

Sleeping site preferences in *Sapajus cay* Illiger 1815 (Primates: Cebidae) in a disturbed fragment of the Upper Paraná Atlantic Forest, Rancho Laguna Blanca, Eastern Paraguay

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Abstract Wild primates can spend up to half of their lives sleeping, during which time they are subjected to many of the same selective pressures that they face when awake. Choosing an appropriate sleeping site can thus have important fitness consequences. We examined the sleeping site preferences of wild hooded capuchins (*Sapajus cay*) in a small degraded fragment of the Upper Paraná Atlantic Forest at Rancho Laguna Blanca (RLB) in eastern Paraguay. Sleeping trees and sites were identified during 5 months of field observations and their physical characteristics were compared to those of non-sleeping trees and sites. Capuchins preferred larger emergent trees with more main and forked branches, no lianas and denser undergrowth directly below. These were found in sites of more mature forest with fewer small trees, less liana coverage and denser undergrowth but more fruiting trees. The species composition of the sleeping sites differed from that of the non-sleeping sites and was dominated by *Albizia niopoides* (Mimosaceae) as well as *Peltophorum dubium* (Fabaceae) and *Anadenanthera colubrina* (Fabaceae). The capuchins were found to sleep most often in these three tree species: 69.23% in *Albizia niopoides* (Mimosaceae), 11.54% in *Peltophorum dubium* (Fabaceae) and 11.54% in

Anadenanthera colubrina (Fabaceae). We found evidence for the predator avoidance, thermoregulatory, social contact and feeding site proximity hypotheses. We found no support for parasite avoidance, given the reuse of sites, although the small size of the forest fragment may have restricted this. Their preference for older-growth forest suggests that selective logging impacts hooded capuchins. However, their persistence in a disturbed fragment shows they are highly adaptable, providing support for the value of conservation and reforestation of even small fragments of the Paraguayan Upper Paraná Atlantic Forest.

Keywords Cebidae · Hooded capuchin · Paraguay · Sleep · Tree characteristics · Upper Paraná Atlantic Forest

Introduction

Primates are subjected to many of the same selective pressures whilst asleep as they face during their active hours, including predation (Albert et al. 2011), thermoregulation and disease (Kowalewski and Zunino 2005). This means that careful sleeping site choice can have important consequences for individual fitness (Day and Elwood 1999; Feilen and Marshall 2014). Sleep and sleeping habits are thus important aspects of the behavioural ecology of any species (Anderson 1984; Feilen and Marshall 2014). For diurnal primates that have specific requirements for their sleeping sites, the availability of suitable sites is crucial to their survival (Di Bitetti et al. 2000). Primates show great variation among species in the type and location of sleeping sites chosen. They may sleep in nests of leaves and sticks (Goodall 1962; Mehlman and Doran 2002; Prasetyo et al. 2009), on steep cliff faces (Crook and Aldrich-Blake 1968; Iwamoto et al. 1996), on

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exposed branches of particular trees within their home range (Soini 1988), or within holes in larger mature trees (Hankerson et al. 2007). Without sites that fulfil the requirements of a species, it is unlikely that a population will be capable of long-term survival.

The hooded capuchin (*Sapajus cay* Illiger 1815) is found in southeast Bolivia, northwest Argentina (Salta and Jujuy provinces) and Brazil (states of Goiás, Mato Grosso and Mato Grosso do Sul), and is the only representative of the genus *Sapajus* found in Paraguay (Lynch-Alfaro et al. 2012; Wallace 2015). It is a diurnal, arboreal primate with an omnivorous diet, eating a large variety of seeds, fruits and arthropods, nestlings, frogs and small mammals (Fragaszy et al. 2004). In Paraguay, this species is confined to the remnants of the humid semideciduous Upper Paraná Atlantic Forest in the east of the country (Stallings 1985; Lowen et al. 1996; Rylands et al. 2013). Across its range, very little is known about its reproduction, movements and activity patterns, home range and social organisation (Pinto 2006; Fernandes 2013; Rylands et al. 2013; Smith and Briggs 2015).

The Atlantic Forest is one of the world's most threatened terrestrial habitats (World Wildlife Fund 2015), and in Paraguay the Upper Paraná Atlantic Forest has been reduced to just 7–13% of its historical range. What remains of this forest now exists as small fragments in a matrix of soy plantations and cattle ranches (Huang et al. 2007). Population pressure is increasing and selective logging, both legal and illegal, further affects wildlife that is surviving in these fragments. In smaller or degraded forest fragments, suitable sleeping sites are likely to be more limited for those species with specific roosting requirements. As a result, it has now become acutely important to focus attention on monitoring the ecology of primates surviving in these small forest fragments in order to gauge their behavioural reactions to the reduction in available habitat. A comprehensive understanding of a species' ecological requirements, such as the physical characteristics of its sleeping sites, may be key to implementing robust conservation initiatives (Chapman and Peres 2001; Seiler et al. 2013).

Several theories have been put forward to explain sleeping site selection (Anderson 1984; Di Bitetti et al. 2000; Kowalewski and Zunino 2005):

- The *predator avoidance hypothesis* states that primates select roosts that allow for increased predator detection and greater ease of escape. Some studies also suggest that primates will shift their sleeping sites on a regular basis to reduce the chance of being discovered by predators (Hrdy 1977; Fan and Jiang 2008; Fei et al. 2012).
- The *parasite avoidance hypothesis* predicts that primates will avoid repeated use of the same roosts to

reduce the risk of gastrointestinal parasite transmission (Di Bitetti et al. 2000; Huffman and Caton 2001; Kowalewski and Zunino 2005).

- According to the *thermoregulation hypothesis*, primates may choose roosts with certain characteristics (such as more branches) to allow groups to huddle together for comfort and, more importantly, to facilitate social contact and conserve energy (Di Bitetti et al. 2000; Liu and Zhao 2004; Kowalewski and Zunino 2005; Cui et al. 2006; Smith et al. 2007; Li et al. 2010).
- The *feeding site hypothesis* predicts that primates prefer sleeping in, or in close proximity to, food sources (von Hippel 1998).

These hypotheses are not necessarily mutually exclusive and other factors may play more limited roles; one example is safety, with primates selecting larger, sturdier trees that are less likely to shed branches or fall in high winds (Di Bitetti et al. 2000).

When investigating the selection of arboreal sleeping sites by a primate species, certain physical characteristics of the sleeping tree and the surrounding area must be taken into consideration in order to allow the results to be applied to existing hypotheses (Garcia and Braza 1993). These characteristics include the tree diameter at breast height (DBH) (Chapman 1989; Di Bitetti et al. 2000), tree height (Tenaza and Tilson 1985; Zhang 1995; Di Bitetti et al. 2000; Wahungu 2001), height of the lowest branch (Day and Elwood 1999), number of forking branches, number of main branches and number of crown joins to surrounding trees (Di Bitetti et al. 2000; Phoonjampa et al. 2010; Bernard et al. 2011), height of lianas and undergrowth, and distance to fruiting trees (Chapman 1989; Heymann 1995; von Hippel 1998;).

In the work reported in this paper, we compared the characteristics of both sleeping trees and sleeping sites to those of non-sleeping trees and sites used by two groups of hooded capuchins at Rancho Laguna Blanca, San Pedro department, northeastern Paraguay. Here, we discuss how our results compare to the predictions offered by the different sleeping site selection hypotheses.

Methods

Study site

This study was carried out at Rancho Laguna Blanca (RLB), San Pedro department, Paraguay (23°49'52.0"S 56°17'42.2"W). RLB contains a small fragment of 243 ha of secondary Upper Paraná Atlantic Forest, characterised by deciduous, mesophytic, broadleaf plants (Lowen et al. 1996). The forest fragment has a history of selective

logging until 2010, when it was classified as a reserve. Reserve status formally ended in February 2015 and until April 2017 there was no utilisation of the forest resources.

RLB is home to two groups of semihabituated capuchins. O group consists of 3 adult males, 5 adult females, 5 subadults, 4 juveniles and 1 infant (demographics according to the protocol detailed in Smith and Briggs 2015), and F group consists of around 16 individuals with unconfirmed group demographics. This study was part of a long-term project (2013–2017) investigating the behaviour of the hooded capuchin groups of RLB. Behavioural data were collected using scan and focal sampling (Altmann 1974). Both groups were followed for 99 days, 4–6 h per day, between February and April 2015 and between July and August 2015.

Sleeping trees vs non-sleeping trees

A sleeping tree is defined as a tree in which one or more individuals spend the night (Di Bitetti et al. 2000). Sleeping trees were identified through field observations; monkeys were assumed to have spent the entire night in the sleeping tree if they were present the following morning at sunrise. After the monkeys had left a tree, its GPS position, species, diameter at breast height (DBH), tree height, height of the lowest branch, crown radius, number of main branches, number of forks, number of crown joins, vertical position in forest strata, undergrowth density around the base of the tree and liana presence/absence were recorded.

The DBH was measured using a measuring tape to give the circumference, which was then divided by π to give the diameter. The tree height and height of the lowest branch were measured using a clinometer. The crown radius was measured by running a measuring tape from the tree trunk to the tip of the widest part of the crown's spread. The number of main branches (primary and secondary from the tree trunk), number of forks and number of crown joins were counted. The trees were then categorised into three groups based on the number of forks: group 1 = 0–4, group 2 = 5–9, group 3 = 10+. They were also categorised based on vertical position as either 1 (emergent), 2 (canopy) or 3 (subcanopy). The undergrowth density of each tree was categorised as either 0 (none), 1 (low), 2 (medium) or 3 (high). Lianas were noted as either present or absent and their lowest extent was measured using a clinometer.

Sleeping sites vs non-sleeping sites

Sleeping sites were defined as particular locations within the group's home range in which the group spent the night. They were analysed using the point-quarter method (Ganzhorn et al. 2011) as 20×20 m plots with four

10×10 m quadrants, using the sleeping tree as the centre point. In locations with multiple sleeping trees, the tree with the most individuals was used as the central tree. Non-sleeping sites, defined as locations in the forest where the capuchins were never observed to spend the night, were chosen by overlaying a numbered 20×20 m grid on the forest and then using a random number generator (in Microsoft Excel) to randomly select a grid square.

For each 20×20 m plot, canopy cover was calculated by measuring the canopy foliage cover of the quadrant borders (in %) and then calculating the mean percentage canopy cover of the four 10×10 m quadrants in the plot (Jennings et al. 1999). The number of large trees (DBH > 25 cm), the number of small trees (DBH < 25 cm) and the number of fruiting trees were counted. Undergrowth density was estimated visually by a single observer and categorised as either 0 (none), 1 (low), 2 (medium) or 3 (high), and liana coverage was estimated by counting the number of trees in the quadrat that contained lianas. The same variables measured for individual trees (above), besides undergrowth density and liana presence/absence, were measured for all large trees (DBH > 25 cm) in each quadrat and the means were estimated.

Statistical analysis

Statistical analyses were carried out in R Studio version 0.99, and a significance level of $\alpha = 0.05$ was adopted unless otherwise stated. We tested for significant differences in (i) the physical characteristics of sleeping trees and non-sleeping trees and (ii) the general and tree-specific characteristics and species compositions of sleeping sites and non-sleeping sites.

The normality and homoscedasticity of noncategorical variables were checked using the Shapiro–Wilk test and nonparametric variables were transformed using $\log(x + 1)$ before applying Student's *t* test. The chi-squared test for goodness of fit was used to compare nominal variables, including species composition. Principal component analyses (PCAs), based on correlation matrices, were also carried out with the package *prcomp* to determine the mean variables leading to the differences between sleeping and non-sleeping trees and sites.

Results

Sleeping site use

Over the course of the study, the monkeys were located on 59 nights, corresponding to a success rate of 59.6% (O group = 32 nights, F group = 27 nights). We recorded 25

sleeping sites throughout the known home ranges of the two groups. The O group was found to use 14 different sleeping sites, two of which were reused more frequently than others, and six on only one occasion. The same site was used for three consecutive nights on one occasion; this was the only consecutive reuse observed. The F group used 13 sleeping sites (two of which were also used by the O group). They were never observed to spend consecutive nights at a single site and did not have a site that they used more frequently than others. The F group used seven of their 13 sleeping sites only once.

Sleeping tree characteristics

Sleeping trees were found to be larger than non-sleeping trees in DBH, tree height, height of the lowest branch and crown radius. They had more main branches and forks and were usually emergent or were less often at the same height as the canopy (Table 1). The above variables were all equally well correlated to PC1, which accounted for 44% of the variation between sleeping and non-sleeping trees (Fig. 1; Table 2). The undergrowth at the bases of sleeping trees was also denser than that for non-sleeping trees, and lianas were more commonly absent (Table 1).

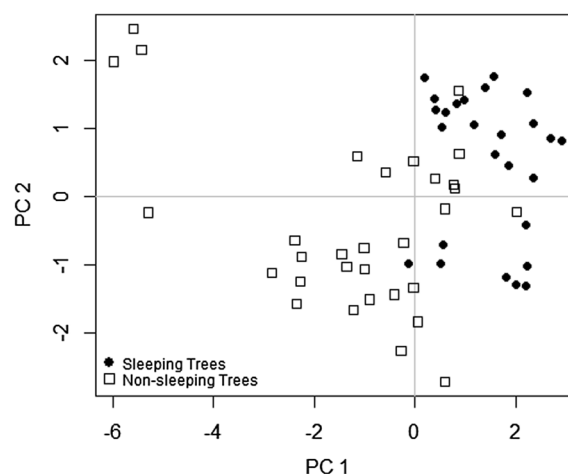


Fig. 1 Differentiation of sleeping and non-sleeping trees based on the principal components of variation between them. PC1 and PC2 together account for 60% of the total observed variance (PC1: 44%, PC2: 16%)

These were most strongly correlated to PC2, which accounted for 16% of the variation between sleeping and non-sleeping trees (Fig. 1; Table 2). Only the number of crown joins was not significantly different for sleeping and non-sleeping trees.

Table 1 Comparison of the physical characteristics of sleeping and non-sleeping trees with mean \pm standard deviation values and *t*-test results of numerical variables and frequency occurrences plus chi-squared test results of categorical variables

Variable	Sleeping trees	Non-sleeping trees	Test values	<i>p</i> value
DBH	46.6 \pm 12.4 cm	38.1 \pm 13.2 cm	$t = -2.81$ $df = 54$	0.007
Tree height	23.7 \pm 3.9 m	15.8 \pm 4.7 m	$t = -6.56$ $df = 50$	<0.0001
Lowest branch height	8.8 \pm 2.1 m	4.5 \pm 2.6 m	$t = -5.52$ $df = 41$	<0.0001
Crown radius	8.1 \pm 1.7 m	4.9 \pm 2.0 m	$t = -5.86$ $df = 45$	<0.0001
Number of main branches	15.1 \pm 5.0	11.2 \pm 5.9	$t = -2.63$ $df = 55$	0.011
Number of crown joins	1.6 \pm 0.9	2.1 \pm 1.7	$t = 0.81$ $df = 54$	0.420
Number of main forks	0–4 forks = 0.0 5–9 forks = 19.2 10+ forks = 80.8	0–4 forks = 16.1 5–9 forks = 22.5 10+ forks = 61.3	$\chi^2 = 19.1$ $df = 2$	<0.0001
Vertical position	Subcanopy = 0.0 Canopy = 13.7 Emergent = 86.3	Subcanopy = 19.3 Canopy = 49.1 Emergent = 31.6	$\chi^2 = 23.4$ $df = 4$	<0.0001
Undergrowth density	None = 0.0 Low = 26.9 Medium = 38.5 High = 34.6	None = 6.5 Low = 45.2 Medium = 19.4 High = 29.0	$\chi^2 = 17.9$ $df = 3$	0.0004
Liana presence/absence	Presence = 34.6 Absence = 65.4	Presence = 74.2 Absence = 25.8	$\chi^2 = 7.46$ $df = 1$	0.006

n = 26 sleeping and 31 non-sleeping trees

Table 2 Correlation coefficients of physical characteristics to the principal components of variance between sleeping and non-sleeping trees

Variable	PC1	PC2
DBH	0.29	-0.25
Tree height	0.35	0.39
Height of lowest branch	0.37	0.02
Crown radius	0.41	-0.01
No. of main branches	0.41	-0.25
No. of crown joins	0.03	-0.35
No. of branch forks	0.35	-0.20
Vertical position	0.41	0.16
Undergrowth height	0.12	0.20
Liana height	0.06	-0.71

PC1 and PC2 account for 44 and 16% of the variance between sleeping vs. non-sleeping trees, respectively

The capuchins slept most frequently in three tree species: *Albizia niopoides* (Mimosaceae) (69.23%), *Peltophorum dubium* (Fabaceae) (11.54%) and *Anadenanthera colubrina* (Fabaceae) (11.54%). These percentages did not differ from the relative abundances of these species at the sleeping sites (Table 6) ($\chi^2 = 0.02$, $df = 2$, $p = 0.99$).

Sleeping and non-sleeping sites

Sleeping sites were found to have fewer small trees (DBH < 25 cm), more fruiting trees, denser undergrowth and lower liana coverage than non-sleeping sites (Table 3). In terms of the tree-specific characteristics, large trees (DBH > 25 cm) in sleeping sites were larger than those in non-sleeping sites in DBH, tree height, height of the lowest branch and crown radius. They also had more main

branches and forks and were usually emergent or were less often at the same height as the canopy (Table 4).

21% of the variance between sleeping and non-sleeping sites is accounted for by PC2 and is correlated with the number of small trees and liana coverage (both of which are much higher in non-sleeping sites) and fruit trees (which are more numerous in sleeping sites); see Fig. 2 and Table 5. However, 23% of the variance between sleeping and non-sleeping sites is represented by PC1 and is correlated with differences in the mean height and vertical position of the large trees they contain, and, to a lesser extent, with differences in crown radius, DBH, number of forks, lowest branch height, number of main branches, undergrowth density and liana coverage (Fig. 2; Table 5).

Tree species composition differed between sleeping and non-sleeping sites ($\chi^2 = 70.4$, $df = 21$, $p = < 0.0001$). This was particularly related to the abundance of *Albizia niopoides* at sleeping sites (Table 6), which was more than twice as abundant as any other species across all sites. *Anadenanthera colubrina* and *Cabrlea canjerana* were also more abundant at sleeping sites. By comparison, the most abundant species at non-sleeping sites were *Jacaratia spinosa*, *Albizia niopoides* and *P. dubium*, and, to a lesser extent, *Acrocomia aculeata*, *Balfourodendron riedelianum* and *Casearia gossypiosperm.*

Discussion

Hooded capuchin monkeys at Rancho Laguna Blanca prefer to sleep in taller, emergent trees that have wider DBHs, wider crowns, higher lowest branches, more main branches and forks, an absence of liana, and denser undergrowth directly beneath the tree. This indicates that capuchins prefer to sleep in areas of more mature forest

Table 3 Comparison of the general physical characteristics of sleeping and non-sleeping sites with mean \pm standard deviation values and *t*-test results of numerical variables and frequency occurrences plus chi-squared test results of categorical variables

Variable	Sleeping sites	Non-sleeping sites	Test values	<i>p</i> value
Canopy cover (%)	89.5 \pm 7.4	88.5 \pm 11.1	$t = -0.39$ $df = 24.03$	0.698
No. of large trees (DBH > 25 cm)	4.1 \pm 1.6	4.7 \pm 1.9	$t = 0.74$ $df = 27.96$	0.466
No. of small trees (DBH < 25 cm)	21.3 \pm 8.2	4.7 \pm 1.9	$t = 2.95$ $df = 28.0$	0.006
Number of fruiting trees	6.8 \pm 5.4	4 \pm 2.4	$t = -2.11$ $df = 27.3$	0.044
Liana coverage (no. of trees)	9.1 \pm 6.4	20.8 \pm 11.7	$t = -3.43$ $df = 28.0$	0.002
Undergrowth density	Low = 17 Medium = 27 High = 57	Low = 13 Medium = 53 High = 33	$\chi^2 = 15.3$ $df = 2$	0.0005

$n = 15$ for both sleeping and non-sleeping sites

Table 4 Comparison of the tree-specific characteristics of all large trees (DBH > 25 cm) at sleeping and non-sleeping sites with mean \pm standard deviation values and *t*-test results of numerical variables and frequency occurrences plus chi-squared test results of categorical variables

Variable	Sleeping site trees	Non-sleeping site trees	Test values	<i>p</i> value
DBH	32.0 \pm 7.9 cm	34.6 \pm SD 7.3 cm	<i>t</i> = -2.83 <i>df</i> = 27.8	0.009
Tree height	18.7 \pm 2.3 m	17.2 \pm 3.1 m	<i>t</i> = -2.9 <i>df</i> = 24.1	0.126
Height of lowest branch	6.0 \pm 1.9 m	5.8 \pm 2.3 m	<i>t</i> = -0.34 <i>df</i> = 26.7	0.736
Crown radius	6.24 \pm 1.3 m	5.1 \pm 0.9 m	<i>t</i> = -3.024 <i>df</i> = 27.5	0.005
Number of crown joins	2.0 \pm 0.7	1.9 \pm 1.	<i>t</i> = -0.53 <i>df</i> = 21.0	0.601
Number of main branches	12.4 \pm 3.5	15.3 \pm 4.0	<i>t</i> = 2.21 <i>df</i> = 27.7	0.036
Number of main forks	0–4 forks = 10.9 5–9 forks = 21.7 10+ forks = 67.4	0–4 forks = 15.9 5–9 forks = 27.3 10+ forks = 56.8	χ^2 = 2.47 <i>df</i> = 2	0.290
Vertical position	Subcanopy = 23.9 Canopy = 32.6 Emergent = 42.5	Subcanopy = 13.6 Canopy = 65.9 Emergent = 20.5	χ^2 = 10.8 <i>df</i> = 4	0.028

n = 15 for both sleeping and non-sleeping sites

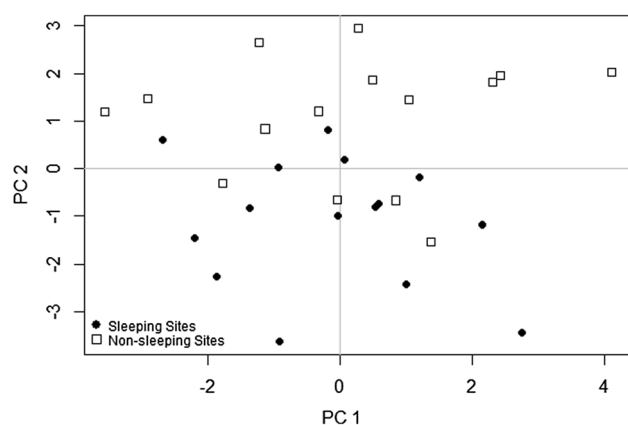


Fig. 2 Differentiation of sleeping and non-sleeping sites based on the principal components of variation between them. PC1 and PC2 together account for 44% of the total observed variance (PC1: 23%, PC2: 21%)

with larger, older, usually emergent trees. Indeed, they clearly avoid more degraded sites with abundant small trees and high liana coverage. The species composition of sleeping sites also contains a greater number of larger species associated with older-growth forest. This indicates that the capuchins are utilising the less disturbed areas, suggesting that while selective logging negatively impacts them, they can adapt to a certain degree of degradation.

Our results partially support the predator avoidance hypothesis. The use of large trees without lianas and higher lowest branches minimises the chance of encountering a terrestrial predator, and a wider crown allows for both

Table 5 Correlation coefficients of physical characteristics to the principal components of variance between sleeping and non-sleeping sites

Variables	PC1	PC2
% Canopy cover	0.08	-0.21
No. of large trees (DBH > 25 cm)	0.20	-0.01
No. of small trees (DBH < 25 cm)	-0.18	0.43
No. of fruiting trees	0.20	-0.42
Undergrowth density	-0.29	0.02
Liana coverage	-0.24	0.48
DBH	-0.29	-0.18
Tree height	-0.37	-0.21
Height of lowest branch	-0.25	-0.20
Crown radius	-0.31	-0.34
No. of crown joins	0.16	-0.06
No. of main branches	-0.23	0.29
No. of forks	-0.28	-0.22
Vertical position	-0.45	-0.07

PC1 and PC2 account for 23 and 21% of the observed variance between sleeping and non-sleeping sites, respectively

easier defence and escape if necessary (Ramakrishnan and Coss 2001; Brotcorne et al. 2014). Though higher undergrowth beneath the sleeping tree could allow an easier access point for terrestrial predators (Tenaza and Tilson 1985), it may be the case that a higher undergrowth blocks the view of terrestrial predators or allows for easier detection of predators by preventing a stealthy approach.

Table 6 Tree species compositions and mean tree heights in capuchin sleeping and non-sleeping sites

Species	Family	Sleeping sites		Non-sleeping sites	
		Species composition (%)	Mean height (m)	Species composition (%)	Mean height (m)
<i>Albizia niopoides</i>	Mimosaceae	36.95	24.15	13.04	19.48
<i>Peltophorum dubium</i>	Fabaceae	6.52	18.93	13.04	18.58
<i>Anadenanthera colubrina</i>	Fabaceae	6.52	21.75	2.17	19.4
<i>Cabranea canjerana</i>	Meliaceae	6.52	15.05	0	NA
<i>Acrocomia aculeata</i>	Arecaceae	4.35	18.1	6.52	15.27
<i>Nectandra lanceolata</i>	Lauraceae	4.35	15.63	10.86	17.72
<i>Nectandra megapotamica</i>	Lauraceae	4.35	16.45	0	NA
<i>Jacaratia spinosa</i>	Caricaceae	4.35	13.78	14.89	10.1
<i>Citharexylum myrianthum</i>	Verbenaceae	4.35	13.03	2.17	15.7
<i>Chrysophyllum gonocarpum</i>	Sapotaceae	4.35	11.1	2.17	15.8
<i>Chlorophora tinctoria</i>	Moraceae	4.35	14.87	0	NA
<i>Cedrela fissilis</i>	Meliaceae	4.35	15.2	4.34	15.65
<i>Parapiptadenia rigida</i>	Fabaceae	2.18	12.9	2.17	10.6
<i>Lonchocarpus leucanthus</i>	Fabaceae	2.17	16.35	0	NA
<i>Albizia saman</i>	Fabaceae	2.17	5.9	4.34	16.7
<i>Syagrus romanzoffiana</i>	Arecaceae	2.17	14.7	0	NA
<i>Balfourodendron riedelianum</i>	Rutaceae	0	NA	8.69	17.43
<i>Casearia gossypiosperma</i>	Salicaceae	0	NA	6.52	19.17
<i>Astronium urundeuva</i>	Anacardiaceae	0	NA	2.17	15.8
<i>Enterolobium timbouva</i>	Fabaceae	0	NA	2.17	14.7
<i>Acacia glomerosa</i>	Fabaceae	0	NA	2.17	18
<i>Cordia trichotoma</i>	Boraginaceae	0	NA	2.17	23

Both groups of capuchins had several sleeping sites throughout their home range, decreasing the need to reuse their sites on consecutive nights and thus reducing the chance that a predator is able to stalk the group (Di Bitetti et al. 2000). Though this preference for trees with larger trunks and wider crowns provides sites that allow for both easier defence and escape from terrestrial predators (Ramakrishnan and Coss 2001; Brotcorne et al. 2014), the behaviour of the monkeys when entering the site did not support the predator avoidance hypothesis. In order to reduce the chance of detection by predators, primates would be expected to enter a site before any nocturnal predators become active and remain silent after entering the sleeping tree to avoid detection by any diurnal predators that are still active (Fei et al. 2012). While the capuchins of RLB did enter their sleeping site before sunset, they were extremely loud, both when moving towards the sleeping site and after entry. On occasions when the capuchins were spread across more than one tree, they could be heard vocalising to each other from a distance of more than 300 m. This may be due to the fact that natural predation pressure at RLB is extremely low. As capuchins are highly social animals, and larger groups have increased vigilance and therefore a higher likelihood of detecting a

potential predator (van Schaik 1983; Chapman 1986; Hirsch 2002), it is possible that rather than entering a sleeping site quietly, capuchins are reliant on each other for predator detection.

As both groups were found to reuse most of their sites on a regular (though nonconsecutive) basis, we did not find support for the parasite avoidance hypothesis. However, little is known about gastrointestinal parasites of wild capuchin monkeys (Phillips et al. 2004; Chinchilla et al. 2010; Parr et al. 2013), and no information is available on the gastrointestinal parasite loads or the diversity of wild hooded capuchins in Paraguay, making it hard to assess the importance of behavioural strategies in parasite avoidance. As the forest fragment in RLB is small and highly disturbed, it may be that there are not enough suitable sleeping sites available to allow parasite avoidance to be a priority for the capuchins. Alternatively, the capuchins of Laguna Blanca may not suffer greatly from gastrointestinal parasites. Further studies of the parasite loads of these groups are required to further investigate the importance of this hypothesis.

We found some support for the thermoregulation and social contact hypotheses. Both the thermoregulation and social contact hypotheses state that primates should sleep

in trees that facilitate increased social contact—those with a greater number of forking branches and large main branches (Cui et al. 2006; Holmes et al. 2011). While the capuchins preferred larger trees with wider crowns, more main branches and greater numbers of forking branches, which are hypothesised to create more opportunities for social contact (Di Bitetti et al. 2000), the capuchins were observed to sleep in small clusters at the very tips of the canopy rather than in the forks of branches. Though this behaviour is not in line with the social contact and thermoregulation hypotheses, it does provide support for the predator avoidance hypothesis. Sleeping at the ends of branches allows both the possibility of rapid escape from aerial predators and the early detection (through vibrations along the branch) of approaching predators (Fan and Jiang 2008; Barnett et al. 2012). In many primate species, including capuchins, vocalisations are an integral part of social behaviour (Seyfarth and Cheney 2010). When the capuchins were sleeping in separate trees at a sleeping site, they vocalised loudly to each other, often for up to an hour. This may indicate that “social contact” may be maintained in this species through vocalising rather than physical body contact. Due to poor visibility and the semi-habituated nature of the capuchins, it was not possible to observe sleeping clusters to further investigate these hypotheses.

The higher prevalence of fruiting trees at sleeping as opposed to non-sleeping sites is congruent with the findings of several other studies that have emphasised the importance of proximity of food resources to sleeping sites (Chapman 1989; Heymann 1995; Anderson 1998; von Hippel 1998; Day and Elwood 1999; Mendes-Pontes and Soares 2005; Smith et al. 2007; Fan and Jiang 2008; Phoojampa et al. 2010). The capuchins were never observed to feed in a tree that they had slept in the previous night, although further study is required to determine if this is simply a result of their semi-habituated nature.

The capuchins were most commonly found to sleep in one of three species: *Albizia niopoides* (Mimosaceae), *Peltophorum dubium* (Fabaceae) or *Anadenanthera colubrina* (Fabaceae). Notably, these three species are also three of the most abundant species found in sleeping sites. However, since the frequencies at which sleeping tree species were used were equal to the relative abundances of these species at sleeping sites, it can be concluded that capuchins select trees based not on the species present but on other factors related to tree size, which itself depends on the maturity of the forest.

In Iguazú National Park, Argentina, *Parapiptadenia rigida* (Fabaceae) was found to be the preferred species of sleeping tree of *Sapajus nigritus* (Di Bitetti et al. 2000). This species produces some of Paraguay’s most valuable timber (Lowen et al. 1996), so, prior to its designation as a “Reserva Natural” in 2010, this was one of the main

species extracted from the forest at Rancho Laguna Blanca over several years of selective logging. On the other hand, *Albizia niopoides* (Mimosaceae), *Peltophorum dubium* (Fabaceae) and *Anadenanthera colubrina* (Fabaceae) do not provide desirable or valuable timber and were infrequently extracted from the forest of RLB. As a result, these species comprise a large percentage of the remaining old growth in the fragment. This indicates that capuchins are willing to adapt their species preference as selective logging removes their original sleeping sites. Although, it may also simply be that *Parapiptadenia rigida* is chosen due to its large size.

Such flexibility in sleeping site preferences may be a crucial factor in the ability of this species to survive in disturbed and fragmented forests. This provides support for the conservation of even small fragments of Paraguayan Upper Paraná Atlantic Forest, and implies that management efforts should include reforestation projects which replace species that have been selectively logged.

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Compliance with ethical standards

Conflict of interest The authors state that there is no conflict of interest.

Ethical standards Our research was approved by the Secretaria del Ambiente and complied with all local laws. The study was non-invasive and followed the American Society of Primatology Code of Best Practices for Field Primatology (2014).

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