *Bagassa* and *Ficus* (mostly epiphytic) nearly always remain intact, and thus can be dispersed with the faeces. But, the role of our cervids in dispersal is obviously of minor importance, because these small seeds are also eaten and dispersed by most arboreal or terrestrial mammals of every body size. Thus, on the whole, the main impact of brockets in the process of forest regeneration could be their negative pressure on seed survival.

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Appendix 1. List of species, parts eaten (fr: entire fruit; pe: pericarp; s: seed; fl: flower) and absolute value of index of usage (++++: more than 0.1; +++: between 0.01 and 0.1; ++: between 0.001 and 0.01; +: less than 0.001) of plants used by the two brockets. Taxonomic nomenclature according to Boggan *et al.* (1997).

Plant species	Red brocket		Grey brocket	
Anacardiaceae				
Spondias mombin	pe, s	+++		
Tapirira guianensis			s	++
Annonaceae				
Duguetia eximia			s	++
Duguetia surinamensis	s	++		
Ephedranthus guianensis			s	+
Guatteria sp.			s	+
Oxandra asbecki	s	+++	s	++
Unonopsis rufescens	s	+	s	+
Unonopsis stipitata			s	+++
Apocynaceae				
Ambelania acida			s	++
Geissospermum cf. *laevis*	s	++		
Pacouria guianensis	fr, s	+++	fr, s	+
Parahancornia fasciculata	s	+	s	++
Araceae				
Heteropsis flexuosa	pe, s	+	fl	+
Monstera adansonii			s	+
Araliaceae				
Schefflera decaphylla	pe, s	++++	pe	++
Arecaceae				
Euterpe oleracea	s, fl	+++	pe, s	++
Jessenia bataua	s	+++		
Oenocarpus bacaba	fr, pe, s	++++	s	++++
Socratea exorrhiza		s	++	
Bignoniaceae				
Schlegelia sp.	pe	+		
Bombacaceae				
Catostemma fragrans	s, fl	++++	s	+++
Eriotheca sp.	s	++++		
Boraginaceae				
Cordia sp.			s	+
Burseraceae				
Dacryodes nitens			s	++
Caesalpiniaceae				
Bauhinia sp.			s	+++
Crudia sp.			pe, s	+++
Dicorynia guianensis			pe, s	++++
Eperua falcata	s, fl	++++	s, fl	++
Macrolobium sp.	s	++		
Swartzia cf. *guianensis*			s	+++
Swartzia panacoco	s	++++		
Swartzia polyphylla	s	+++	s	+++
Caricaceae				
Carica microcarpa	s	++		
Jacaratia spinosa			s	+
Caryocaraceae				
Caryocar glabrum	fl	+++	fl	++
Cecropiaceae				
Cecropia obtusa	s	++++	s	+++
Cecropia sciadophylla	fr, s	++++	fr, s	+++
Coussapoa angustifolia	fr	+	fr, fl	++
Pourouma spp.	fr	+	fr, pe, s	+++
Chrysobalanaceae				
Hirtella racemosa			s	+++
Licania micrantha			s	++
Clusiaceae				
Clusia sp.	s	+++	s	+
Moronobea coccinea	fr	++		
Platonia insignis			fr	+++
Rheedia benthamiana			pe, s	++
Rheedia sp.			s	+
Symphonia globulifera	pe, s	++	s	+++
Tovomita sp.			s	+++

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Appendix 1. Continued.

Plant species	Red brocket		Grey brocket	
Convolvulaceae				
Dicranostyles guianensis	fr, s	+++	s	+++
Maripa scandens	pe, s	+++	s	+++
Cucurbitaceae				
Cayaponia sp.	s	+	fr	+
Gurania sp.			pe, s	++
Cyclanthaceae				
Cyclanthus bipartitus	fr, s	++++		
Ebenaceae				
Diospyros sp.	pe	+	s	++
Euphorbiaceae				
Conceveiba guianensis	pe, s	++	fl	+
Mabea sp.			fr, pe	+++
Fabaceae				
Andira surinamensis	pe, s	++		
Gnetaceae				
Gnetum sp.			s	+++
Hippocrateaceae				
Cheiloclinium sp.			s	+++
cf. *Salacia* sp.	s	+++		
Humiriaceae				
Humiria balsamifera			s	+
Hugoniaceae				
Roucheria sp.	s	++		
Icacinaceae				
Emmotum fagifolium			pe	+
Poraqueiba guianensis	pe, s	+++		
Lauraceae				
Ocotea schomburgkiana			pe, s	+++
Rhodostemonodaphne grandis	fr, s	+++	pe	++
Sextonia rubra	fr, pe, s	+++		
Lecythidaceae				
Eschweilera congestiflora	fl	+++		
Eschweilera grandiflora			fl	+++
Eschweilera micrantha			fl	++
Eschweilera parviflora			fl	+++
Eschweilera spp. (*M. americana*: 2 spp.; *M. gouazoubira*: 1 sp.)	s, fl	++++	pe, s, fl	++++
Gustavia augusta			s	+++
Lecythis corrugata			s	+++
Lecythis persistens			s	++++
Lecythis pneumatophora	s, fl	+++		
Lecythis cf. *poiteaui*	s	++		
Lecythis spp. (*M. americana*: 2 spp.; *M. gouazoubira*: 1 sp.)	s	+	s	+++
Loganiaceae				
Strychnos spp. (*M. americana*: 2 spp.; *M. gouazoubira*: 1 sp.)	s	+	pe, s	++
Melastomataceae				
Miconia sp.	s	+++		
Mouriri nervosa	s	+++		
Meliaceae				
Carapa cf. *guianensis*	pe, s	++++	s	+++
Guarea gomma			s	+++
Guarea grandifolia	fr, s	++++	fr, s	+++
Guarea kunthiana	s	++		
Guarea silvatica			s	+
Mendonciaceae				
Mendoncia sp.			s	+
Mimosaceae				
Inga spp. (*M. americana*: 1 sp.; *M. gouazoubira*: 3 spp.)	fr, pe, s	+++	pe, s	++++
Parkia sp.			s	+
Stryphnodendron polystachyum			s	+++
Moraceae				
Bagassa guianensis	fr, s, fl	++++	fr, s	+++
Brosimum acutifolium			fr, s	+++
Brosimum guianense			pe, s	++++
Brosimum parinarioides			pe, s	+++
Ficus insipida			s	+++
Ficus nymphaeifolia			fr, s	++
Ficus spp. (*M. americana*: 2 spp.; *M. gouazoubira*: 2 spp.)	fr, pe, s, fl	++++	s	++++
Helicostylis cf. *tomentosa*			s	+
Trymatococcus oligandrus			s	+++

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Appendix 1. Continued.

Plant species	Red brocket		Grey brocket	
Myristicaceae				
Virola kwatae	s	++++	s	++
Virola michelii	fr, s	++	s	++++
Virola surinamensis	pe, s, fl	++++	s	++++
Virola sp.	s	+	pe	++
Myrtaceae				
Eugenia coffeifolia			s	++
Olacaceae				
Minquartia guianensis			s	+++
Opiliaceae				
Agonandra silvatica	pe, s	++++		
Passifloraceae				
Passiflora sp.	s	++	s	+
Polygalaceae				
Moutabea guianensis	pe, s	++	fr, s	+++
Rubiaceae				
Posoqueria latifolia	s	++		
Schradera surinamensis			fr	+++
Sapindaceae				
Cupania sp.			s	+
Paullinia capreolata	pe, s	++++		
Paullinia venosa	s	++		
Talisia spp.	pe	+	pe	+
Sapotaceae				
Chrysophyllum cuneifolium			s	+++
Chrysophyllum pomiferum			s	+
Chrysophyllum prieurii	s	+++	s	++++
Chrysophyllum spp. (*M. americana*: 1 sp.; *M. gouazoubira*: 2 spp.)	fr, s	+++	fr, pe	++
Ecclinusa cf. *guianensis*	s	++		
Micropholis guyanensis			s	+++
Micropholis melinoniana			s	+++
Micropholis spp.			pe, s	+++
Pouteria brachyandra	fr, s	+	s	++
Pouteria cayennensis	s	+++		
Pouteria coriacea			fr, s	+++
Pouteria egregia			s	++
Pouteria guianensis	s	++++		
Pouteria sp.	s	+		
Smilacaceae				
Smilax sp.			s	+
Solanaceae				
Solanum spp. (*M. americana*: 1 sp.; *M. gouazoubira*: 2 spp.)	fr, s	+++	s	+
Verbenaceae				
Avicennia germinans	fr, s	+++		
Total number of identified families 47	38		39	
Total number of identified species 142	79		107	

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