

## Spatial Distribution and Exploitation of Trees Gouged by Common Marmosets (*Callithrix jacchus*)

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**Abstract** Resource distribution shapes many aspects of primate behavioral ecology. Though the spatial patterning of fruits, leaves, and insects has been explored among primate foods, comparatively less is known about exudate distributions. Tree exudates are a renewable resource, provide long-term evidence of exploitation, and may be selectively exploited to manipulate spatial distribution. We assessed the spatial patterning of trees gouged by common marmosets (*Callithrix jacchus*) to determine if they exhibit a uniform, random, or clumped distribution. We also asked whether marmosets selectively gouge trees in home range centers, which may afford them exclusive access to exudates. We explored whether spatial or physical characteristics of trees predict how intensely gouged trees were exploited. The mean nearest neighbor distance of gouged trees was significantly closer than expected for a random distribution and Ripley's *K*-function showed that gouged trees were clumped across all spatial scales in our study area. Clumping may enable marmosets to reduce day and home ranges and facilitate

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repeated gouging of trees. Gouged trees were not closer to marmosets' home range centers than peripheries, nor were centrally located trees more intensely gouged. Increased gouging intensity was associated with larger tree circumferences, although this effect was primarily driven by interspecific differences in circumference. Although marmosets may benefit from exploiting clumped exudates, they do not concentrate gouging in areas where they are more likely to gain exclusive access. Species-specific tree characteristics such as exudate quality and/or bark properties may play a larger role in determining gouging patterns than intergroup feeding competition.

**Keywords** Callitrichids · Exudativory · GIS · Intergroup competition · Renewable resources · Resource distribution

## Introduction

The distribution of resources in the environment is a key factor influencing many aspects of primate ecology, behavior, and life history. Resource distribution has been empirically linked to home range size and shape (Izumiyama *et al.* 2003; Tsuji and Takatsuki 2004), temporal shifts in activity and ranging patterns (Fashing 2007; Kumar *et al.* 2007; Oates 1987; Tsuji and Takatsuki 2004), density of individuals (Chapman *et al.* 1995; Fashing 2007; Izumiyama *et al.* 2003; Rassmussen 1980; Vasudev *et al.* 2008), dispersal patterns (Boinski *et al.* 2005), sex ratios (Clark 1978), and reproductive potential (Ferrari and Lopes Ferrari 1989). Given these relationships, it is not surprising that resource distribution is also a fundamental variable in many ecological and socio-ecological models of primate behavior (Clutton-Brock and Harvey 1977; Sterck *et al.* 1997; Sussman and Garber 2007, 2011; van Schaik 1989; Wrangham 1980).

Primates often rely on resources that are spatially and temporally clumped (Chapman 1990; Oates 1987; Tuomisto *et al.* 2003). Research has focused on the distribution of more traditional primate foods such as fruits, leaves, and insects. Insects are generally regarded as randomly or uniformly dispersed in primate habitats (Rylands 1987), and fruits are distributed in a clumped fashion (Go 2010; Leighton and Leighton 1982; Strier 1989). Despite the overall abundance of leaves in many environments, the leaves consumed by primates are often distributed in clumps (Go 2010; Oates 1994; Snaith and Chapman 2005) because their nutritional and mechanical qualities can vary considerably in time and space (Milton 1979; Teaford *et al.* 2006). Resources located in clumps can be more easily monopolized permitting cooperative resource defense by groups (Bacon *et al.* 1991; Emlen and Oring 1977; Grant 1993; Johnson *et al.* 2002; Slobodchikoff 1984; Snaith and Chapman 2007; van Schaik 1983, 1989; Wrangham 1980). Accordingly, clumped resources are predicted to generate intergroup contest competition (Reeve and Hölldobler 2007; Sterck *et al.* 1997; Travis and Slobodchikoff 1993; van Schaik 1989). Conversely, uniform or randomly distributed resources are less feasible to monopolize and defend, which should lead to scramble competition (Sterck *et al.* 1997; van Schaik 1989). The decision to defend resources is also a function of resource renewal and depletion rates (Isbell *et al.* 1998; Pruettz and Isbell 2000; Shopland 1987; Waser 1981; Waser and Waser 1985), with rapid renewal rates (or short depletion times) decreasing the benefits of contesting resources (Chancellor and Isbell 2009; Pruettz and Isbell 2000; Waser and Waser 1985).

Tree gouging and exudativory by marmosets (*Callithrix*, *Mico*, and *Cebuella* spp.) offers an interesting case study for examining the spatial distribution of food resources. Marmosets mechanically injure trees to elicit exudate flow (Fig. 1a) and repeatedly gouge the same marks across multiple trees to sustain this flow (Fig. 1b) (Coimbra-Filho and Mittermeier 1977; Garber 1992; Nash 1986; Rylands 1984; Stevenson and Rylands 1988; Vinyard *et al.* 2009). These gouge marks persist for years, providing long-term documentation of resource exploitation. Relatively little is known about the spatial distribution of these resources, despite evidence that exudates can comprise >70 % of marmoset diet during specific seasons (Digby *et al.* 2011). Exudates are also somewhat unusual among primate foods in that they are a relatively renewable (or nondepleting) resource (Garber and Porter 2010) that are reliably available and exploited year round (Digby *et al.* 2011; Stevenson and Rylands 1988).

The distribution of exudates may have important implications for marmoset behavioral ecology. For instance, marmoset species that feed more heavily on exudates tend to have smaller home ranges (Ferrari and Lopes Ferrari 1989; Rylands 1984; Rylands and de Faria 1993). Smaller home range size in marmoset species relative to the more frugivorous tamarins (*Saguinus*, *Leontopithecus* spp.) has similarly been attributed to an increased reliance on exudates (Ferrari and Lopes Ferrari 1989). Day path lengths are shorter in marmosets than tamarins (Digby *et al.* 2011; Harrison and Tardiff 1994; Kinzey 1997) and in black-tufted marmosets (*Callithrix penicillata*) travel increases during seasonal periods of high fruit consumption (Vilela and de Faria 2004). Some groups of marmosets use a specific area of their home range as a “home base” where they spend large amounts of time with short day ranges reflecting one or two excursions from the home base to foraging areas (Hubrecht 1985; Maier *et al.* 1982). Spatial clumping of resources would provide sufficient food in concentrated areas, enabling marmosets to reduce travel time between multiple exudate resources. Such a clumped distribution would also facilitate repeated gouging of trees to ensure continued exudate production.

The spatial distribution of exudate tree exploitation also has implications for intergroup competition. Marmosets live in small social groups that engage in frequent and aggressive encounters with neighbors (Decanini and Macedo 2008; Hubrecht 1985; Lazaro-Perea 2001; Rylands 1986; Stevenson and Rylands 1988). The role resource defense plays in these encounters remains relatively unexplored, although encounters are known to facilitate intergroup sexual behavior (Lazaro-Perea 2001). If intergroup competition reduces available food for individual group members, then marmosets should selectively exploit resources within central areas of their home range where they are more likely to have exclusive access.

Beyond spatial location, many additional factors have the potential to influence selective gouging of exudate trees. More than 80 tree species have been identified as exudate sources for *Callithrix* spp. (Smith 2010) and we do not understand what characteristics of tree species drive preference in gouging (if preferences exist). Physical and mechanical factors influencing the ability to produce gouge holes, such as the depth or mechanical properties of bark, may play a role (Rylands 1984; Vinyard *et al.* 2009). Marmosets also use trees with larger trunks for both gouging and locomotion (Jackson 2011; Lacher *et al.* 1984; Youlantos 2009), which may indicate that the ability to grasp certain trunks is an important criterion (Hamrick 1998). In addition, nutritional qualities of the exudates themselves could impact

**Fig. 1** Gouge holes created by common marmosets. **a** Close-up of recent gouging holes made in *Astronium fraxinifolium* demonstrating gum flow from the wound created by a marmoset. **b** *Enterolobium contortilicium* (center) with numerous gouging holes of different ages demonstrating the intensity of gouging by marmosets as well as the long-term record of resource exploitation by these individuals. (Note individual at base of tree for scale). (**b** reprinted with permission from Vinyard *et al.* 2009).



preference in gouged trees (Nash 1986; Power 1996; Smith 2000, 2010) as could the quantity of exudates produced (Garber and Porter 2010) or abundance of a particular tree species in the habitat. Finally, increased tree cover may provide greater protection from predators (Lacher *et al.* 1984) and group-specific behavioral traditions of exploiting certain trees or areas (Fragazy and Perry 2003) may also impact the choice of gouged trees.

We examined the spatial distribution of trees gouged by common marmosets (*Callithrix jacchus*) at Tapacurá Field Station, in the Atlantic Coastal forest, near Recife, Brazil. We address the following questions: 1) What is the distribution of exudate resources exploited by marmosets throughout their environment? We test the hypotheses that resources exhibit either a clumped, uniform, or random distribution. The quantitative predictions for these spatial distributions are listed in Table I. 2) Do marmosets selectively exploit gouging trees near the center of their ranges to increase exclusive access to exudate resources? Based on the prevalence of intergroup aggression in common marmosets, we predict that marmoset gouging trees will be concentrated near home range centers (Table I). 3) Are patterns of gouge intensity related to spatial location? We predict that heavily gouged trees will be spatially clumped (reflecting concentrated areas of intense resource use) and/or focused in the center of home ranges (Table I). 4) Lastly, we assess whether gouge intensity is related to other nonspatial characteristics of gouged trees. Though data are not currently available to evaluate fully all potential factors influencing tree gouging, we will assess the effects of tree species (which is likely to

**Table I** Potential spatial distributions of gouged trees and quantitative expectations

Distribution	Expectations	Supported
Uniform	1) Trees' nearest neighbor distance (NND) should be similar for all pairs.	N
	2) The CV of NND should be at or near 0.	N
Random	1) NND of trees should be normally distributed.	N
	2) Average NND should equal $0.5\sqrt{M}$ . <sup>a</sup>	N
	3) NND of actual trees and between pairs of random points should not differ significantly.	N
Clumped	1) The distribution of NND should be positively skewed.	Y
	2) Average NND should be $< 0.5\sqrt{M}$ .	Y
	3) NND of gouge trees should be significantly shorter than random points.	Y
	4) Trees that are heavily gouged should be spatially proximate.	N
Intergroup resource competition	1) Gouged trees should be located closer to home range centers than boundaries.	N
	2) Fewer than 25 % of gouged trees should be located in the peripheral 25 % of home range area.	N
	3) Gouged trees in the center of the home range should be more heavily gouged. <sup>b</sup>	N

<sup>a</sup> Where  $M$  is the reciprocal of gouged tree density (Cottam and Curtis 1956)

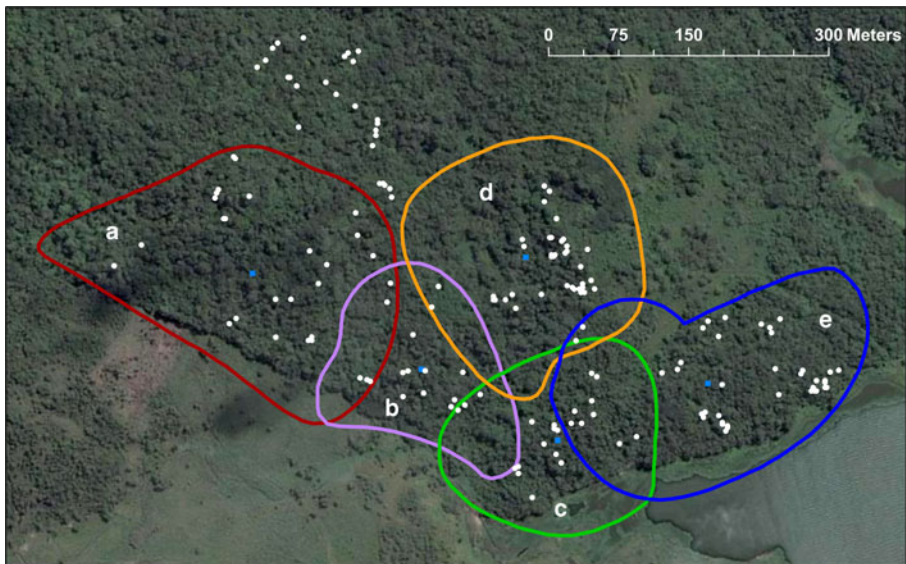
<sup>b</sup> Although use by more than one group could increase gouge intensity in home range overlap areas

significantly influence many of the afore mentioned variables) and trunk size on patterns of exudate exploitation.

## Methods

### Field Site

The study area encompassed a *ca.* 25-ha section of forest tract in the western portion of the Estação Ecológica do Tapacurá near Recife in Pernambuco, Brazil (08° 03 S, 35°12 W) (Fig. 2). The ecological field station is located within the Atlantic coastal forest (Mata Atlântica) and is maintained by the Universidade Federal Rural de Pernambuco. The field station is 100–200 m above sea level and is composed predominantly of semideciduous, secondary growth, broadleaf perennials (Hubrecht 1984, 1985; Scanlon *et al.* 1988, 1989). The wet season at Tapacurá is from May to August and the dry season is from September to April. Common marmosets have been studied intermittently at the field site for three decades (Faulkes *et al.* 2003; Hubrecht 1984, 1985; Melo 2001; Scanlon *et al.* 1988, 1989; Vinyard *et al.* 2009). The primary study area included the home ranges of five marmoset groups ranging in size from 6 to 14 individuals per group (Faulkes *et al.* 2003; Monteiro da Cruz 1998; Scanlon *et al.* 1988). Permission to conduct this research was provided by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) and the Universidade Federal Rural de Pernambuco (UFRPE).



**Fig. 2** Satellite image of Tapacurá field station showing distribution of gouged trees (white dots), home range centroids (blue squares), and home range boundaries for different marmoset groups in the study area (a = red, b = purple, c = green, d = orange, e = blue).

## Data Collection

We collected spatial data on gouged trees ( $N=145$ ) between January and March 2003 using a grid of  $50 \times 50$  m transects (Monteiro da Cruz 1998; Scanlon *et al.* 1988, 1989). All transects were systematically walked and trees with gouge marks identified. In areas where growth prohibited effective visualization of trees up to the adjacent transect, we conducted additional walks between transects. We identified the species of each gouged tree and collected the tree's latitude and longitude using a handheld GPS (Garmin GPS 12). We measured tree circumference 1 m off the ground and ranked the number of gouges for each tree into one of three ordinal categories: low (1–9 gouges), medium (10–25), and high (>25). The large number of gouge marks on highly used trees (Fig. 1b) made it unfeasible to count individual gouge marks on all trees.

We collected gouge hole dimensions on a randomly chosen subset of trees and gouging holes per tree (within researcher standing height). We measured depth, length, and width of gouge holes for 352 gouges for 50 individual trees from 14 species (although seven species had only one individual), resulting in a mean of seven measured gouge holes per tree (range=1–20). We used these measurements to obtain the volume of bark excavated for a gouge hole by calculating the volume of a half ellipsoid  $\left[\frac{1}{2} \left(\frac{4}{3} \times \pi \times l \times w \times d\right)\right]$ . As repeated gouging events will likely increase the size of gouge holes, this measurement is used as an indicator of the frequency of gouging for a particular hole. We also considered the depth of gouges as a second index of gouge intensity. We computed mean values for both volume and depth for individual trees.

We analyzed spatial relationships among trees using ArcGIS® (Environmental Systems Research Institute, Inc., Redlands, CA). We imported home range maps previously collected for marmoset groups at Tapacurá (Monteiro da Cruz 1998) into ArcGIS and georeferenced to GPS data marking forest transect intersections throughout the study area. These home range data were obtained from follows conducted over a 4-year period from 1993 to 1997. All groups were followed 12–24 d/mo and the grid cell quadrats ( $50 \times 50$  m) entered by each were recorded. This method of home range measurement was identical for all groups. We computed home range area, geometric centroids of each home range, and home range overlap area in ArcGIS. We used Hawth's tools for ArcGIS (Beyer 2004) to calculate the distance of each gouged tree to 1) the nearest home range centroid, 2) the nearest home range boundary, and 3) the nearest neighboring gouged tree (NND). We also used Hawth's tool to generate 50 sets of random points ( $N=145$ ) within the combined home ranges' boundaries for comparison to gouged trees.

## Data Analysis

*Spatial Distribution* We tested the distribution of NND for gouged trees for normality using a Shapiro–Wilks test. [Kolmogorov–Smirnov tests for normality yielded similar statistical results.] We compared mean values and skewness  $\left(g_1 = \frac{\frac{1}{N} \sum (x_i - \bar{x})^3}{\left(\frac{1}{N} \sum (x_i - \bar{x})^2\right)^{\frac{3}{2}}}\right)$  for the NND of gouged trees to the distribution of mean NND values and skewness

obtained from the randomly generated sets of points via *t*-tests. We also tested whether the mean skewness of gouged tree NND differed from zero (i.e., a symmetrical distribution) via a one sample *t*-test. High positive skewness (i.e., many trees have close nearest neighbors) indicate that trees are clumped. We calculated the expected NND in a random distribution as  $E(x) = 0.5\sqrt{M}$ , where  $M$  is the reciprocal of gouging tree density (Cottam and Curtis 1956). Lower than expected values of  $E(x)$  indicate clumping of trees.

We used Ripley's *K*-function to evaluate the spatial scale of clumping (Ripley 1977). This test generates iterations of random points within the study area and then tallies the number of points within varying radii ( $d$ ) of each point. These random values are then compared to the same tallies generated from the observed data. Using ArcGIS we calculated a common transformation of the

*K*-function as  $L(d) = \sqrt{\frac{A \sum_{i=1}^N \sum_{j=1, j \neq i}^N k(i,j)}{\pi N(N-1)}}$  where  $N$  is the number of gouged trees,  $A$  is the area of the study site, and  $k(i, j)$  is a weight applied by a boundary correction method. To adjust for edge effects (i.e. the absence of samples outside of the study range) we used the "simulate outer boundary values" algorithm within ArcGIS (ESRI 2011). We generated a 99 % confidence interval of the *K*-function for the expected random distribution. Observed values above this interval indicate gouged trees are significantly clumped at a given spatial scale.

We used paired *t*-tests to compare the distance of each gouged tree to its home range's geometric centroid and nearest boundary. Given that distances can vary widely due to the differing shape of home ranges, we also assessed these differences using a nonparametric Wilcoxon signed rank tests. Outcomes were consistent between tests and only paired *t*-tests are reported. For each gouged tree we also calculated the ratio of the distances to the home range centroid and nearest home range boundary (centrality ratio). We  $\log_{10}$  transformed the centrality ratio to achieve normality (Shapiro-Wilks test for normality: S-W=0.99,  $P=0.454$ ). The  $\log_{10}$  centrality ratio reflects the relative spatial position of a tree within its home range with positive values indicating a tree is closer to the boundary and negative values reflecting proximity to the center.

We arbitrarily defined the central region of home ranges as 75 % of the area surrounding the geometric centroid, with the remaining 25 % near the home range boundary considered the periphery. We tallied the number of gouged trees in center and peripheral areas and binomial tests were conducted for each home range using expected probabilities based on the 75 %/25 % proportion of center versus periphery. In addition, because overlap areas may display increased gouging intensity due to use by more than one group, we conducted binomial tests to assess whether more trees were present in overlap areas than would be expected based on the percent area in home range overlap zones. Overlap areas were likely underestimated for home ranges A, D, and E because not all neighboring group ranges were known.

*Gouge Intensity* We assessed intensity of gouging on individual trees in two ways: 1) by ordinal gouge intensity ranks based on the number of gouges per tree and 2) by dimensions (depth and volume) of gouge holes. To assess specifically whether trees



with higher gouge intensity ranks were located closer to the center of home ranges, we conducted a  $\chi^2$  test on the relationship between gouge intensity rank and location in the central (75 %) vs. peripheral (25 %) areas of home ranges for trees in all home ranges. We conducted Pearson's correlation between NND and both gouge hole depth and volume to assess whether more intensely gouged trees were spatially clumped.

To determine the predictors of gouge intensity rank, we performed an ordinal logistic regression including tree circumference, the  $\log_{10}$  centrality ratio, and location in the overlap zone as predictor variables. We included gouge intensity of the nearest neighbor tree as a predictor variable to assess whether the spatial distribution of gouge intensity was clumped. We considered presence of a tree in the home range periphery in an initial model, but removed this nonsignificant variable to reduce the number of interrelated predictor variables. Using presence in the overlap rather than home range periphery has the added benefit of assessing whether gouging is more or less intense in areas without exclusive access by individual groups. Though we acknowledge that the number of individuals within groups may also affect gouge intensity, the long-term persistence of gouge holes and variable size of groups over time make testing this relationship impractical for the present study.

We found that circumference was a significant predictor of gouge intensity in the logistic model. To determine if this relationship was driven by tree size or preferences for species with larger circumferences, we conducted the above ordinal regression controlling for species identity. Sample sizes were low ( $\leq 5$ ) for some tree species in the model, but statistical results were similar when restricting the sample to species with more than five individuals in the data set. Results including all species are reported. We also conducted an ANOVA to assess the amount of variation in circumference explained by species identity. For each tree species with more than 10 representatives, we compared circumference to gouge intensity ranks by Jonckheere–Terpstra tests for ordered alternatives to assess intraspecific preference for circumference by marmosets.

We performed multiple regressions to determine the factors driving gouge hole depth and volume. We used the  $\log_{10}$  centrality ratio, location in the overlap area, and tree circumference as independent variables. We assessed the effect of species on gouge hole depth and volume via one-way ANOVAs. For gouge dimension data, seven species had only one representative in the data set. We conducted tests both including and excluding these species. Statistical results were the same for the regressions and only tests including all species are reported. Both results are reported for the ANOVAs. We used a two-tailed  $\alpha=0.05$  for all tests.

**Study Limitations** Our data set has several restrictions worth highlighting. First, the measurement of home ranges and survey of gouged trees were conducted 6 years apart. It is therefore possible that home range boundaries may have shifted from the time of measurement to when gouged trees were sampled. Though this temporal gap may raise concerns, some studies have argued that common marmoset home ranges are relatively stable over time (Hubrecht 1985; Mendes Pontes and Da Cruz 1995; Scanlon *et al.* 1989). In addition, if gouge marks persist over extended periods (i.e. years) on trees, then many of the surveyed gouge marks may have been contemporaneous with home range measurements. Indeed, tree wounds caused from bark stripping by red deer (*Cervus elaphus*) and moose (*Alces alces*) in Scottish and Lithuanian

forest stands, respectively, have been found to persist for >14 years (Vasiliauskas 1998; Welch *et al.* 1997). Similarly, in a bark stripping experiment of tropical medicinal trees, 5 of 12 species had healing rates (i.e., bark replacement) of <30 cm<sup>2</sup>/year (Delvaux *et al.* 2010). For comparison, mean gouge hole area in our data set was 194.1 cm<sup>2</sup>. Though we do not have quantitative data on how long marmoset gouge holes last, the long-term persistence of similar tree wounds implies that our gouge hole survey data do have some temporal association with the earlier home range measurements.

Second, because these home range measures were georeferenced from a previous study (Monteiro da Cruz 1998), we have only geometric, rather than use frequency data on marmoset home ranges. Our tests are accordingly limited to the geometric effects of tree location within home ranges (e.g., center vs. periphery) rather than tests regarding dispersion of trees in relation to areas of frequent use. Geometric effects can have important biological significance given that home range peripheries represent areas where groups are more likely to encounter neighboring competitors and may be subject to intergroup feeding competition. As an illustrative example, white-faced capuchins were more likely to win intergroup encounters when they occurred near the long-term center of their range (i.e., the mean *x*- and *y*-coordinate locations) but not necessarily in areas of recent high use frequency (Crofoot *et al.* 2008). We acknowledge, however, that some peripheral areas in our study border habitat edges that may result in edge effects.

Lastly, although we recorded the location of gouged trees, we have no spatial information on the underlying distribution of ungouged trees from these exploited species. Accordingly we cannot draw comparisons between the characteristics of trees that were gouged vs. not gouged or determine whether the spatial distribution of gouged trees simply reflects the underlying distribution for that tree species. Instead we focus on 1) the resulting spatial distribution of trees that marmosets did choose to exploit and 2) compare between the characteristics of heavily vs. nonheavily exploited trees.

## Results

### Spatial Distribution of Gouged Trees

Home range area and the density of gouge trees within each range varied among groups (home range area: A: 6.90 ha, B: 3.20, C: 3.79, D: 5.21, E: 5.80; gouged tree density: A: 4.20 trees/ha, B: 6.56, C: 6.33, D: 7.68, E: 9.31; Fig. 2). The NND distribution of gouged trees (from trees across all home ranges) deviated significantly from normality (Shapiro–Wilks test:  $S-W=0.86$ ,  $P<0.001$ ) and was positively skewed (Table II and Fig. 3), indicating clumping of gouged trees. Skewness of gouged trees (Table II) was significantly greater than 0 (one-sample *t*-test:  $t=32.42$ ,  $df=144$ ,  $P<0.001$ ). This was higher than the mean skewness from randomly generated sets of points (Table II), but the difference was not significant (one-sample *t*-test:  $t=1.15$ ,  $df=49$ ,  $P=0.257$ ), likely because some random sets contained trees with high NND values (Fig. 3). The coefficient of variation (CV) of gouged tree NND was also >0, indicating a nonrandom distribution, and was also higher than the NND for random points (Table II). Lastly, mean NND of gouged trees (Table II) was lower than the expected value of 20.72 m based on the study area's size and number of gouged trees. Gouged tree NND was also lower than the entire range of mean NND generated from random sets

**Table II** Nearest neighbor distance (NND) statistics for gouged trees and randomly generated points within marmoset home ranges

Sample	Range (m)	$\bar{x}$ (m)	CV (%)	Skewness
Gouged trees <sup>a</sup>	36.80	9.75	95.9	1.15
Random points <sup>b</sup>	56.46	19.93	55.4	0.87

<sup>a</sup> Gouged trees:  $N=145$

<sup>b</sup> Random points: average of 50 samples of  $N=145$  points

(range=17.8–21.3 m; one-sample  $t$ -test:  $t=-11.76$ ,  $P<0.001$ ), indicating that gouge trees are spatially clumped. Ripley's  $K$  further verified this pattern, with observed  $K$  values being significantly greater than expected across all spatial scales of the study area including scales as small as 10 m (Fig. 4). Each gouged tree had a mean of 1.7 ( $\pm 1.8$ ) gouged trees within 10 m.

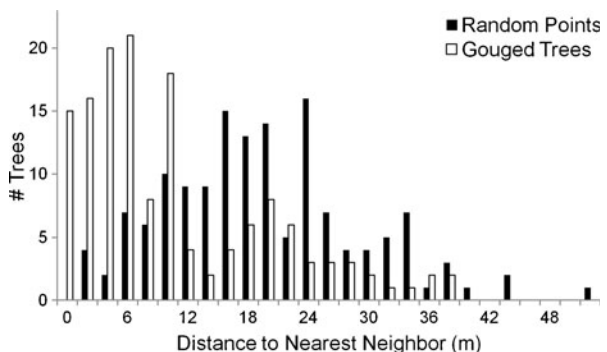
### Centralization Within Home Ranges

Gouged trees were not significantly closer to home range centers than boundaries (Table III). Contrary to our prediction, two home ranges (A, E) had gouged trees that were significantly closer to the boundary (Table III). Binomial comparisons of the number of trees in central vs. peripheral areas of individual home ranges yielded conflicting patterns (Table III). The number of trees in home range overlap zones were not larger than would be expected from the size of overlap areas (binomial test: A:  $P=0.131$ ,  $N=29$  total gouged trees; B:  $P=0.890$ ,  $N=21$ ; C:  $P=0.160$ ,  $N=23$ ; D:  $P=0.135$ ,  $N=40$ ; E:  $P=0.100$ ,  $N=54$ ) although overlap area was likely underestimated for groups A, D, and E (see Methods).

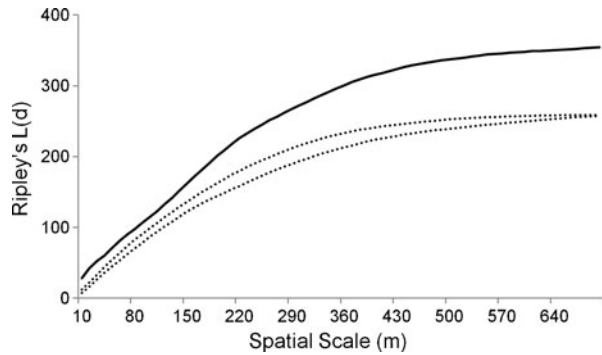
### Gouge Intensity

Tree circumference was the only significant predictor of gouge intensity rank in the logistic regression (Table IV, Fig. 5), suggesting that larger trees tended to be more intensely gouged. The odds ratio for this variable was low, which may result from the broadly defined gouge rank categories. However, when tree species was

**Fig. 3** Distribution of nearest neighbor distances (NNDs) for gouged trees and a representative set of random points across all marmoset home ranges.



**Fig. 4** Ripley's *K*-function [L(d)] of gouged trees over different spatial scales. Solid line = observed values, dotted lines = 99 % confidence interval. Observed values greater than confidence limits indicate significant clumping.



controlled for in the model, the effect of circumference was no longer significant (ordinal logistic regression: Wald  $\chi^2=0.08$ ,  $P=0.783$ ). Moreover, species identity explains a large proportion of the variance in circumference among gouging trees (partial  $\eta^2=53.5\%$ ; ANOVA:  $F=11.58$ ,  $df=13$ ,  $P<0.001$ ) (Table V).

The ordinal logistic regression found that increasing gouge intensity of nearest neighbor trees did not significantly increase the likelihood that gouged trees would have a high gouge intensity rank (i.e., gouge intensity was not clumped) (Table IV). The centrality ratio was also not a significant predictor of gouge intensity rank (Table IV). A  $\chi^2$  test corroborated the finding that gouge intensity rank was not related to home range center/peripheral areas when overlap trees ( $N=22$ ) were either included in the data set ( $\chi^2=0.08$ ,  $df=2$ ,  $P=0.960$ ) or excluded ( $\chi^2=0.12$ ,  $df=2$ ,  $P=0.941$ ).

When using gouge hole dimensions as indicators of intensity, multiple regression found that circumference had a significant effect on gouge hole depth and volume (Table IV). Neither the centrality ratio nor location in the overlap zone were significant predictors of gouge hole depth or volume. Likewise, gouged tree NND was not correlated with gouge hole dimensions (Pearson's correlation: depth:  $r=0.05$ ,  $P=0.761$ ,  $N=48$ ; volume:  $r=0.04$ ,  $P=0.771$ ,  $N=48$ ), indicating that

**Table III** Distribution of gouged trees relative to common marmoset home range centers

Home range	Paired <i>t</i> -test					Center/periphery binomial test		
	$\bar{x}$ Distance to centroid (m)	$\bar{x}$ Distance to boundary (m)	<i>t</i> -statistic	df	<i>P</i> -value	No. of trees in center	No. of trees in periphery	<i>P</i> -value
A	102.10	46.57	-4.67	28	<b>&lt;0.001<sup>a</sup></b>	18	11	<b>0.047<sup>a</sup></b>
B	55.26	42.89	-1.17	20	0.258	18	3	0.117
C	51.72	46.87	-0.43	22	0.670	20	3	0.088
D	56.99	67.30	1.38	39	0.176	36	4	<b>0.011</b>
E	90.26	44.78	-6.28	53	<b>&lt;0.001<sup>a</sup></b>	31	23	<b>0.002<sup>a</sup></b>

<sup>a</sup> Significant in the direction contrary to predictions

Significant values ( $\alpha=0.05$ ) in **bold**

**Table IV** Regression models for variables explaining gouge intensity rank, gouge hole depth, and gouge hole volume

Predictor variable	Gouge intensity rank <sup>a</sup>			Gouge hole depth <sup>b</sup>			Gouge hole volume <sup>b</sup>		
	Wald $\chi^2$	P-value	Odds ratio	Standardized $\beta$	t	P-value	Standardized $\beta$	t	P-value
Centrality ratio	<0.01	0.956	-0.021	0.04	0.27	0.785	0.11	0.81	0.422
Overlap	0.30	0.584	-0.279	0.01	0.11	0.916	0.03	0.24	0.809
Circumference	11.05	<b>0.001</b>	0.013	0.52	3.87	<b>&lt;0.001</b>	0.58	4.42	<b>&lt;0.001</b>
NN Gouge Intensity									
Low-Medium	0.04	0.837	-0.075	—	—	—	—	—	—
Medium-High	1.76	0.184	-0.615	—	—	—	—	—	—

<sup>a</sup> Ordinal logistic regression model

<sup>b</sup> Multiple linear regression model

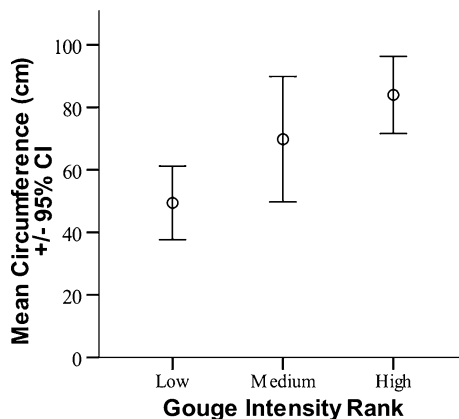
Significant values ( $\alpha=0.05$ ) in **bold**

For gouge intensity rank model:  $R^2=0.13$ , depth:  $R^2=0.51$ ; volume:  $R^2=0.56$

NN = nearest neighbor

trees with closer neighbors were not gouged more intensely. Similar to results for gouge intensity rank, species identity explained a large proportion of the variance in gouge hole volume (all species: partial  $\eta^2=70.7\%$ ; ANOVA:  $F=6.31$ ,  $df=13$ ,  $P<0.001$ ; species with more than one individual: partial  $\eta^2=30.8\%$ ; ANOVA:  $F=2.53$ ,  $df=6$ ,  $P=0.04$ ) (Table V). For gouge hole depth, species only differed significantly when all tree data were included (all species: partial  $\eta^2=65.2\%$ ; ANOVA:  $F=4.90$ ,  $df=13$ ,  $P<0.001$ ; species with more than one individual: partial  $\eta^2=24.8\%$ ; ANOVA:  $F=1.87$ ,  $df=6$ ,  $P=0.115$ ). For species with >10 individuals, the Jonckheere–Terpstra tests did not find a significant increase in circumference with increased gouge intensity rank suggesting that intraspecific differences in circumference do not influence gouge intensity.

**Fig. 5** Mean ( $\pm 95\%$  confidence interval) circumference of gouged trees by gouge intensity rank.



**Table V** Distribution of gouge intensity variables and circumference by tree species

Species	Family	N	No. of trees in gouge intensity ranks			Average circumference (cm)	Average GH depth (mm)	Average GH volume (cm <sup>3</sup> )
			Low	Medium	High			
<i>Acacia paniculata</i>	Fabaceae	13	12	1	0	20.25	3.20	1.83
<i>Allophylus edulis</i>	Sapindaceae	3	1	1	1	25.60	1.77	5.44
<i>Anacardium occidentale</i>	Anacardiaceae	1	0	0	1	146.00	5.02	5.38
<i>Anadenanthera peregrina</i>	Fabaceae	16	8	2	6	97.42	2.84	0.95
<i>Astronium fraxinifolium</i>	Anacardiaceae	48	13	10	25	72.82	9.13	11.27
<i>Coccoloba</i> sp.	Polygonaceae	15	4	5	6	38.23	2.13	1.51
<i>Didymopanax morotoni</i>	Araliaceae	5	3	1	1	60.39	4.32	2.07
<i>Enterolobium contortilicium</i>	Fabaceae	15	0	1	14	114.78	11.11	8.84
<i>Heteropterys</i> sp.	Malpighiaceae	1	1	0	0	22.50	1.88	0.40
<i>Inga fagifolia</i>	Fabaceae	1	1	0	0	14.00	3.14	1.82
<i>Pithecolobium saman</i>	Fabaceae	2	2	0	0	32.25	3.22	0.99
<i>Spondias mombin</i>	Anacardiaceae	5	1	2	2	138.26	4.43	3.99
<i>Stryphnodendron pulcherrimum</i>	Fabaceae	14	5	2	7	41.14	2.35	0.94
<i>Talisia esculenta</i>	Sapindaceae	6	5	1	0	25.33	1.90	0.61

GH = gouge hole

## Discussion

Our data indicate that the trees marmosets choose to gouge are spatially clumped within their home ranges (Table I). Clumped resource distributions are generally associated with the ability to monopolize resources and for group-living animals, the potential for cooperative defense (Emlen and Oring 1977; Reeves and Hölldobler 2007; Slobodchikoff 1984; van Schaik 1989; Wrangham 1980). Despite the fact that intergroup encounters are often aggressive in marmosets, we found minimal evidence that marmosets choose to exploit trees located near the centers of ranges, where they are most likely to have exclusive access. Likewise, intergroup overlap zones, which should reflect areas of nonexclusive access, did not contain fewer gouged trees, nor were trees in these areas less intensely exploited (Table I). Trees with larger circumferences were gouged more intensely, although this preference was largely driven by species-specific differences in circumference.

### Intergroup Competition for a Renewable Resource

It is possible the lack of association between home ranges and the spatial distribution of exploited gouged trees is driven by the unique nature of competition over exudates. For resource defense to be advantageous, foods must be both defendable and worth the costs of defense (Brown 1964). When resources are quickly renewable (or conversely, difficult to deplete), the benefit of gaining exclusive access decreases,

while the costs of defense remain constant, resulting in a net decrease in the selective advantage of active defense (Waser 1981; Waser and Waser 1985). Exudates are a renewable resource (Garber and Porter 2010), and hence defense of these trees may not be worth the costs as visitation by competing groups may not greatly reduce the amount of exudates available in subsequent visits. Access to these resources, however, may also lead to smaller home range size, which could lower the costs of defense. If the renewable nature of exudates does reduce the benefits of their defense, then the territorial aggression seen in common marmosets may reflect disputes over more depletable resources that are more economical to contest such as fruits. Indeed, in a separate study intergroup encounters occurred in home range overlap areas that had high densities of fruit trees, but not exudate trees (Lazaro-Perea 2001). Yet as a caveat to this interpretation, Lazaro-Perea noted that aggressive encounters still occurred during the nonfruiting season and the study did not specifically examine food defense as a drive for intergroup aggression. It has been similarly noted that intergroup encounters tend to occur in favored fruit trees (Rylands 1986), although encounters are also known to serve a sexual function in repelling same sex competitors and gaining extragroup copulations (Decanini and Macedo 2008; Hubrecht 1985; Lazaro-Perea 2001).

It is also possible that frequently used areas of the home range, rather than the geometric center and peripheral areas, are more relevant measures for resource defense and exploitation. The study population at Tapacurá showed preferential use of certain habitat types within the home range (Hubrecht 1985), and areas of greater use had higher densities of tree species that marmosets exploit, although not necessarily gouged trees (Scanlon *et al.* 1989). It is possible that marmosets defend access to exudate trees in frequented areas regardless of proximity to neighboring competitors. Our study is limited in that we do not have continuous ranging data by marmoset groups to calculate use frequency within home ranges and that we do not know the underlying distribution of individual trees (gouged and ungouged) of exploited species.

### Selectivity in Tree Gouging

Our data support the hypothesis that gouged trees are spatially clumped at scales pertinent to marmoset ecology (Table 1). Exploiting clumped resources may offer advantages such as decreased day path length and smaller home range size. By having a number of steady and reliable exudate resources close to one another, marmosets may be able to reduce the energetic costs of traveling widely to exploit alternate resources such as fruits that are more temporally and spatially dispersed. Smaller home ranges and clumping of resources may also enable marmosets to easily revisit gouged trees to harvest exudates. Smaller home ranges are likewise more defensible and could allow groups to better maintain exclusive access to food resources (exudates or otherwise) and mates. The fact that gouged trees in our study were clumped at small spatial scales (i.e. 10 m) through scales comparable to home range size indicates that marmosets at Tapacurá are likely gaining benefits from the clumped spatial distribution of exudate resources. Unfortunately, our study is unable to assess short-term (e.g. daily, monthly, seasonal) patterns of exudate exploitation and hence cannot determine whether multiple trees within a clump are actually

exploited during a single visit. Behavioral studies linking the distribution of food resources exploited by marmosets on these short time scales with ranging data are needed to test this hypothesis.

The clumped distribution of gouged trees may also reflect the underlying distribution of tree species throughout the site with exploitation by marmosets reflecting a random, proportionate sample of available trees. Support for this argument appears equivocal, although there are limited data available on the distribution of existing versus unexploited gouged trees in marmoset habitats. In our sample, three gouged tree species had nearest neighbors of the same species more often than expected, although four species did not (the remaining tree species did not have enough trees to analyze). When all species were considered together, gouged trees did have nearest neighbors of the same species more frequently than expected, even though this characterized only 30 % of trees in our sample. Likewise, two of the four most frequently exploited species in our sample (*Astronium fraxinifolium* and *Coccoloba* sp.) were significantly clumped at all spatial scales using Ripley's  $K$ , whereas the remaining two displayed significant clumping only at radius scales  $>150$  m (*Anadenanthera peregrina*) and  $>60$  m (*Enterolobium contortiticicum*). This contrasts with the majority of tropical tree species that are strongly clumped at small spatial scales ( $<50$  m), but are often only weakly aggregated at scales above *ca.* 150 m (Condit *et al.* 2000; Seidler and Plotkin 2006). Indeed, some of the gouged species in this study have been reported as spatially clumped (*Acacia paniculata*: de Oliveira *et al.* 2007; *Astronium fraxinifolium*: Leite 2001; *Anadenanthera peregrina*: Malhado and Petreire 2004), although these studies often did not assess spatial aggregation at multiple or larger scales. However, even at small scales, as the number of gouged species sampled increases, the spatial distribution of these independently clumped species will become more uniform. As an example, gouged trees for one marmoset habitat were clumped for the three most exploited tree species, although their collective distribution was not clumped (Lacher *et al.* 1984). Neither Lacher's nor our study evaluated the spatial distribution of exploited relative to unexploited trees throughout the habitat. Yet, the mean NND between gouged trees in our study (9.75 m) was far greater than the mean NND that has been reported between conspecifics (gouged and ungouged) of three species marmosets used in Lacher's (1984) study (0.82–2.42 m), as well as those reported for a large number of tree species in a dry tropical forest (range: 0.7–1.6 m,  $N=61$ ) (Hubbell 1979). Similarly, for the three species in Lacher's study (which were not present in our sample), 40 % of individual trees were not gouged. Given the relatively small home ranges of common marmosets, the fact that such a large percentage of trees from habitually gouged species were not exploited suggests that marmosets exhibit some preference (spatial or otherwise) for individual trees.

Though gouged trees in our study were spatially clumped, intensely gouged trees were not necessarily spatially proximate to one another. This confirms observations that highly gouged trees are frequently found alongside trees of the same species without gouges (Stevenson and Rylands 1988). Marmosets at Tapacurá more intensely gouged trees with larger circumferences, consistent with former studies on gouge patterns and locomotion preferences (Jackson 2011; Lacher *et al.* 1984; Youlantos 2009). We found that this relationship was driven by interspecific differences in circumference rather than intraspecific variation. This finding suggests that intense



gouging reflects a preference for larger tree species, rather than older (i.e.) larger, trees of a given species. However, it is currently unknown whether preference is determined by trunk size or other species-specific characteristics. It is possible that the larger trunk size of heavily gouged trees is related to marmoset locomotor preferences or that marmosets prefer trees with more surface area available for gouging. There may also be a tendency for large trunked species to possess other properties desirable for gouging such as nutritional quality and quantity of the exudate produced, mechanical properties of the bark that facilitate gouging, an improved capacity to continue producing exudate despite intense gouging, or other qualities such as increased cover from predators.

Our findings suggest that the distribution of gouged trees exploited by marmosets is spatially clumped within home ranges, although the intensity of exploitation is not. Although this distribution may have important implications for the ranging behavior of marmosets, we found no clear relationship between gouged tree distribution and the center or peripheral areas of home ranges. This may indicate that the frequent intergroup aggression seen in marmosets is not driven by competition over exudates, although we did not assess marmoset behaviors directly. Marmosets gouged larger trees more intensely, but this pattern was driven by interspecific differences in trunk size rather than preference for larger trees. We suggest that future research focus on the structural, mechanical, and nutritional variables driving gouging tree preference in marmosets.

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## References

- Bacon, P. J., Ball, F., & Blackwell, P. (1991). A model for territory and group formation in a heterogeneous habitat. *Journal of Theoretical Biology*, *148*(4), 445–468.
- Beyer, H.L. (2004). Hawth's analysis tools for ArcGIS. Available at <http://www.spatial ecology.com/htools>.
- Boinski, S., Kauffman, L., Ehmke, E., Schet, S., & Vreedzaam, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*): I. Divergent costs and benefits. *Behaviour*, *142*(5), 525–632.
- Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *The Wilson Bulletin*, *76*(2), 109–208.
- Chancellor, R. L., & Isbell, L. A. (2009). Food site residence time and female competitive relationships in wild gray-cheeked mangabeys (*Lophocebus albigena*). *Behavioral Ecology and Sociobiology*, *63*(10), 1447–1458.
- Chapman, C. (1990). Ecological constraints on group size in three species of Neotropical primates. *Folia Primatologica*, *55*(1), 1–9.
- Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*(1), 59–70.
- Clark, A. (1978). Sex ratio and local resource competition in a prosimian primate. *Science*, *201*(4351), 163–165.
- Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology*, *183*(1), 1–39.

- Coimbra-Filho, A. F., & Mittermeier, R. A. (1977). Tree-gouging, exudate-eating and the “short-tusked” condition in *Callithrix* and *Cebuella*. In D. G. Kleiman (Ed.), *The biology and conservation of the callitrichidae* (pp. 105–115). Washington, DC: Smithsonian Institution Press.
- Condit, R., Ashton, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S. P., Foster, R. B., Itoh, A., LaFrankie, J. V., Lee, H. S., Losos, E., Manokaran, N., Sukumar, R., & Yamakura, T. (2000). Spatial patterns in the distribution of tropical tree species. *Science*, *288*(5470), 1414–1418.
- Cottam, G., & Curtis, J. T. (1956). The use of distance measures in phytosociological sampling. *Ecology*, *37*(3), 451–460.
- Crofoot, M. C., Gilby, I. C., Wikelski, M. C., & Kays, R. W. (2008). Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. *Proceedings of the National Academy of Sciences of the USA*, *105*(2), 577–581.
- de Oliveira, R., Lins Neto, E., Araújo, E., & Albuquerque, U. (2007). Conservation priorities and population structure of woody medicinal plants in an area of *Caatinga* vegetation (Pernambuco State, NE Brazil). *Environmental Monitoring and Assessment*, *132*(1), 189–206.
- Decanini, D., & Macedo, R. (2008). Sociality in *Callithrix penicillata*: II. Individual strategies during intergroup encounters. *International Journal of Primatology*, *29*(3), 627–639.
- Delvaux, C., Sinsin, B., & Van Damme, P. (2010). Impact of season, stem diameter and intensity of debarking on survival and bark re-growth pattern of medicinal tree species, Benin, West Africa. *Biological Conservation*, *143*(11), 2664–2671.
- Digby, L. J., Ferrari, S. F., & Saltzman, W. (2011). Callitrichines: The role of competition in cooperatively breeding species. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 91–107). New York: Oxford University Press.
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223.
- ESRI. (2011). *ArcGIS Desktop: Release 10*. Redlands: Environmental Systems Research Institute.
- Fashing, P. J. (2007). African colobine monkeys: Patterns of between-group interaction. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 201–224). New York: Oxford University Press.
- Faulkes, C. G., Arruda, M. F., & Monteiro Da Cruz, M. A. O. (2003). Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus*. *Molecular Ecology*, *12*(4), 1101–1108.
- Ferrari, S., & Lopes Ferrari, M. (1989). A re-evaluation of the social organisation of the callitrichidae, with reference to the ecological differences between genera. *Folia Primatologica*, *52*(3–4), 132–147.
- Fragaszy, D. M., & Perry, S. (2003). *The biology of traditions: Models and evidence*. Cambridge: Cambridge University Press.
- Garber, P. A. (1992). Vertical clinging, small body size, and the evolution of feeding adaptations in the callitrichinae. *American Journal of Physical Anthropology*, *88*(4), 469–482.
- Garber, P. A., & Porter, L. M. (2010). The ecology of exudate production and exudate feeding in *Saguinus* and *Callimico*. In A. M. Burrows & L. T. Nash (Eds.), *The evolution of exudativory in primates* (pp. 89–108). New York: Springer.
- Go, M. (2010). Seasonal changes in food resource distribution and feeding sites selected by Japanese macaques on Koshima Islet, Japan. *Primates*, *51*(2), 149–158.
- Grant, J. W. A. (1993). Whether or not to defend? The influence of resource distribution. *Marine Behaviour and Physiology*, *23*(1–4), 137–153.
- Hamrick, M. W. (1998). Functional and adaptive significance of primate pads and claws: evidence from New World anthropoids. *American Journal of Physical Anthropology*, *106*(2), 113–127.
- Harrison, M. L., & Tardif, S. D. (1994). Social implications of gummivory in marmosets. *American Journal of Physical Anthropology*, *95*(4), 399–408.
- Hubbell, S. P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, *203*(4387), 1299–1309.
- Hubrecht, R. (1984). Field observations on group size and composition of the common marmoset (*Callithrix jacchus jacchus*), at Tapacura, Brazil. *Primates*, *25*(1), 13–21.
- Hubrecht, R. (1985). Home-range size and use and territorial behavior in the common marmoset, *Callithrix jacchus jacchus*, at the Tapacura Field Station, Recife, Brazil. *International Journal of Primatology*, *6*(5), 533–550.
- Isbell, L. A., Pruett, J. D., & Young, T. P. (1998). Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behavioral Ecology and Sociobiology*, *42*(2), 123–133.

- Izumiyama, S., Mochizuki, T., & Shiraishi, T. (2003). Troop size, home range area and seasonal range use of the Japanese macaque in the northern Japan Alps. *Ecological Research*, 18(5), 465–474.
- Jackson, C. (2011). The positional behavior of pygmy marmosets (*Cebuella pygmaea*) in northwestern Bolivia. *Primates*, 52(2), 171–178.
- Johnson, D. D. P., Kays, R., Blackwell, P. G., & Macdonald, D. W. (2002). Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution*, 17(12), 563–570.
- Kinzey, W. G. (1997). *New world primates: Ecology, evolution, and behavior*. New York: Aldine de Gruyter.
- Kumar, R. S., Mishra, C., & Sinha, A. (2007). Foraging ecology and time-activity budget of the Arunachal macaque *Macaca munzala* – a preliminary study. *Current Science*, 93(4), 532–539.
- Lacher, T. E., Bouchardet da Fonseca, G. A., Alves, C., & Magalhaes-Castro, B. (1984). Parasitism of trees by marmosets in a central Brazilian gallery forest. *Biotropica*, 16(3), 202–209.
- Lazaro-Perea, C. (2001). Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Animal Behaviour*, 62, 11–21.
- Leighton, M., & Leighton, D. R. (1982). The relationship of size of feeding aggregate to size of food patch: Howler monkeys (*Alouatta palliata*) feeding in trichilia cipo fruit trees on Barro Colorado Island. *Biotropica*, 14, 81–90.
- Leite, E. J. (2001). Spatial distribution patterns of riverine forest taxa in Brasília, Brazil. *Forest Ecology and Management*, 140(2–3), 257–264.
- Maier, W. C., Alonso, C., & Langguth, A. (1982). Field observations on *Callithrix jacchus jacchus* L. *Zeitschrift für Säugetierkunde*, 47, 334–346.
- Malhado, A. C., & Petrere, M. (2004). Behaviour of dispersion indices in pattern detection of a population of angico, *Anadenanthera peregrina* (Leguminosae). *Brazilian Journal of Biology*, 64(2), 243–249.
- Melo, L.C.O. (2001). *Seleção de recursos alimentares por Callithrix jacchus – sagui-do-nordeste: Um foco sobre a teoria de otimização*. Master's thesis, Brazil: Universidade Federal de Pernambuco.
- Mendes Pontes, A., & Monteiro da Cruz, M. (1995). Home range, intergroup transfers, and reproductive status of common marmosets *Callithrix jacchus* in a forest fragment in north-eastern Brazil. *Primates*, 36(3), 335–347.
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys – test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, 114(3), 362–378.
- Monteiro da Cruz, M.A. (1998). *Dinâmica Reprodutiva em uma População de Sagui-do-Nordeste (Callithrix jacchus) na Estação Ecológica do Tapacurá, Pernambuco*. Ph.D. thesis, Brazil: Universidade de São Paulo.
- Nash, L. T. (1986). Dietary, behavioral, and morphological aspects of gummivory in primates. *American Journal of Physical Anthropology*, 29(S7), 113–137.
- Oates, J. F. (1987). Food distribution and foraging behavior. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 197–209). Chicago: University of Chicago Press.
- Oates, J. F. (1994). The natural history of African colobines. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour, and evolution* (pp. 75–128). Cambridge: Cambridge University Press.
- Power, M. L. (1996). The other side of callitrichine gummivory: Digestibility and nutritional value. In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of Neotropical primates* (pp. 97–110). New York: Plenum Press.
- Pruetz, J. D., & Isbell, L. A. (2000). Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioral Ecology and Sociobiology*, 49(1), 38–47.
- Rasmussen, D. (1980). Clumping and consistency in primates' patterns of range use: Definitions, sampling, assessment and applications. *Folia Primatologica*, 34(1–2), 111–139.
- Reeve, H. K., & Hölldobler, B. (2007). The emergence of a superorganism through intergroup competition. *Proceedings of the National Academy of Sciences of the USA*, 104(23), 9736–9740.
- Ripley, B. D. (1977). Modelling spatial patterns. *Journal of the Royal Statistical Society B (Methodological)*, 39(2), 172–212.
- Rylands, A. B. (1984). Exudate-eating and tree-gouging by marmosets (Callitrichidae, Primates). In A. C. Chadwick & S. L. Sutton (Eds.), *Tropical rain forest: The Leeds Symposium* (pp. 155–168). Leeds: Leeds Philosophical and Literary Society.
- Rylands, A. B. (1986). Ranging behaviour and habitat preference of a wild marmoset group, *Callithrix humeralifer* (Callitrichidae, Primates). *Journal of Zoology*, 210(4), 489–514.

- Rylands, A. B. (1987). Primate communities in Amazonian forests: Their habitats and food resources. *Cellular and Molecular Life Sciences*, 43(3), 265–279.
- Rylands, A. B., & de Faria, D. S. (1993). Habitats, feeding ecology, and home range size in the genus *Callithrix*. In A. B. Rylands (Ed.), *Marmosets and tamarins: Systematics, behaviour, and ecology* (pp. 262–272). Oxford: Oxford University Press.
- Scanlon, C., Chalmers, N., & Monteiro da Cruz, M. (1988). Changes in the size, composition, and reproductive condition of wild marmoset groups (*Callithrix jacchus jacchus*) in northeast Brazil. *Primates*, 29(3), 295–305.
- Scanlon, C., Chalmers, N., & Monteiro da Cruz, M. (1989). Home range use and the exploitation of gum in the marmoset *Callithrix jacchus jacchus*. *International Journal of Primatology*, 10(2), 123–136.
- Seidler, T. G., & Plotkin, J. B. (2006). Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, 4(11), 2132–2137.
- Shopland, J. M. (1987). Food quality, spatial deployment, and the intensity of feeding interference in yellow baboons (*Papio cynocephalus*). *Behavioral Ecology and Sociobiology*, 21(3), 149–156.
- Slobodchikoff, C. N. (1984). Resources and the evolution of social behavior. In P. W. Price, C. N. Slobodchikoff, & S. W. Guad (Eds.), *A new ecology: Novel approaches to integrative systems* (pp. 227–251). New York: John Wiley & Sons.
- Smith, A. C. (2000). Composition and proposed nutritional importance of exudates eaten by saddleback (*Saguinus fuscicollis*) and mustached (*Saguinus mystax*) tamarins. *International Journal of Primatology*, 21(1), 69–83.
- Smith, A. C. (2010). Exudativory in primates: Interspecific patterns. In A. M. Burrows & L. T. Nash (Eds.), *The evolution of exudativory in primates* (pp. 45–87). New York: Springer.
- Snaith, T. V., & Chapman, C. A. (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Ptilocolobus tephrosceles*). *Behavioral Ecology and Sociobiology*, 59(2), 185–190.
- Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evolutionary Anthropology: Issues, News, and Reviews*, 16(3), 94–106.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291–309.
- Stevenson, M. F., & Rylands, A. B. (1988). The marmosets, genus *Callithrix*. In R. A. Mittermeier, A. B. Rylands, & A. F. Coimbra-Filho (Eds.), *Ecology and behavior of Neotropical primates* (pp. Vol. II, pp. 131–177). Washington, DC: World Wildlife Fund.
- Strier, K. B. (1989). Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). *Folia Primatologica*, 52(1–2), 70–77.
- Sussman, R. W., & Garber, P. A. (2007). Cooperation and competition in primate social interactions. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 636–651). New York: Oxford University Press.
- Sussman, R. W., & Garber, P. A. (2011). Cooperation, collective action, and competition in primate social interactions. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 587–598). New York: Oxford University Press.
- Teaford, M. F., Lucas, P. W., Ungar, P. S., & Glander, K. E. (2006). Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology*, 129(1), 99–104.
- Travis, S. E., & Slobodchikoff, C. N. (1993). Effects of food resource distribution on the social system of Gunnison's prairie dog (*Cynomys gunnisoni*). *Canadian Journal of Zoology*, 71(6), 1186–1192.
- Tsuji, Y., & Takatsuki, S. (2004). Food habits and home range use of Japanese macaques on an island inhabited by deer. *Ecological Research*, 19(4), 381–388.
- Tuomisto, H., Ruokolainen, K., & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299(5604), 241–244.
- van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87(1–2), 120–144.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 195–218). Oxford: Blackwell.
- Vasiliauskas, R. (1998). Patterns of wounding and decay in stems of *Quercus robur* due to bark peeling. *Scandinavian Journal of Forest Research*, 13(1–4), 437–441.
- Vasudev, D., Kumar, A., & Sinha, A. (2008). Resource distribution and group size in the common langur *Semnopithecus entellus* in southern India. *American Journal of Primatology*, 70(7), 680–689.

- Vilela, S. L., & de Faria, D. S. (2004). Seasonality of the activity pattern of *Callithrix penicillata* (Primates, Callitrichidae) in the cerrado (scrub savanna vegetation). *Brazilian Journal of Biology*, *64*(2), 363–370.
- Vinyard, C. J., Wall, C. E., Williams, S. H., Mork, A. L., Armfield, B. A., Melo, L. C. O., Valença-Montenegro, M. M., Valle, Y. B. M., Oliveira, M. A. B., Lucas, P. W., Schmitt, D., Taylor, A. B., & Hylander, W. L. (2009). The evolutionary morphology of tree gouging in marmosets. In S. M. Ford, L. M. Porter, & L. C. Davis (Eds.), *The smallest anthropoids* (pp. 395–409). New York: Springer.
- Waser, P. M. (1981). Sociality or territorial defense? The influence of resource renewal. *Behavioral Ecology and Sociobiology*, *8*(3), 231–237.
- Waser, P. M., & Waser, M. S. (1985). *Ichneumia alhicauda* and the evolution of viverrid gregariousness. *Zeitschrift für Tierpsychologie*, *68*(2), 137–151.
- Welch, D., Scott, D., & Staines, B. W. (1997). Bark stripping damage by red deer in a sitka spruce forest in western Scotland III. Trends in wound condition. *Forestry*, *70*(2), 113–120.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262–299.
- Youlatos, D. (2009). Locomotion, postures, and habitat use by pygmy marmosets (*Cebuella pygmaea*). In S. M. Ford, L. M. Porter, & L. C. Davis (Eds.), *The smallest anthropoids* (pp. 279–297). New York: Springer.