Diet plasticity of black-horned capuchin monkey

# DIET PLASTICITY OF A WILD SOUTHERN BLACK-HORNED CAPUCHIN MONKEY GROUP IN AN URBAN FRAGMENT

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Abstract: *Sapajus nigritus* popularly known as southern black-horned capuchin monkey is a medium-sized arboreal primate endemic to the Atlantic Forest. They have high trophic and behavioral plasticity, which allows them to adapt to different environments, including highly fragmented landscapes and urban areas. This study aimed to understand the patterns and variations in the diet and feeding activity of capuchin monkeys living in an urban area by comparing areas with different habitat composition.

Keywords: Atlantic Forest, Foraging behavior, Platyrrhini, Sapajus nigritus, seasonality.

#### INTRODUCTION

The increase in human activity over the decades has contributed to changes in the structure of forest landscapes, and currently the primary neotropical forest is found isolated into fragments (Fahrig et al. 2003; Gilbert 2003) especially in the Brazilian Atlantic Forest (Rezende et al. 2018). Changes in land use associated with the process of habitat fragmentation have negative effects on biodiversity, promoting changes in the ecology and behavior of those animal species that resist the changes in habitat reduction (Ramsay et al. 2023). Under those conditions small and medium sized mammals can present dietary shifts, changes in home range size and reproduction (Luccas & Izar et al. 2021; Martins et al. 2022).

Primates are directly affected by anthropogenic fragmentation because they depend, at least in part, on forest cover for most of their life history traits (Chapman et al. 2013; Rovero et al. 2015; Stevenson 2016). Furthermore, the process of anthropogenic fragmentation may force these organisms to seek alternative food sources, reducing their trophic specialization and thus increasing their omnivorous behavior by consuming available resources (Bicca-Marques and Calegaro-Marques 1994; Silver and Marsh 2003). In this scenario, primates may alternatively consume non-native and/or cultivated species, such as monocultures of maize, sugarcane, and pine trees, causing damage to farmers (Bicca-Marques and Calegaro-Marques, 1994; Rocha 2000; Mikich & Liebsch, 2014; Hill 2017).

Trophic plasticity is common in primates (Singh et al. 2002; Irwin 2008), but the magnitude of these dietary changes leads to the evolution of new foraging and predatory behaviors (Bicca-Marques et al. 2009; Baoping et al. 2009). When living in urban forest remnants, the habitat conditions alter population dynamics in different primates (Ramsay et al. 2023), including robust capuchin monkeys *Sapajus* sp. (Back et al. 2019; Suscke et al. 2021). Under these conditions, capuchin species tend to consume large amounts of hypercaloric anthropogenic resources, which may lead to increased body fat, behavioral changes over time (e.g., dependence on anthropogenic foods), and exposure to pathogens and parasites (Maréchal et al. 2016; Suzin et al. 2017).

The Atlantic Forest is one of the most degraded forests in Brazil, with approximately 80% of its remaining forest found in small and isolated patches, and these patches are smaller than 50 ha (Ribeiro et al. 2009; Rezende et al. 2018). Among the several primate species endemics to this

biome *Sapajus nigritus*, also known as black-horned capuchins, is a medium-sized arboreal primate found in southeastern and southern Brazil and northeastern Argentina (Silva-Junior 2001; Vilanova et al. 2005). This species plays an important role in forest regeneration through seed dispersal (Mikich et al. 2015) and has the capacity to maintain population densities facing habitat fragmentation (Hendges et al. 2017). Although *S. nigritus* have a diet composed mainly of fruits throughout the year, they may also consume invertebrates, small vertebrates, leaves and stems at different frequencies between seasons (Izawa 1979; Galetti and Pedroni 1994; Fragaszy et al. 2004; Milano and Monteiro-Filho 2009; Gómez-Posada 2012; Albuquerque et al. 2014; Genty and Cäsar 2014).

The aim of this study was to investigate the dietary patterns and foraging activity of a population of urban black-horned capuchin monkeys living on a university campus. We compared areas within the campus with different habitat composition within the group's home range. We hypothesize that (1) there are differences in *Sapajus nigritus* diet between natural and anthropic areas. It is expected that feeding records at anthropic areas will show a higher diversity of food items due to greater anthropogenic disturbance, which may force capuchins to change their diet to adapt to new food sources. The second hypothesis is that (2) capuchin monkeys will spend more time during feeding in anthropic areas due to less diversity of native plant species and the presence of non-natural food resources. It is also expected that (3) diet composition will vary in response to seasonal changes, as native plant species may not be present throughout the year. Additionally, we assessed inter-individual variation by comparing the feeding pattern among different sex-age classes.

#### MATERIAL AND METHODS

#### Study site

The study was carried out at the State University of Londrina (UEL), located in the municipality of Londrina, State of Paraná (23°19'19" S and 51°12'04" W). The campus is in the

urban region of Londrina and includes fragments of natural seasonal semi-deciduous forest, woods and riparian forests, inserted in an urbanized area with impermeable surfaces such as buildings, streets, parking lots and agricultural crops and pastures. The campus total area is 1,692,582.354 m<sup>2</sup>, of which 236,062.01 m<sup>2</sup> is composed by mature semi-deciduous seasonal forest fragments. This study was conducted during the COVID-19 pandemic, which reduced the university community at UEL to a few graduate and undergraduate students and university staff. For those present, most of the daily diet consisted of packed lunches provided by the university itself, rather than the usual consumption of meals in campus restaurants and cafes, which changed the leftover types in trash cans.

Anthropic areas were defined as areas with the presence of artificial structures such as buildings, dumpsters, and impermeable areas (roads and parking lots), which also included exotic and native tree conglomerates that are considered urban forestation, where natural food resources may also be available at some level. We considered as part of the natural areas the forest patches that have a non-impermeable soil, forest cover and the presence of vegetation in the understory. However, as in Suzin et al. (2017), we considered as part of natural areas the regions within two meters of the fragment edge (Fig. 1).

## Study group

A group of southern black-horned capuchin (*Sapajus nigritus*) has the university campus as part of the group's home range from up to 30 years (Rocha, 1998). This monkey troop has direct anthropic contact, with access to urban areas of the campus (e.g., dumpsters, experimental fields and laboratory greenhouses), where they can find food from natural sources and humanmediated. This subspecies ranges from southern São Paulo State through Paraná, Santa Catarina, Rio Grande do Sul, in Brazil, and northern Argentina (Groves, 2001) and is considered near threatened with declining populations in the IUCN Red List (Ludwig et al., 2022). During this study the population of *Sapajus nigritus* was composed of 39 individuals of different sex-age classes, such as male and female adults, juveniles and infants (Supplementary Data SD1). From May/2021 to August/2021, the researchers were habituated to the group and the individuals were identified using facial and body recognition according to Izawa (1980).



Figure 1. Study area at the campus of the State University of Londrina (UEL), Londrina, PR, Brazil.

## Sampling design

Data were collected between August/2021 and August/2022, spanning dry and wet seasons, for a total of 257 sampling days, of which 67 days individuals were sighted. Individuals were sampled equally in the morning and afternoon for three hours or until visual contact was lost.

We sampled feeding episodes by direct observation using the focal animal method (Altmann 1974; Bateson and Martin 2021) using 5-min sampling interval for recording the

feeding behavior of focal individuals, and 5-min intervals for changing focal individuals, giving preference to unsampled individuals.

During sampling, we recorded the time (in seconds) of each feeding episode, so one or more feeding episodes may be present in a 5-minute sample. We identified the food item, classified according to its source (i.e. natural or anthropic), the age-sex class (adult male, adult female or juvenile) of the individual and the type of area (natural or anthropic) where the feeding episode occurred. Focal samples that contained different food items were considered as independent events. We did not collect samples from infant individuals, their diet is composed of breast milk.

When food items were plant parts, we identified at the lower possible taxonomic level, according to Souza and Harri (2012). In the absence of information about the species or uncertain identification, we requested the identification from a specialist (Dr. José Eduardo Lahoz da Silva Ribeiro). To classify plants according to its origin (i.e. native and exotic), we used Reflora Brasil Database (2024).

It is important to mention that the university campus is forested with native and exotic species, both in natural and in anthropic areas. Hence, it is possible that there are episodes of natural feeding recorded in anthropic areas. Similarly, green areas can also be visited by humans, leaving human food behind, so it is also possible that there are episodes of anthropogenic feeding in natural areas.

# Statistical procedure

We used a PERMANOVA based on a similarity matrix of Bray-Curtis to test the differences in time spent feeding in each item between areas. The pseudo-F statistic resulting from this analysis was tested using the Monte Carlo method with 999 randomizations. We used the permutational analysis of multivariate dispersions (PERMDISP, Anderson 2006) to test for variability in time spent feeding among individuals, where niche width was measured by the

spatial dispersion of food in space. We calculated the distance to the centroid using Principal Coordinate Analysis (PCoA). The centroid was calculated using the Bray-Curtis dissimilarity measure, which allows comparison of the mean dissimilarity of individual observations within the group. We tested the diet composition using three dependent variables: (i) area (i.e., anthropic versus forest fragment); (ii) seasonality (i.e., rainy versus dry season); (iii) age-sex class (i.e., adult female, adult male, and juvenile) in a second PERMANOVA. However, due to the binary nature of our data (i.e. presence and absence of food type in the focal sample), the similarity matrix was based on Jaccard similarity. The pseudo-F statistic resulted was tested by the Monte Carlo method using 999 randomizations. We used a permutation analysis of multivariate dispersions to evaluate potential variations in the species niche breadth across response variables (PERMDISP; Anderson 2004). We also compared areas through general proportion of feeding episodes in each item as in Gonçalves et al. (2022) and additionally, we tested the proportion of exotic-native and for exclusive-non-exclusive plant species using Z-test for proportions.

All statistical procedures were performed in the R software (R Core Team 2023) using the "vegan" (Oksanen et al. 2018), "spaa" (Zhang 2016), and "devtools" (Wickham et al. 2021) packages, and figures were created using the "ggplot2" package (Wickham 2016).

# RESULTS

We recorded 175 focal samples, including feeding behavior, divided into 237 independent feeding episodes, 196 collected in anthropic areas and 36 episodes in natural areas. Differences in the number of samples in each area were because capuchins spent most of their time in anthropic areas during data collection.

The study group consumed a total of 60 food items, divided into natural and anthropic resources (Table 1). Capuchins consumed 55 types of natural resources, such as plant items (i.e., fruit, leaf, stem, root, flower, and seed), invertebrates, and vertebrates. They consumed three items classified as anthropic resources: packaged lunch, dairy and industrial beverage. When comparing

the number of food items, capuchins had a more diverse diet in anthropic areas (51 items) than in natural areas (17 items) (Table 1). The study group consumed 54 plant species divided into 27 families, Fabaceae (7 sp., 35 records) and Anacardiaceae (1 sp., 33 records) being the most abundant plant families in this study (Table 1). Capuchins fed on four exotic species with 16 records out of 36 total plant records in natural areas, and in anthropic areas we registered twelve exotic species with 89 records out of 167 total plant records consumed (Table 1, Fig. 2). However, there was no significant difference between the proportions of food resources observed by area (Z-test, chi-squared = 0.00022356, df = 1, p-value = 0.988).

**Table 1.** – Food resources consumed by *Sapajus nigritus* in anthropic and natural areas, during the dry and rainy seasons, between the months of August/2021 to August/2022. \* =non-native species.

| Food items                              |                            | Feeding episode | Area |           |         |
|---|----------------------------|-----------------|------|-----------|---------|
| Plants                                  | Feeding part               | Duration(s)     | n    | Anthropic | Natural |
| ARAUCARIACEAE<br>Araucaria angustifolia | Seed                       | 81              | 1    | 1         | -       |
| LAURACEAE                               |                            |                 |      |           |         |
| Persea americana                        | Flower, Fruit and Leaf     | 834             | 6    | 4         | 2       |
| Ocotea puberula                         | Fruit                      | 106             | 2    | 2         | -       |
| ARACEAE                                 |                            |                 |      |           |         |
| Epipremnum aureum*                      | Leaf                       | 614             | 4    | -         | 4       |
| Thaumatophyllum bipinnatifidum          | Fruit                      | 566             | 2    | 2         | -       |
| Syngonium sp.*                          | Stem                       | 232             | 4    | 3         | 1       |
| ARECACEAE                               |                            |                 |      |           |         |
| Syagrus romanzoffiana                   | Fruit and Leaf             | 574             | 5    | 3         | 2       |
| Livistona chinensis*                    | Fruit and Leaf             | 466             | 3    | 3         | -       |
| Euterpe edulis                          | Fruit, Root and Stem       | 267             | 5    | 5         | -       |
| BROMELIACEAE                            |                            |                 |      |           |         |
| Tillandsia sp.                          | Leaf and Root              | 249             | 3    | 3         | -       |
| POACEAE                                 |                            |                 |      |           |         |
| Saccharum officinarum L.*               | Stem                       | 622             | 4    | 4         | -       |
| Bambusa textilis*                       | Leaf and Stem              | 456             | 5    | 5         | -       |
| Zea mays                                | Fruit                      | 389             | 2    | -         | 2       |
| Guadua angustifólia                     | Stem                       | 165             | 1    | -         | 1       |
| Axonopus compressus                     | Stem                       | 114             | 1    | 1         | -       |
| Digitaria insularis*                    | Stem                       | 108             | 1    | 1         | -       |
| FABACEAE                                |                            |                 |      |           |         |
| Cassia fistula*                         | Flower, Fruit and Stem     | 1876            | 10   | 10        | -       |
| Cenostigma pluviosum                    | Fruit, Leaf, Root and Stem | 1010            | 11   | 9         | 2       |

| Food items                |                            | Feeding episode Area |    | a         |         |
|---------------------------|----------------------------|----------------------|----|-----------|---------|
| Plants                    | Feeding part               | <b>Duration</b> (s)  | n  | Anthropic | Natural |
| Inga marginata            | Fruit and Leaf             | 985                  | 7  | 6         | 1       |
| Hymenaea courbaril        | Fruit and Stem             | 163                  | 2  | 2         | -       |
| Bauhinia forficata        | Leaf, Stem and Root        | 160                  | 3  | 3         | -       |
| Tipuana tipu              | Flower and Stem            | 137                  | 2  | 2         | -       |
| Piptadenia gonoacantha    | Stem                       | 92                   | 1  | 1         | -       |
| Fabaceae sp1.             | Stem                       | 68                   | 1  | 1         | -       |
| Delonix regia             | Stem                       | 43                   | 1  | 1         | -       |
| ROSACEAE                  |                            |                      |    |           |         |
| Eriobotrya sp. *          | Fruit and Stem             | 2025                 | 15 | 11        | 4       |
| Malus sp.                 | Fruit                      | 162                  | 1  | 1         | -       |
| MORACEAE                  |                            |                      |    |           |         |
| Artocarpus heterophyllus* | Fruit, Root and Stem       | 1457                 | 12 | 12        | -       |
| Ficus sp.                 | Leaf                       | 146                  | 1  | 1         | -       |
| Ficus eximia              | Leaf                       | 46                   | 1  | -         | 1       |
| Ficus pumila              | Leaf                       | 21                   | 1  | 1         | -       |
| URTICACEAE                |                            |                      |    |           |         |
| Urera bacífera            | Leaf and Stem              | 310                  | 3  | -         | 3       |
| JUGLANDACEAE              |                            |                      |    |           |         |
| Carya illinoinensis*      | Fruit                      | 56                   | 1  | 1         | -       |
| EUPHORBIACEAE             |                            |                      |    |           |         |
| Alchornea triplinervia    | Stem                       | 66                   | 1  | -         | 1       |
| COMBRETACEAE              |                            |                      |    |           |         |
| Terminalia catappa*       | Fruit, Leaf, Root and Seed | 2526                 | 16 | 16        | -       |
| MYRTACEAE                 |                            |                      |    |           |         |
| Campomanesia pubescens    | Fruit and Stem             | 1039                 | 5  | 5         | -       |
| Eugenia uniflora          | Leaf and Stem              | 474                  | 5  | 5         | -       |
| Syzygium cumini           | Fruit, Leaf and Stem       | 438                  | 6  | 5         | 1       |
| ANACARDIACEAE             |                            |                      |    |           |         |
| Mangifera indica*         | Fruit, Seed and Stem       | 4093                 | 33 | 26        | 7       |
| SAPINDACEAE               |                            |                      |    |           |         |
| Dimocarpus longan*        | Fruit                      | 265                  | 1  | 1         | -       |
| MELIACEAE                 |                            |                      |    |           |         |
| Cabralea canjerana        | Stem                       | 82                   | 1  | -         | 1       |
| Trichilia clausseni       | Stem                       | 70                   | 1  | 1         | -       |
| Cedrela fissilis          | Fruit                      | 35                   | 1  | 1         | -       |
| PHYTOLACCACEAE            |                            |                      |    |           |         |
| Phytolacca dioica         | Leaf                       | 135                  | 1  | -         | 1       |
| SOLANACEAE                |                            |                      |    |           |         |
| Solanaceae sp.            | Leaf                       | 55                   | 1  | 1         | -       |
| BIGNONIACEAE              |                            |                      |    |           |         |
| Jacaranda mimosifolia*    | Seed                       | 130                  | 1  | 1         | -       |
| Amphilophium crucigerum   | Stem                       | 71                   | 1  | -         | 1       |
| ANNONACEAE                |                            |                      |    |           |         |

| Food items                                | Feeding episode | Feeding episode     |    |           |         |
|---|-----------------|---------------------|----|-----------|---------|
| Plants                                    | Feeding part    | <b>Duration</b> (s) | n  | Anthropic | Natural |
| Annona squamosa                           | Fruit           | 165                 | 2  | 1         | 1       |
| APOCYNACEAE<br>Aspidosperma polyneuron    | Leaf            | 210                 | 2  | 2         | -       |
| CALOPHYLLACEAE<br>Calophyllum brasiliense | Stem            | 36                  | 1  | 1         | -       |
| RUTACEAE<br>Citrus spp.*                  | Fruit           | 74                  | 2  | 2         | -       |
| ASPARAGACEAE<br>Dracaena fragrans         | Stem            | 95                  | 1  | 1         | -       |
| VERBENACEAE<br>Duranta erecta             | Fruit           | 95                  | 1  | 1         | -       |
| PIPERACEAE                                |                 |                     |    |           |         |
| Piper aduncum                             | Fruit           | 26                  | 1  | 1         | -       |
| Invertebrate                              |                 |                     |    |           |         |
| Artropods                                 | -               | 2361                | 23 | 23        | -       |
| Vertebrate                                |                 |                     |    |           |         |
| Bird eggs                                 | -               | 196                 | 2  | 2         | -       |
| Other                                     |                 |                     |    |           |         |
| Honeycomb                                 | -               | 61                  | 1  | 1         | -       |
| Processed                                 |                 |                     |    |           |         |
| Packaged lunch                            |                 | 1016                | 5  | 5         | -       |
| Dairy Beverage                            | -               | 340                 | 2  | 2         | -       |
| Industrialized beverage                   | -               | 45                  | 1  | 1         | -       |

The feeding pattern observed in anthropic areas is characterized by Fruit (35.19%), Stem (13.39%), Seed (11.29%), Leaf (8.36%), Invertebrate (7.94%), Processed (3.34%), Root (1.25%) and Flower (0.8%). In natural areas, capuchins fed exclusively on Fruit (6.17%), Invertebrate (2.51%), Leaf (4.6%) and Stem (4.18) (Fig. 3). However, the proportion of fruit in the diet was not significantly different between anthropic and natural areas (chi-squared = 0.42862, df = 1, p-value = 0.2563).



**Figure 2.** Frequency of *Sapajus nigritus* feeding records on native and exotic plants in natural and anthropic areas at the campus area of the Universidade Estadual de Londrina.



Figure 3. Plant parts consumption frequency in natural and anthropic areas by *Sapajus nigritus* at campus area of the Universidade Estadual de Londrina.

Diet composition

The diet composition of *S. nigritus* varied significantly between natural and anthropic areas (pseudo $F_{[1,177]} = 2.016$ ; p = 0.015). There are differences in the consumption of plants that are exclusively present in each area, as the proportion of exclusive plants per area (i.e. species richness) were higher in anthropic areas (33 sp. out of 42 species) than in natural areas (nine sp. out of 18 species (Z-test, chi-squared = 3.6319, df = 1, p-value = 0.02834) (Fig. 4). The number of feeding records was also higher in anthropic compared to natural areas (chi-squared = 3.0511, df = 1, p-value = 0.04034)



**Figure 4.** *Sapajus nigritus* exclusive and non-exclusive feeding records in natural and anthropic areas at the campus area of the Universidade Estadual de Londrina.

Comparing the seasons, capuchins had a different diet composition throughout the seasons (PERMANOVA, pseudoF<sub>[1,177]</sub> = 5.601; p = 0.001). Considering exotic plant species, we did not observe significant variation when all plant parts were combined (chi-squared = 2.1252, df = 1, p-value = 0.07245) (Fig. 5), but also considering only the Fruit category (chi-squared = 3.5497e-31, df = 1, p-value = 1). However, when we compared the consumption of Fruit from native plant species, the proportion were significantly lower in the dry than rainy season (chi-squared = 6.54,

df = 1, p-value = 0.005274). The consumption of all parts from native species per season was not



significantly different (chi-squared = 1.4855, df = 1, p-value = 0.2229).

**Figure 5.** Feeding records of *Sapajus nigritus* on native and exotic plants during the rainy and dry seasons at the campus area of the Universidade Estadual de Londrina.

Nevertheless, diet composition was not influenced by sex-age class (pseudo $F_{[2,177]} = 1.245$ ;

p = 0.124), nor by the interactions of age-sex and other variables (season or area) (Table 2).

|                                     | Df  | SumOfSqs | R <sup>2</sup> | F      | p-value |
|-------------------------------------|-----|----------|----------------|--------|---------|
| Area                                | 1   | 0.911    | 0.01094        | 2.0165 | 0.015   |
| Seasonal                            | 1   | 2.532    | 0.03038        | 5.6012 | 0.001   |
| Sex-age class                       | 2   | 1.125    | 0.01351        | 1.2451 | 0.124   |
| Seasonal vs. Area                   | 1   | 0.595    | 0.00714        | 1.3165 | 0.135   |
| Seasonal vs. Sex-age class          | 2   | 1.122    | 0.01347        | 1.2412 | 0.153   |
| Area vs. Sex-age class              | 2   | 1.156    | 0.01388        | 1.2793 | 0.107   |
| Seasonal vs. Area vs. Sex-age class | 2   | 0.848    | 0.01018        | 0.9383 | 0.599   |
| Residual                            | 166 | 75.027   | 0.9005         |        |         |
| Total                               | 177 | 83.316   | 1              |        |         |

**Table 2.** Multilevel permutational analysis of variance (PERMANOVA) results applied to the *Sapajus nigritus* Diet Composition between areas (anthropic x natural); seasons (rainy x dry); sex-age class (Adult male x Adult female x Juvenile). Bold numbers represent p-value significance (<0.05).

Inter-individual variation in *Sapajus nigritus* only occurred between anthropic and natural areas (PERMDISP, ANOVA:  $F_{[1,176]} = 5.66$ , p = 0.01), and this variability is relatively greater in anthropic areas (Average distance to centroid = 0.68). However, the analysis did not reveal any inter-individual variability accounting to other variables (i.e. season and sex-age effects) (Table 3).

# Feeding duration

The duration of feeding differed significantly between areas, being longer in anthropogenic areas (PERMANOVA: pseudoF<sub>[1,176]</sub> = 2.031; p = 0.005) (Table 3). Moreover, feeding duration can significantly vary among individuals depending on the areas (PERMIDISP, ANOVA:  $F_{[1,176]}$  = 7.3043, p = 0.007).

| (Permdisp)<br>Average distance to centroid |           |              |            |      | p-value |
|--|-----------|--------------|------------|------|---------|
| Area                                       | Anthropic | Natural      | -          | 5 66 | 0.01    |
|  | 0.68      | 0.66         |            | 5.00 | 0.01    |
| Seasonal                                   | Rainy     | Dry          | -          | 0.45 | 0.5     |
|  | 0.66      | 0.67         |            | 0.43 | 0.5     |
| Sex-age class                              | Juvenile  | Adult Female | Adult Male | 171  | 0.19    |
|  | 0.68      | 0.67         | 0.68       | 1./1 | 0.18    |

**Table 3.** Multivariate Dispersion Permutation Analysis (PERMDISP) results on *Sapajus nigritus* interindividual diet. Bold numbers represent p-value significance (<0.05).

## DISCUSSION

Black-horned capuchin monkeys can alter their diet as a foraging strategy to adapt to the availability of new food resources when living in urban forest fragments, which matches the pattern observed in *Sapajus* by Fragaszy et al. (2004). As evidence supporting our first hypothesis, capuchins had a different diet in natural and anthropic areas in that some plant species were consumed exclusively in natural areas, while there were also some items exclusive to anthropic

areas. Furthermore, we observed that episodes in different areas differed in feeding duration, which is also expressed by inter-individual variation (i.e., individuals spend time eating differently). Lastly, there are seasonal variations in both diet composition and feeding duration.

While capuchins frequently consume natural food sources, a large proportion of their diet consists of exotic plants that may also act as invasive alien species in this area. The consumption of exotic plant species on the university campus was proportional in natural and anthropic areas, indicating a concerning pattern in these urban fragments. We observed seasonal variations in the presence/absence and number of records of native plant species. This shows that capuchin monkeys can acquire other sources of food, such as exotic plants, when they experience a reduction in their natural diet (Suzin et al. 2017). When primates experience a reduction or unavailability of key food resources, they may shift their diet to maintain their energy intake (McLennan et al. 2017). This has been observed in both Old-World primates (*Hylobates albibarbis*, Marshall and Leighton 2006; *Macaca sylvanus*, Maibeche et al. 2015; *Chlorocebus djamdjamensis*, Mekonnen et al. 2018) and New-World primates (*Alouatta guariba clamitans*, Chaves and Bicca-Marques 2016; *Sapajus cay*, Suzin et al. 2017).

Food-related shifts are expected in *S. nigritus* as they are known for their behavioral flexibility to keep up changes in the amount of valuable food items (Fragaszy 2004; Sabbatini et al. 2007; Izar et al. 2012; Luccas & Izar 2021). Our results show that the presence of differential food sources in anthropic areas modulate foraging decisions in this group, not because there is human food but because there are different exotic and native plant species in more anthropogenic areas. The top frequent exotic plants such as the mango (*Mangifera indica*), jackfruit (*Artocarpus heterophyllus*), the Japanese loquat (*Eriobotrya japonica*), and several other exotic species, are present in both anthropic and natural areas whereas these species are used as green cover. Although capuchins here spent most of their time at anthropic areas, the foraging decisions were not only associated to the presence of processed food (i.e. human-provided food nor human-leftovers).

Consumption of exotic plant species is of particular concern because of the role that primates can play as seed dispersers (Bufalo et al. 2016; Fuzessy et al. 2022). Black-horned capuchins are primates that tolerate some degree of habitat fragmentation, so their role as seed dispersers can have both negative and positive effects on the provision of ecosystem services (Hendges et al. 2017). They can disperse native species that promote forest regeneration, but they can also disperse exotic species that alter the disturbance regime in forest remnants (Mikich et al. 2015; Hendges et al. 2017). Life history studies have shown that baboons (*Papio anubis*) feeding on an exotic prickly pear cactus may have increased the invasion of this species in Kenya (Strum et al., 2019).

The pandemic situation directly affected conservation programs and primate studies across the world. As a result, many researchers had their studies neglected to some extent (Reuter et al. 2022). We gathered our data during an abnormal situation when most university community members were absent due to the Covid-19 pandemic. This could be the reason for the significant number of group encounters observed in the anthropic areas, as we visited those areas at the same effort and followed the group whenever they would go (i.e. same research effort).

The seasonal effect observed here may be associated with the lower availability of native species and, consequently, the lower availability of fruits throughout the year. Therefore, capuchins consumed whatever resources were available during the dry season. Black-horned capuchins already been seen feeding on other sources when preferred (mostly, fleshy native fruits) were scarce or absent, in forestry areas (Mikich & Liebsch 2014); on fallback food sources, such as cassava (*Manihot suculenta*, Ludwig et al. 2005); and became seed predators and flower eaters (Galetti & Pedroni, 1994). This seems to be a pattern in different *Sapajus* species, as *S. libidinosus* are also known for using tool-use for the consumption of encased food when they face reduced fruit availability.

The scarcity of natural preferred food sources caused urban robust capuchin monkeys (*Sapajus* sp.) to consume higher proportions of human-derived food (Suzin et al. 2017). Our data

contrasts with Suzin (2017) in part, there capuchins consumed both natural (i.e. exotic plant species) and anthropogenic food items (e.g. processed food), here events of anthropogenic food were lower, but the exotic plant consumption was expressive.

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