



Exotic Plant Consumption by Black-Tufted Capuchin Monkeys (*Sapajus nigritus*) in an Urban Fragment of Atlantic Forest Across Two Wet Seasons

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Abstract

Cities near protected areas facilitate the introduction of exotic plants, reshaping ecological interactions, particularly those involving frugivore primates. Characterizing the consumption of exotic plants in urban areas is important to understand how primates persist under anthropogenic environments. We studied the diet of a group of black-tufted capuchin monkeys (*Sapajus nigritus*) living in Mata de Santa Genebra, an urban Atlantic Forest fragment in Brazil, in two consecutive wet seasons. Three decades ago, the capuchins at our study site relied partially on neighboring fields of *Zea mays*, which no longer exist at the time of our study. We recorded the capuchins' diet using field observations and fecal analyses in August 2019–March 2020 and October 2020–February 2021. The capuchins consumed 80 plant species, with a higher number of exotic species than previously (23 vs. 4). Most of the exotic species in the capuchins' diet during our study were urban and zoochorous. Pulp (35.7%) and aril fruits (23%) were the main items. Food items differed between wet seasons, but the species consumed did not. Exotic plant consumption varied across months and peaked in December. Also, exotic seeds, particularly those of *Psidium guajava* and *Morus nigra*, were abundant in feces. The availability, predictability, energetic value, and opportunistic use of resources in the city may explain the variation in exotic plant consumption across months. Exotic seeds in feces indicate potential seed dispersal



Badges earned for open practices: Open Data and Open Analytical Code. Experiment materials and data are available in the repository at ____.

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within the reserve. Our findings highlight how dietary flexibility and the urban matrix reshape capuchin monkey feeding ecology through the incorporation of exotic plants.

Keywords Feeding · Diet · Primates · Invasive plants · Nonnative plants

Resumo

Cidades próximas a áreas protegidas facilitam a introdução de espécies exóticas, mudando interações ecológicas, como as que envolvem primatas frugívoros. Caracterizar o consumo de plantas exóticas por primatas em áreas urbanas possibilita entender como persistem em ambientes antrópicos. Caracterizamos a dieta de um grupo de macacos-prego-de-tufo-preto (*Sapajus nigritus*) vivendo na Mata de Santa Genebra, fragmento urbano de Mata Atlântica no Brasil, durante duas estações chuvosas. Três décadas atrás, a dieta era composta principalmente por *Zea mays*. Hoje não existem mais plantações no entorno. Registramos a dieta em observações de campo e fezes entre agosto 2019-março 2020 e outubro 2020-fevereiro 2021. Os macacos-prego consumiram 80 espécies vegetais, com mais espécies exóticas (23 vs. 4) do que registradas anteriormente. A maioria das espécies exóticas atuais são zoocóricas e urbanas. Frutos com polpa (35,7%) e arilo (23%) foram os principais itens consumidos. Os itens mudaram entre as estações chuvosas, mas não ao nível de espécies, indicando mudança relativa na contribuição dos itens consumidos. O consumo de plantas exóticas variou entre os meses, como o pico de consumo em dezembro. Sementes exóticas foram mais abundantes do que as nativas, principalmente de *Psidium guajava* e *Morus nigra*. A disponibilidade, previsibilidade, valor energético e uso oportunístico dos alimentos urbanos podem explicar essa variação ao longo dos meses. Além disso, as sementes exóticas nas fezes indicam potencial de dispersão para dentro da reserva. Nossos resultados mostram como a flexibilidade da dieta e a matriz urbana influenciam na ecologia alimentar dos macacos-prego pela incorporação de plantas exóticas.

Palavras-chave Alimentação · Dieta · Primatas · Plantas invasoras · Plantas não nativas

Introduction

Urbanization is one of the leading causes of ecosystem changes globally. Most of the human population lives in cities, which also have been expanding rapidly (Grimm *et al.*, 2008). In the future, this scenario is likely to worsen, because population growth will accelerate urbanization worldwide (UNPD, 2025). As urbanization expands, cities become closer to protected areas, with numerous consequences for conservation, including biodiversity loss and habitat degradation (Magle *et al.*, 2012; McDonald *et al.*, 2008). Wildlife must adjust their behavior or physiology to human-disturbed landscapes, or they may decline and become locally extinct (Lowry *et al.*, 2013). While many native species decline under urbanization, other species are favored by

it, such as introduced alien species (Borden & Flory, 2021; McKinney, 2008; Santana Marques *et al.*, 2020).

Humans have introduced alien species for centuries, but globalization has markedly intensified this process (Meyerson & Mooney, 2007; Pyšek *et al.*, 2020). Urban areas often act as primary points of introduction for alien species (Padayachee *et al.*, 2017). Urban environments present conditions that may benefit invasive species, such as food resources with reduced natural predation and sites for reproduction and establishment (Borden & Flory, 2021; Francis & Chadwick, 2015; Santana Marques *et al.*, 2020). For example, invasive plants are introduced for horticulture, fruit production, or to restore ecosystem services in cities (Potgieter *et al.*, 2019; Reichard & White, 2001; Richardson & Rejmánek, 2011). However, the presence of invasive plants in urban contexts has only recently received increased attention. Invasive plants might change ecological dynamics and interactions with other animals, especially frugivores and herbivores, and native plants (Carneiro *et al.*, 2025; Heleno *et al.*, 2013; Richardson & Rejmánek, 2011; Vilà *et al.*, 2011). Mutualistic relationships can emerge and affect interaction networks between frugivores and native plants, which might lead exotic plants to become invasive (Back & Bicca-Marques, 2019; Kueffer *et al.*, 2009; Martin-Albarracín *et al.*, 2026; Rojas *et al.*, 2019).

The invasive process of exotic fruiting plants is often facilitated by seed dispersal. Birds are usually considered the main dispersers of invasive plants (Gosper *et al.*, 2005; Pejchar *et al.*, 2025). Some mammals may also contribute to the spread of invasive plants, but their role in interacting with nonnative fruits has received comparatively little attention (Bicca-Marques, 2023; De Luca *et al.*, 2025). Among mammals, primates are considered some of the most important frugivorous seed dispersers in the tropics (Bufalo *et al.*, 2016; Chapman & Onderdonk, 1998). As contact with urban matrices and humans has increased, primates have adapted to fragmented and urban landscapes (Jaman & Huffman, 2013; Lousa *et al.*, 2024; Nogueira *et al.*, 2025). Primates in human-modified landscapes frequently incorporate invasive plant species in their diet, with the potential to introduce them into conservation areas (Bicca-Marques & Calegario-Marques, 1994; Chaves & Bicca-Marques, 2013; Cunha *et al.*, 2006; Freitas *et al.*, 2008; Hockings *et al.*, 2009; Jaman & Huffman, 2013; Parpinelli *et al.*, 2024; Reinegger *et al.*, 2023; Verçosa & Setz, 2020). Primates can also benefit from human provisioning or from fruiting trees and shrubs in gardens or streets, altering their feeding ecology (Back & Bicca-Marques, 2019; Bicca-Marques, 2023; Bicca-Marques & Calegario-Marques, 1994; Scarabelo & Setz, 2025; Verçosa & Setz, 2020).

Capuchin monkeys are an ideal system to investigate how urbanization and invasive plants may influence changes in primate diets in highly modified landscapes, because they have become common in many urban areas in Brazil (Nogueira *et al.*, 2025; Scarabelo & Setz, 2025). Capuchins are split into untufted, or gracile, capuchins (genus *Cebus*) and tufted, or robust, capuchins (genus *Sapajus*). Capuchin groups are multimale-multifemale and are hierarchical with a dominant alpha male (Fragaszy *et al.*, 2004; Lynch Alfaro, 2007). Their groups are usually large, with high fission–fusion dynamics and male-biased dispersal (Lynch Alfaro, 2007). Capuchin groups forage across small (e.g., 80 ha) to large home ranges (120–290 ha), with fruit availability

being the most important factor in space use (Di Bitetti, 2001; Fragaszy *et al.*, 2004; Martins *et al.*, 2022; Oliveira *et al.*, 2004; Zhang, 1995). The genus *Sapajus* has the most diverse plant diet, in terms of number of species, of any Atlantic Forest primates (Vasquez *et al.*, 2025). Their varied diet includes mainly fruits and arthropods, but also seeds, stems, flowers, leaves, and vertebrates (Fragaszy *et al.*, 2004; Freitas *et al.*, 2008; Galetti & Pedroni, 1994; Martins *et al.*, 2022; Oliveira *et al.*, 2004; Rasec-Silva *et al.*, 2023), allowing a highly flexible response to resource availability (Gonçalves *et al.*, 2022; Sabbatini *et al.*, 2008). This flexible generalist diet may be a key trait that has enabled capuchins to persist in altered environments (Freitas *et al.*, 2008; Gonçalves *et al.*, 2022; Martínez De Zorzi *et al.*, 2024; Schulte *et al.*, 2020; Smith *et al.*, 2022). For instance, capuchins may incorporate high-energy foods into their diet, such as *Zea mays*, to compensate for seasonal or spatial scarcity of resources, particularly in fragmented landscapes where restricted home ranges can limit foraging options (Di Bitetti, 2001; Freitas *et al.*, 2008; Galetti & Pedroni, 1994). Tufted capuchin monkeys frequently occur in forest fragments and near urban areas (Pinto *et al.*, 2009). Many of these forest remnants are a result of historical land use (Adami *et al.*, 2014; Ellis & Ramankutty, 2008). These human-modified landscapes offer new opportunities for monkeys' diet due to changes in availability and composition of food resources.

The Mata de Santa Genebra (MSG, Campinas, São Paulo, Brazil) consists of a remnant of semideciduous Atlantic Forest (252 ha) inhabited by *Sapajus nigritus* (black-tufted capuchin monkeys). The Mata de Santa Genebra is an interesting place to study capuchins' diet, because it is a fragment that has changed due to edge effects, natural disturbances, secondary succession, and urban expansion (Farah *et al.*, 2014; Guirao & Teixeira Filho, 2011; José, 2024). The landscape surrounding MSG reflects a long history of land-use change associated with urban expansion and socio-economic transformations (Adami *et al.*, 2014). The capuchin monkeys at MSG were last studied three decades ago when the forest was already a fragment (Galetti & Pedroni, 1994). In 1988–1991, capuchins consumed 71 species from 34 plant families: 40 species of zoochorous fruits (35 native, five exotic), 13 native anemochorous fruits, and two native autochorous fruits (Galetti & Pedroni, 1994). At that time, the capuchins mainly fed on *Zea mays* planted in a neighboring field, which no longer exists. Fragmentation and urbanization have increased since that study (Farah *et al.*, 2014; Guirao & Teixeira Filho, 2011). In 2013, a 10 ha area caught fire (Chudnobsky *et al.*, 2015; G1, 2013). Additionally, in 2014, a windstorm struck the mid-forest and toppled and killed almost 200 trees (G1, 2014). Residential development in the surroundings has also increased (José, 2024). The Mata de Santa Genebra also has invasive plants (Guaratini *et al.*, 2008). These disturbances mean that the study area has been repeatedly altered, and the continued presence of capuchins reflects their persistence in a human-modified landscape. This provides an opportunity to understand the capuchins' diet in an environment that has suffered numerous changes over time. Given the loss of *Z. mays* plantations and increasing urbanization near the MSG, we aimed to characterize the diet of a group of black-tufted capuchin monkeys during the wet season, when food availability is high, allowing us to evaluate their diet under resource rich conditions, and to assess variation in their diet between consecutive years. Because MSG was closed during

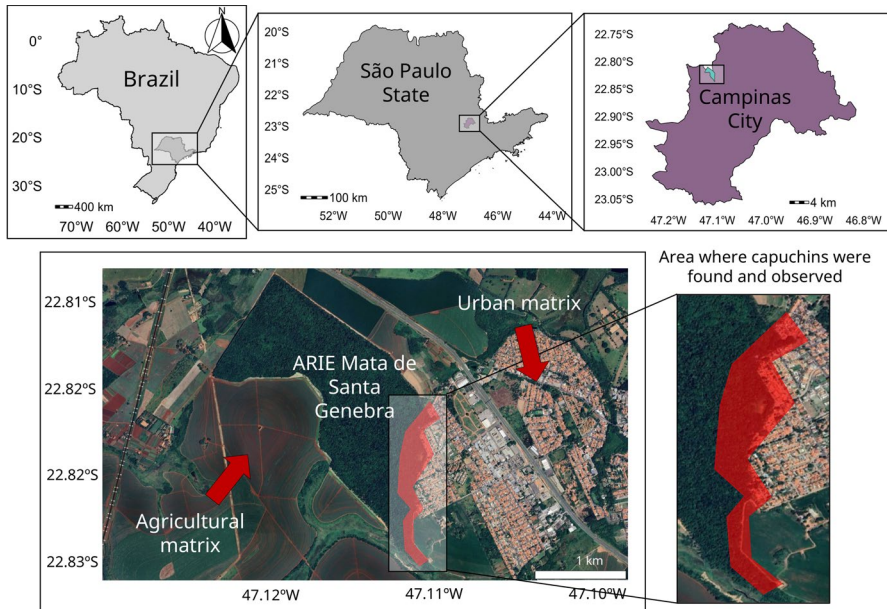


Fig. 1 Mata de Santa Genebra Biological Reserve, a forest fragment surrounded by urban and agricultural matrices (red arrows). The site is shown at multiple spatial scales, from national (Brazil) to state (São Paulo), municipal (Campinas), and local (Mata de Santa Genebra). We highlighted, in red, the area in which we encountered our study group of black-tufted capuchin monkeys (*Sapajus nigritus*) in August 2019–March 2020 and October 2020–February 2021.

the dry season, due to COVID-19 restrictions, we limited sampling to wet season months.

Methods

Study Site

We conducted the study at the Federal Reserve Area of Relevant Ecological Interest (in Portuguese, Área de Relevante Interesse Ecológico-ARIE) Mata de Santa Genebra (MSG), a 252 ha semideciduous Atlantic Forest in southeast Brazil (Campinas, State of São Paulo; coordinates 22°81' S, 47°11' W; Fig. 1). The climate is markedly seasonal, with a warm and wet season from October to March and a cooler, drier season from April to September, including transitional periods in March–April and September–October, when more than 70% of leaf fall occurs, mainly in July and August (Morellato, 1991). The flowering and fruiting period starts at the beginning of wet season (September–October), especially for pulp fruits (Morellato, 1991). Fabaceae, Rubiaceae, and Myrtaceae are the most common plant families (Guaratini *et al.*, 2008). The Mata de Santa Genebra is an isolated forest fragment between the city and rural agricultural zones. The surrounding agricultural matrix previously



Fig. 2 Study group of black tufted capuchin monkeys (*Sapajus nigritus*) (September 2019–March 2020 and October 2020–February 2021) at Mata de Santa Genebra Biological Reserve, Campinas, São Paulo, Brazil. (a) Subadult male eating an exotic *Artocarpus heterophyllus* on the ground; (b) a juvenile eating a native *Annona cacans*; (c) an adult eating a chicken egg while an infant observes; (d) adults and (e) an infant eating seeds in *Handroanthus albus*; (f) a juvenile eating the exotic *Hovenia dulcis*.

included *Zea mays*, *Glycine max*, *Coffea arabica*, and *Gossypium hirsutum* plantations. As drought severely reduced *Z. mays* yields, it was replaced by *G. max*.

Study Species and Study Group

Sapajus nigritus, *Alouatta guariba*, and recently arrived *Callithrix* sp. (*Callithrix penicillata* morphospecies, possibly hybridized with *C. jacchus*) inhabit MSG. Two groups of *Sapajus nigritus* live in the forest. We focused on a group that occupies the urban edge of the reserve (Fig. 2). This group has approximately 20–30 individuals, in which we recognized the alpha male and a male with a cleft lip, and is habituated to humans. The other group lives on the other side of the forest fragment out of contact with the urban matrix. We characterized the study group as urban-exposed based on repeated encounters along the forest edge and adjacent urban areas during systematic searches of the reserve.

We searched for the capuchin group once a week and, when we found them, followed them for as long as possible, as in the previous study (Galetti & Pedroni, 1994). We began recording their feeding behavior and foods consumed as soon as we found them. We conducted fieldwork from late August 2019 to March 2020 and from October 2020 to February 2021. We did not conduct fieldwork during the dry season (April–September 2020) because MSG was closed due to COVID-19. Our total effort (i.e., time spent in the field, with or without monkey

observations) was 437 h 50 min (241 h 32 min between August 2019 and March 2020, 196 h 18 min between October 2020 and February 2021), with an effective effort (i.e., time spent in the field observing monkeys) of 213 h 19 min (130 h 50 min between August 2019 and March 2020, 82 h 29 min between October 2020 and February 2021), across 29 days for each period. We did not follow the monkeys in complete days (from dawn to dusk). Instead, we observed them opportunistically from the moment we first encountered them until we were no longer able to follow them or maintain visual contact.

Diet Characterization

We characterized the capuchins' diet using all occurrence sampling (Altmann, 1974; Galetti & Pedroni, 1994), recording every feeding bout. We defined each feeding bout as a continuous feeding period, from the time an individual started feeding until it stopped. If feeding stopped for less than one minute and then resumed, we considered it part of the same feeding bout. We considered a new feeding bout when feeding stopped for more than 1 min and then resumed. Given that capuchin monkeys have high fission–fusion dynamics, we sampled all visible individuals whenever we encountered a subgroup. We moved between subgroups when the capuchins stopped feeding on a patch or item. If capuchins from a subgroup were already feeding on an item when we found them, we recorded this as a feeding bout, even if we did not observe the start. Thus, the duration of a bout is an underestimate of the true duration. As in most tropical forest studies, visibility constraints (because of dense vegetation and lianas, for example) may have limited the detection of some feeding bouts. We used Olympus Coleman 8×25 binoculars for observations.

We classified the items consumed by capuchin monkeys as animal (invertebrates or vertebrates) or plant part (roots, stems, flowers or inflorescences, pulp or aril fruits, or seeds). We separated aril fruits, with a thin tegument covering the seed, from pulp fruits, with a thicker and fleshier tegument. We identified plants using guides and tree lists for semideciduous forests (Guaratini *et al.*, 2008; Ramos *et al.*, 2015) and with the help of botanical specialists at the University of Campinas (UNICAMP) and at MSG (see [Acknowledgments](#)). We considered unidentified plant species as “morphospecies.” Our study covered mainly the wet summer season (from October to March), the period with most pulp fruits (Morellato, 1991).

We also identified food items from fecal samples we collected opportunistically during the study. We took the feces to the laboratory, washed them in running water and passed them through 1-mm and 0.5-mm mesh size sieves. We placed the sieved samples in Petri dishes and sorted out seeds and animal parts manually. If the seeds were smaller than 0.5 mm, we could not separate and identify them. We identified the seeds by using guides (Frigieri, 2016; Souza Junior & Brancalion, 2016) and with help from specialists at the UNICAMP and staff of the MSG plant nurseries (see [Acknowledgments](#)). All scientific names follow those in “Flora e Funga do Brasil” (Flora e Funga do Brasil, 2026). We could

not identify seeds present in a small number of feces and categorized these as “morphoseeds.”

Statistical Analyses

We calculated the percentage contribution of each feeding category (invertebrates, vertebrates, roots, stems, flowers, seed, pulp and aril fruits) or species as the number of feeding bouts recorded for that category or species divided by the total number of feeding bouts. To compare years, we restricted analyses to equivalent wet-season months, when fruit availability is typically higher (Morellato, 1991): Wet Season 1 (October 2019 to February 2020), and Wet Season 2 (October 2020 to February 2021).

We conducted analyses in R (version 4.4.0), using the packages *dplyr*, *tidyr*, *ggplot2*. We assessed differences in the proportion of food item categories between the two wet seasons using a Pearson’s chi-square test, as the data consisted of frequency counts across categorical variables. We grouped food items with low frequencies into ecologically meaningful categories (combining seeds and dry fruits; and roots and stems) to reduce potential effects of items with low frequencies. The expected frequencies met the assumptions of the chi-square test.

To evaluate differences in diet composition between the two wet seasons at species level, we used a permutational multivariate analysis of variance (PERMANOVA), with Bray–Curtis dissimilarity, (*adonis2* function in the *vegan* package). We treated monthly samples as independent replicates in each period. We verified homogeneity of multivariate dispersion using a permutation test (*betadisperser* function).

We explored whether the consumption of exotic plants differed between consecutive wet seasons by using two complementary approaches. First, we used Pearson’s chi-square test to compare the total number of feeding bouts on exotic versus native plant species between wet seasons. Second, we calculated the monthly proportion of feeding bouts involving exotic items to account for temporal variation and to avoid potential bias from unequal sampling effort. We used a Wilcoxon rank-sum test to compare these monthly proportions between wet seasons, as the data did not follow normality assumptions.

We explored the similarity between our findings and those from the previous study (Galetti & Pedroni, 1994) in terms of the total number of species, number of native species, and number of exotic species consumed, using the Sørensen-Dice Coefficient (Krebs, 1999), expressed as $SDC = \frac{2a}{2a+b+c}$, where “a” is the number of species common to both studies, “b” is the total number of species recorded in our study, and “c” is total number of species in the Galetti and Pedroni (1994) study. The SDC is a measure of similarity between two samples and ranges from zero to one. If SDC is closer to zero, there is low similarity between diets. However, if the SDC is closer to 1, there is more similarity in the diets. As the studies were carried out with different sampling methods and efforts, we conducted our comparison in an exploratory manner and similarity values should be interpreted cautiously. We updated plant species names

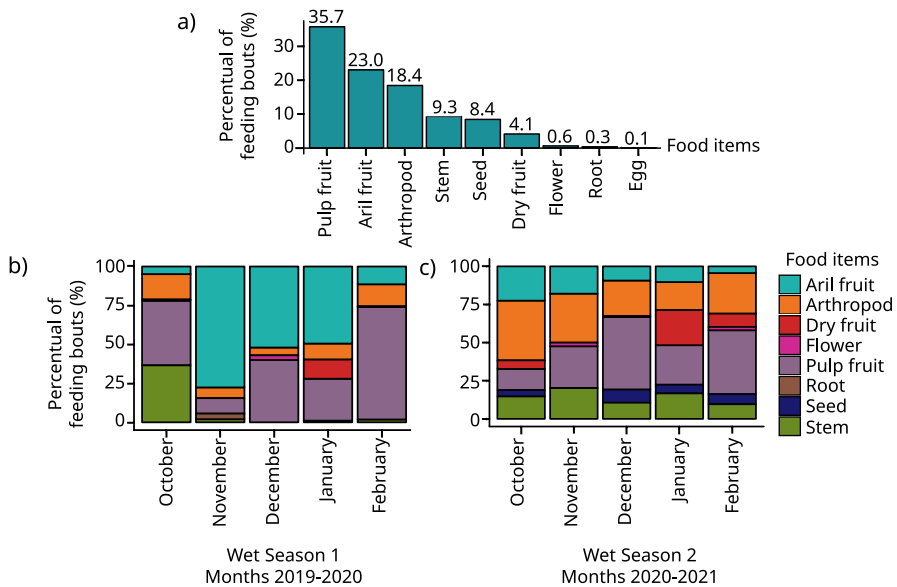


Fig. 3 Items consumed by black-tufted capuchin monkeys (*Sapajus nigritus*) in Semideciduous Atlantic Forest Mata de Santa Genebra (Campinas, São Paulo, Brazil). (a) August 2019 to March 2020, and October 2020 to February 2021 combined (N=3,235); (b) October 2019 to February 2020 (N=1,329); and (c) October 2020 to February 2021 (N=1299). Percentages and feeding bouts per item are given in Supplementary file 1.

that have changed since the Galetti and Pedroni (1994) list, according to “Flora e Funga do Brasil” (Flora e Funga do Brasil, 2026).

The script and data are available in the Zenodo repository, with additional files provided in the Supplementary Information (files 1, 2 and 3). See the *Data Availability* section for further details.

Ethical Statement

This study adhered to the legal requirements of Brazil (SISBIO 70343–1) and the International Primatology Society Code of Best Practices for Field Primatology.

Results

Diet Composition

The capuchins at Mata de Santa Genebra mostly consumed plant parts (82.5%; N=2,638/3,235), but also animal parts (18.5%; N=597/3,235) (Fig. 3). The most plant parts consumed were fruits (62.8%; N=2,033/3,235), divided between pulp (35.7%; N=1,155/3,235), aril fruits (23.0%; N=744/3,235), and dry fruits (4.1%;

N=134/3,235) (Fig. 3). Other plant parts included stems (9.3%; N=302/3,235), seeds (8.4%; N=273/3,235), flowers (0.6%; N=19/3,235), and roots (0.3%; N=11/3,235). The capuchins consumed 47 species of zoochorous aril and pulp fruits (29 native, 12 exotic, and six undetermined), and five seeds from anemochorous fruits (four natives and one exotic) (Table I). The distribution of food item categories consumed differed significantly between the two wet seasons ($\chi^2=399.56$; $df=5$; $p<0.001$; Supplementary file 1). Capuchins consumed aril (51% more than expected from parity across seasons) and pulp fruits (8%) more in wet season 1, and they consumed arthropods (45%), seeds (54%), and vegetative parts (41%) more in wet season 2.

The capuchins consumed 80 plant species from 34 families (Table I). Fabaceae (N=13) and Arecaceae (N=9) families had the highest number of consumed plant species (Supplementary file 1). Fabaceae showed the highest proportion of feeding bouts (21.2%; N=559/2,638), followed by Myrtaceae (7.5%, N=197/2,638), Bignoniaceae (7.1%; N=188/2,638), Peraceae (6.6%; N=174/2,638), Poaceae (5.4%; N=143/2,638), Moraceae (5.4%; N=142/2,638), and Piperaceae (5.1%; N=134/2,638). We also recorded ten morphospecies (three from feeding bouts and seven from feces) that we could not identify at any taxonomic level. Therefore, the true number of plant species and families consumed may be higher.

The fruit of *Inga vera affinis* was the most consumed food type (13.7%; N=362/2,638), followed by the seeds of *Handroanthus albus* (7%; N=184/2,638) and the arils of *Pera glabrata* fruits (6.6%; N=174). *I. v. affinis* (24%; N=284/1,185), *P. glabrata* (14.7%; N=174/1,185), and *Zanthoxylum roifolium* (7.8%; N=92/1,185) were the main items consumed during wet season 1, whereas *Piper* sp. (9.1%; N=85/938), *I. v. affinis* (8.3%; N=78/938), and *Malpighia emarginata* (6.6%; N=62/938) were the main items during wet season 2. However, diet composition at species level did not differ significantly between wet seasons (PERMANOVA, $F_{1,8}=1.05$; $R^2=0.116$; $p=0.33$). Multivariate dispersion did not differ significantly between groups (ANOVA, $F_{1,8}=0.14$; $p=0.71$), showing that results were not influenced by differences in within-group variability.

Invertebrates comprised 18.4% (N=596/3,235) of the capuchins' diet. They also ate chicken eggs taken from a nearby house (0.1%; N=2/3,235). Among the invertebrates, they ate termites, ants, beetles, cicadas, caterpillars, moths, flies, insect larvae, and some millipedes (Table I). We could not identify arthropod prey at species level because capuchins usually consumed prey completely without leaving identifiable remains.

We collected 123 capuchin monkey fecal samples (92 between September 2019 and March 2020; 31 between October 2020 and February 2021; Table II). The number of seeds (total N=8,578) ranged from 0 to 594 per sample, with 14 samples without seeds, and a mean $\pm$ SD of 92.9 ± 129.1 seeds per sample. The mean number of seed species per fecal sample was $1.7 \pm$ SD 1.3, with the most diverse sample containing eight seed species. Exotic *Morus nigra*, *Psidium guajava*, and cultivated *Oxalis* sp., were the most common seeds in the feces (Table II). Native species included wild *Jacaratia spinosa*, *Cissus sicyoides*, *Cecropia hololeuca*, and *Ficus* sp. (Table II, Supplementary file 2). Exotic seeds were more abundant than native ones (Table II).

Table 1 Items consumed by black-tufted capuchin monkeys (*Sapajus nigritus*) in September 2019 to March 2020 and October 2020 to February 2021 at Mata de Santa Gen- ebra (Campinas, São Paulo, Brazil). O = Observed during fieldwork; F = seed found in feces; N = number of feeding bout records; % = percentage of feeding bouts in relation to the total (calculation records of percentages are in Supplementary file 1); Origin of the item in the study site; Fruit type, if a fruit or seed; Months of item recording

Plants	Item	Method	No. feed- ing bouts	% of feed- ing bouts	Origin	Fruit type	Months eaten
Acanthaceae							
<i>Sanchezia spectiosa</i>	Stem	O	6	0.2	Exotic		Oct/20
<i>Thunbergia erecta</i>	Flower	O	1	0.0*	Exotic		Nov/20
Anacardiaceae							
<i>Mangifera indica</i>	Pulp fruit	O	55	2.1	Exotic	Zoochorous	Nov-Dec/19, Jan-Feb, Oct-Dec/20, Jan-Feb/21
Annonaceae							
<i>Annona cacans</i>	Pulp fruit	O/F	7	0.3	Native	Zoochorous	Mar/20, Feb/21
Araceae							
<i>Syngonium podophyllum</i>	Stem	O	19	0.7	Exotic		Dec/20, Feb/21
Areaceae							
<i>Acrocomia aculeata</i>	Art fruit	O	15	0.6	Native	Zoochorous	Jan/20, Jan/21
Areaceae sp. 1	Pulp fruit	O	3	0.1	Undetermined	Zoochorous	Feb/20
Areaceae sp. 2	Pulp fruit	O	17	0.6	Undetermined	Zoochorous	Mar/20
Areaceae sp. 3	Pulp fruit	F	-	-	Undetermined	Zoochorous	Feb-Mar/20
<i>Euterpe edulis</i>	Pulp fruit	O	11	0.4	Native	Zoochorous	Feb/21
<i>Syagrus romanzoffiana</i>	Pulp fruit	O	63	2.4	Native	Zoochorous	Sep/19, Oct, Nov/20
Bignoniaceae							
Bignoniaceae sp. 1	Flower	O	1	0.0*	Undetermined		Feb/21
Bignoniaceae sp. 2	Flower	O	2	0.1	Undetermined		Dec/20
Bignoniaceae sp. 3	Flower	O	1	0.0*	Undetermined		Mar/20
<i>Handroanthus albus</i>	Seed	O	184	7.0	Native	Anemochorous	Sep/19

Table 1 (continued)

Item	Method	No. feed- ing bouts	% of feed- ing bouts	Origin	Fruit type	Months eaten
Boraginaceae						
<i>Cordia africana</i>	F	-	-	Exotic	Zoochorous	Jan/20
<i>Cordia ecayculata</i>	O	36	1.4	Native	Zoochorous	Feb-Mar/20
<i>Cordia sellowiana</i>	F	-	-	Native	Zoochorous	Oct/20
<i>Cordia</i> sp.	F	-	-	Native	Zoochorous	Mar/20
Caricaceae						
<i>Jacaratia spinosa</i>	O/F	62	2.3	Native	Zoochorous	Jan-Mar, Nov/20, Jan-Feb/21
	O	2	0.1	Native		Oct/20
<i>Carica papaya</i>	O	1	0.0*	Exotic	Zoochorous	Oct/20
Cucurbitaceae						
<i>Citrullus lanatus</i>	O	2	0.1	Exotic	Zoochorous	Sep/19
<i>Momordica charantia</i>	O/F	3	0.1	Exotic	Zoochorous	Jan-Feb, Dec/20
Euphorbiaceae						
<i>Manihot esculenta</i>	O	11	0.4	Native		Nov/19
<i>Croton</i> sp.	O	4	0.1	Native		Dec/20, Feb/21
Fabaceae						
<i>Bauhinia forficata</i>	O	11	0.4	Native		Feb, Oct-Nov/20
	O	4	0.1	Native		Dec/19, Nov/20
	O	27	1.0	Exotic		Jan/21
<i>Caesalpinia pulcherrima</i>	O	25	1.0	Native	Zoochorous	Sep-Nov/19, Feb, Nov/20
<i>Hymenaea courbaril</i>	O	10	0.4	Native	Zoochorous	Sep/19
<i>Inga</i> sp.	O/F	362	13.7	Native	Zoochorous	Nov-Dec/19, Jan-Mar, Oct-Dec/20, Jan/21
<i>Inga vera affinis</i>	O	47	1.8	Native	Zoochorous	Nov/19
<i>Inga marginata</i>	O	8	0.3	Native		Nov/19, Jan/20
<i>Fabaceae</i> sp. 1						

Table 1 (continued)

	Item	Method	No. feed- ing bouts	% of feed- ing bouts	Origin	Fruit type	Months eaten
Fabaceae sp. 2	Seed	O	4	0.1	Native	Anemochorous	Dec/20
Fabaceae sp. 3	Seed	F	-	-	Undetermined		Mar/20
<i>Leucaena leucocephala</i>	Seed	O	15	0.6	Exotic	Anemochorous	Feb/21
<i>Platypodium elegans</i>	Stem	O	27	1.0	Native		Mar/20, Feb/21
Heliconiaceae							
<i>Heliconia</i> sp.	Stem	O	9	0.3	Exotic		Oct-Nov/20
Lauraceae							
<i>Persea americana</i>	Pulp fruit	O	12	0.4	Exotic		Sep/19, Dec/20
Lecythidaceae							
<i>Cariniana legalis</i>	Seed	O	12	0.4	Native	Anemochorous	Sep/19, Dec/20
Malpighiaceae							
<i>Dicella bracteosa</i>	Seed	O	10	0.4	Native	Autochorous	Jan/21
<i>Malpighia enarginata</i>	Pulp fruit	O	130	4.9	Exotic	Zoochorous	Sep/19, Oct-Nov/20
Malvaceae							
<i>Malvaviscus arboreus</i>	Flower	O	1	0.0*	Exotic		Feb/20
Meliaceae							
<i>Cabralea canjerana</i>	Aril fruit	O	26	1.0	Native	Zoochorous	Oct-Nov/20, Feb/21
<i>Guarea kunthiana</i>	Aril fruit	O	60	2.3	Native	Zoochorous	Nov/19, Oct-Nov/20
Moraceae							
<i>Artocarpus heterophyllus</i>	Pulp fruit	O	80	3.0	Exotic	Zoochorous	Oct/19, Dec/20
<i>Morus nigra</i>	Pulp fruit	O/F	46	1.7	Exotic	Zoochorous	Sep-Nov/19, Jan-Mar, Oct-Dec/20
<i>Ficus guaranitica</i>	Pulp fruit	O/F	16	0.6	Native	Zoochorous	Oct/19, Dec/20, Feb/21
Musaceae							
<i>Musa</i> sp.	Pulp fruit	O	74	2.8	Exotic	Zoochorous	Sep, Nov-Dec/19, Jan-Feb, Nov-Dec/20

Table 1 (continued)

	Item	Method	No. feeding bouts	% of feeding bouts	Origin	Fruit type	Months eaten
Myrtaceae							
<i>Eugenia involucrata</i>	Pulp fruit	O	5	0.2	Native	Zoochorous	Oct/20
<i>Eugenia uniflora</i>	Pulp fruit	O	28	1.0	Native	Zoochorous	Oct-Dec/20
<i>Myrciaria glazioviana</i>	Pulp fruit	O	52	2.0	Native	Zoochorous	Dec/19, Feb-Mar/20, Feb/21
Myrtaceae sp. 1	Pulp fruit	O	12	0.4	Native	Zoochorous	Sep/19
Myrtaceae sp. 2	Pulp fruit	F	-	-	Native	Zoochorous	Oct/20
<i>Psidium guajava</i>	Pulp fruit	O	100	3.8	Exotic	Zoochorous	Aug/19, Jan-Feb, Dec/20, Feb/21
Nyctaginaceae							
<i>Guapira opposita</i>	Pulp fruit	O	12	0.4	Native	Zoochorous	Dec/20
Orchidaceae							
<i>Oeceoclades maculata</i>	Stem	O	14	0.5	Exotic		Oct/19, Oct, Dec/20
<i>Bulbophyllum granulatum</i>	Stem	O	2	0.1	Exotic		Nov/19
Oxalidaceae							
<i>Oxalis</i> sp.	Pulp fruit	F	-	-	Native	Autochorous	Oct-Dec/19, Jan-Mar/20
Peraceae							
<i>Pera glabrata</i>	Aril fruit	O	174	6.6	Native	Zoochorous	Oct-Nov/19
Phytolacaceae							
<i>Seguiera americana</i>	Dry Fruit	F	-	-	Exotic		Dec/20
Piperaceae							
<i>Piper</i> sp.	Dry fruit Stem	O, F O	109 25	4.1 0.9	Native Native	Zoochorous	Jan/20, Jan-Feb/21 Oct-Dec/20, Jan/21
Poaceae							
<i>Saccharum officinarum</i>	Stem	O	47	1.8	Exotic		Sep/19
Poaceae sp. 1	Stem	O	35	1.3	Undetermined		Oct/19, Feb, Nov-Dec/20
Poaceae sp. 2	Flower	O	1	0.0*	Undetermined		Oct/19

Table 1 (continued)

	Item	Method	No. feed- ing bouts	% of feed- ing bouts	Origin	Fruit type	Months eaten
<i>Merostachys</i> sp.	Stem	O	12	0.4	Native		Feb, Nov-Dec/2020
<i>Zea mays</i>	Seed	O	48	1.8	Exotic	Zoochorous	Oct, Dec/20
Polygalaceae							
<i>Diclidanthera laurifolia</i>	Pulp fruit	F	-	-	Native	Zoochorous	Oct/20
Rhamnaceae							
<i>Hovenia dulcis</i>	Aril fruit	O	22	0.8	Exotic	Zoochorous	Mar/20
Rhamnaceae sp. 1	Pulp fruit	O	30	1.1	Undetermined	Zoochorous	Jan/20
Rhamnaceae sp. 2	Pulp fruit	O	24	0.9	Undetermined	Zoochorous	Jan-Mar/20
Rutaceae							
<i>Esenbeckia leiocarpa</i>	Stem	O	39	1.5	Native		Oct/19, Oct-Nov/20, Jan-Feb/21
<i>Zanthoxylum rholfolium</i>	Pulp fruit	O	92	3.5	Native	Zoochorous	Feb/20
Solanaceae							
<i>Solanum cf. granuloseprosum</i>	Pulp fruit	F	-	-	Native	Zoochorous	Dec/19
Urticaceae							
<i>Cecropia hololeuca</i>	Pulp fruit	O/F	11	0.4	Native	Zoochorous	Sep-Oct/19, Feb-Mar, Oct/20
<i>Cecropia pachystachia</i>	Pulp fruit	O/F	109	4.1	Native	Zoochorous	Dec/19, Jan-Feb, Oct-Dec/20
Violaceae							
<i>Pombalia atropurpurea</i>	Dry fruit	O	25	0.9	Native	Anemochorous	Oct/20
Vitaceae							
<i>Cissus sicyoides</i>	Pulp fruit	O/F	58	2.2	Native	Zoochorous	Nov/19, Jan-Feb/20, Feb/21
Unidentified							
Morphospecie 1	Stem	O	19	0.7	Native		Oct/19
Morphospecie 2	Pulp fruit	O	10	0.4	Undetermined		Jan/21
Morphospecie 3	Flower	O	1	0.0*	Undetermined		Feb/21
Animals							
Phasianidae							

Table 1 (continued)

	Item	Method	No. feed- ing bouts	% of feed- ing bouts	Origin	Fruit type	Months eaten
<i>Gallus Gallus domesticus</i>	Vertebrate egg	O	2	0.1	Exotic		Oct/20
Blattodea							
Termites	Arthropod	O	14	2.3	Undetermined		Oct/20
Coleoptera							
Beetles (adult)	Arthropod	O/F	4	0.7	Undetermined		Nov/19, Jan, Nov/20
Beetle (larva)	Arthropod	O	1	0.2	Undetermined		Sep/19
Diplopoda							
Millipedes	Arthropod	O/F	9	1.5	Undetermined		Oct/19, Oct-Dec/20
Diptera							
Fly	Arthropod	O	1	0.2	Undetermined		Dec/20
Homoptera							
Cicadas	Arthropod	O	4	0.7	Undetermined		Oct/19
Hymenoptera							
Ants	Arthropod	O/F	20	3.4	Undetermined		Jan/20, Nov-Dec/20, Jan/21
Lepidoptera							
Caterpillars	Arthropod	O	5	0.8	Undetermined		Oct, Nov/19, Feb, Dec/20, Feb/21
Moth	Arthropod	O	1	0.2	Undetermined		Feb/21
Pupa	Arthropod	O	1	1.2	Undetermined		Nov/20
Orthoptera							
Grasshoppers	Arthropod	O	2	0.3	Undetermined		Nov/19, Feb/20
Unidentified	Arthropod	O	534	90.0	Undetermined		All months

*Rounded from two decimal places (0.04 values) to one decimal place 0.0

Table II Seeds found in 123 fecal samples from black-tufted capuchin monkeys (*Sapajus nigritus*) in September 2019–March 2020 and October 2020–February 2021 at Mata de Santa Genebra (Campinas, São Paulo, Brazil). Morphoseeds are seeds not identified at species level. We provide images of the seeds in Supplementary file 2 for reference

Seed species	No. samples	Total no. seeds	Origin	Months recorded
Annonaceae				
<i>Annona cacans</i>	2	2	Native	Mar/20
Boraginaceae				
<i>Cordia africana</i>	1	8	Exotic	Jan/20
<i>Cordia ecalyculata</i>	2	7	Native	Feb–Mar/20
<i>Cordia sellowiana</i>	5	41	Native	Oct/20
<i>Cordia</i> sp.	2	20	Native	Mar/20
Arecaceae				
<i>Arecaceae</i> sp. 3	5	11	Undetermined	Feb–Mar/20
Caricaceae				
<i>Jacaratia spinosa</i>	7	24	Native	Jan–Mar/20
Cucurbitaceae				
<i>Momordica charantia</i>	1	5	Exotic	Feb/20
Fabaceae				
<i>Inga vera affinis</i>	1	2	Native	Dec/20
<i>Fabaceae</i> sp. 3	2	3	Undetermined	Mar/20
Moraceae				
<i>Morus nigra</i>	45	2045	Exotic	Nov/19, Jan–Mar/20, Oct–Dec/20
<i>Ficus guaranitica</i>	7	315	Native	Oct, Dec/19, Dec/20
Myrtaceae				
<i>Myrtaceae</i> sp. 2	1	8	Undetermined	Oct/20
<i>Psidium guajava</i>	31	1952	Exotic	Aug/19, Jan–Mar/20, Oct, Dec/20, Feb/21
Oxalidaceae				
<i>Oxalis</i> sp.	44	3441	Native	Oct–Dec/19, Jan–Mar/20

Table II (continued)

Seed species	No. samples	Total no. seeds	Origin	Months recorded
Peraceae				
<i>Pera glabrata</i> *	2	2	Native	Nov/19
Piperaceae				
<i>Piper</i> sp.	7	354	Native	Jan-Feb/20
Phytolacaceae				
<i>Segutieria americana</i>	1	3	Exotic	Dec/20
Polygalaceae				
<i>Diclidanthera laurifolia</i>	1	4	Native	Dec/20
Solanaceae				
<i>Solanum</i> cf. <i>granulosoleprosum</i>	1	94	Native	Dec/19
Urticaceae				
<i>Cecropia hololeuca</i>	8	160	Native	Sep-Oct/19, Feb/20, Oct/20
<i>Cecropia pachystachia</i>	2	33	Native	Oct/20
Vitaceae				
<i>Cissus sicyoides</i>	10	29	Native	Dec/19, Feb-Mar/20, Oct, Dec/20
Unidentified				
Morphoseed 1	1	1	Undetermined	Mar/20
Morphoseed 2	1	3	Undetermined	Nov/19
Morphoseed 3	2	2	Undetermined	Feb-Mar/20
Morphoseed 4	1	1	Undetermined	Dec/20
Morphoseed 5	2	2	Undetermined	Feb-Mar/20
Morphoseed 6	1	4	Undetermined	Oct/20
Morphoseed 7	2	3	Undetermined	Feb-Mar/20

*This item was not a seed, but a distinctive part that served to characterize the fruit species

Presence of Exotic Plants in the Diet of *Sapajus nigritus*

The capuchins consumed exotic plants in all months (Fig. 4a). They ate 21 species of exotic plants (26.8%; $N=705/2,638$), most of these outside the reserve. For instance, *Malpighia emarginata* (4.9%; $N=130$), and *Psidium guajava* (3.8%; $N=100$), both commonly used in urban gardens and as street trees, were the fourth and fifth most eaten species, respectively. Capuchins also ate bananas, papayas, and watermelons in houses or in a park near the Reserve. We also observed capuchins entering houses and leaving with cookies and bread. Capuchins have also made off with dog food, instant noodles, and various fruits from kitchens in neighboring houses (Thomaz Barrella, personal communication, 2020).

The proportion of feeding bouts on exotic plants consumed differed significantly between the two wet seasons ($\chi^2=155.34$, $df=1$, $p<0.001$; Supplementary file 1), with an overall increase in the number of feeding bouts in wet season 2 compared with wet season 1, 54% higher than expected, based on equal frequencies between periods. In contrast, this pattern was not consistent across months. The monthly proportion of feeding bouts on exotic plants (i.e., the number of feeding bouts on exotic plants divided by the total number of feeding bouts per month) was numerically higher in wet season 2 (mean = $0.28 \pm SD\ 0.18$, median = 0.20) than in wet season 1 (mean = $0.18 \pm SD\ 0.22$, median = 0.10), but this difference was not statistically significant (Wilcoxon rank-sum test, $W=5$, $p=0.15$). This lack of significance is probably because of high variability in monthly proportions of feeding bouts on exotic plants within each wet season ($SD=0.18\text{--}0.22$), leading to overlap between periods. The higher proportion of feeding bouts on exotic plants during wet season 2 was not driven by sample size, as the proportion remained higher than in wet season 1, despite fewer total number of plant feeding bouts (wet season 1 = 1,185; wet season 2 = 938). The number of feeding bouts involving exotic plants peaked in December of wet season 2 (222 feeding bouts across 10 exotic species), exceeding the number of feeding bouts on native plants in the same months (117 feeding bouts across 11 native species). *Malpighia emarginata*, *Musa* sp., *Psidium guajava*, *Artocarpus heterophyllus*, and *Zea mays* (obtained from chicken feed near the reserve) were the main items consumed in December and are all exotic. Exotic plants also dominated the capuchins' diet in September 2019 (145 feeding bouts on six species). *M. emarginata* was the main exotic item consumed at this time, followed by *P. guajava*, *A. heterophyllus*, and *Musa* sp. (Fig. 4b). *M. emarginata* consumption was especially high in September 2019 ($N=68$) and December 2020 ($N=52$), although *Saccharum officinarum* ($N=47$) also contributed to the high value for exotic items in September (Fig. 4b).

The number of plant families ($n=35$) and species ($n=80$) were similar to those in the capuchins' diet from 1988 to 1991 (Galetti & Pedroni, 1994). However, the diet composition was different ($SDC=0.2$), even for native species ($SDC=0.3$). The number of exotic or urban species consumed by capuchins at MSG increased almost sixfold between 1988–1991 and 2019–2020, from four to 23 species, and similarity was low ($SDC=0.1$).

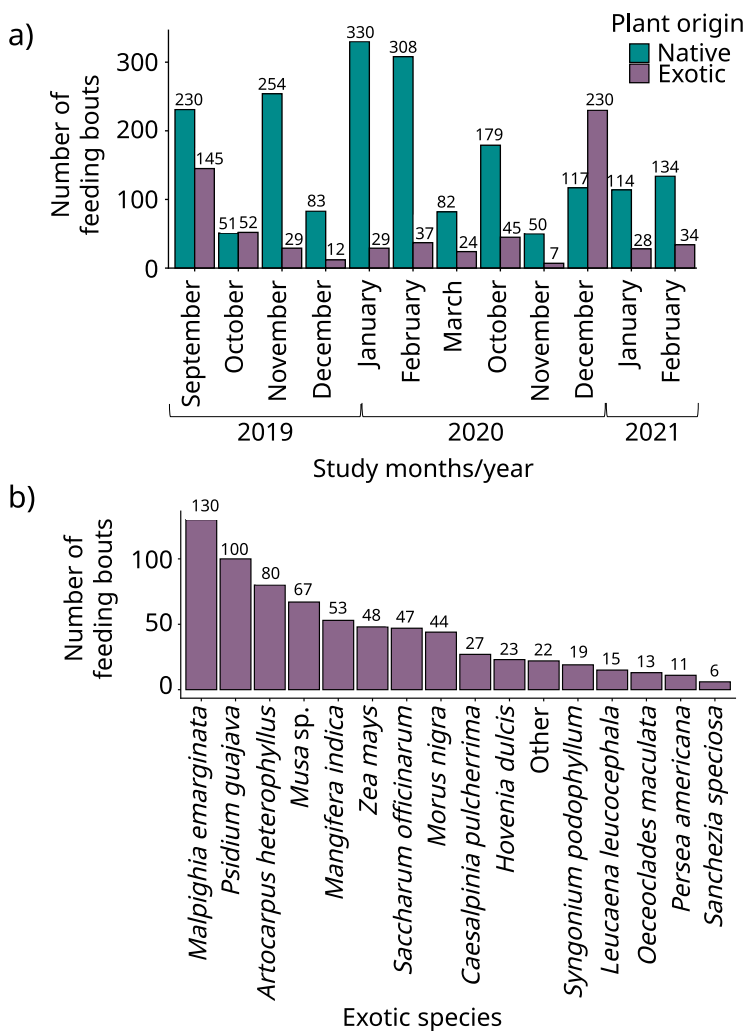


Fig. 4 (a) Native and exotic plants consumed monthly and (b) exotic plant species ranked by number of feeding bouts for black-tufted capuchin monkeys (*Sapajus nigritus*) in Semidecidual Atlantic Forest Mata de Santa Genebra (Campinas, São Paulo, Brazil) in October 2019 to February 2020. Complete feeding bout values are given in the Supplementary file 1.

Discussion

The diet of *Sapajus nigritus* was dominated by fruits and invertebrates but also was strongly influenced by exotic plants associated with the surrounding urban matrix at Mata de Santa Genebra, in the Atlantic Forest in Brazil. The frequency of different items in their diet changed between two consecutive wet seasons, probably due to plant availability. Although comparisons with the previous study should be interpreted with caution because of differences in methodology and season, the

exotic items contrast with those reported for 1988–1991, in which *Zea mays* was the main item in the capuchins' diet (Galetti & Pedroni, 1994). The capuchins' diet has changed from including a cultivated resource to the use of urban exotics. In our study, the consumption of exotics was high even during months with high resource availability, suggesting that capuchins favor exotics over native plants. The consumption of these new exotic plants may have consequences for capuchin's natural history (e.g., activity pattern, feeding behavior), their interactions with humans, and the ecological process (e.g., seed dispersal) and dynamics of forest fragments (Cordero *et al.*, 2023; Magioli *et al.*, 2022; McLennan *et al.*, 2017; Suzin *et al.*, 2017). In sum, our findings show that capuchin diet changes between consecutive wet seasons, and that urban-associated exotic plants play an increasingly important role in black-tufted capuchin feeding ecology in this highly modified landscape.

Diet Composition

The capuchins had a diverse diet, comprising 80 plant species. Although our study covered a shorter sampling period than the previous study (Galetti & Pedroni, 1994), we recorded a similar number of species. The frugivorous and insectivorous nature of our study group is consistent with the findings of previous studies (Fragaszy *et al.*, 2004; Freitas *et al.*, 2008; Galetti & Pedroni, 1994; Martins *et al.*, 2022). Fruits provide essential carbohydrates, invertebrates are key protein sources, and items, such as stems and seeds, offer fibers and lipids, respectively (Garber, 1987).

Capuchins usually consume more fruits during the wet season and other items, such as seeds, during the dry season (Freitas *et al.*, 2008). Although we detected differences in food item frequencies between wet seasons, fruits remained the dominant resource in both periods. Arthropods, stems, and seed consumption was higher in wet season 2 than wet season 1, which may indicate a shift in availability of aril fruits. Tropical plant species fruit continuously, annually, biannually, or supra-annually, including irregular or mast-fruiting events (Heideman, 1989; Mendoza *et al.*, 2018; Norden *et al.*, 2007; Wheelwright, 1986). Even among species that fruit annually, fruit production and availability can vary substantially among or within individuals, due to individual variation or environmental factors (Herrera, 1988; Wheelwright, 1986). This could explain the observed changes in food item categories, but not in species composition, between the two wet seasons. For example, *Inga vera affinis* was the main resource in wet season 1 but became the second most consumed item in wet season 2, alongside increased consumption of *Piper* sp. and *Malpighia emarginata*.

Changes in resource availability driven by anthropogenic factors may further influence diet composition over longer temporal. The higher representation of seeds on capuchins' diet in the 1990s is explained by consumption of *Zea mays*, highlighting the influence of anthropogenic resources on the capuchins' diet composition. *Z. mays* was available in the agricultural matrix at MSG during the 1990s and was the main item in the capuchins' diet between January and July, covering both wet and dry months (Galetti & Pedroni, 1994). When *Z. mays*

is available, it can be used as a fallback or a preferred item (Freitas *et al.*, 2008; Galetti & Pedroni, 1994; Ludwig *et al.*, 2005). *Z. mays* has now been replaced by *Glycine max* fields at our study site and other food items appear to have gained importance. For example, seeds of *Handroanthus albus* were the most consumed seed items in September during our study but were not previously recorded in the diet of capuchins at our study site (Galetti & Pedroni, 1994). These seeds may be an important food resource during the transition between the dry and wet seasons when other resources are scarce (Morellato, 1991). The aril fruit *Inga vera affinis* (Fabaceae) and exotic plants were also substantial components of the capuchins' diet in our study. They also ate new exotic plant species (e.g., *Mangifera indica*, *Leucaena leucocephala*, *Morus nigra*), showing high flexibility and diversity in the capuchins' diet. This flexibility may facilitate their persistence in the fragment despite the urban-influenced disturbances.

Impact of Exotic Plants and Provided Items on the Diet of *Sapajus nigritus*

Exotic plant species were an important component of the capuchins' diet in our study. The previous study conducted at the same site reported four exotic species in their diet (Galetti & Pedroni, 1994), although differences in sampling methods and effort between studies limit direct comparisons. The current species composition in the diet, including species from urban forestry and cultivated plants, such as *Psidium guajava*, *Morus nigra*, *Musa* sp., *Mangifera indica*, *Artocarpus heterophyllus*, *Hovenia dulcis*, *Saccharum officinarum*, *Oeceoclades maculata* and *Bulbophyllum granulatum* (ornamental orchids), and *Leucaena leucocephala*, highlights the importance of urban areas as foraging sites for capuchins.

The similar proportion of feeding bouts on exotic plants between consecutive wet seasons shows their importance in the capuchins' diet, including in periods of high fruit availability. This indicates that rather than being used as fallback resources during periods of scarcity (Cunha *et al.*, 2006; Freitas *et al.*, 2008; Parpinelli *et al.*, 2024), exotic species may represent consistent or complementary resources for capuchins in human-modified landscapes. The high consumption of exotic plants in December, a month typically associated with peak fruit availability at our study site (Morellato, 1991), further supports this interpretation. Variation in exotic plant consumption over the months suggests that resource use may be influenced by short-term fluctuations in availability, as well as opportunistic foraging, individual preferences, and the heterogeneous and often unpredictable phenology of urban plant species. In addition, increased human presence during vacation months may enhance access to intentional provisioned items, such as bananas, which humans frequently offered to capuchins in December. This may lead capuchins to substitute wild resources with provisioned items, including exotic fruits, a pattern also reported for *Alouatta guariba* (Bicca-Marques, 2023; Chaves & Bicca-Marques, 2013).

Given the high contribution of exotic fruits to the capuchins' diet, seed dispersal is a key potential ecological consequence of their diet. Capuchins are the second largest frugivorous mammal at MSG and are considered good seed dispersers (Bufalo *et al.*, 2016; de Albuquerque Teixeira *et al.*, 2024). Some seeds are usually not consumed but

are instead spat out (e.g., *Inga vera affinis*, *Syagrus romanzoffiana*, *Malpighia emarginata*) due to seed size and toxicity (Ancorenaz *et al.*, 2006; Dominy & Duncan, 2005; Flores, 2020). In contrast, wood sorrel seeds were abundant in fecal samples, and this species has potential zoochorous dispersal despite being considered autochorous (Li *et al.*, 2020). Moreover, most of the exotic species in the capuchins' diet are fleshy fruits, whose seeds can be dispersed. *Psidium guajava* and *Morus nigra* are the main conservation concerns in terms of potential seed dispersal and invasiveness because of the high number of seeds per fruit. *Psidium guajava* is considered one of the most invasive plants owing to its regrowth ability, allelopathy, and easy seed dispersal by animals, with documented impacts on ecosystem composition, structure, and function (Berens *et al.*, 2008; Chapla & Campos, 2010; Guézou *et al.*, 2010; Marciniak *et al.*, 2024; Ruwanza & Dondofema, 2020; Urquía *et al.*, 2019; Walsh *et al.*, 2008). *M. nigra* is also a common invasive plant in urban areas in Brazil, although its ecological impacts on native plant communities and frugivores interactions are not well understood (Ahlawat *et al.*, 2016; Corrêa *et al.*, 2018; Gasperin & Pizo, 2012; José, 2024; Vieira *et al.*, 2018). Other exotic seeds with potential for dispersal occurred at a low frequency. The impact and consequences of the dispersal of the seeds of nonnative plants by primates should be investigated further in urban and peri-urban forest fragments.

The incorporation of urban and exotic plants in the capuchins' diet may change ecosystem functionality, favoring nonnative species over native ones and reshaping plant–animal interaction networks within the reserve (Cordero *et al.*, 2023; Hardy *et al.*, 2025; McConkey *et al.*, 2012). Other frugivores can be affected in a cascade, such as invasive plants associated with reduced birds abundance and richness (Da Silva *et al.*, 2020). *Alouatta guariba* also eat *Morus nigra* fruits at MSG (José, 2024). Invasive plants may affect the diversity of items consumed by frugivorous. For example, a bird community diet became less diverse, in number of species consumed, because they started eating more invasive *Psidium guajava* instead of native fruit species (Marciniak *et al.*, 2024). Furthermore, consuming fruits in the urban matrix may increase contact with human-modified environment and potential human-wildlife conflicts (Basak *et al.*, 2023; Nogueira *et al.*, 2025).

Fruit provisioning and access to urban resources affect the capuchins' diet at MSG. They eat items offered by humans or taken from neighboring houses. Fruit provisioning has become common in areas where primates interact with humans, altering monkeys' behavior, social relationships, and potentially leading to primate-human conflict (Hill, 1999; Mikich & Liebsch, 2014; Rangel *et al.*, 2013; Sabbatini *et al.*, 2008; Scarabelo & Setz, 2025; Smith *et al.*, 2022; Suzin *et al.*, 2017). In addition, provisioning can have serious consequences for primate health (e.g., obesity, dental problems, other diseases), because store-bought fruits and ultra-processed foods, for example, have more sugar, sodium, and preservatives (Araújo *et al.*, 2016; Costa *et al.*, 2011; Pontzer, 2023; Soto-Calderón *et al.*, 2016). Capuchins consume exotic and urban items at other sites (Cunha *et al.*, 2006; Gonçalves *et al.*, 2022; Mikich & Liebsch, 2014; Rasec-Silva *et al.*, 2023; Sabbatini *et al.*, 2006; Scarabelo & Setz, 2025; Schulte *et al.*, 2020; Smith *et al.*, 2022; Spagnoletti *et al.*, 2017). Such resources tend to be more accessible, predictable, and energy-rich and are preferred, reducing the consumption of wild and native fruits and enhancing reproduction, increasing population growth (Back & Bicca-Marques, 2019; Gonçalves *et al.*, 2022; Magioli *et al.*, 2022). The biologist at Mata de Santa Genebra

observed that the group size of the capuchins we studied increased over the years (Thomaz Barrella, personal communication, 2020), which may be due to the new items provided by the urban matrix. Together, these observations suggest that access to urban food resources may be reshaping capuchin natural history at MSG.

Conclusions

The highly flexible and diverse diet of capuchins at MSG, including urban-associated exotic plants, reveals important shifts in resource use since the 1990s. While *Zea mays* was the main dietary item in the 1990s, the current diet is now centered on *Inga vera affinis* and exotic plant species with variation in the consumption of food items between wet seasons, indicating dietary flexibility rather than changes in species composition. These findings have important implications for the future of forests near urban areas, particularly as contact between wildlife and exotic plants increases. For example, the incorporation of exotic and urban items into the primates' diet raises concerns about the long-term sustainability of the ecological processes in the fragment and the changing relationship between capuchins, plants, and other animals, including humans. The influence of the anthropic matrix on foraging for capuchins and other frugivores also leads to human-wildlife conflicts (e.g., roadkill, disease transmission), due to increasing interaction with humans. These questions are relevant to understanding how capuchin monkeys and other animals are dealing with invasive species and the long-term consequences for protected areas in urbanized landscapes.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10764-026-00566-x>.

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Authors' Contribution JVAV: Conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, software, validation, visualization, writing – original draft. EZFS: Conceptualization, supervision, project administration, funding acquisition, validation, writing – review & editing.

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Data Availability All data and scripts generated and analyzed during this study are included at Zenodo repository (<https://zenodo.org/records/19833044>) and in this published article supplementary information files. Supplementary Information: Supplementary file 1 consists of an Excel spreadsheet (divided into files, containing monthly feeding bout records by item category and plant species, items percentual, records of seeds found in scats, monthly arthropod consumption data, Sørensen-Dice similarity index calculations, and chi-square test results). Supplementary file 2 consists of seeds figures found in the scat samples. Supplementary file 3 is the R script.

Declarations

Inclusion and Diversity Statement - The author list includes contributors from the location where the research was conducted, who participated in study conceptualisation, study design, data collection, analysis, and/or interpretation of the findings.

- One of the authors of this paper self-identifies as a member of the LGBTQ+ community.
- While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

Conflict of Interest The authors declare that they have no conflict of interest.

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