

# Plant community and native primate as drivers of habitat use by an exotic primate (*Saimiri* spp. Linnaeus, 1758) in an Atlantic Forest fragment

## Research Article

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## Abstract

Understanding how and why exotic species use their habitats is crucial for defining effective conservation strategies. We aimed to investigate habitat use by an exotic population of squirrel monkeys living in an Atlantic Forest fragment and identify factors associated with their habitat preferences. Over 6 months of scan sampling observations, we collected data on native and exotic plants consumed by the squirrel monkeys, food availability, and interactions between the squirrel monkeys and the native common marmosets. We also georeferenced the estimated centroid point of the study group during each scan. Squirrel monkeys used Secondary Old Forest habitats more often than the other habitats available. The consumption of native and exotic plants and the association with common marmoset appear to have influenced the habitat use of the exotic squirrel monkeys; however, the choice habitat did not demonstrate to be associated with food availability. The exotic squirrel monkeys preferred to use less disturbed habitats to consume a high amount of food (often associated with the common marmoset), potentially optimizing their food intake. Our findings demonstrated the adaptive success of an exotic primate in its non-natural habitat and the key role of the plant community in maintaining this population.

## Introduction

To aid our understanding of ecological niches, we must investigate habitat use and preferences of both native and exotic species (Castro & Huber 2003; Kuprijanov 2017). Exotic species are organisms introduced outside their natural range and natural dispersal potential (Olenin *et al.* 2010). Exotic species, especially, can assume the role of competitors and predators of native species, potentially limiting food resources and spreading diseases within habitats (Primack & Rodrigues 2001; Moura-Brito & Patrocínio 2006; Camarotti *et al.* 2015). Moreover, such species can also increase fruit production by pollination processes (Pavé *et al.* 2009), thereby attracting animals to consume and disperse their seeds, increasing the potential risk to local biodiversity (Hendges *et al.* 2012; Canale *et al.* 2016). Additionally, the establishment of a given exotic organism can be facilitated for another exotic one. This relationship between exotic species is commonly known as an invasional meltdown (Simberloff & Von Holle 1999). If a species is invasive, it will quickly expand its population in the new territory, potentially becoming dominant (Valéry *et al.* 2008). Thus, studying behavioural and ecological aspects of exotic organisms with a high potential to become invasive is crucial in helping habitat management and the conservation of areas.

The relationship between animals and their habitats constitutes a central component in wildlife ecology (Morrison *et al.* 2006). To increase their chances of survival and reproduction, animals can select and preferentially use specific areas and avoid others (Gaillard *et al.* 2010). Several factors are responsible for animal habitat preferences, including canopy height, vegetation coverage, availability and distribution of food resources, and the presence of other organisms (Manly *et al.* 2007; Herfindal *et al.* 2009).

The habitat use by mammals is strongly associated with food availability and distribution in their habitat (Hanya *et al.* 2020; Kinap *et al.* 2021). Neotropical primates, for example, inhabiting predictable environments in terms of food production, such as tropical rainforests, tend to choose their habitat type according to the presence/absence of specific food belonging to their diet (Heiduck 2002). For instance, during periods of high fruit production, black-fronted titi monkeys (*Callicebus nigrifrons* Spix, 1823) use central areas of their home range (Nagy-Reis & Setz 2017), and masked titi monkeys (*Callicebus melanochir* Wied-Neuwied 1820) often

exploit undisturbed areas due to the high availability of food (Heiduck 2002). In these habitats, both species appeared to search for food resources highly nutritious (i.e., fruits) to maintain their daily energy. The type of food available – that is, native or exotic – may also influence habitat use. The consumption of exotic *Artocarpus heterophyllus* Lam. fruits by golden-headed lion tamarins (*Leontopithecus chrysomelas* Kuhl, 1820), for instance, affects the use of cacao plantations by this primate species (Oliveira *et al.* 2011).

Mixed-species groups include associations between at least two groups of different species or between an individual of a species and a group of another species (Terborgh 1983). Such associations increase the group's overall size, which may lead to increased direct resource competition. Still, they can improve predator detection or defence or have other foraging-related benefits (Terborgh 1983; Cords 2000; Rehg 2006). The benefits of foraging during mixed-species association may include a greater chance of detecting and obtaining food (Terborgh 1983; Peres 1996). Time spent foraging can also increase because of cooperative anti-predator surveillance behaviour. Callitrichids, for example, scan for potential predators visually, compromising much of the daily activity time (Ferrari & Lopes Ferrari 1989). Thus, a decrease in vigilance can lead to an increase in time spent foraging and feeding. For example, when small groups of *L. chrysomelas* are associated with Wied's marmoset (*Callithrix kuhlii* Coimbra-Filho 1985) groups, they use areas of lower forest canopy levels (Almeida-Rocha *et al.* 2015). Considering the complex alarm calling system often observed in primates (e.g., Cäsar & Zuberbuehler 2012), other advantages related to predation include the increased probability of detecting a predator (Norconk 1990) and a lower probability of being captured (Roberts 1996).

The squirrel monkeys (genus *Saimiri*) have been illegally introduced outside their natural distribution – Amazonian Forest – in several parts of Brazil (Rosa *et al.* 2017). In North-eastern Brazil, the species can be found inhabiting Atlantic Forest fragments in Salvador, Alagoas and two municipalities in Pernambuco: Tamandaré (Mendes-Pontes *et al.* 2007) and Recife (PAN PriNE 2013). In Recife Forest fragments, the exotic squirrel monkeys have been reported as a potential seed disperser of native trees (Oliveira-Silva *et al.* 2018). They seem to possess flexible ecological and behavioural patterns to adapt to the Atlantic Forest (Campêlo *et al.* 2019). In Atlantic Forest fragments in Tamandaré, the presence of the species has been reported to negatively influence the behavioural pattern of a local primate, the common marmoset, *Callithrix jacchus* Linnaeus, 1758 (Camarotti *et al.* 2015).

The present study aimed to investigate the use of an urban fragment of Atlantic Forest in North-eastern Brazil by the exotic squirrel monkey, *Saimiri* spp. We investigated if habitat use by exotic squirrel monkeys was associated with the consumption of exotic and native plant species, the presence of native common marmosets, and monthly fruit production. In this sense, we predicted that (i) exotic squirrel monkeys would preferentially use areas where exotic plants were prevalent, due to their preference for this food source in the study site (Campêlo *et al.* 2019); (ii) the presence of common marmosets (*Callithrix jacchus* Linnaeus, 1958) does not affect habitat choice of exotic squirrel monkeys due to the lack of agonistic interactions previously observed between the species in the study area (Campêlo *et al.* 2019); furthermore, due to different feeding habits between common marmoset and exotic squirrel monkeys (e.g., Castro & Araújo 2006; Paim *et al.* 2017; Schiel & Souto 2017; Oliveira-Silva *et al.* 2018), the species would not share the same habitat, and (iii) exotic squirrel monkeys would

preferentially use habitat where the fruit production is increased (Boinski 1987; Silva *et al.* 2003; Veiga 2006; Mercês and de Paula 2018).

### Study site

We carried out the study in a 106-ha urban Atlantic Forest fragment at Mata do Curado Wildlife Refuge (8°04'50"S, 34°58'21"W), located in Recife, Pernambuco, North-eastern Brazil. The area has many plant species from the families Monimiaceae and Melastomataceae (Lins-e-Silva & Rodal 2008). The tree density is 780 individuals/ha, basal area of 24.7 m<sup>2</sup> ha<sup>-1</sup>, and the mean height of the tree canopies is 11.3 m (Lins-e-Silva & Rodal 2008). Over the ten years before our study (2006–2016), the mean monthly rainfall from December to March was 188.6 ± 110 mm (range: 67.7 mm–335.2 mm). During the study period (December 2016 to May 2017), the monthly rainfall ranged between 67.8 mm (December) and 397.7 mm (May) with an average of 157.7 ± 154.5 mm (APAC 2017). Because the study area is inserted in the urban area, many exotic plant species exist, such as *Artocarpus heterophyllus* Lam., *Mangifera indica* L., *Musa* sp., and *Elaeis guineensis* Jacq. Furthermore, such plants are uniformly distributed under high densities in the home range of the study squirrel monkey group (6.83 individuals/ha) (Campêlo *et al.* 2019).

## Material and methods

### Data collection

From December 2016 to May 2017, we collected behavioural and ecological data from a population of exotic squirrel monkeys. We observed the apparent fission–fusion division of the population during the systematic monitoring, resulting in at least five subgroups averaging 59 individuals (± SD 45: 25–139 individuals). Expeditions lasted ten continuous days per month. The fieldwork activities occurred from 05:00 to 17:00, using the scan sampling method (Altmann 1974) at 10 minutes intervals, totalling 147 hours of observations (mean number of records/scans: 11 ± SD 2). We have used the pattern procedure to collect behavioural data for primates (see Zuberbühler & Wittig 2011). This procedure consisted in recording the behavioural activity separately of each individual in the view. Thus, if there were four individuals during the scan, and, two individuals could be feeding, one resting, and the last moving on the trees each behaviour was separately recorded. When the monitored individuals of the subgroup were visually lost, the scan sampling was stopped and resumed when the observer reencountered the animals, and when a given monitored subgroup was lost, the first subgroup or even the previously monitored was found, the scan was returned. We recorded several behavioural categories during the scans, including rest, feed, move, and social interaction (adapted from Campêlo *et al.* 2019). In this study, we only used data from feeding on native and exotic plants in the present study. When the animals were consuming any plant parts (i.e., fruit, leaf, flower, seed), the plant source was marked with vinyl tape and numbered; when it was not possible to identify the plant in the field, a fertile branch was collected for identification at Geraldo Mariz herbarium at the Universidade Federal de Pernambuco.

### Habitat characterization

Before characterizing the habitat, we established the home range limits of the exotic squirrel monkey group over the study period. These limits were based on the minimum convex polygon, with

100% of the points georeferenced in each scan. We used this estimator as the kernel density estimators often overestimate home range size when the sample size is small (Boyle *et al.* 2009). We used the software ArcGis 9.3 with the Home Range Extension (Rodgers & Carr 1998). We overlapped a raster of the forest structure over the exotic squirrel monkeys' home range limits, aiming to characterize its structure. The raster was provided by the Woods Hole Research Center (<http://whrc.org/publications-data/datasets/detailed-vegetation-height-estimates-across-the-tropics/>) obtained from LiDAR (light detection and ranging). This system provided information on vegetation height at a pixel resolution of  $30 \times 30$  m, allowing for the classification of the exotic squirrel monkeys' home range into three categories: (i) Disturbed Forest (trees between 0–5 m); (ii) Secondary Initial Forest (6–12 m); and (iii) Secondary Old Forest (>12 m) (adapted from Oliveira-Silva *et al.* 2018).

### Food availability

To quantify the food availability within the home range of the exotic squirrel monkeys and thus verify a possible association with the used habitat (Freitas *et al.* 1997; Pinotti 2010; Camaratta *et al.* 2017), we installed 50 fruit traps in five transects. These transects were randomly distributed within the limits of the home range of the study group. Each transect was set up at least 100 m apart and received ten fruit traps (1 m  $\times$  1 m) 2 m apart from one another (Oliveira-Silva *et al.* 2018). Thus, the total trapped area was 50 m<sup>2</sup>. We fortnightly revised the traps from December 2016 to May 2017, when all fruits and seeds were collected and taken to the laboratory for analysis. The trapped fruits and seeds were identified to their highest taxonomic level possible. Still, when it was impossible to identify the seed/fruit, we classified them as morphotypes based on their general morphological characteristics (e. g., size, form, colour).

### Presence of common marmosets

During the scan sampling, we registered the native common marmosets (*Callithrix jacchus*) using the same area as the exotic squirrel monkeys if they were within a 50-m radius (Oates & Whitesides 1990). We recorded the estimated distance between the common marmosets and the exotic squirrel monkeys. Also, when the exotic squirrel monkeys were engaged in feeding behaviour, we recorded whenever the common marmoset was in the same tree. We recorded whether the common marmosets were eating the same food item, a different item, or not eating at all.

### Data analysis

To determine the different types of habitats used by exotic squirrel monkeys during each scan sampling, we georeferenced the central location of the observed group using a handheld Garmin 60CSx GPS. Furthermore, whenever a plant source – native or exotic plant – was consumed, we identified, marked, and georeferenced the source. We then mapped the location of native and exotic plant species that were part of the exotic squirrel monkey diet within their home range. Therefore, at the end of this procedure, we had the geographical location of (i) native and exotic consumed plants; (ii) feeding behaviour; and (iii) the presence of common marmosets.

Although there is a fission–fusion dynamic in exotic squirrel monkeys, we treated all the population as a unit sampling. Thus, all the behavioural and ecological events within each month were summed. Firstly, we used the abundance of resources in the traps to classify the months with low and high food availability

extremes. We considered the period of low availability when abundance was lower than the lower limit of the 95% confidence interval (CI). In contrast, abundance was higher than its upper limit in high availability month. We have used such extreme values because there is a strong association among these periods on the behaviour and ecology of Neotropical primates (Chaves & Bicca-Marques 2016; Nagy-Reis & Setz 2017; Souza-Alves *et al.* 2021a, 2021b). Thus, following the 95% confidence interval (range = 176–597), the month with the lowest availability was December, and the month with the highest availability was May. Therefore, such months were chosen to verify the potential influence of low and high availability periods on the habitat use of exotic squirrel monkeys.

For the frequency of consumption of native and exotic plants across months, we have quantified the total frequency for both and calculated the relative frequency (%) using the formula:  $p_i = n_i/N \times 100$ , where  $p_i$  = percentage of the total number of records for fruits,  $n_i$  = number of records of fruits, and  $N$  = total number of records collected during the study period (Cullen & Valladares-Pádua 1997).

To verify if exotic squirrel monkeys engaged in true associations, remaining in contact more often than it would be expected by chance, we used the ideal gas model proposed by Waser (1982) and Hutchinson & Waser (2007). First, we calculated the expected values of frequency of association using the following equation to generate expected values of the encounter due to chance:

$$S_{ij} = 2\rho Dv$$

where  $S$  is the frequency that group  $i$  will form an association with group  $j$  given the density of each group ( $\rho$ ), the distance used to define the association between groups ( $D$ ), and the mean relative velocity ( $v$ ). We assumed the Maxwell-Boltzmann distributions of velocity in both groups; therefore,  $v$  was calculated following Hutchinson & Waser's (2007) equation:

$$v = \sqrt{\bar{u}^2 + \bar{v}^2}$$

where  $v$  is the mean relative velocity,  $\bar{u}$  is the mean velocity for the group  $i$  and,  $\bar{v}$  is the mean velocity for the group  $j$ . Velocities for exotic squirrel monkeys and common marmosets represent the mean distances travelled per full-day follow (0.81 km/d–0.90 km/d) were obtained from Campêlo *et al.* (2019) and Digby *et al.* (2011), respectively. We tested whether observed results differed significantly from predictions by comparing the variance in mean monthly observations of encounter rate to the expected encounter rate with a t-test procedure (Hutchinson & Waser 2007). We produced 95% confidence intervals by multiplying the standard error of the mean for monthly encounter rates by the 95% confidence interval for the T distribution and adding and subtracting from the mean (Hutchinson & Waser 2007). If the predicted encounter rate fell outside the confidence intervals, the observed encounter rate was significantly different from chance. We used a square-root transformation to normalize the data.

To obtain the proportion of the different types of habitats within the home range, we used the total pixel count within the limits of the home range of the study group ( $N = 880$  pixels). The observed proportion of each type of habitat and the variables used (food availability, presence of common marmosets, presence of exotic and native trees) was determined by the presence of at least one scan within a defined habitat.





**Fig. 1** Home range extracted through minimum polygon convex using 100% (red line) of the collected points of the exotic squirrel monkeys and three different types of habitats (0–5 m: Disturbed Forest; 6–12: Secondary Initial Forest; <12 m: Secondary Old Forest).

The observed frequencies were obtained through of quantification of each pixel based on (i) the presence of native and exotic plants consumed (prediction #1); (ii) the presence of exotic squirrel monkeys during the periods with low and high food availability (prediction #2); and (iii) presence of common marmosets (prediction #3).

To determine the expected frequency of habitat used by exotic squirrel monkeys, we considered the percentage of each type of habitat within the home range calculated from the number of pixels. We then considered the observed frequency of the habitats used in association with the predictive variable, that is, the presence of exotic and native plant species consumed by exotic squirrel monkeys. Thus, it was possible to calculate the expected frequency for the consumption of exotic and native plant species by exotic squirrel monkeys in the different habitats using the following equation:

$$\text{Freq}_{exp} = \frac{\sum \text{Freq}_{obs} \times \%Hbd}{100}$$

where  $\text{Freq}_{exp}$  is the expected frequency of the records,  $\text{Freq}_{obs}$  is the observed frequency of records for each predictive variable in each habitat, and Hbd is the percentage of the type of habitat available.

For the other predictive variables (i.e., common marmoset presence, food availability), we first calculated the percentage of each type of habitat used by the exotic squirrel monkeys. Then, we calculated the observed frequency referring to the habitats for each predictor variable aforementioned. From these results, it was possible to calculate the expected frequency of the habitat used with the variables using the equation:

$$\text{Freq}_{exp} = \frac{\sum \text{Freq}_{obs} \times \%Hbu}{100}$$

where  $\text{Freq}_{exp}$  is the expected frequency of the records,  $\text{Freq}_{obs}$  is the observed frequency of records for each predictive variable in each habitat, and Hbu is the percentage of habitat type used.

To verify if habitat type used by exotic squirrel monkeys was associated with the predictor variables (difference between expected and observed frequency), we used Fisher's tests of independence based on 999 randomizations through the *DescTools* package (Signorell *et al.* 2019) in the RStudio version 1.1.463 (RStudio Team 2019). Statistical significance was set at  $p < 0.05$ .

## Results

### Habitat characterization

A total of 880 pixels were registered in the exotic squirrel monkey home range. Sixty-three per cent ( $N = 561$  pixels) of the study area was characterized as Secondary Old Forest, with the other two categories of forest occupying less than 40% of the area, Secondary Initial Forest = 295 (33%)/Disturbed Forest = 24 (3%) (Figure 1, Table 1). In general, the exotic squirrel monkey preferred Secondary Old Forest habitats when considering the observed and expected frequency (Table 1 – Fisher's test:  $p = 0.001$ ).

### Fruit availability

A total of 2,323 fruits and seeds (monthly mean =  $387 \pm 201$  SD) were collected in the traps while monitoring the exotic squirrel monkeys' behaviours. December ( $N = 110$ ) presented the lowest number of food available, while May ( $N = 709$ ) showed the highest values (Table 2). Of the 18 fruit species collected, it was possible to identify five native plants (*Tapirira guianensis* Aubl., *Schefflera morototoni* Aubl., *Parkia pendula* (Willd.) Benth. ex Walp., *Inga edulis* Mart., *Guaera Guidonia* (L.) Sleumer) and one exotic species

**Table 1.** Habitat available in the study area observed and expected frequencies of the habitat type used by exotic squirrel monkeys in the study urban Atlantic Forest fragment in North-eastern Brazil

Habitat	Habitat available (# pixel)	Habitat available (%)	Observed frequency of habitat use (%)	Expected frequency of habitat use (%)
Disturbed forest	24	3	5 (1)	21 (3)
Secondary initial forest	295	33	108 (14)	263 (33)
Secondary Old Forest	561	64	672 (85)	500 (64)

**Table 2.** Estimative of fruit productivity across the study period. We measured monthly productivity from 50 fruit traps installed in the home range of the exotic squirrel monkeys

Species	Status	Monthly productivity					
		Dec	Jan	Feb	Mar	Apr	May
<i>Tapirira guianensis</i>	Native	98	93	57	395	298	687
<i>Parkia pendula</i>	Native	12	–	8	10	6	–
<i>Inga edulis</i>	Native	–	–	–	1	3	4
<i>Schefflera morototoni</i>	Native	–	16	67	12	10	–
<i>Artocarpus heterophyllus</i>	Exotic	–	7	–	1	–	–
<i>Guaera Guidonia</i>	Native	–	–	5	–	3	–
Morphotype 1	Native	–	316	–	–	–	–
Morphotype 2	Native	–	–	49	–	–	–
Morphotype 3	Native	–	–	51	–	6	–
Morphotype 4	Native	–	–	4	–	–	–
Morphotype 5	Native	–	–	7	–	–	–
Morphotype 6	Native	–	–	–	10	8	–
Morphotype 7	Native	–	–	5	–	–	–
Morphotype 8	Native	–	–	–	1	–	–
Morphotype 9	Native	–	–	–	–	–	–
Morphotype 10	Native	–	–	–	–	41	–
Morphotype 11	Native	–	–	–	–	4	4
Morphotype 12	Native	–	–	3	–	7	14
Total abundance		110	432	256	430	386	709

(*Artocarpus heterophyllus*) (Table 2). *Tapirira guianensis*, morphotype 1, and *S. morototoni* were the most abundant species (Table 2).

### Distribution of food sources and food item consumption

Exotic squirrel monkeys consumed 194 plant food sources during the study period. One hundred seventy food sources (88%) consisted of exotic plants, while 24 (12%) were native plants. Within the exotic plants, we found *A. heterophyllus* (Moraceae), *M. indica* (Anacardiaceae), *E. guineensis* (Arecaceae), *Syzygium jambos* (L.)

Alston (Myrtaceae), *Anacardium occidentale* (L.) (Anacardiaceae), *Musa* sp. (Musaceae), *Spondias mombin* L. (Anacardiaceae), and *Syzygium cumini* (L.) Skeels (Myrtaceae). The native species were *I. edulis* (Fabaceae), *Bowdichia* sp. (Fabaceae), *Talisia* sp. (Sapindaceae), and four morphotypes. We found 22 native plant food sources inserted in the Secondary Old Forest and two native plant sources in the Secondary Initial Forest (Figure 2). Only 22 exotic plant food sources were found in the Secondary Initial Forest, while 148 exotic plant food sources were recorded in the Secondary Old Forest (Figure 2).

Exotic squirrel monkeys consumed the native plant species only three out of six months of the study period (Figure 3). In contrast, exotic plant species were consumed across the study period (Figure 3). The lowest frequencies of feeding records on both native and exotic plant species were recorded in the month with the lowest food availability (i.e., December). On the other hand, the highest native and exotic plant consumption frequencies occurred in May, that is, the month with the highest food availability (Figure 3). Although the monthly percentages demonstrate an increase in the consumption of native plants in the last 2 months, when we consider the absolute values, the exotic plants were most frequently consumed (Figure 4).

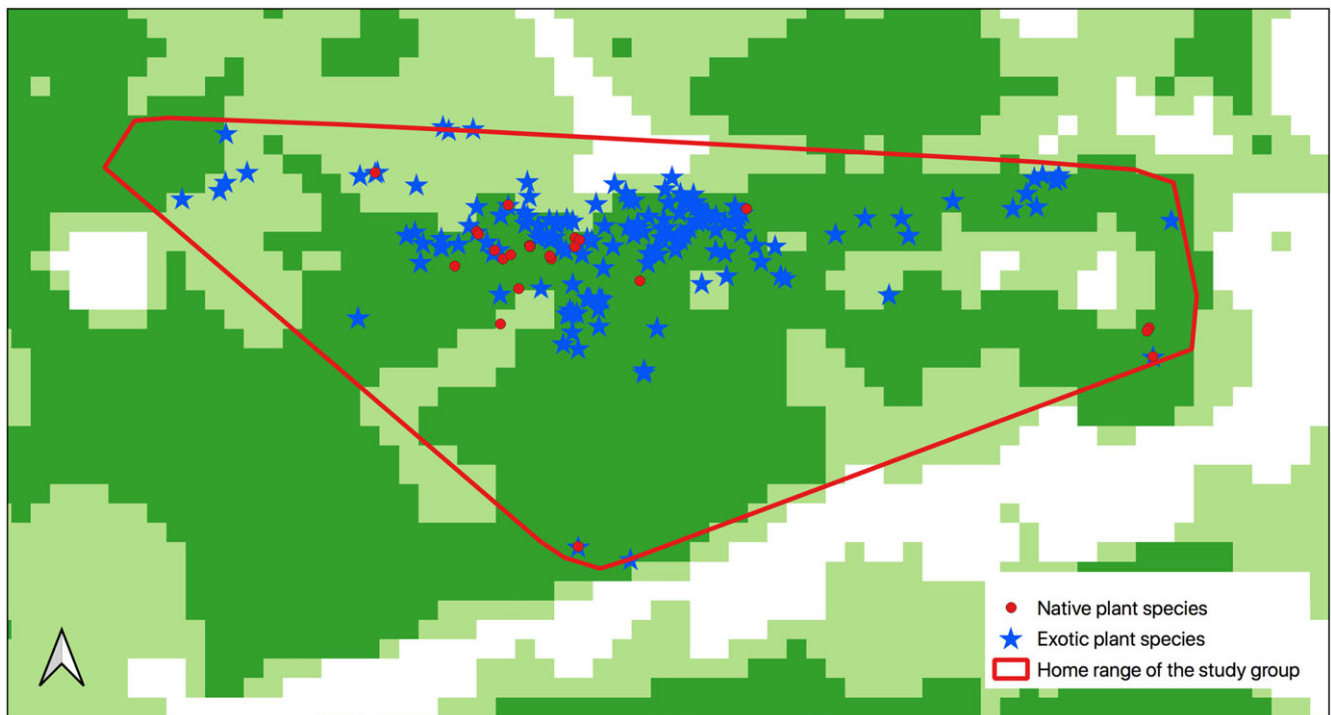
### Presence of common marmosets

We observed exotic squirrel monkeys interacting with common marmosets throughout the study period in 220 events (3% of total de records). The mean number of individual common marmosets in contact with the exotic squirrel monkeys ranged from 1.5 ( $\pm 0.8$  individuals) in March to 3.1 individuals in February ( $\pm 2.0$  individuals) and April ( $\pm 2.6$  individuals). We observed 35 events of interaction (16%) occurring in the Secondary Initial Forest and 185 events (84%) in the Secondary Old Forest; no event was recorded in the Disturbed Forest (Table 3). The expected encounter rate was 0.74 and 0.54 events for the duration of the study period (147 hours) in the Secondary Initial Forest and the Secondary Old Forest, respectively.

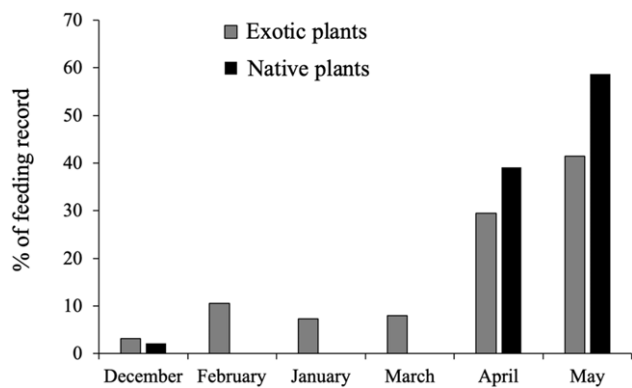
### Potential correlates of habitat use by exotic squirrel monkeys

From the scans, we obtained 7,069 records of exotic squirrel monkey habitat use. The total number of feeding records represented 11% ( $N = 795$  records). The consumption of exotic plants by the exotic squirrel monkeys represented 76% ( $N = 603$  records), while the consumption of native plants represented 6% ( $N = 46$  feeding records). The other feeding records (18%) were for different food items such as invertebrates. We found that 84% of the consumption records of exotic plants occurred in Secondary Old Forest (84%) (Table 3). Similarly, native plants were primarily consumed in the Secondary Old Forest (96%) (Table 3). There was a preference for Secondary Old Forest habitats to consume exotic and native plants by the exotic squirrel monkeys (Fisher's test:  $p = 0.001$ ), thus supporting prediction #1.

There was no variation concerning the expected and observed frequencies of associations between exotic squirrel monkeys and common marmoset in the different habitats (Fisher's test:  $p = 0.781$ ). Nevertheless, the frequency of interaction did not appear to be by chance in one type of habitat. According to the 95% confidence interval for Secondary Initial Forest (0.20–2.70 events), the values for expected encounters between exotic squirrel monkeys and common marmosets demonstrated that such interaction was by chance. On the other hand, the interaction between species in the Secondary Old Forest habitat (95% CI: 5.14–13.5 events) was not by chance (prediction #2 was supported).



**Fig. 2** Distribution of native and exotic plant species consumed by exotic squirrel monkeys in their home range during the study period. The red line represents the limits of the home range.

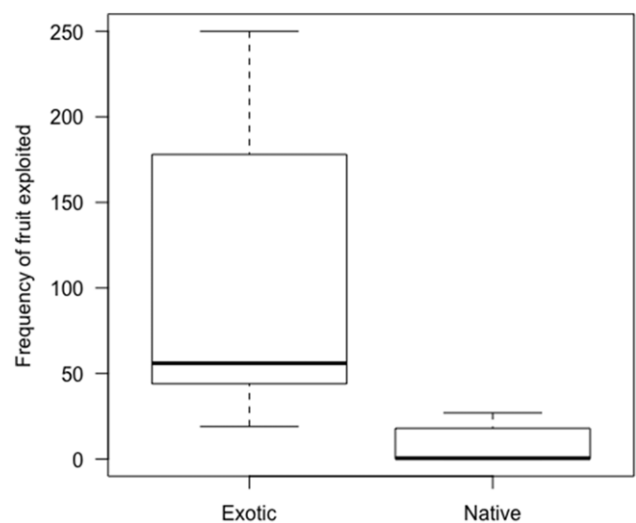


**Fig. 3** Relative frequency (%) of the feeding records for native and exotic plant species exploited by exotic squirrel monkeys.

During the study period, 785 scan samples were performed. We obtained 28% of the scan records ( $N = 218$  scans) during the months of low food availability and 19% ( $N = 148$ ) during the months of high food availability. For both periods, most of the records took place in the Secondary Old Forest (80% of records – low food availability/89% of records – high food availability) (Table 3). There were no differences between the observed and the expected frequencies for the period of low availability (Fisher’s test:  $p = 0.139$ ) and high availability (Fisher’s test:  $p = 0.195$ ) of fruits. Thus, exotic squirrel monkeys did not prefer any habitat during the months with low and high food availability (prediction #3 was not supported).

**Discussion**

Our findings demonstrated that the use of the habitat by the exotic squirrel monkeys appears to be highly flexible and related to the



**Fig. 4** Consumption of exotic and native plant species by exotic squirrel monkeys living in an Atlantic Forest fragment in Northeast Brazil. The boxplot shows the absolute values of consumption. The dark line inside the box represents the median, and the top and bottom edges of the box mark the 1st and 3rd quartile, respectively. The error bars are the standard deviation.

consumption of native and exotic food sources. The consumption of exotic and native plant species contributed to the exotic squirrel monkey preferences for non-disturbed habitats. The presence of the native common marmosets did not prevent the use of the habitat. We found that the association between common marmosets and exotic squirrel monkeys in the Secondary Old Forest habitat was not by chance. The use of the habitat by exotic squirrel monkeys was not related to food availability. Nevertheless, the high availability of food in Secondary Old Forest appeared to be related

**Table 3.** Observed/expected frequencies of potential correlate as habitat use of exotic squirrel monkeys in the present study

Habitat type	Presence of <i>C. jacchus</i>	Feeding on exotic plants	Feeding on native plants	High productivity	Low productivity
Disturbed Forest	0/1	0/5	0/1	0/1	4/1
Secondary initial forest	35/30	27/57	2/15	29/20	20/30
Secondary Old Forest	185/158	143/108	44/29	119/127	194/187

to the increased use of native and exotic food sources and the high frequency of food consumption. Previous studies have demonstrated that exotic plants are essential for the maintenance of exotic animal populations, including deer (Relva *et al.* 2010), carnivores (Hardesty-Moore *et al.* 2020), snails (Meza-Lopez & Siemann 2015), and primates (Cunha *et al.* 2006).

Primate responses to the availability of both native and exotic food sources will vary by species and the context in which they are placed (McLennan & Hockings 2014). Some primates tend to use areas with more native resources (Riley 2008; Terada *et al.* 2015; Bryson-Morrison *et al.* 2017), while others use areas with high densities of exotic plants (Eppley *et al.* 2015). However, highly aggregated and predictable food resources, such as exotic and cultivated vegetation, can also be attractive to species (Hill 2005; Hockings *et al.* 2009; Hoffman & O'Riain 2011). In the Mata do Curado Wildlife Refuge, there is a high density of exotic plant species (*A. heterophyllus*, *S. cumini*, *E. guineenses*, *M. indica*) that dominate the diet of this exotic squirrel monkey population (Oliveira-Silva *et al.* 2018; Campêlo *et al.* 2019). Such plant species are widely distributed in Secondary Old Forest habitats. Moreover, exotic plant species produce year-round large fleshy fruits that attract frugivorous species (Piedade-Kill & Ranga 2000; Ziller 2001; Kueffer *et al.* 2009; Traveset & Richardson 2014). In our study, the use of the Secondary Old Forest areas by the exotic squirrel monkeys was associated with native and exotic plant consumption and the high availability of food sources. The use of primary forest and the late-successional forest was also reported for *Saimiri orstedii* (Reinhardt, 1872) when low food availability (Boinsky 1987). Undisturbed habitats favour the high availability of food resources due to an increase in plant species richness, tree basal (López *et al.* 2005; Arroyo-Rodríguez & Mandujano 2006), which can positively influence the habitat choice of a primate species (Heiduck 2002; Tinsman *et al.* 2022; Trapanese *et al.* 2022; Yazezew *et al.* 2022). The fact that the exotic squirrel monkeys use these areas at a higher frequency seems to be an essential adaptation for maintaining the population in this habitat and consuming foods presenting higher availability and most likely high energetic content.

Few studies have demonstrated interspecific associations between native and exotic primates (Ruiz-Miranda *et al.* 2000). As a result of these associations, an increase in competition for food resources can occur (Ruiz-Miranda *et al.* 2000; Morais 2005; Morais *et al.* 2008). In our study, the presence of common marmosets did not contribute to the exotic squirrel monkeys' preference for a given habitat. Likewise, variability in food availability is often highlighted as a key factor for habitat use in primates (Peres 1994; Clutton-Brock & Harvey 1997; Camaratta *et al.* 2017). Even though we worked with only one month of low and high fruit production – which are months of extreme productivity – the difference between them is evident, and the formation of mixed groups in a habitat with increased food availability was demonstrated. Therefore, our findings suggest that the interspecific associations formed by exotic squirrel monkeys and common marmosets were not by chance. It is likely to be associated with increased fruit

abundance in the habitat. Constant and abundant fruit production over the year by exotic plants may have increased the likelihood of both primates consuming fruits in Secondary Old Forest habitats at any time.

The population of exotic squirrel monkeys appears to be well-adapted to the ecological conditions found and offered in this urban forest fragment, preferring to use habitats with the presence of exotic plants (and native), and where they were frequently observed to eat and rest (see Campêlo *et al.* 2019). Contrary to our predictions, the variation of food availability did not affect the exotic squirrel monkeys' preference for some type of habitat. Meanwhile, the resource consumption and their location of food sources likely favoured the high frequency of exotic squirrel monkeys in Secondary Old Forest during the low availability month. Although they are miles away from their natural habitat (i.e., Amazonian Forest), suitable feeding strategies (e.g., consuming exotic plants) increase the chances of this species becoming well-established (high number of infants were reported during the study period: A. Campêlo, pers. comm.). Furthermore, our study also introduced the possibility that an invasional meltdown effect positively affects the exotic squirrel monkey population. This study made it possible to broaden our knowledge on the ecological and behavioural flexibility of an exotic population in a habitat out of their native range.

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