available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/actoec

Original article

Seed dispersal services by coatis (*Nasua nasua*, Procyonidae) and their redundancy with other frugivores in southeastern Brazil

Cecília P. Alves-Costa[a,*], *Paula C. Eterovick*[b,1]

[a]*Laboratório de Interação Vertebrado-Planta, Departamento de Zoologia, IB, Universidade Estadual de Campinas, CP 6109 Campinas, SP, Brazil*
[b]*Departamento de Biologia Geral, ICB, Universidade Federal de Minas Gerais, 30161-970 Belo Horizonte, MG, Brazil*

ARTICLE INFO

Article history:
Received 5 September 2006
Accepted 12 March 2007
Published online 2 May 2007

Keywords:
Atlantic forest
Defaunation
Fragmentation
Germination success
Nasua nasua
Residual frugivores
Redundancy
Seed dispersal services

ABSTRACT

Coati effectiveness as seed dispersers and their potential in maintaining this service through an annual cycle were evaluated during 33 months in an Atlantic forest fragment in southeastern Brazil. We determined the range of fruit and seed traits consumed by coatis, the phenology of fruit consumption, the patterns of fruit consumption and seed defecation, and the effects of ingestion in the speed and success of seed germination. In addition, we assessed redundancy among the seed dispersal services provided by coatis and other resident frugivores. Coatis consumed fruits of 53 species and dispersed seeds of at least 49 out of these species. Most consumed plant species were pioneer (59%), had fruits >15 mm diameter (58%), and were yellow or green (54%). Seeds were found in 54.5% out of 288 faecal samples. The number of seeds in faeces correlated negatively to seed mass and ranged from 1 to 1209 seeds; 50% of the faeces had <50 seeds. Passage through coatis gut did not alter speed or success of seed germination of tested species, except for *Myrcia guajavaefolia*, whose germination success was increased approximately 50% after pulp removal by coatis. Considering fruit colour and seed size, redundancy of seed dispersal services between coatis and other frugivores ranged from 39 to 70%. In defaunated fragments, coatis may provide a 'key role' in maintaining seed dispersal services for a large variety of species and they may promote gene flow among forest patches and the regeneration of disturbed sites.

1. Introduction

From 50 to over 90% of tropical trees and shrubs produce fleshy fruits and rely on frugivorous vertebrates to disperse their seeds, by offering them energetic rewards, such as lipids, carbohydrates, and protein (Howe and Smallwood, 1982). Seed dispersal provides many advantages for plants, including occupancy of vacant sites (colonization), avoidance of sites

* *Correspondence to: Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Pernambuco, Av.* Moraes Rego s/n, Cidade Universitária, 50670-901 Recife, PE, Brazil.
E-mail addresses: cepacosta@yahoo.com.br (C.P. Alves-Costa), eterovick@yahoo.com (P.C. Eterovick).
[1] Present address: Pontifícia Universidade Católica de Minas Gerais, Programa de Pós Graduação em Zoologia de Vertebrados, 30535-610 Belo Horizonte, MG, Brazil.
1146-609X/$ – see front matter © 2007 Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.actao.2007.03.001

occupied by relatives or other individuals of the same species (escape from distance or density-dependent mortality), and occupancy of specific microsites critical for establishment (directed dispersal) (for reviews see Howe and Smallwood, 1982; Willson and Traveset, 1992). In fragmented landscapes, seed dispersal by frugivores may guarantee the possibility of gene flow among natural vegetation patches (Jordano and Godoy, 2002) and the regeneration of degraded areas (Grime and Hillier, 1992; Duncan and Chapman, 2002).

However, due to habitat loss, fragmentation and hunting, some frugivorous species, mainly large-bodied such as tapirs, deer, and peccaries, are becoming scarce or even extinct in forest fragments (Willis, 1979; Chiarello, 1999; Cullen et al., 2000; Roldán and Simonetti, 2001). With the defaunation of these and other frugivores, some plant species may suffer a decrease in seed dispersal and, consequently, in seedling recruitment and/or survival (Terborgh and Wright, 1994; Dirzo and Miranda, 1990; Pizo, 1997; Cordeiro and Howe, 2001; Galetti et al., 2003; Alves-Costa, 2004). However, the impact of frugivore defaunation could be reduced, if frugivorous species that are more resistant or even benefit from anthropogenic impacts are able to disperse seeds of a great variety of morphological fruit types, compensating, at least partially, for the decline of other frugivores.

Coatis are medium-sized (3–6 kg) gregarious Procyonids, common throughout most Neotropical forests [*Nasua nasua* (Linnaeus) in South America and *N. narica* (Linnaeus) in Central and North America], where they are often the most abundant species of the order Carnivora (see Gompper and Decker, 1998). These mammals are omnivorous, feeding on fruits, small vertebrates and forest floor invertebrates (*N. narica*: Russell, 1982; Gompper, 1996; *N. nasua*: Gompper and Decker, 1998; Alves-Costa et al., 2004). Seeds are found in 30–77% of coati faeces, depending on the season and the availability of other food resources (Alves-Costa et al., 2004). Coatis thrive in disturbed fragments (Terborgh, 1990; Bisbal, 1993; Chiarello, 1999) and should be an important species for the maintenance of seed dispersal services in such habitats.

We evaluated some aspects of coati effectiveness (*sensu* Schupp, 1993) as seed dispersers and their potential in maintaining this service throughout the year in fragmented forest remnants with an impoverished community of large frugivores. For this purpose, we determined the range of fruit and seed characteristics consumed by *Nasua nasua*, patterns of fruit consumption and seed defecation, the phenology of seed species in faeces over 33 months, and the effects of ingestion in speed and success of seed germination for some of the most consumed fruit species. In addition, we assessed the redundancy among the seed dispersal services provided by coatis and other frugivorous species that frequently persist in defaunated fragments in southeastern Brazil.

2. Materials and methods

2.1. Study area

The study was conducted in the Mangabeiras Park; a reserve located near the Curral mountain range, in the city of Belo Horizonte, state of Minas Gerais in southeastern Brazil (19°56′S, 43°54′W; 1040–1175 m a. s. l.). Annual rainfall averages 1767 mm, with a marked dry season (April–September), when rainfall averages 217 mm. Most of the precipitation falls from October to March (1551 mm), and mean annual temperature is approximately 26 °C (details in Alves-Costa et al., 2004).

The park encompasses 236 ha, including semideciduous Atlantic forest (covering 40% of the area), cerrado vegetation (a Brazilian savanna, 30%), and grasslands at higher elevations (30%), and represents a transition zone between the Atlantic forest and the cerrado biomes. The cerrado includes open areas (with scattered trees) as well as areas in transition to forest (called Cerradão). There is a total of about 320 plant species in the Park area and the most common families are Compositae (mainly genera *Eremanthus*), Leguminosae (*Bauhinia*, *Dalbergia*, *Inga*), Melastomataceae (*Miconia* and *Tibouchina*), Myrtaceae (*Myrcia*) and Solanaceae (*Solanum*) (Pedersoli, 1997). Access for tourists is limited to some paved trails and entertainment areas, which encompass approximately 4% (10 ha) of the total area. The park is surrounded by iron mining, residential areas and some natural vegetation along the highest ranges of the mountains. Hunting is forbidden, but occurs.

Coatis are frequently seen in the Park. On one occasion (August 1996, during the mating period), 70 individuals were seen together in the study area (CPAC, pers. observation). Females with six puppies were frequent, reflecting a high birth rate compared with literature data (commonly 3–4 puppies; Gompper and Decker, 1998). Other frugivorous species $>$500 g in the study area are limited to *Penelope superciliaris* Temminck (Rusty-margined guan, Cracidae), *Didelphis albiventris* Lund (White-eared opossum, Didelphidae) and *Cerdocyon thous* Hamilton Smith (Crab-eating fox, Canidae). Smaller non-volant frugivorous mammals are *Callithrix penicillata* E. Geoffroy (Black tufted-ear marmoset, Callitrichidae), *Sciurus aestuans* Linnaeus (Guianan squirrel, Rodentia), *Philander frenata* Linné (Gray four-eyed opossum, Didelphidae), *Marmosops incanus* Lund (Mouse opossum, Didelphidae) and *Gracilianus agilis* Burmeister (Agile gracile mouse opossum, Didelphidae) (Câmara and Lessa, 1993; Lessa et al., 1998). In addition, there are 159 bird species (almost 25% of the Minas Gerais state avifauna), but large frugivorous birds, such as cotingas (Cotingidae), toucans (Ramphastidae) and trogons (Trogonidae) are absent (Jr. Melo et al., 1996). There are no studies on bats in that area.

2.2. Fruits consumed by coatis

From April 1995 to December 1997, weekly field visits were conducted in order to determine the fruit species consumed by coatis. During each visit, some areas frequently visited by coatis as well as trails crossing the Park (including urbanized areas, forest and cerrado habitats) were walked in search of coatis and/or their fresh faeces. Faeces were identified by their characteristic size, shape and smell and by coati footprints found nearby. Direct observations of fruit consumption were included when the animals could be located while foraging. The faeces were washed (within 24 h after collection) using two superimposed sieves of 0.7 and 0.4 mm. The seeds were counted (for faeces with about 300 or more seeds, the number of seeds was estimated by dividing the total seed mass by the individual seed mass), weighed (after drying at 40 °C for 8 days), measured (largest diameter), classified in morphospecies, and stored in labelled plastic pots. During trail walking, fruiting plants were collected and their seeds were compared with those found in faeces, allowing taxonomic identification of the species whose fruits were consumed. The fruits of the consumed species were characterized by their colour, diameter, and the number of seeds per fruit. Plant habitat, life form, and successional stage were recorded according to Lorenzi (2002) or Wanderley et al. (2002). To estimate the maximum number of fruits ingested by coatis, the maximum number of seeds found in the faeces was divided by the minimum and maximum number of seeds per fruit. This yields a conservative estimative of number of fruits consumed, as the seeds consumed in a single meal might be dropped in more than one faecal pellet. To test whether species with different seed sizes are associated with clumps of different seed densities after dispersal by coatis, the mean number of seeds from each plant species in faecal samples was related to individual seed mass through a Pearson correlation. Data were log-transformed for normality.

2.3. *Effects of ingestion by coati on seed germination*

To test if seed ingestion by coatis affects seed germination, species represented by 30 or more seeds in individual faecal samples and whose seeds could be obtained from fruiting plants were used in germination trials. Such fruits were in the same ripening phase both in faeces and fruiting plants, as determined by the colour of pulp remnants found in faeces. After being washed, seeds from faeces were distributed in Petri dishes (30 seeds of a single faecal sample per Petri dish) on a wet filter paper. Uningested seeds directly obtained from ripe fruits of the same species were used as controls (30 seeds of a single plant per dish). These seeds were washed and separated from the fruit pulp. The number of replicates (Petri dishes) per treatment varied according to the availability of faeces and plants with seeds. To test whether gut passage affects seeds only due to pulp removal, uningested seeds with pulp (intact fruits) were distributed in Petri dishes (30 fruits of a single plant per dish). This was done just for the species with one-seeded fruits. All Petri dishes were put in an incubating chamber with temperature between 26 °C and 30 °C and continuous light. The Petri dishes were watered and checked for germinating seeds in 2–5 day intervals, when both germinating and visibly dead seeds were counted and removed. When fungi infested a Petri dish, the seeds were washed in water and put on a new wet filter paper. The trials were finished when no more seeds germinated for two consecutive weeks or when fungal infection could not be controlled by the procedures above.

Each Petri dish was considered as a sample unit (different dishes had seeds from different faecal samples or plants), and the variables used for analyses were proportion of germinated seeds (germination success) and number of days the first seed took to germinate (speed of seed germination). For seeds with pulp only germination success was tested, as seedling emergence could only be seen after the plant tore the pulp, leading to an overestimation of time to germination. Due to the small sample sizes, non-parametric tests were used to compare treatments: Mann–Whitney tests were used to compare the germination in cases with only two treatments: ingested (i) and uningested (u) seeds, and Kruskal–Wallis tests were used in the cases with three treatments: ingested seeds (i), uningested seeds without pulp (u), and uningested seeds with pulp (up). For germination experiments conducted in two consecutive years (1996 and 1997), the proportion of germinated seeds in each treatment was compared between the years (Mann–Whitney tests) and, whenever there were no significant differences, data were pooled to compare treatments.

2.4. *Redundancy among resident frugivores on seed dispersal services*

To know if seed dispersal services provided by coatis could be redundant with those provided by other resident frugivorous species, we evaluated the frequency of fruit consumption, the number and colour of fruit species consumed, the seed size of dispersed species and the home range of these frugivores. The largest bodied frugivorous species in the study area are *Penelope superciliaris*, *Callithrix penicillata*, *Cerdocyon thous* and *Didelphis albiventris*. In addition, we included 26 small bird species present in the Park and the bat *Artibeus lituratus* (very common in forest fragments in southeast Brazil, Galetti and Morellato, 1994; Zortéa and Chiarello, 1994). For each frugivore, we compiled published data (found through Google Scholar and Web of Science, until October 2005) on fruit species consumed in Cerrado and/or forest fragments in southeast Brazil. As the number of fruit species consumed by different frugivores can be affected by sample size, we restricted the comparison of this parameter to same sample sizes. For this, a same number of feeding bouts, feeding roosts and faeces were considered equivalents. Due to possible differences among fruit abundance and plant species composition in the different study sites, we used just fruit traits (per fruit species consumed) to evaluate the seed dispersal service redundancy among frugivorous species. We assume that the frequency of consumption of fruits with different traits might reflect frugivore preferences, despite differences among plant species composition at different sites. Thus, for each consumed plant species, we determined fruit colour, the largest seed diameter and fruit diameter. For each frugivore, we calculated the relative frequency of fruit traits in the set of plant species consumed. For this purpose, we considered four categories of seed sizes (0–6, >6–12, >12–25, >25 mm) and six categories of fruit colours (wine or red, green, purple or black, brown, yellow or orange, other), which were combined in 24 categories to assess redundancy between coatis' and other frugivores' diets. In order to determine the redundancy on traits of the plant species dispersed by coatis and those dispersed by other frugivores, we calculated the percentage overlap of fruits with specific traits between pairs of frugivores through the Schoener overlap index (Jr. Wallace, 1981; Krebs, 1989). When available, data about the home range of each species are presented as an indicative of frugivore potential to provide long-distance seed dispersal.

3. Results

3.1. *Fruits consumed by coatis and their traits*

During the 33 months of study, we collected 288 faecal samples of which 54.5% ($n = 157$ faeces) contained seeds. In total, we recorded the consumption of 53 fruit species by coatis (Table 1), which were verified by seed occurrence in the faeces (49 species) and/or by direct observation of coati feeding (4 additional species). Seeds of just one species, *Mangifera indica*, were not ingested by coatis, but its pulp consumption was verified by direct observation. The fruits consumed by coatis included at least 23 genera and 17 families, considering the 34 species in which identification was possible at least until genera (Table 1). Seeds of 19 morphospecies recorded in the faeces could not be identified, as fruits with similar seeds were not found.

Fruit diameter of the identified species varied between 4 and 120 mm (mean $= 27.2 \pm 32.8$ SD, median $= 20.2$, $n = 22$ species, excluding legume infructescence), with 42% <15 mm and 37% between 15–30 mm diameter. Seed diameter of consumed fruits varied from 0.8 mm (*Miconia* and *Ficus*) to 80 mm (*Mangifera indica*), but the maximum seed size ingested by coatis during this study was 18 mm diameter (mean $= 5.5 \pm 4.2$ SD, median $= 4.0$, $n = 52$ species).

Seventy-one percent of the species whose fruits were consumed by coatis are from the forest, 17% are from cerrado and at least 12% occur in both vegetation types (Table 1). The large majority are trees (81%), followed by shrubs (15%) and lianas (4%). Fifty-nine percent of consumed species are pioneers and the remaining are secondary or shadow tolerant (Table 1). Yellow and green fruits were the most consumed (34.6% and 19.2%, respectively) followed by purple (15.4%), black (11.5%), beige (7.7%), brown (7.7%) and blue (3.8%) fruits (Table 3). The height at which coatis foraged varied greatly, from fruits fallen onto the ground to fruits on the trees up to about 20 m high.

3.2. *Patterns of seed deposition*

Fifty-one percent (25 species) of the dispersed species had seeds in just one faecal sample and 24% (11 species) occurred in six to 30 samples (Table 1). The number of seeds per faecal sample varied from a single seed to 1209 seeds, but half of the samples had less than 50 seeds (Fig. 1). The mean number of seeds of each plant species per faecal sample was negatively correlated with individual seed mass (Fig. 2, $r_{\text{Pearson}} = -0.84$, $P < 0.0001$, $n = 15$ species, including only species recorded in 3 or more faecal samples).

The estimated maximum number of fruits ingested by coatis varied from about 3–4 fruits (of *Ficus* and *Passiflora*) to 124 fruits (*Lithraea molleoides*) (Table 1). As coati groups are usually comprised of about 20 individuals, it is possible to infer that a single visit can mean the ingestion of 60–80 to 2480 fruits.

Coati faeces contained seeds from 1–4 different plant species, with a mean of 1.3 ± 0.6 SD species per faecal sample (median $= 1$ species/sample, $n = 157$ samples with seeds). Most faecal samples (75%) contained seeds of a single plant species, 17% contained seeds from two species, 7% contained seeds from three species and just 1% contained seeds from four species. Seeds from the same combination of plant species were repeatedly found in four faecal samples at most (in the case of *Guazuma ulmifolia* + *Cecropia pachystachya*).

3.3. *Phenology of fruit consumption*

Seeds were recorded in faeces in 32 out of the 33 months studied (Fig. 3). There was a tendency to regular oscillations on frequency of fruit consumption, but they were not correlated with monthly rainfall (Fig. 3; $r_s = -0.31$, $P = 0.08$, $n = 32$ months). Most plant species were found in coati faeces during a short period: 73–86% occurred in one or two months per year and the remaining occurred in up to three (*Lithraea molleoides*, *Miconia* spp., *Vismia brasiliensis*) or four (*Cecropia pachystachya*, *Ficus* spp., *Guazuma ulmifolia*, *Miconia flammea*, *Myrcia guajavaefolia*, *Passiflora* spp.) months per year. *Guazuma ulmifolia* was the most regular species in coati faeces, occurring in August–October during the three studied years. Other species that occurred in all years were *Cecropia* spp. and *Ficus* spp. (mainly from August to November), *Passiflora* spp. (exclusively between July and October), and *Emmotum* sp., *Myrcia guajavaefolia*, *Casearia lasiophylla*, and *Miconia* spp. (Fig. 3).

3.4. *Effects of seed ingestion by coatis on germination*

The seeds recovered from coati faeces did not show any physical evidence of damage. For six species, it was possible to obtain a number of seeds sufficient to conduct germination tests: *Casearia lasiophylla* (Flacourtiaceae), *Cecropia pachystachya* (Cecropiaceae), *Ficus obtusifolia* (Moraceae), *Guazuma ulmifolia* (Sterculiaceae), *Lithraea molleoides* (Anarcadiaceae), and *Myrcia guajavaefolia* (Myrtaceae). For *C. pachystachya*, *G. ulmifolia*, and *M. guajavaefolia*, experiments were conducted in two consecutive years (1996 and 1997). Both years could be pooled for *C. pachystachya* and *G. ulmifolia*, as the proportion of germinating seeds in each treatment did not differ between years (ingested seeds: $U = 17.0$, $n_{1996} = 6$, $n_{1997} = 7$, $P = 0.57$; uningested seeds: $U = 14.0$, $n_{1996} = 3$, $n_{1997} = 12$, $P = 0.56$ for *C. pachystachya*, and ingested seeds: $U = 3.0$, $n_{1996} = 3$, $n_{1997} = 5$, $P = 0.18$; uningested seeds: $U = 30.0$, $n_{1996} = 6$, $n_{1997} = 17$, $P = 0.14$ for *G. ulmifolia*). For *Myrcia guajavaefolia*, data from both years could not be pooled ($U = 19.0$, $n_{1996} = 8$, $n_{1997} = 12$, $P = 0.01$).

The ingestion of seeds by coatis did not alter speed or success of seed germination for any of the species tested, except for *M. guajavaefolia*. In this case there was a negative effect of pulp on germination. Manual removal of fruit pulp increased seed germination in 60–75% and coati removal increased in about 50% (Table 2). Seeds obtained from faeces and from

Table 1 – Fruit species consumed by coatis in Mangabeiras Park. SF – semidecidual forest

Family	Species[a]	Mean number of seeds per faeces ± SD (min-max)	% of faeces with seeds (*n*)	Mean seed weight in mg ± SD (*n*)	Range number of seeds per fruit (*n*)	Estimated maximum number of fruits consumed per meal per individual	Fruit type/ Life form	Successional stage/habitat
Anarcadiaceae	*Lithraea molleoides* (Vell.)	37.8 ± 44.7 (2–124)	3.8 (6)	33.47 ± 6.19 (5)	1 (10)	124	Drupe/Tree	Pioneer/SF
Cecropiaceae	*Cecropia pachystachya* Trécul.	234.2 ± 311.2 (10–1209)	15.3 (24)	0.82 ± 0.05 (10)	>1000	–	Polyachene/Tree	Pioneer/SF
Clusiaceae	*Vismia brasiliensis* Choisy	135.1 ± 187.8 (3–415)	4.5 (7)	0.85 ± 0.17 (10)	–	–	Berry/Tree	Secondary/SF
Flacourtiaceae	*Casearia lasiophylla* Eichler	98.2 ± 92.4 (3–332)	11.5 (18)	11.7 ± 3.3 (5)	4–6 (10)	55.3–83	Berry/Tree	Secondary/SF
Melastomataceae	*Miconia albicans* (Sw.)	169.4 ± 190.5 (5–577)	Up to 8.3 (13)	1.13 ± 0.17 (5)	10–18 (10)	32–58	Berry/Shrub	Cerrado
	Miconia trianaei Cogn.	Included above[b]		0.64 ± 0.10 (5)	10–30 (30)	20–58	Berry/Shrub	Cerrado
	Miconia flammea Casar.	25.8 ± 27.5 (1–84)	7 (11)	11.86 ± 2.33 (5)	1–2 (15)	42–84	Berry/Shrub	Cerrado
Moraceae	*Ficus obtusifolia*	322.5 ± 306.4 (5–1114)	15.3 (24)	0.24 ± 0.06 (5)	291–486 (13)	3–4	Syconium/Tree	Shade tolerant/SF
Myrtaceae	*Myrcia guajavaefolia* O. Berg	34.4 ± 29.9 (4–90)	10.8 (17)	39.97 ± 13.69 (4)	1–3 (31)	30–90	Berry/Tree	Secondary/SF
Passifloraceae	*Passiflora edulis* Sims.	72.8 ± 106.0 (1–288)	8.3 (13)	24.61 ± 1.32 (5)	85–134 (5)	3–4	Berry/Liane	Shade tolerant/SF, Cerrado
Sterculiaceae	*Guazuma ulmifolia* Lam.	44.7 ± 44.2 (4–137)	19.1 (30)	5.40 ± 0.86 (5)	12–81 (40)	2–12	Capsule/Tree	Pioneer/SF

a Species with seeds in <5 faecal samples: Caricaceae: *Carica* sp., Cecropiaceae: *Cecropia glaziovi* Snethlage, *Cecropia hololeuca* Miq., Flacourtiaceae: *Casearia* sp., Icacinaceae: *Emmotum* sp., Leguminosae: *Senna macranthera* Irwin et Barneby, Melastomataceae: *Miconia* spp. (include at least 4 species), Moraceae: *Ficus insipida* Willd., *Maclura tinctoria* (L.) D. Don ex Steud., Myrtaceae: *Campomanesia* sp., *Psidium guajava* Raddi, Nyctaginaceae: *Guapira graciliflora* (Mart. ex Schmidt), Passifloraceae: *Passiflora* sp., Rubiaceae: *Amaioua guianensis* Aubl. and *Guettarda viburnoides* Cham. et Schlecht., Styracaceae: *Styrax ferrugineus* Nees et Mart. and other 19 non-identified species. Species recorded only during direct observation of coati feeding: Anacardiaceae: *Mangifera indica* L., Lauraceae: *Cryptocarya aschersoniana* Mez., Leguminosae: *Inga uruguensis* Hook. and Arn. and Piperaceae: *Piper aduncum* L. sp.

b Seeds of *Miconia albicans* and *M. trianaei* were not differentiated in 13 faecal samples in which they occurred.

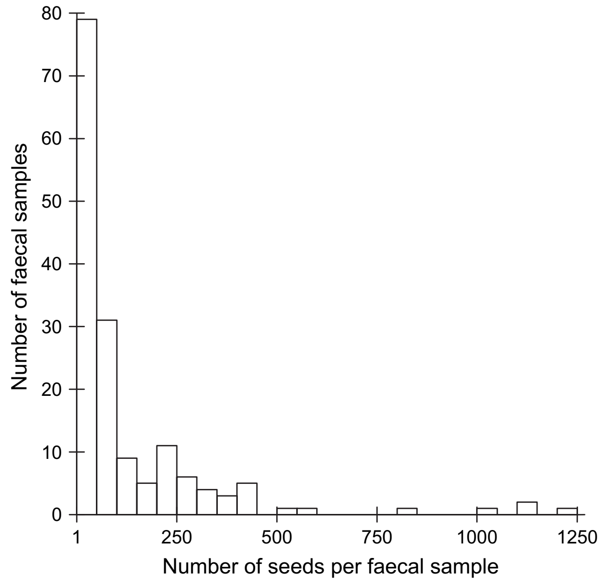


Fig. 1 – Absolute frequency of faecal samples with different numbers of seeds.

fruits (without pulp) took the same time for germination (Table 2).

3.5. *Redundancy among resident species on seed dispersal services*

The data of each frugivorous species corresponds to at least 10 months of dietary studies (see Appendix 1 for additional details). In total, fruits of at least 161 species were consumed by the frugivores analysed in this study (Appendix 2). *Penelope superciliaris* was the most frugivorous (seeds were found in 96.8% of its faecal samples), followed by *Didelphis albiventris* and *Cerdocyon thous* (Table 3). Seeds occurred in 54.5%

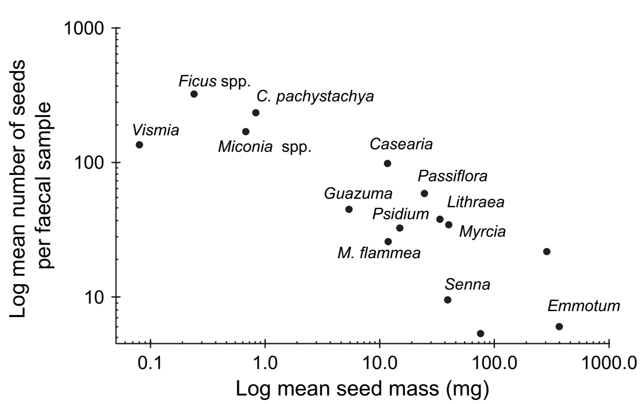


Fig. 2 – Mean number of seeds per coati faeces in relation to seed mean mass for different plant species. $r_{Pearson} = -0.84$, $P < 0.0001$, $n = 15$ species. Complete names of plant species are listed in Table 1.

of coati faeces, which consumed the largest number of fruit species (Table 3). However, considering a same sample size, *P. superciliaris* and *C. thous* consumed seeds of a number of species about 26 and 28% larger than coatis (Fig. 4).

All frugivores consumed fruits of at least five of the six fruit colour categories (Table 3). Small birds and *D. albiventris* were only able to disperse small seeds (up to 12 mm), while the other frugivores dispersed larger seeds of up to 25 mm. *Artibeus lituratus* was the only one being able to disperse seeds >25 mm (Table 3). Between 60–70% of plants whose fruits were consumed by *A. lituratus*, small birds, *C. thous*, and *D. albiventris* had the same fruit traits of those explored by coatis. *Callithrix penicillata* and *P. superciliaris* had the smallest overlap, with 50 and 39%, respectively (Table 3). *C. thous* and *N. nasua* had a much larger home range than the other frugivores (Table 3).

4. Discussion

4.1. *Effectiveness of seed dispersal by coatis*

Disperser effectiveness is defined by the quantity of seeds dispersed, which depends on number of visits and number of seeds dispersed per visit, as well as quality of seed dispersal, which in turn depends on treatment of seeds in the gut and on quality of deposition sites (Schupp, 1993). Because coatis have a large body size and forage in large groups (up to 70 individuals at the study site), a single visit can be enough to promote removal of a large proportion of a fruit crop. While some individuals remove fruits directly from the plant, others remain on the ground and consume dropped fruits. Thus, coatis' foraging behaviour likely contributes to reduced seed waste compared to exclusively arboreal or terrestrial frugivores. In addition, seeds in their faeces remained intact and viable. In the case of *Myrcia guajavaefolia*, germination success was strongly reduced in the presence of pulp. Pulp removal during ingestion increased germination success up to 50%. The germination success of ingested seeds was not as high as that of uningested seeds without pulp, which may be due to the fact that ingested seeds maintained some pulp attached to the seed. Pulp may contain germination inhibitors or may increase the chances of seed infection by fungal or other pathogens (Traveset, 1998). Pulp removal can be an important frugivore service to the plant fitness, but its effect is rarely determined (Samuels and Levey, 2005).

Post-dispersal fate of seeds and seedlings is another critical determinant of offspring survival for many plant species (Hampe, 2004). Because animals often deposit seeds from more than one species in their faeces, they can influence post-dispersal fate of seeds through effects on interspecific seedling competition (Loiselle, 1990). This is unlikely for seeds dispersed by coatis, as they eat a large variety of food items (Alves-Costa et al., 2004), so that fruit consumption is interposed by consumption of other resources and thus seeds of different plants are often deposited in different faecal pellets.

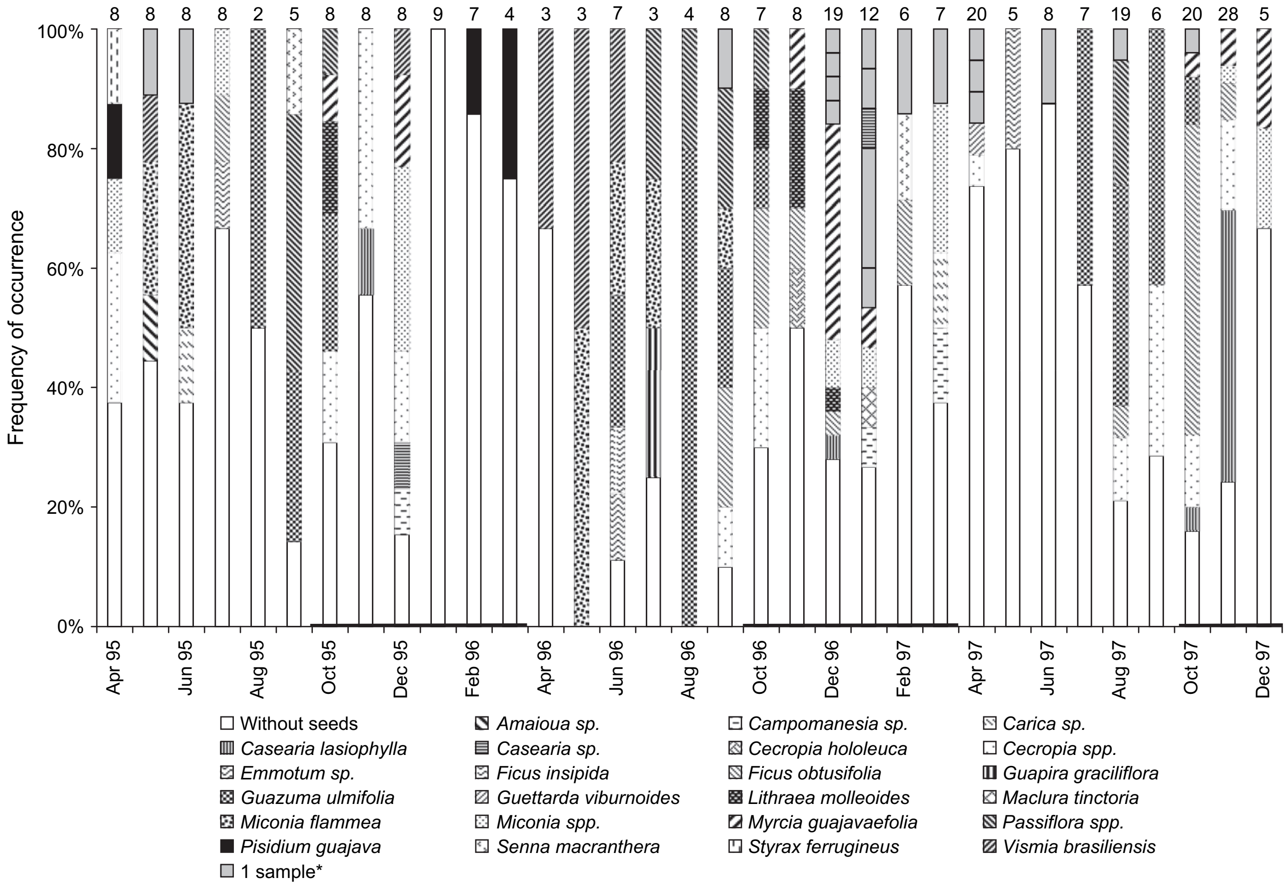


Fig. 3 – Monthly percentage of faeces without seeds and with seeds of different species. Numbers above the bars indicate numbers of faecal samples. Wet seasons are indicated with thicker lines in the x axis. *Unidentified species occurring in just one sample.

Other determinants of post-dispersal fate of seeds are the density of seeds in faeces and deposition sites. Coatis defecated on the soil, trunks, stones and paved ground while on the soil or in the canopy. They did not seem to have any preference for defecation sites (see also Kaufmann, 1962), so that the spatial distribution of defecations mainly depends on the time coatis dispend in each habitat. In the study site, coatis used all available habitats, but most group locations were recorded in cerrado (51%) and forest (35%) habitats, followed by areas with infrastructure for visitors (17%) and grasslands (7%) (CPAC, unpublished telemetry data of a group with about 25 individuals located weekly between May 1998 and May 1999). Based on the percentage of cover of the different habitats in the study site (respectively, 30%, 40%, 4% and 30%), cerrado and areas with infrastructure were used proportionately more often than expected, grasslands much less, and forest a little less. Thus, early successional species (59% of the dispersed species) can succeed in reaching open areas when dispersed by coatis. In addition, seed dispersal by coatis probably promotes seed deposition far from the parent plant because coatis walk large daily distances (about 2 km in the study area, CPAC, unpubl. telemetry data; 2.3–4.6 km to *N. narica*, Valenzuela and Ceballos, 2000) and have relatively long retention times (2–3 h for two three-month-old puppies; CPAC, pers. observation). Thus, species that need to escape from near the parent plant can also benefit from seed dispersal by coatis.

Coatis can also promote a reduction in mortality by density-dependent factors as seeds were frequently deposited in clumps with less than 50 seeds. However, small seeds were frequently dropped in clumps with hundreds of seeds. Thus, for small seeds, dispersal by coatis may not be efficient in reducing density-dependent mortality. However, species frequently dispersed in dense seed clumps, such as the genera *Cecropia* and *Ficus* (see Knogge and Heymann, 2002; Wehncke et al., 2003, for *Ficus* review Shanahan et al., 2001), may have evolved chemical or mechanical defences against density-dependent mortality factors (Howe, 1989). Climax species frequently have large seeds and can escape from both distance- and density-dependent mortality factors when dispersed by coatis. However, coatis did not disperse these species during this study. Studies on larger and well-conserved fragments are needed to address whether our results are due to coati limitation on seed dispersal or if they reflect the vegetation structure of the study site.

Table 2 – Trial duration, mean time to germination ± SD (sample size) and mean percentage of germination ± SD (sample size) of seeds defecated by coatis and of uningested seeds (without and with fruit pulp). Sample size is the number of Petri dishes (each dish had 30 seeds). Significant differences (P < 0.05) are in bold-font

Species	Trial duration (d)	Time to germination (days)			P-value	Germination percentage			P-value	
		Ingested	Uningested		(ingested vs. uningested)	Ingested	Uningested		(ingested vs. uningested)	(uningested with × without pulp)
			Without	With pulp			Without	With pulp		
Casearia lasiophylla	20[a]	4.0 ± 1.0 (12)	5.5 ± 1.7 (4)	–	0.14	81.4 ± 17.2 (13)	84.2 ± 11.7 (4)	–	1.0	–
Cecropia pachystachya	82	6.8 ± 2.1 (13)	6.9 ± 2.4 (13)	–	0.73	69.3 ± 23.0 (13)	76.3 ± 19.0 (15)	–	0.31	–
Ficus obtusifolia	78	8.7 ± 3.6 (13)	12.2 ± 3.4 (6)	–	0.06	86.0 ± 12.4 (13)	80.0 ± 23.3 (6)	–	0.72	–
Guazuma ulmifolia	130	38.7 ± 18.9 (8)	35.5 ± 22.6 (22)	–	0.72	7.3 ± 12.6 (8)	7.7 ± 14.0 (23)	–	0.55	–
Lithraea molleoides	44	6.0 (1)	5.0 ± 2.8 (2)	4.5 ± 1.9 (8)	0.40	3.3 ± 4.6 (2)	26.7 ± 28.3 (2)	13.0 ± 13.0 (10)	0.34	–
Myrcia guajavaefolia 1996	45	2.5 ± 0.7 (2)	1.8 ± 1.0 (8)	–	0.31	**73.3 ± 9.3 (2)**	**99.6 ± 1.0 (8)**	**24.7 ± 14.7 (12)**	**0.01**	**< 0.001**
M. guajavaefolia 1997	52	–	–	–	–	–	**79.0 ± 34.7 (12)**	**19.3 ± 8.3 (6)**	–	**0.02**

a Trials terminated due to fungal infection.

4.2. *Temporal patterns of seed defecation*

Coatis dispersed seeds of a large diversity of plant species but few were recorded repeatedly in their faeces, providing evidence of opportunistic fruit consumption. The most frequently consumed fruit species were recorded up to 3 or 4 months per year, generally encompassing dry and wet seasons. All the most frequent species in faeces were consumed during the dry season, suggesting the importance of plants fruiting in this season for the maintenance of coati populations. *Guazuma ulmifolia*, for example, reached the largest monthly and total consumption frequencies and was consumed just during the dry season. Among the most consumed species are also those of the genera *Ficus* and *Cecropia*, recorded as frequent in the diet of several other vertebrates, including bats, primates, carnivores and birds (Estrada and Coates-Estrada, 1986; Kays, 1999; Knogge and Heymann, 2002; Shanahan et al., 2001; Wehncke et al., 2003).

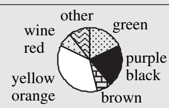
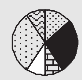
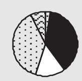
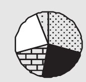
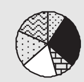
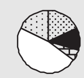
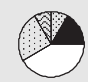
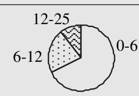
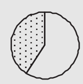
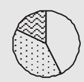
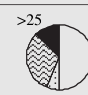
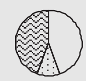
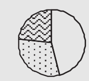
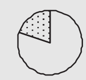
4.3. *Seed dispersal redundancy among frugivores and implications for conservation*

The Atlantic forest is highly fragmented. In the state of São Paulo, more than 70% of protected forest fragments are <1000 ha and 80% of unprotected fragments are <50 ha (Cullen, 1997; Ditt, 2002). Thus, the size of the Mangabeiras Park is similar to several other Atlantic forest remnants. In fragments like these, the residual large-bodied frugivores are mainly the Rusty-margined Guan *Penelope superciliaris* (Willis, 1979; Pizo, 2004), and the mammals *Didelphis* spp., *Callithrix* spp., *Cerdocyon thous*, and *Nasua nasua* (the last three can persist in fragments as small as 9 ha; see Gheler-Costa, 2002). Sometimes, *Cebus* spp. and *Allouata* spp. are also reported from small fragments (Chiarello, 1999, 2000, 2003; Pontes et al., 2006). Thus, in these fragments, large-seeded and/or large-fruited plant species may depend exclusively on these few frugivorous species for seed dispersal services.

Based on attributes evaluated in this study, the seed dispersal services provided by coatis are more similar to those provided by *C. thous*, as both dispersed species of similar seed size and fruit colour and both have the potential to disperse seeds over large distances. *P. superciliaris* consumed a large number of species and provided seed dispersal services to species with other fruit morphologies than coatis. As expected for birds, *P. superciliaris* consumed mainly plants with red and black fruits (74% of the fruits vs. 28% in the case of coatis) while coatis and other mammals concentrated mainly in plants with yellow fruits followed by green, black or brown fruits.

The residual frugivorous fauna analysed here failed to guarantee seed dispersal services to species with seeds >25 mm diameter. Bats, like *A. lituratus*, are the only exception, because they carry seeds outside the body and thus are able to disperse larger seeds. This may also be true for some rodent species, although they are mainly seed predators (Jansen and Forget, 2001). Therefore, species with seeds

Table 3 – Traits related to fruit consumption by some frugivorous species common in forest fragments in southeastern Brazil. Data source is Appendix 1

Parameters \ Frugivores	*Nasua nasua*	26 small bird species	*Penelope superciliaris*	*Artibeus lituratus*	*Callithrix penicillata*	*Cerdocyon thous*	*Didelphis albiventris*
% of faeces with seeds	54.5	--	96.8	--	--	43-69	71.8
Total of consumed fruit species (range)[a]	53	36	52	20 (11-13)	15	27 (6-14)	18
Fruit colour of plant species consumed[b]							
Seed size (mm) of dispersed seeds[b]							
% overlap with *N. nasua* (Schoener's index)	--	66	39	70	50	63	61
Home range (x±SD or min-max, ha)[c]	90.6-141.6	?	~11	?	8.3-18.5	532±272 (48-1042)	0.6-2.7

a Range was presented when more than one study was analysed.
b Data compiled from Appendix 2.
c Data compiled from: Alves-Costa, unpublished data from Mangabeiras Park; Guix and Ruiz (1997); Miranda and Faria (2001); MacDonald and Courtenay (1996); Cáceres (2003) for the *Didelphis aurita*.

>25 mm are probably the most vulnerable to a collapse of their reproductive process in defaunated fragments where, despite of the presence of residual frugivorous species, they may depend exclusively on large bats to seed dispersal services.

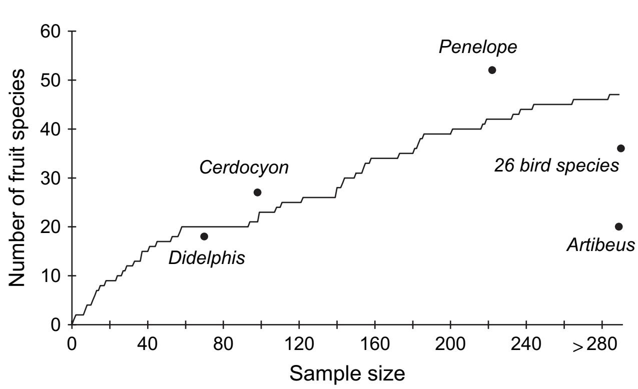


Fig. 4 – Number of fruit species in relation to sample size for coatis (line) and other frugivores (points). To small birds the sample unit is feeding bout, to *A. lituratus* is feeding roost and to others species is faeces. See Appendix 1 for detailed information about each study.

All residual frugivores provided seed dispersal to small seeded species (<15 mm), which could be less affected by large-bodied frugivore defaunation. So, for these species we would expect a high redundancy on seed dispersal services among frugivores. However, as most of residual frugivores are small, and consequently have shorter seed retention time and smaller home range (Lindstedt et al., 1986; Traveset, 1998), seed dispersal services provided by them may become restricted to short distances. This may result in populations of endozoochorous plant species that are tightly clumped and with limited seed flow through the landscape, resulting in spatial aggregation of close relatives, and a severe reduction in genetic diversity (Pacheco and Simonetti, 2000; Jordano and Godoy, 2002). Thus, in a fragmented landscape, the disperser effectiveness could also depend on the frugivores' ability to move long distances and cross matrix habitat. Most small birds, for example, are usually unable to cross more than 100–200 m of inhospitable habitat (Offerman et al., 1995; Bierregaard and Dale, 1996; Silva et al., 1996). Procyonidae and Canidae are mesopredators that thrive in disturbed landscapes and are capable of movements between islands of vegetation through a relatively inhospitable matrix (Crooks, 2002). They routinely ingest fleshy fruits (e.g. Bisbal, 1986; Herrera, 1989; Motta-Junior et al., 1994; Facure and Monteiro-Filho, 1996; Kays, 1999; Engel, 2000) and can assume a crucial role as alternative seed dispersers in defaunated and fragmented landscapes. In Atlantic Forest fragments, these families are represented mainly by *N. nasua* and *C. thous*. Both are habitat generalists and move long distances daily (coatis: about 2 km in the study area, pers. observation; *N. narica*: about 2–4 km, Valenzuela and Ceballos, 2000; *C. thous*: about 10 km, Juarez and Marinho-Filho, 2002). Such opportunistic fruit consumers, together with bats and guans, may then provide crucial seed dispersal services for the maintenance of a relatively high variety of plant populations and species in remaining areas of this highly fragmented biome.

5. Conclusion

In a fragmented and defaunated forest scenario seed disperser effectiveness must be defined not only by the quantity and quality of seeds dispersed, but also by the frugivores' ability to persist in these landscapes and to guarantee some seed flux among forest patches. Coatis can be a key to seed dispersal processes in this context because: (a) they are tolerant to and even benefit from some anthropogenic disturbances; (b) they are able to ingest and disperse intact seeds of a large variety of plants with seeds up to 2.5 cm; (c) they have a large body size, forage in groups, and have ability to forage in all strata of the forest, so that they can remove a large proportion of a plant's seed crop; and (d) they move large distances daily using different habitats and forest patches. Therefore, coatis can be an important component of the patchy landscape where they occur, potentially promoting regeneration of disturbed sites and gene flow between forest fragments. In the Atlantic Forest, other complementary seed disperser species in this context are frugivorous bats, like *Artibeus lituratus*, and the canid *Cerdocyon thous*. Within a defaunated fragment, *Penelope superciliaris* also dispersed a large variety of species and could offer complementary seed dispersal services as preferred fruits whose colours were little attractive to coatis.

Acknowledgements

We thank G.C. Araújo, J.E. Côrtes-Figueira, G.A.B. Fonseca, R.P. Martins, and J.A. Santos for their substantial support; and the administration of the Parque das Mangabeiras for logistic and financial support. We also thank C. Christófaro, A. Siqueira and R. Mendes for help in field and laboratory activities, J.A. Lombardi and R. Stehmann for plant identification and A.G. Chiarello, T.R. Engel, C. Knogge, D.J. Levey and R.J. Young for valuable suggestions on the manuscript. Financial support was provided by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais), FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) and PMBH (Prefeitura Municipal de Belo Horizonte).

Appendix 1. Details about the studies included in redundancy analyses

Frugivores/Study conditions	Duration (months)	Method	Habitat	Area size (ha)	References
Nasua nasua	33	288 faeces	Semidecidual forest Cerrado/Field	236	This study
26 small bird species	44	385 feeding bouts	Semidecidual forest	250	Galetti and Pizo, 1996
Penelope superciliaris	20	223 faeces	Semidecidual forest	245	Zaca, 2003
Artibeus lituratus	21	Seeds under 144 feeding roosts	Semidecidual forest	250	Galetti and Morelatto, 1994
	13	Seeds under 189 feeding roosts	Rain forest	8	Zórtea and Chiarello, 1994
Callithrix penicillata	10	436 h of direct observation	Cerrado	9800	Miranda and Faria, 2001
Cerdocyon thous	10	41 faeces	Cerrado	150	Motta-Junior et al., 1994
	120	19 stomachs	Semidecidual forest	–	Facure and Monteiro-Filho, 1996
	7	39 faeces	Semidecidual forest/ Cerrado	20,000	Juarez and Marinho-Filho, 2002
Didelphis albiventris	12	71 faeces	Araucarian forest	2.5 and 5	Cáceres, 2002

Appendix 2. Fruit colour, fruit size and seed size of plant species whose fruits are consumed by some bird or mammal species common in forest fragments in southeastern Brazil. Data compiled from references of Appendix 1

Plant species	Plant family	Fruit color class	Fruit size (mm)	Seed size (mm)	26 bird species	*Artibeus lituratus*	*Callithrix penicillata*	*Cerdocyon thous*	*Didelphis albiventris*	*Nasua nasua*	*Penelope superciliaris*
Aegiphila sellowiana	Verbenaceae	Wine-red	7	5							X
Alchornea triplinervia	Euphorbiaceae	Wine-red	8	5							X
Alibertia sp.	Rubiaceae						X				
Allagoptera arenaria	Arecaceae	Yellow-orange	25	20				X			
Allophyllus sp.	Sapindaceae										X
Amaioua guianensis	Rubiaceae	Wine-red	20	4				X		X	X
Anacardium humile	Anacardiaceae	Yellow-orange	20	17				X			
Andira sp.	Fabaceae					X					
Annona crassiflora	Annonaceae	Green	140	18				X			
Blepharocalyx salicifolius	Myrtaceae	Wine-red	10	5			X				
Brosimum gaudichaudii	Moraceae	Yellow-orange	36	21			X				
Cabralea canjerana	Meliaceae	Brown	27	11	X						
Callophyllum brasiliensis	Clusiaceae	Green	28	1.8		X					
Calyptranthes clusiifolia	Myrtaceae	Wine-red	7.7	5							X
Campomanesia guazumaefolia	Myrtaceae	Yellow-orange	25	10							X
Campomanesia sp.	Myrtaceae	Yellow-orange						X			
Campomanesia sp.	Myrtaceae	Yellow-orange		4.0						X	
Carica papaya	Caricaceae	Yellow-orange	150	6				X			
Carica sp.	Caricaceae	Yellow-orange		4.5						X	
Casearia lasiophylla	Flacourtiaceae	Yellow-orange	7.5	5						X	
Casearia sylvestris	Flacourtiaceae	Yellow-orange	4	2							X
Casearia sp.	Flacourtiaceae									X	
Cecropia glaziovi	Cecropiaceae	Brown	140	2.5						X	
Cecropia hololeuca	Cecropiaceae	Purple-black	160	3		X				X	
Cecropia pachystachya	Cecropiaceae	Brown	130	2	X	X				X	
Cestrum sp.	Solanaceae				X						
Chamissoa altissima	Amaranthaceae	Other	5	4	X						
Chrysophyllum gonocarpum	Sapotaceae	Yellow-orange	28	13		X					
Citharexylum myrianthum	Verbenaceae	Wine-red	11	10	X						
Citrus sp.*	Rutaceae								X		
Coccocypselum sp.	Rubiaceae										X
*Coffea arabica**	Rubiaceae	Wine-red	13	10							X
Copaifera langsdorffi	Caesalpiniaceae	Purple-black	14	12	X						X
Cordia sellowiana	Boraginaceae	Yellow-orange	13	10							X
Cordia sp.	Boraginaceae				X						
Cryptocarya aschersoniana	Lauraceae	Yellow-orange	20.4	17.2						X	
Cucumis sp.	Cucurbitaceae								X		
Cupania vernalis	Sapindaceae	Purple-black	20	11							X
Cyphomandra corymbiflora	Solanaceae								X		
Daphnopsis brasiliensis	Thymeliaceae	Other	13.6	12							X
Dendropanax cuneatum	Araliaceae	Purple-black	10	4	X						
Didymopanax angustissimum	Araliaceae	Wine-red	8.3	5.8							X

(continued on next page)

(continued)

Plant species	Plant family	Fruit color class	Fruit size (mm)	Seed size (mm)	26 bird species	*Artibeus lituratus*	*Callithrix penicillata*	*Cerdocyon thous*	*Didelphis albiventris*	*Nasua nasua*	*Penelope superciliaris*
Didymopanax macrocarpum	Araliaceae	Wine-red	14	7				X			
Diospyros inconstans	Ebenaceae	Purple-black	22.3	18							X
Duguetia furfuraceae	Annonaceae	Yellow-orange	50	14			X				
Emmotum sp.	Icacinaceae	Green	23	11						X	
*Eriobothria japonica**	Rosaceae	Yellow-orange	20	11		X					
Erythroxylum argentinum	Erythroxyllaceae	Wine-red	10.3								X
Erythroxylum deciduum	Erythroxylaceae	Wine-red	10	8					nd		
Eugenia brevipedunculata	Myrtaceae	Purple-black									X
Eugenia involucrata	Myrtaceae	Wine-red	28	10							X
Eugenia sp.	Myrtaceae							X			X
Eugenia uniflora	Myrtaceae	Wine-red	28	13							X
Eugenia uvalha	Myrtaceae	Yellow-orange	21.7								X
Ficus enormis	Moraceae	Wine-red	13	1.3		X					
Ficus glabra	Moraceae	Green	12.5	1		X					
Ficus insipida	Moraceae	Green	24	2						X	
Ficus luschnatiana	Moraceae	Purple-black	14.5	1.1	X	X					
Ficus obtusifolia	Moraceae	Green	17	1						X	
Ficus sp.	Moraceae							X			
*Fragaria vesca**	Rosaceae	Wine-red	15	1				X			
Gomidesia affinis	Myrtaceae	Purple-black	21	12	X						
Guapira graciliflora	Nyctaginaceae	Wine-red	15	12			X			X	
Guapira opposita	Nyctaginaceae	Wine-red	9.3	8							X
Guazuma ulmifolia	Sterculiaceae	Purple-black	22.5	2.7						X	
Guettarda viburnoides	Rubiaceae	Yellow-orange	22	13						X	X
Holocalyx balansae	Fabaceae	Green	30	23		X					
*Hovenia dulcis**	Rhamnaceae	Brown	35	6				X			
Ilex sp.	Aquifoliaceae		6.4								X
Inga sp.	Fabaceae						X			X	
Inga uruguensis	Fabaceae	Other	80	18		X					
Lantana sp.	Verbenaceae				X						
Leandra australis	Melastomataceae	Purple-black	8.5	1					X		
Lithraea molleoides	Anacardiaceae	Other	6	3.5						X	po
Maclura tinctoria	Moraceae	Green	24	2.7	X	X				X	
*Mangifera indica**	Anacardiaceae	Yellow-orange	80	55		X		nd	nd	nd	
Maytenus aquifolium	Celastraceae	Yellow-orange	12	5	X						
Melothria cucumis	Cucurbitaceae	Green	47	5					X		
Miconia albicans	Melastomataceae	Other	6	1.2			X			X	
Miconia cinnamomifolia	Melastomataceae	Purple-black	4	1.3							X
Miconia discolor	Melastomataceae	Purple-black	4	2	X						
Miconia elegans	Melastomataceae	Wine-red	4	1	X						
Miconia ferruginata	Melastomataceae	Other	5	1.5			X				
Miconia flammea	Melastomataceae		6	4						X	
Miconia trianaei	Melastomataceae	Purple-black	6.0	0.9			po			X	po
Miconia sp.	Melastomataceae				X		X	X		X	
Momordica charantia	Euphorbiaceae	Yellow-orange	80	9	X						

*Morus nigra**	Moraceae	Purple-black	19	2					X		
*Musa acuminata**	Musaceae	Yellow-orange	10					X			
Myrcia guajavaefolia	Myrtaceae	Purple-black	8	6						X	
Myrcia rostrata	Myrtaceae	Purple-black	8	5							X
Myrcia sp.	Myrtaceae		13.7								X
*Myrciaria cauliflora**	Myrtaceae	Purple-black	27	8		X		X			
Myrsine coriacea	Myrsinaceae	Purple-black	3.4	3							X
Ocotea cf. *macropoda*	Lauraceae										
Ocotea corimbosa	Lauraceae	Green	10	8	X						X
Ocotea diospyrifolia	Lauraceae	Purple-black	20	15							
Palicourea sp.	Rubiaceae				X						
Parinari obtusifolia	Lecythidaceae	Brown	4					X			
Passiflora actinia	Passifloraceae	Yellow-orange	35	4					X		
Passiflora edulis	Passifloraceae	Yellow-orange	50	7.5						X	
Passiflora sp.	Passifloraceae						X		X	X	
Paullinia rhomboidea	Sapindaceae	Wine-red	13	4	X						
Paullinia sp.	Sapindaceae				X						
Pera glabrata	Euphorbiaceae	Wine-red	13	5	X						
Pereskia aculeata	Cactaceae	Yellow-orange	11	5	X						
*Persea americana**	Lauraceae	Green	100	50				nd			
Persea cf major	Lauraceae		10	8	X						
Persea pyrifolia	Lauraceae	Purple-black	9.5	7							X
Piper aduncum	Piperaceae	Green	117	1						X	
Piper gaudichaudianum	Piperaceae	Other	100	1					X		
Piper sp.	Piperaceae			1	X						
Pouteria sp.	Sapotaceae										X
Protium heptaphyllum	Burseraceae	Wine-red	20	12	X						
Prunus myrtifolia	Rosaceae	Purple-black	10.9	9.7							X
Prunus sellowii	Rosaceae	Wine-red	12.6	8							X
*Psidium guajava**	Myrtaceae	Yellow-orange	50	5		X		X		X	
Psidium guineense	Myrtaceae	Green	20	5				X			
Psidium sp.	Myrtaceae							X			
Psychotria sessilis	Rubiaceae	Purple-black	7								X
Rhipsalis sp.	Cactaceae				X						
Rubus erythrocladus	Rosaceae	Wine-red	15	3					X		
Rubus rosaefolius	Rosaceae	Wine-red	13.3	1.5					X		X
Rubus sp.	Rosaceae				X						
Rudgea jasminoides	Rubiaceae	Yellow-orange	10	6.3							X
Saccharum officinalis	Poaceae		3.6	3.5				X			
Salacia crassifolia	Hippocrateaceae	Yellow-orange	27	7				X			
Sapium glandulatum	Euphorbiaceae	Wine-red	13	4							X
Scheflera macrocarpum	Araliaceae	Purple-black	11				X				
Schinus terebinthifolius	Anacardiaceae	Wine-red	4.7	3							X
Senna macranthera	Leguminosae	Purple-black	230	7						X	
Simarouba versicolor	Simaroubaceae	Green	30	23			X				
Siphoneugena densiflora	Myrtaceae	Purple-black	15.9	9.5			X				
Smilax sp.	Liliaceae										X
Solanum americanum	Solanaceae	Purple-black	5	1				X			

(continued on next page)

(continued)

Plant species	Plant family	Fruit color class	Fruit size (mm)	Seed size (mm)	26 bird species	*Artibeus lituratus*	*Callithrix penicillata*	*Cerdocyon thous*	*Didelphis albiventris*	*Nasua nasua*	*Penelope superciliaris*
Solanum granulosoleprosum	Solanaceae	Green	11	2		X					
Solanum inaequale	Solanaceae	Yellow-orange	15			X					
Solanum lycocarpum	Solanaceae	Green	120	7				X			
Solanum maioranthum	Solanaceae		4						X		
Solanum sanctaecatharinae	Solanaceae	Purple-black	8.5	3.18					X		
Solanum spp.	Solanaceae							X	X		X
Strychnos brasiliensis	Loganiaceae	Wine-red	12.6	9							X
Styrax ferrugineus	Styracaceae	Purple-black	9	7						X	
Styrax pohlii	Styracaceae	Purple-black	20	15							X
Syagrus romanzoffiana	Arecaceae	Yellow-orange	24	22		po		X	nd	po	po
Symplocos laxiflora	Symplocaceae	Other	18.7								X
Symplocos mosenii	Symplocaceae	Purple-black									X
*Syzygium jambolana**	Myrtaceae	Purple-black	40	20		X	X				
Talauma ovata	Magnoliaceae	Wine-red	120	8	X						
Tapura amazonica	Dichapetalaceae	Yellow-orange	20	18			nd				
*Terminalia cattapa**	Combretaceae	Green	60	40		X					
Trema micrantha	Ulmaceae	Yellow-orange	2.5	2.1	X						
Trichilia claussenii	Meliaceae	Wine-red	12	10	X						
Urera baccifera	Urticaceae	Other	3.2	3	X						
Vassobia breviflora	Solanaceae	Yellow-orange	7	1					X		
Vismia brasiliensis	Guttiferae	Yellow-orange	8	3						X	
Vitex polygama	Verbenaceae	Purple-black	17.5	12							X
*Vitis vinifera**	Vitaceae		10.1					X			
Xylopia brasiliensis	Annonaceae	Green	28	8	X						
Zanthoxylum hyemale	Rutaceae	Purple-black	7	3	X						
Zanthoxylum rhoifolium	Rutaceae	Purple-black	4	2.5							X

* Cultivated species; nd, seed non dispersed; po, personal observation (CPAC).

REFERENCES

Alves-Costa, C.P., 2004. Efeitos da defaunação de mamíferos herbívoros na comunidade vegetal. PhD thesis. Universidade Estadual de Campinas, Campinas, SP, Brazil.

Alves-Costa, C.P., Fonseca, G.A.B., Christófaro, C., 2004. Variation in the diet of the brown-nosed coati (*Nasua nasua*) in southeastern Brazil. J. Mamm. 85, 478–482.

Bierregaard, R., Dale, V.H., 1996. Island in an everchanging sea: the ecological, socioeconomic dynamics of Amazonian Rainforest fragments. In: Schelhas, J., Greenberg, R. (Eds.), Forest Patches in Tropical Landscapes. Island Press, Washington, pp. 187–204.

Bisbal, F.J., 1986. Food habits of some neotropical carnivores in Venezuela (Mammalia, Carnivora). Mammalia 50, 329–339.

Bisbal, F.J., 1993. Human impact on the carnivores of Venezuela. Stud. Neotrop. Fauna Environ. 28, 145–156.

Cáceres, N., 2002. Food Habits and seed dispersal by the white-eared opossum *Didelphis albiventris* in southern Brazil. Stud. Neotrop. Fauna Environ. 37, 97–104.

Cáceres, N., 2003. Use of the space by the opossum *Didelphis aurita* Wied-Newied (Mammalia, Marsupialia) in a mixed forest fragment of southern Brazil. Rev. Bras. Zool. 20, 315–322.

Câmara, E.M.V.C, Lessa, L.G., 1993. Amostragem diversificada da mastofauna do Parque das Mangabeiras. Technical report. Partially published in http://www.pbh.gov.br/mangabeiras/index01.htm. Consulted in 9 April/2005.

Chiarello, A.G., 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol. Cons. 89, 71–82.

Chiarello, A.G., 2000. Conservation value of a native forest fragment in a region of extensive agriculture. Rev. Bras. Biol. 60, 237–247.

Chiarello, A.G., 2003. How do howler monkeys cope with habitat fragmentation? In: Marsh, L.K. (Ed.), Primates in Fragments: Ecology and Conservation. Kluwer Academic Plenum Publishers, New York, pp. 283–303.

Cordeiro, N.J., Howe, H.F., 2001. Low recruitment of trees dispersed by animals in African forest fragments. Conserv. Biol. 15, 1733–1741.

Crooks, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv. Biol. 16, 488–502.

Cullen, L. Jr., 1997. Hunting and biodiversity in Atlantic forest fragments, São Paulo, Brazil. Masters dissertation, University of Florida, Florida, USA.

Cullen Jr., L., Bodmer, R.E., Valladares-Pádua, C., 2000. Effects of hunting in habitat fragments of the Atlantic forests. Brazil. Biol. Conserv. 95, 49–56.

Dirzo, R., Miranda, A., 1990. Contemporary neotropical defaunation and forest structure, function, and diversity – a sequel to John Terborgh. Conserv. Biol. 4, 444–447.

Ditt, E.H., 2002. Fragmentos Florestais no Pontal do Paranapanema. Meio Ambiente Vol. 207, Annablume editora, São Paulo.

Duncan, R.S., Chapman, C.A., 2002. Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB International, Wallingford, pp. 437–450.

Engel, T.R., 2000. Seed Dispersal and Natural Forest Regeneration in a Tropical Lowland Biocoenosis (Shimba Hills, Kenya). Logos, Berlin, GE.

Estrada, A., Coates-Estrada, R., 1986. Frugivory by howling monkeys (*Allouata palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. In: Estrada, A., Fleming, T.H. (Eds.), Frugivory and Seed Dispersal. Dr. W. Junk Publishers, Dordrecht, pp. 93–104.

Facure, K.G., Monteiro-Filho, E.L.A., 1996. Feeding habitats of the crab-eating fox, *Cerdocyon thous* (Carnivora, Canidae), in a suburban area of southeastern Brazil. Mammalia 60, 147–149.

Galetti, M., Morellato, L.P.C., 1994. Diet of the large fruiting bat *Artibeus lituratus* in Southeast Brazil. Mammalia 58, 661–665.

Galetti, M., Pizo, M.A., 1996. Fruit eating birds in a forest fragment in southeastern Brazil. Ararajuba 4, 71–79.

Galetti, M., Alves-Costa, C.P., Cazetta, E., 2003. Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. Biol. Conserv. 111, 269–273.

Gheler-Costa, C., 2002. Mamíferos não-voadores do Campus ''Luís de Queiróz'', da Universidade de São Paulo, em Piracicaba, Estado de São Paulo. Master dissertation, ESALQ. Universidade de São Paulo, Piracicaba, SP, Brazil.

Gompper, M.E., 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging cost and benefits. Behav. Ecol. 7, 254–263.

Gompper, M.E., Decker, D.M., 1998. Nasua nasua. Mammal. Sp. 580, 1–9.

Grime, J.P., Hillier, S.H., 1992. The contribution of seedling regeneration to the structure and dynamic of plant communities and larger units of landscape. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CAB International, Wallingford, pp. 349–364.

Guix, J.C., Ruiz, X., 1997. Weevil larvae dispersal by guans in southeastern Brazil. Biotropica 29, 522–525.

Hampe, A., 2004. Extensive hydrochory uncouples spatiotemporal patterns of seedfall and seedling recruitment in a 'bird-dispersed' riparian tree. J. Ecol. 92, 797–807.

Herrera, C.M., 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55, 250–262.

Howe, H.F., 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79, 417–426.

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13, 201–228.

Jansen, P.A., Forget, P.M., 2001. Scatterhoarding rodents and tree regeneration. In: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, M. (Eds.), Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer Academic Publishers, Netherlands, pp. 275–288.

Jordano, P., Godoy, J.A., 2002. Frugivore-generated seed shadow: a landscape view of demographic and genetic effects. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB International, Wallingford, pp. 305–321.

Juarez, K.M., Marinho-Filho, J., 2002. Diet, habitat use, and home ranges of sympatric canids in central Brazil. J. Mammal. 83, 925–933.

Kaufmann, J.H., 1962. Ecology and social behavior of the coati, Nasua narica, on Barro Colorado Island, Panama. PhD Thesis, University of California, California.

Kays, R.W., 1999. Food preferences of kinkajous (*Potos flavus*): a frugivorous carnivore. J. Mammal. 80, 589–599.

Knogge, C., Heymann, E.W., 2002. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. Fol. Primat. 74, 33–47.

Krebs, C.J., 1989. Ecological Methodology. Harper and Row, New York.

Lessa, L.G., Câmara, E.M.V.C., Nascimento, L.B., 1998. Novas ocorrências de mamíferos para o parque das Mangabeiras (Belo Horizonte, Minas Gerais). Bios: Cadernos do Departamento de Ciências Biológicas da PUC. Belo Horizonte 6, 69–72.

Lindstedt, S.L., Miller, B.J., Buskirk, S.W., 1986. Home range, time and body size in mammals. Ecology 67, 413–418.
Loiselle, B.A., 1990. Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. Oecologia 82, 494–500.
Lorenzi, H., 2002. Árvores Brasileiras. In: Manual de identificação e Cultivo de Plantas Arbóreas do Brasil, second ed., Vol. 1 and 2. Instituto Plantarum, Nova Odessa.
MacDonald, D.W., Courtenay, O., 1996. Enduring social relationships in a population of crab-eating zorros, *Cerdocyon thous*, in Amazonian Brazi (Carnivora, canidae). J. Zool. 239, 329–355.
Melo Jr., T.A., Freitas, C.T., Vianna, C.R., 1996. Aves do Parque das Mangabeiras. Technical report. Partially published in http://www.pbh.gov.br/mangabeiras/index01.htm. (consulted in 9 April/2005).
Miranda, G., Faria, D., 2001. Ecological aspects of Black-Pincelled Marmoset (*Callithix penicillata*) in the Cerradão and Dense Cerradão of the Brazilian Central Plateau. Braz. J. Biol. 61, 397–404.
Motta-Junior, J.C., Lombardi, J.A., Talamoni, S.A., 1994. Notes on Crab-eating fox (*Dusicyon thous*): seed dispersal and food habits in southeastern Brazil. Mammalia 58, 156–159.
Offerman, H., Dale, V.H., Pearson, S.M., Bierregaard Jr., R.O., O'Neill, R.V., 1995. Effects of forest fragmentation on neotropical fauna: current research and data availability. Environ. Rev. 3, 191–211.
Pacheco, L., Simonetti, J.A., 2000. Genetic structure of a mimosoid tree deprived of its seed disperser, the spider monkey. Conserv. Biol. 14, 1766–1775.
Pedersoli, J.L., 1997. Sub-projeto – Vegetação. Resultados e relação das plantas do Parque das Mangabeiras. Technical report. Partially published in http://www.pbh.gov.br/mangabeiras/index01.htm. (consulted in 9 April/2005).
Pizo, M.A., 1997. Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic Forest of southeastern Brazil. J. Trop. Ecol. 13, 559–578.
Pizo, M.A., 2004. Frugivory and habitat use by fruit-eating birds in a fragmented landscape of southeast Brazil. Ornitol. Neotrop. 15, 117–126.
Pontes, A.R.M., Peres, P.H.A.L., Normande, I.C., Brazil, C.M., 2006. Mamíferos. In: Porto, K.C., Almeida-Cortez, J.J.S., Tabarelli, M. (Eds.), Diversidade Biológica e Conservação da Floresta Atlântica ao Norte do Rio São Francisco. Ministério do Meio Ambiente, Brasília, DF, pp. 303–324.
Roldán, A.I., Simonetti, J.A., 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. Conserv. Biol. 15, 617–623.
Russell, J.K., 1982. Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resource. In: Leight Jr., E.G., Rand, A.S., Windsor, D.M. (Eds.), The Ecology of a Tropical Forest – Seasonal Rhythms and Long-Term Changes. Smithsonian Institution Press, Washington, pp. 413–431.
Samuels, I.A., Levey, D.J., 2005. Effects of gut passage on seed germination: do experiments answer the question they ask? Funct. Ecol. 19, 365–368.
Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108, 15–29.
Shanahan, M., Samson, S.O., Compton, S.G., Corlett, R., 2001. Fig-eating by vertebrate frugivores: a global review. Biol. Rev. 76, 529–572.
Silva, J.M.C., Uhl, C., Murray, G., 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned pastures. Conserv. Biol. 10, 419–503.
Terborgh, J., 1990. The role of felid predators in Neotropical forest. Vida Silv. Neotr. 2, 3–5.
Terborgh, J., Wright, S.J., 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. Ecology 75, 1829–1833.
Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. Persp. Plant Ecol. Evol. Syst. 1/2, 151–190.
Valenzuela, D., Ceballos, G., 2000. Habitat selection home range and activity of the white-nosed coati (*Nasua narica*) in a Mexican tropical dry forest. J. Mamm. 81, 810–819.
Wallace Jr., R.K., 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. Bethesda 110, 72–76.
Wanderley, M.G.L., Shepherd, G.J., Giulietti, A.M., 2002. Flora fanerogâmica do estado de São Paulo. Vol. 2 and 3, HUCITEC/FAPESP, São Paulo, SP, p. 391.
Wehncke, E.V., Hubbell, S.P., Foster, R.B., Dalling, J.W., 2003. Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. J. Ecol. 91, 677–685.
Willis, E.O., 1979. The composition of avian communities in remanescent woodlots in southern Brasil. Pap. Avul. Zool. 31, 1–25.
Willson, M., Traveset, A., 1992. The ecology of seed dispersal. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities, second ed. CAB International, Wallingford, pp. 85–110.
Zaca, W., 2003. Dieta de *Penelope superciliaris* Spix, 1825 (Aves, Cracidae) em um fragmento de mata semidecídua de altitude no sudeste brasileiro. Master dissertation, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais.
Zortéa, M., Chiarello, A.G., 1994. Observations on the big fruit-eating bat, *Artibeus lituratus*, in an Urban Reserve of South-east Brazil. Mammalia 58, 665–670.