TITLE

High density of white-faced capuchins (*Cebus capucinus*) and habitat quality in the
Taboga Forest of Costa Rica

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Capuchin density in the Taboga Forest

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ABSTRACT

Across the globe, primate species and habitats are threatened by human activity. This is especially true for species found in tropical dry forests, which are widely distributed and comprise diverse habitats that remain largely unprotected. Evidence suggests that some primate species endemic to tropical dry forests may be more sensitive to anthropogenic disturbance than others, but our ability to predict primate abundance in the face of disturbance also depends on the specific variables for each site. Here, we consider the factors that explain the high density of white-faced capuchins (*Cebus capucinus*) found in the Taboga Forest, Costa Rica, a relatively small fragment of tropical dry forest surrounded by agricultural fields. Our analyses suggest that, for capuchins (and potentially for mantled howler monkeys, *Alouatta palliata*), the size and disturbance of a forest fragment may matter less than the composition and availability of key resources, like above-ground water. Group sightings for both species were higher near permanent water sources, but group sightings did not vary between edge and interior forest. These findings help explain why some primate species can flourish even alongside anthropogenic disturbance and thus carry important implications for conservation efforts. Smaller forest fragments, like Taboga, may be able to support high densities of some species because they provide a mosaic of habitats and key resources that buffer adverse ecological conditions. Future studies will assess the extent to which primates in the Taboga Forest rely on the canals versus the river and will consider how the high density of capuchins in Taboga influences ranging patterns, home range overlap, and the frequency and intensity of intergroup encounters.

KEYWORDS

Conservation, edge effect, fragmentation, tropical dry forest, *Cebus imitator*

RESEARCH HIGHLIGHTS

- Here we introduce a new white-faced capuchin study site in the Taboga Forest, Costa Rica, a fragmented tropical dry forest.
- Forest fragments like Taboga may support high primate densities because they provide a mosaic of habitats and key resources.

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INTRODUCTION

The majority of primate species across the globe are either under threat of extinction or experiencing population declines (Estrada et al., 2018). Non-human primate densities tend to decrease in unprotected areas, yet non-human primates (hereafter, “primates”) can nevertheless still flourish in areas of human activity, suggesting both a vulnerability and a resilience to anthropogenic disturbance (Cavada, Barelli, Ciolli, & Rovero, 2016). Some human activities (e.g., those contributing to climate change) tend to be more disruptive than others (e.g., habitat fragmentation), but different primate species also exhibit differential responses to each threat. Some species show remarkable behavioral flexibility and quickly adjust to new habitats, while others get pushed closer to extinction (Kulp & Heymann, 2015; Laurance et al., 2007; Ries, Fletcher, Battin, & Sisk, 2004). This variation is likely due to a number of factors, from species-specific characteristics (i.e., dietary breadth) to habitat characteristics (i.e., species richness). For example, in Bornean forests tree density predicts primate species richness much better than the degree of habitat disturbance does (Bernard et al., 2016). Understanding how species and habitat characteristics together contribute to resilience is critical for effective conservation efforts.

One key primate habitat that remains relatively understudied is the tropical dry forest. Tropical dry forests are widely distributed and diverse habitats that simultaneously support a number of endemic species while also experiencing significant anthropogenic disturbance (Dryflor et al., 2016; Miles et al., 2006). Despite warnings about the vulnerability of these habitats (e.g., Janzen, 1988), tropical dry forests worldwide remain

unprotected and understudied (Dexter et al., 2018). For example, over 90% of the tropical dry forests in North and Central America are vulnerable to anthropogenic disturbance (Miles et al., 2006). However, a variety of primate species are found in tropical dry forests, with some even continuing to flourish in fragments. Most notably, white-faced capuchins (*Cebus capucinus*), howler monkeys (*Alouatta palliata*), and spider monkeys (*Ateles geoffroyi*) are common sympatric species, yet they demonstrate markedly divergent responses to fragmentation and other forms of anthropogenic disturbance (e.g., Williams-Guillén, Hagell, Otterstrom, Spehar, & Gómez, 2013).

Understanding how different species respond to anthropogenic disturbance has important implications for conservation and reforestation efforts. This is especially true when it comes to tropical dry forests, which were once the predominant forest type on the west coast of Central America (Gillespie, Grijalva, & Farris, 2000). While spider monkeys are rarely found in small fragments (instead requiring large territories to support their frugivorous diet: Williams-Guillén et al., 2013), both capuchins and howlers can thrive there. As large-bodied omnivores, capuchins, in particular, can opportunistically exploit a broad array of plants and animals (Ford & Davis, 1992; Rose, 1994; Panger et al., 2002; Perry 2012) and can adapt to anthropogenic disturbances that threaten many other species (i.e., showing neutral or even positive edge effects: Bolt et al., 2018 [*C. capucinus*]; surviving in fragmented habitats: Lins & Ferreira, 2019 [*Sapajus flavius*]; Cunha, Vieira, & Grelle, 2006 [*C. sp.*]). However, certain factors may constrain capuchin densities. For example, low capuchin densities in Nicaraguan forest fragments have been attributed to human hunting, poaching, and the pet trade

(Williams-Guillén et al., 2013). In addition, capuchin populations in dry forests, where rainfall is scarce for months at a time, may be constrained by access to reliable above-ground water (Fedigan & Jack, 2001). Howler monkeys, in contrast, may be less reliant on above-ground water sources because of the high water content in the leaves in their diet (Fedigan & Jack, 2001). Moreover, howlers are expected to do well in disturbed habitats in general, and data tend to support this (i.e., showing neutral or positive edge effects: Bolt et al., 2018 [*A. palliata*]; Lenz, Jack, & Spironello, 2014 [*A. macconelli*]; surviving in fragmented habitats: Asensio, Arroyo-Rodríguez, Dunn, & Cristóbal-Azkarate, 2009 [*A. palliata mexicana*]; Boyle & Smith, 2010 [*A. macconelli*]). Despite this resilience under certain circumstances howler monkeys can still be negatively impacted by fragmentation (Arroyo-Rodríguez & Dias, 2010; Horwich, 1998). For example, a 1976 census of howlers at Taboga suggested that the population was in decline, if not at a nadir (Heltne, Turner, & Scott, 1976).

Here, we studied plant and wildlife abundance in the Taboga Forest (hereafter, “Taboga”) of Costa Rica. Taboga presents an ideal opportunity to understand primate abundance in relation to habitat quality for a number of reasons. First, the Taboga Forest has an extremely high density of capuchins compared to other forests in the region (see Table 2). Second, the forest is relatively small (516 hectares) and irregularly shaped with a high proportion of edge to interior (almost 40%: Fig. 1). Third, the forest is dissected by a series of canals used in irrigation and has been completely surrounded by sugar cane and rice farmland for decades. Therefore, we are able to look at the long-term impacts of two types of human disturbance: habitat fragmentation and year-round,

artificial water sources. This is particularly important because Taboga is a tropical dry forest, where the dry season would normally limit the viability of many fauna that depend on above-ground water.

One of our primary goals is to estimate the density of white-faced capuchins in the forest (as well as the mantled howlers to serve as a comparison species). Specifically, we address the following questions: (1) What is the density of capuchins in Taboga, and how does this compare to other long-term sites with white-faced capuchins? To answer this, we first compare group size and home range size of known groups across long-term capuchin sites. (2) Does the large amount of edge habitat contribute to capuchin abundance at Taboga? To answer this, we next compare the plant composition of edge and interior forest. We predict higher species richness, mean diameter at breast height (DBH), and canopy coverage in interior compared to edge forest (Bolt et al., 2018). Third, we expect to find significant seasonal effects on canopy coverage, with lower coverage during the dry season. However, because capuchins have been shown to have neutral or even positive edge effects (e.g., Bolt et al., 2018), we expect to find no significant differences in species richness and mean DBH for tree species associated with capuchins (i.e., that capuchins use for food or fur-rubbing). Fourth, because of the long-term anthropogenic disturbance around Taboga, we expect to find significant differences in the species richness and DBH for indicator tree species associated with the first stage of forest succession in tropical dry forests (Kalacska et al., 2004).

Finally, we ask: (3) Do forest characteristics differentially affect capuchin as compared to howler abundance? We expect that both howler and capuchin monkeys will show neutral edge effects (Bolt et al., 2018). However, because Taboga is a tropical dry forest, we expect to find higher primate abundance within 100 m of reliable water sources (i.e., rivers and large canals), but this should mainly apply to capuchin groups, as howler monkeys are less dependent on above-ground water (Fedigan & Jack, 2001).

METHODS

Study site and subjects

We conducted this study at the Capuchins at Taboga research site, established in June 2017 in la Reserva Forestal Taboga (the Taboga Forest Reserve; i.e., Taboga) in Guanacaste province, Costa Rica. The reserve was established in 1978 and contains 296 hectares of largely tropical dry forest (~3 x 4 km), representing an important piece of the fragmented biological corridor connecting the Guanacaste Mountains to the Tempisque River Basin (Fig. 1). The Universidad Técnica Nacional (UTN) of Costa Rica operates an experimental farm of 702 hectares that encompasses the reserve along with agricultural land. The UTN farm consists of irrigated land dedicated to the cultivation of sugarcane (100 hectares), rice (30 hectares), and grass for cattle (4.5 hectares). There is also a tilapia farm and research center as well as a water research laboratory. As such, Taboga is characterized by distinct forest edges (i.e., farm land and roads) as well as more transitional or “natural” forest edges (i.e., canals and rivers). The reserve is almost exclusively bordered by sugarcane and rice fields, aside from a 2 km perimeter that borders private forested land and 1 km bordering public forested land.

Figure 1. Location of the Taboga Forest in Costa Rica. The official Taboga Forest Reserve boundary is within this larger reserve held by the Universidad Técnica Nacional (see Fig. 3a). However, for simplicity, we refer to this entire area as the Taboga Forest or “Taboga”.

Taboga is largely characterized by seasonally dry tropical forest, a highly threatened ecosystem that features a closed canopy and seasonal deciduousness (Janzen, 1988; Miles et al., 2006). In addition to the dry forest, there are also riparian, semi-deciduous forests around the river and a palm forest dominated by the native species *Attalea rostrata*, part of which becomes inundated during the wet season. The area experiences two distinct seasons (Fig. 2): a hot, dry season from Nov-Apr (mean daily maximum temperature = 35.38 °C +/- 0.20 SE; mean daily rainfall = 0.66 mm +/- 0.27 SE) and a cooler wet season from May-Oct (mean daily maximum temperature = 32.57 °C +/- 0.21

SE; mean daily rainfall = 8.93 mm +/- 1.09 SE). Mean daily minimum temperatures remain consistent throughout the year (dry season: 26.25 °C +/- 0.10 SE; wet season: 25.46 °C +/- 0.11 SE). The river provides fresh water year-round and many of the canals used by the UTN farm for irrigation are consistently full during the dry season (Fig. 3C).

Figure 2. Temperature (black triangles) and rainfall (grey boxes) data from the Taboga Forest from Jul 2017 - May 2019. Numbers along the x-axis indicate the number of days of weather data measured per month.

The Capuchins at Taboga research project (directed by Thore Bergman, Jacinta Beehner, Marcela Benítez, Elizabeth Tinsley Johnson) is focused on the behavioral biology, endocrinology, and cognition of wild white-faced capuchins (*C. capucinus*). Note that the taxonomy of Central American capuchins is in flux and some authors refer to Costa Rican capuchins as *C. capucinus imitator* (Ruiz-Garcia et al., 2012; Lynch Alfaro et al., 2014; Melin et al., 2017; Hogan et al., 2018). However, we prefer the more general name *C. capucinus* because the defining feature of the capuchins first described as “imitator” is a frontal tuft in females, something that is clearly absent in our populations (Thomas, 1903). Our research group has identified at least 12 distinct capuchin groups in the reserve since July 2017. We collect GPS data on group movements and behavioral data on three of these groups (“Tenori”, “Mesas”, and “Palmas”), including regular group scans (all groups) and weekly focal follows of each individual (in Tenori group and some individuals in Mesas group). Whenever possible, groups are followed from their morning sleeping site to their evening sleeping site. The Tenori group is entirely habituated to observers on foot, and the Mesas and Palmas groups are mostly habituated. These three groups range in size from 16 (Mesas) to 17 (Tenori) to 36 individuals (Palmas). The breakdown of age / sex categories can be found in Table 1.

218

Table 1. Group size and composition for three habituated white-faced capuchin groups

Group	Adult males	Adult females	Subadults and juveniles	Infants	Total
Mesas	2	4	6	4	16
Tenori	3	4	7	3	17
Palmas	5	8	12	4	29

219

220

221 *Ranging data*

222 We collected ranging data for three capuchin groups (Tenori, Mesas, and Palmas)
 223 between Jan 2018 and Apr 2019 (Fig. 3d). We spent a total of 1482 hours (220
 224 observation days) with Tenori, 481 hours (72 days) with Mesas, and 486 hours (81
 225 days) with Palmas. Observers recorded group locations on handheld GPS units
 226 (Garmin eTrex 10 and 20) using the “track” function, which marks a point every 10 m or
 227 10 sec, whichever comes first. When observers lost sight of their group they turned the
 228 track function off. Location data were uploaded to Google Earth Pro version 7.3.2.5776
 229 (Google LLC 2019) and used to create convex polygons encompassing each group’s
 230 home range. All three group range polygons contained areas not traversed by the
 231 monkeys (agricultural fields, buildings, and cattle pasture) that were excluded from the
 232 polygon area measures (Di Bitetti, 2001). The river area was conserved in ranging area,
 233 as canopy cover is generally continuous over the river and the capuchins crossed it
 234 freely.

235

236 *Vegetation survey*

237 From Jul-Nov 2018 (wet season), we conducted a vegetation survey of the reserve to
 238 examine edge and interior forest habitats (Fig 3b-c). Edge forest was defined as forest
 239 within 100 m of a forest boundary (following (Bolt et al., 2018). Edges in this forest were
 240 created by agricultural and cattle pasture fields, land cleared for buildings, and various
 241 roads that traverse the reserve. Transects were dispersed randomly within edge (n =
 242 20) and interior (n = 20) forest using a random number generator selecting numbers
 243 associated with points on a grid overlaid on a map of Taboga. Each 50 m transect was
 244 walked in a random direction selected by a spin of a compass bezel. If the direction
 245 selected did not allow for a full 50 m transect, then the opposite direction was chosen.

246

247 Along each transect and within 2.5 m of either side of the transect, we recorded the
 248 species and diameter at breast height (DBH) of every tree with a circumference at
 249 breast height >10 cm (FAO, 2004). We recorded canopy coverage on a scale from 1-4
 250 (1 = 1-25% coverage; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%) every meter along the
 251 transect line, first during the wet season (Jul-Nov 2018) and again during the dry
 252 season (Mar-Apr 2019).

253

254 For each transect, we calculated the following: mean DBH, mean canopy cover (wet
 255 and dry season), density (trees/m²), species richness (S, i.e., the number of tree
 256 species), and Shannon's Diversity Index (H, which accounts for both species richness
 257 and the distribution of individuals across the species represented in the sample:

Shannon & Weaver, 1949; Spellerberg, 2005). To determine whether forest edges contained more resources for capuchins and to quantify the stage of forest regeneration seen along the edges, we also categorized tree species into two groups: (1) those used by capuchins for foraging or fur rubbing, and (2) those characteristic of the early stage of successional forests (following Kalacska et al., 2004); see Table S1). Then, for each group (edge vs. interior), we calculated mean DBH, density, species richness, and Shannon's Diversity Index.

Finally, for ease of comparison across sites, we calculated overall mean Shannon's diversity index and Shannon's equitability (J' , i.e., the distribution of individuals across the species in a sample: DeJong, 1975; Pielou, 1969). Shannon's equitability ranges from 0-1, with 0 indicating an uneven distribution and 1 an equitable distribution of species (DeJong, 1975; Pielou, 1969; see Table S2).

Vegetation survey analyses

First, we examined whether there were vegetation differences between edge and interior forest types. Because our data were not normally distributed, we used Mann-Whitney U tests to compare edge and interior transects with respect to mean DBH, density (trees/m²), species richness (S), and Shannon's Diversity Index (H). Identical comparisons were conducted: (1) after restricting species to those used by capuchins for foraging and locomotion, and (2) after restricting species to those characteristic of the early stage of successional dry forests (Kalacska et al., 2004; see Table S1). Second, to test whether canopy cover varied between edge and interior forest and/or if

canopy cover changed seasonally, we fit a linear mixed model with transect location (edge or interior), season (wet or dry), and the interaction between the two as fixed effects. We controlled for transect number as a random effect and log transformed canopy cover as the dependent variable.

Primate survey

Between Feb-Apr 2019, we conducted a primate population survey using 32 line transects comprising pre-existing roads and paths (i.e., along canals or firebreaks) and a network of trails created by the project (19 cut trails total, each at least 0.2 km apart; Fig. 3b). Transect lengths ranged from 0.2 km to 2.2 km and we walked most transects twice (once in the morning between 6:00-10:00 and once in the afternoon between 14:00-16:00), each time in an alternate cardinal direction, for a total of 55 km in transects. Three transects were only walked once due to lack of maintenance. Transects were not surveyed when it was raining.

Transects were walked by teams of observers (typically 2 and no more than 5), traveling at a speed of 1.5 km/h and stopping every 100 m for 2 min of detailed observation (Bolt et al., 2018; Pruetz & Leason, 2002). When more than one team searched on the same day, teams walked transects that were more than 0.2 km apart to avoid double-counting primate groups. Upon encountering a primate group (defined here as sighting one or more individuals), observers recorded the time of day, primate species, and location (using a Garmin eTrex 10 or 20 handheld GPS unit). Observers paused for 10 min to

count individuals of each age/sex class, when possible, and then returned to the transect.

Primate survey analyses

We then determined whether observations of primate groups were more likely in different forest type (i.e., edge vs. interior; Fig. 3c) or proximity to a permanent water source (i.e., <100 m vs. >100 m; Fig. 3c). For each species of monkey (i.e., capuchins, howlers), we fit a generalized linear mixed model where the dependent variable was the number of observations of primate groups for each species. We assumed the number of encounters on each transect followed a Poisson distribution whose log mean depended on forest type and proximity to water as fixed effects and transect number as a random effect. We also added a constant offset term to each model to account for different research effort on transects of different lengths.

We fit all the models with the lme4 package (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2016; RStudio Team, 2016). Figures were created using the ggplot2 package (Wickham, 2009).

Figure 3a-d. Maps of (a) the UTN Estate and the Taboga Forest Reserve (together, the “Taboga Forest”), with overlays displaying: (b) both primate and vegetation transect locations, (c) 0.1 km buffer zones for forest edges and year-round water sources, and (d) home ranges for three groups of wild white-faced capuchins.

RESULTS

Capuchin density and home range size

The density of capuchins in the Taboga Forest is higher than that reported from all other long-term white-faced capuchin sites (Table 2). This high density emerges whether we use the mean group and homerange size from individual groups (21.65 individuals / km²) or the total population and total useable area (36.17 individuals / km²). For other

sites, the group-based estimates range from 7.97-12.93 individuals / km²; and the total population-based estimates range from 5.60-20.00 individuals / km² (Table 2).

Therefore, with the exception of BCI, the Taboga population is 2-6 times more dense than other white-faced capuchin sites. Moreover, we believe the total estimate from the Taboga Forest is a conservative estimate because we suspect that several capuchin groups were not censused during our primate surveys (the forest continues into private land that we are not allowed to survey). We estimate that there are three additional capuchin groups here that also range into the Taboga Forest.

With respect to our habituated groups, Tenori had the smallest range size (60.5 ha, 70% of which was “edge” habitat) in comparison with Mesas (129.4 ha, 60% edge) and Palmas (102.1 ha, 57% edge) groups (Fig. 3d). We do not yet have accurate estimates of how much our capuchin groups overlap. We will soon have data from another group (Escameka group) that overlaps with the Mesas group, providing us with two points of overlap (Tenori and Palmas groups, and Mesas and Escameka groups).

Table 2. Group size and density comparison for this ("Taboga") and other white-faced capuchin sites.

Site	Description	Individuals	km2	Individuals / km2	Source
Lomas	Mean (3 groups)	29.00	3.64	7.97	Vogel, 2004
Lomas	Total population	216.00	36.99	5.84	Perry, pers comm
Palo Verde	Total population	-	-	9.40	Panger et al., 2002
Santa Rosa	Mean (7 groups)	20.10	1.98	10.15	Campos et al. 2014, Fedigan & Jack 2012
Santa Rosa	Total population	673.00	57.70	11.66	Campos, pers comm
BCI	Mean (4 groups)	15.00	1.16	12.93	Crofoot, 2007
BCI	Total population	300.00	15.00	20.00	Crofoot, 2007
BCI (after 2010 crash)	Total population	84.00	15.00	5.60	Milton & Giacalone, 2014
Taboga	Mean (3 groups)	21.00	0.97	21.65	Tinsley Johnson et al., this publication
Taboga	Total population	187.00	5.17	36.17	Tinsley Johnson et al., this publication

Vegetation survey

Contrary to our predictions, we found no significant differences in the interior and in the edge for mean tree DBH (Mann Whitney U; $U = 185.5$, $p = 0.70$; Table 3), mean tree species richness ($U = 234.5$, $p = 0.37$; Table 3), mean tree density ($U = 203.5$, $p = 0.94$; Table 3), or Shannon's Diversity Index ($U = 244$, $p = 0.24$; Table 3). In comparing just trees used by capuchins, we again found no significant differences due to transect location for mean tree DBH (Mann Whitney U; $U = 185$, $p = 0.70$; Table 3), mean tree species richness ($U = 264.5$, $p = 0.08$; Table 3), mean tree density ($U = 241$, $p = 0.27$; Table 3), or Shannon's Diversity Index ($U = 264$, $p = 0.09$; Table 3). For indicator trees, we found that trees on the edge had a significantly greater DBH than indicator trees in the interior (Mann-Whitney U; $U = 274$, $p = 0.046$; Table 3). We found no difference between edge and interior forest for mean indicator species richness ($U = 144.5$, $p =$

0.132; Table 3), mean tree density ($U = 234.5$, $p = 0.36$; Table 3), or Shannon's Diversity Index ($U = 153$, $p = 0.20$; Table 3).

Table 3. Mean $\pm$ standard error of vegetation measures in the edge and interior of all trees, monkey food trees, and indicator tree species. Bold indicates significant differences between edge and interior, * denotes $p < 0.05$.

	Overall		Monkey Food Trees		Indicator Trees	
	Edge	Interior	Edge	Interior	Edge	Interior
DBH (cm)	12.53 $\pm$ 1.31	14.30 $\pm$ 1.72	12.85 $\pm$ 1.31	15.23 $\pm$ 1.96	16.21 $\pm$ 1.55	11.30 $\pm$ 1.72 *
Density (trees/m²)	0.13 $\pm$ 0.01	0.15 $\pm$ 0.03	0.08 $\pm$ 0.01	0.07 $\pm$ 0.04	0.03 $\pm$ 0.01	0.08 $\pm$ 0.03
Richness	12.30 $\pm$ 1.01	11.15 $\pm$ 1.23	7.40 $\pm$ 0.61	6.90 $\pm$ 1.50	3.00 $\pm$ 0.61	4.45 $\pm$ 0.72
Diversity index (H)	2.10 $\pm$ 0.11	1.89 $\pm$ 0.14	1.65 $\pm$ 0.12	1.34 $\pm$ 0.13	0.67 $\pm$ 0.15	0.99 $\pm$ 0.17

We found that in the dry season, interior transects had significantly less canopy cover than edge transects (Interior x Wet season; Beta = 0.42, SE = 0.17, $p = 0.020$). We found that there was more canopy coverage in the wet season months than in the dry season (GLM; Wet Season, Beta = 0.31, SE = 0.12, $p = 0.014$). We also found a significant effect of edge over the interior (Interior, Beta = -0.44, SE = 0.13, $p = 0.001$; Fig. 4). In other words, the edge forest is able to better maintain its canopy cover throughout the dry season, while the interior forest does not, following a typical deciduous pattern where trees lose their leaves during the dry season.

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Figure 4. Mean canopy cover score ($\pm$ standard error) across season and transect type.

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380

381 *Population survey*

382 As predicted, both capuchins and howlers showed neutral edge effects (i.e., no
383 significant difference between group encounter rates in edge vs. interior forest).

384 Capuchin encounter rates were lower overall (compared to howler encounters) and did
385 not differ between edge (0.34 groups/km; CI: -2.10, 0.48) and interior forest (0.46
386 groups/km; CI: -0.48, 2.10; $p = 0.25$; Fig. 5a). Although there was a higher encounter
387 rate for howlers in edge (1.31 groups/km; CI: -0.38, 0.85) compared to interior forest
388 (0.75 groups/km; CI: -0.85, 0.38; Fig. 5c), this difference was not significant ($p = 0.43$).

389

As predicted, capuchin group encounters were higher near permanent water sources (i.e., the river or large canals: 0.78 groups/km; CI: 1.42, 4.41) compared to farther from water (0.15 groups/km; CI: -4.41, -1.42; $p = 1.73 \times 10^{-4}$; Fig. 5b). Contrary to our predictions, however, howler group encounter rates were also significantly higher near water sources (1.69 groups/km; CI: 0.42, 1.72) compared to farther from water (0.57 groups/km; CI: -1.72, -0.42; $p = 1.24 \times 10^{-3}$; Fig. 5d).

Figure 5a-d. Mean group encounter rate (groups/km walked $\pm$ standard error) by forest type in Taboga. **(a)** capuchin groups in edge and interior forest; **(b)** capuchin groups near (<0.01 km) or far (>0.01 km) from a permanent water source; **(c)** howler groups in edge and interior forest; **(d)** howler groups near and far from a permanent water source.

DISCUSSION

The Taboga Forest of Costa Rica has one of the highest densities of white-faced capuchins thus far recorded. Here, we asked whether specific features of the forest might allow these capuchins to survive and reproduce at such high densities. Our results suggest that the presence of reliable year-round water sources is critical for capuchins (and possibly for howlers) living in a seasonally dry habitat. For example, capuchins in Santa Rosa National Park (another tropical dry forest in Costa Rica) rely on a limited number of water holes during the dry season, and access to these water holes is thought to be the primary constraint on the capuchin population (Fedigan & Jack, 2001; Fedigan, Rose, & Avila, 1996, 1998). In contrast, Taboga has two types of year-round water supply: the river and a system of canals. We did not test whether forest characteristics varied significantly according to distance from water sources. However, because the canals have cement bottoms, we think that it is unlikely that the canals impact the surrounding flora all that much. We will implement future studies to test how forest characteristics vary with proximity to the river (and the associated riparian/semi-deciduous forest type). For example, riparian forests may contain certain fruiting trees central to the capuchin diet, overall larger trees due to year-round water supply, and/or year-round canopy cover. Our results also suggest that howlers at Taboga may be more dependent on permanent water sources than at other sites, as they were also frequently found near permanent water sources. However, this may have more to do with the forest subtype near the river (i.e., evergreen and riparian) than the need to drink water daily (Fedigan & Jack, 2001).

In line with previous research that found neutral edge effects for both species (e.g., (Bolt et al., 2018), we found no difference between capuchin (or howler) group encounter rates when we compared edge vs. interior forest. Combined with the overall high capuchin population density, this suggests that despite a large percentage of edge forest (nearly 40% of the 516 hectares), capuchins appear to thrive in forest fragments (Cunha et al., 2006). Indeed, we found that capuchins were equally likely to find staple food and fur-rubbing species in the edge compared to the interior forest and that the size of these staple species (i.e., DBH) did not vary significantly between edge and interior. Other features of the forest, like canopy height (Fleagle & Mittermeier, 1980) and canopy cover (Fedigan & Jack, 2001) have been useful in explaining forest use by other primate taxa. Although we did not record canopy height in this study, we found that the DBH for our trees did not differ from the edge to the interior. Canopy cover showed a very different pattern though. The edge forest in Taboga maintained canopy cover even throughout the dry season, while the interior forest was more deciduous (we expand on possible reasons for this below). For primates, semi-evergreen forest can provide shade and may stay cooler through the hottest months (Fedigan & Jack, 2001; Fedigan et al., 1996), and therefore both capuchins and howlers might spend more time in edge forest during the dry season (when our primate survey took place) than they do during the wet season. Longitudinal data will determine whether ranging patterns vary seasonally.

Together, our data suggest that the difference between edge and interior forest at Taboga is less than that from other sites (e.g., Arroyo-Rodríguez & Mandujano, 2009;

Bolt et al., 2018; Harris, 1988; Lehman, Rajaonson, & Day, 2006; Saunders, Hobbs, & Margules, 1991). This may be because the initial anthropogenic disturbance (i.e., creation of pastures and croplands around the reserve) happened some time ago and the forest is actually in the intermediate stages of regeneration (Kalacska et al., 2004). Three lines of evidence support this hypothesis. First, both edge and interior forest at Taboga exhibit high species richness and diversity, which also characterize intermediate tropical dry forest succession at nearby Santa Rosa (Kalacska et al., 2004). Second, tree species that characterize the first stage of tropical dry forest succession (of which many remain through stages 2 & 3) are well-established in the forest edge. Specifically, these trees had a significantly higher mean DBH in edge forest compared to interior forest. Third, the early stages of dry forest succession are characterized by a high percentage of deciduous trees (Kalacska et al., 2004). Yet, we found that the edge forest in Taboga was semi-evergreen throughout the dry season. This, of course, raises the question of why the interior forest is more deciduous. It may be that the Taboga Forest is small enough that it lacks a true “interior” (Banks-Leite, Ewers, & Metzger, 2010), and therefore the entire forest represents different stages of regeneration. Alternatively, much of the interior forest is also more elevated and may lack year-round water sources. Finally, flood-irrigation of agricultural land during the dry season might spill-over into edge forests, thus allowing for year-round canopy maintenance.

Our survey indicates that the Taboga Forest is actually composed of at least three distinct forest types: (1) the deciduous tropical dry forest that extends from the North

boundary of the farm down to the river, (2) the riparian semi-deciduous forest that follows the river, and (3) a moist palm forest that retains canopy cover year-round. Future studies should distinguish between these subtypes to test how different microclimates alter edge effects. In addition, the severity of edge effects on forest composition can vary according to the type of disturbance (i.e., road, pastureland, sugar cane/rice plantation, etc.). Thus, the universal 100 m buffer used here may not apply equally to each forest type found in Taboga (Didham et al., 2015; Harper et al., 2005). For capuchins living in a highly seasonal environment, having distinct habitats may provide a buffer from extreme fluctuations in temperature and rainfall (indeed, preliminary data suggest group ranging varies significantly by forest type between seasons). For example, in 2010, a capuchin population crash on Barro Colorado Island was caused by unusually heavy rains that decimated the arthropod population (a key source of protein for capuchins) (Milton & Giacalone, 2014). In Taboga, the wet and evergreen forest may be less vulnerable to drought or El Niño events (e.g., Campos, Jack, & Fedigan, 2015), while the deciduous tropical dry forest may be less vulnerable to unusually heavy rains and flooding.

The abundance of the capuchins in Taboga has important implications for conservation efforts. For certain species, the size and disturbance of a forest fragment may matter less than the composition and availability of key resources, like above-ground water. Our analysis here adds to our understanding of factors that influence primate abundance, and also establishes Taboga as critical case study in tropical dry forest dynamics. Future studies will provide a more fine-grained analysis of the possible

491 interaction between edge effects, habitat type, and season, and how these factors
 492 influence primate sightings (Gogarten et al., 2012). For example, we were not able to
 493 test here whether primates prefer the river over human-made canals (or vice-versa),
 494 though we predict that howlers sightings may be more frequent along the river (i.e., that
 495 howlers prefer riverine habitat over others but do not necessarily need to be close to an
 496 above-ground water source). For capuchins, the next question is how the high density in
 497 Taboga influences ranging patterns, home range overlap, and the frequency and
 498 intensity of intergroup encounters (Perry, 1996; Perry 2012). Preliminary data suggest
 499 that intergroup encounters are higher at Taboga than at other sites, but that the intensity
 500 of such encounters is lower, which may represent a behavioral adaptation to frequent
 501 encounters.

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REFERENCES

- Arroyo-Rodríguez, V., & Dias, P. A. D. (2010). Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology*, 72(1):1-16.
- Arroyo-Rodríguez, V., & Mandujano, S. (2009). Conceptualization and measurement of habitat fragmentation from the primates' perspective. *International Journal of Primatology*, 30:497–514.
- Asensio, N., Arroyo-Rodríguez, V., Dunn, J. C., & Cristóbal-Azkarate, J. (2009). Conservation value of landscape supplementation for howler monkeys living in forest patches. *Biotropica*, 41(6):768-773.
- Banks-Leite, C., Ewers, R. M., & Metzger, J.-P. (2010). Edge effects as the principal cause of area effects on birds in fragmented secondary forest. *Oikos*, 119(6):918-926.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R., Singmann, H., & Others. (2015). Lme4: Linear mixed-effects models using Eigen and S4 (Version 1.1-7). 2014.
- Bernard, H., Bili, R., Matsuda, I., Hanya, G., Wearn, O. R., Wong, A., & Ahmad, A. H. (2016). Species richness and distribution of primates in disturbed and converted forest landscapes in Northern Borneo. *Tropical Conservation Science*, 9(4), 1940082916680104.
- Bolt, L. M., Schreier, A. L., Voss, K. A., Sheehan, E. A., Barrickman, N. L., Pryor, N. P., & Barton, M. C. (2018). The influence of anthropogenic edge effects on primate

525 populations and their habitat in a fragmented rainforest in Costa Rica. *Primates*,
526 59(3):301–311.

527 Boyle, S. A., & Smith, A. T. (2010). Can landscape and species characteristics predict
528 primate presence in forest fragments in the Brazilian Amazon? *Biological*
529 *Conservation*, 143(5):1134–1143.

530 Campos, F. A., Jack, K. M., & Fedigan, L. M. (2015). Local and global climate effects on
531 white-faced capuchin population growth and demography. *American Journal Of*
532 *Physical Anthropology*, 156:100.

533 Campos, F. A., Bergstrom, M. L., Childers, A., Hogan, J. D., Jack, K. M., Melin, A. D.,
534 Mosdossy, K. N., Myers, M. S., Parr, N. A., Sargeant, E., Schoof, V. A. M., &
535 Fedigan, L.M. (2014). Drivers of home range characteristics across
536 spatiotemporal scales in a Neotropical primate, *Cebus capucinus*. *Animal*
537 *Behaviour*, 91:93-109.

538 Cavada, N., Barelli, C., Ciolli, M., & Rovero, F. (2016). Primates in human-modified and
539 fragmented landscapes: The conservation relevance of modelling habitat and
540 disturbance factors in density estimation. *PloS One*, 11(2), e0148289.

541 Crofoot, M. C. (2007). Mating and feeding competition in white-faced capuchins (*Cebus*
542 *capucinus*): The importance of short- and long-term strategies. *Behaviour*,
543 144(12):143-1495.

544 Cunha, A. A., Vieira, M. V., & Grelle, C. E. V. (2006). Preliminary observations on
545 habitat, support use and diet in two non-native primates in an urban Atlantic
546 forest fragment: The capuchin monkey (*Cebus* sp.) and the common marmoset

547 (*Callithrix jacchus*) in the Tijuca forest, Rio de Janeiro. *Urban Ecosystems*,
548 9:351–359.

549 DeJong, T. M. (1975). A comparison of three diversity indices based on their
550 components of richness and evenness. *Oikos*, 26:222.

551 Dexter, K. G., Pennington, T., Oliveira-Filho, A. T., Bueno, M. L., Silva de Miranda, P.
552 L., & Neves, D. (2018). Inserting tropical dry forests into the discussion on biome
553 transitions in the tropics. *Frontiers in Ecology and Evolution*,
554 <https://doi.org/10.3389/fevo.2018.00104>

555 Di Bitetti, M. S. (2001). Home-range use by the tufted capuchin monkey (*Cebus apella*
556 *nigratus*) in a subtropical rainforest of Argentina. *Journal of Zoology*, 253(1):33–
557 45.

558 Didham, R. K., Barker, G. M., Bartlam, S., Deakin, E. L., Denmead, L. H., Fisk, L. M., ...
559 Schipper, L. A. (2015). Agricultural intensification exacerbates spillover effects on
560 soil biogeochemistry in adjacent forest remnants. *PloS One*, 10(1):e0116474.

561 Dryflor, K. B.-R., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-
562 Filho, A., Prado, D., ... Others. (2016). Plant diversity patterns and their
563 conservation implications in neotropical dry forests. *Science*, 353:1383–1387.

564 Estrada, A., Garber, P. A., Mittermeier, R. A., Wich, S., Gouveia, S., Dobrovolski, R., ...
565 Setiawan, A. (2018). Primates in peril: the significance of Brazil, Madagascar,
566 Indonesia and the Democratic Republic of the Congo for global primate
567 conservation. *PeerJ*, 6:e4869.

568 FAO. (2004). *National Forest Inventory Field Manual: Template*. Food and Agriculture
569 Organization (FAO) of the United Nations, Rome.

- 570 Fedigan, L. M., & Jack, K. (2001). Neotropical primates in a regenerating Costa Rican
571 dry forest: A comparison of howler and capuchin population patterns.
572 *International Journal of Primatology*, 22(5):689–713.
- 573 Fedigan, L. M. & Jack, K. M. (2012). Tracking neotropical monkeys in Santa Rosa:
574 Lessons from a generating Costa Rican dry forest. In: P. M. Kappeler & D. P.
575 Watts (Eds.), *Long-Term Field Studies of Primates*. Berlin: Springer-Verlag.
- 576 Fedigan, L. M., Rose, L. M., & Avila, R. M. (1996). See how they grow: tracking
577 capuchin monkey (*Cebus capucinus*) populations in a regenerating Costa Rican
578 dry forest. *Adaptive Radiations of Neotropical Primates*, 289–307.
- 579 Fedigan, L. M., Rose, L. M., & Avila, R. M. (1998). Growth of mantled howler groups in
580 a regenerating Costa Rican dry forest. *International Journal of Primatology*,
581 19(3):405–432.
- 582 Fleagle, J. G., & Mittermeier, R. A. (1980). Locomotor behavior, body size, and
583 comparative ecology of seven Surinam monkeys. *American Journal of Physical*
584 *Anthropology*, 52(3):301–314.
- 585 Ford, S. M., & Davis, L. C. (1992). Systematics and body size: implications for feeding
586 adaptations in New World monkeys. *American Journal of Physical Anthropology*,
587 88(4):415–468.
- 588 Gillespie, T. W., Grijalva, A., & Farris, C. N. (2000). Diversity, composition, and structure
589 of tropical dry forests in Central America. *Plant Ecology*, 147(1):37–47.
- 590 Gogarten, J. F., Brown, L. M., Chapman, C. A., Cords, M. A., Doran-Sheehy, D.,
591 Fedigan, L. M., Grine, F. E., Perry, S., Pusey, A. E., Sterck, E. H. M., Wich, S. A.,
592 & Wright, P. C. (2012). Seasonal mortality patterns in non-human primates:

593 Implications for variation in selection pressures across environments. *Evolution*,
594 66(10):3252-3266.

595 Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosfokske, K. D., Saunders, S.
596 C., ... Esseen, P.-A. (2005). Edge Influence on forest structure and composition
597 in fragmented landscapes. *Conservation Biology*, 19(3):768–782.

598 Harris, L. D. (1988). Edge effects and conservation of biotic diversity. *Conservation*
599 *Biology*, 2(4):330–332.

600 Heltne, P. G., Turner, D. C., & Scott, N. J., Jr. (1976). Comparison of census data on
601 *Alouatta villosa* (= *pallata*) from Costa Rica and Panama. In R. J. Thorington &
602 P. G. Heltne (Eds.), *Neotropical Primates: Field Studies and Conservation* (10-
603 19). Washington, D. C.: National Academy of Sciences.

604 Hogan, J. D., Fedigan, L. M., Hiramatsu, C., Kawamura, S., & Melin, A. D. (2018).
605 Trichromatic perception of flower colour improves resource detection among New
606 World monkeys. *Scientific Reports*, 8:10883.

607 Horwich, R. H. (1998). Effective Solutions for Howler Conservation. *International*
608 *Journal of Primatology*, 19(3), 579–598.

609 Janzen, D. H. (1988). Management of habitat fragments in a tropical dry forest: growth.
610 *Annals of the Missouri Botanical Garden*, 75(1):1-5-116.

611 Kalacska, M., Sanchez-Azofeifa, G. A., Calvo-Alvarado, J. C., Quesada, M., Rivard, B.,
612 & Janzen, D. H. (2004). Species composition, similarity and diversity in three
613 successional stages of a seasonally dry tropical forest. *Forest Ecology and*
614 *Management*, 200(1), 227–247.

- 615 Kulp, J., & Heymann, E. W. (2015). Ranging, activity budget, and diet composition of
616 red titi monkeys (*Callicebus cupreus*) in primary forest and forest edge. *Primates*,
617 56(3), 273–278.
- 618 Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ewers, R. M.,
619 Harms, K. E., ... Ribeiro, J. E. (2007). Habitat fragmentation, variable edge
620 effects, and the landscape-divergence hypothesis. *PloS One*, 2(10), e1017.
- 621 Lehman, S. M., Rajaonson, A., & Day, S. (2006). Edge Effects on the Density of
622 *Cheirogaleus major*. *International Journal of Primatology*, 27(6), 1569–1588.
- 623 Lenz, B. B., Jack, K. M., & Spironello, W. R. (2014). Edge effects in the primate
624 community of the biological dynamics of forest fragments project, Amazonas,
625 Brazil. *American Journal of Physical Anthropology*, 155:436–446.
- 626 Lins, P. G. A. de S., & Ferreira, R. G. (2019). Competition during sugarcane crop raiding
627 by blond capuchin monkeys (*Sapajus flavius*). *Primates*, 60(1), 81–91.
- 628 Lynch Alfaro, J. W., Izar, P., & Ferreira, R. G. (2014). Capuchin monkey research
629 priorities and urgent issues. *American Journal of Primatology*, 76:705-720.
- 630 Melin, A. D., Chiou, K. L, Walco, E. R., Bergstrom, M. L., Kawamura, S., & Fedigan, L.
631 M. (2017). Trichromacy increases fruit intake rates of wild capuchins (*Cebus*
632 *capucinus imitator*). *PNAS*, 114(39):10402-10407.
- 633 Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., ... Gordon, J.
634 E. (2006). A global overview of the conservation status of tropical dry forests.
635 *Journal of Biogeography*, 33(3), 491–505.
- 636 Milton, K., & Giacalone, J. (2014). Differential effects of unusual climatic stress on
637 capuchin (*Cebus capucinus*) and howler monkey (*Alouatta palliata*) populations

638 on Barro Colorado Island, Panama. *American Journal of Primatology*, 76(3),
639 249–261.

640 Panger, M. A., Perry, S., Rose, L., Gros-Louis, J., Vogel, E., Mackinnon, K. C., & Baker,
641 M. (2002). Cross-site differences in foraging behavior of white-faced capuchins
642 (*Cebus capucinus*). *American Journal of Physical Anthropology*, 119(1):52-66.

643 Perry, S. (1996). Intergroup encounters in wild white-faced capuchins (*Cebus*
644 *capucinus*). *International Journal of Primatology*, 17(3):309-330.

645 Perry, S. (2012). The behavior of wild white-faced capuchins: Demography, life history,
646 social relationships, and communication. *Advances in the Study of Behavior*,
647 44:135-181.

648 Pielou, E. C. (1969). *An Introduction to Mathematical Ecology*. New York, NY: Wiley
649 Interscience.

650 Pruetz, J. D., & Leason, H. C. (2002). Survey of three primate species in forest
651 fragments at La Suerte Biological Field Station, Costa Rica. *Neotropical*
652 *Primates*, 10(1), 4–9.

653 R Core Team. (2016). R: A Language and Environment for Statistical Computing.
654 Retrieved from <https://www.R-project.org/>

655 Ries, L., Fletcher, R. J., Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat
656 edges: Mechanisms, models, and variability explained. *Annual Review of*
657 *Ecology, Evolution, and Systematics*, 35(1), 491–522.

658 Rose, L. M. (1994). Sex differences in diet and foraging behavior in white-faced
659 capuchins (*Cebus capucinus*). *International Journal of Primatology*, 15(1), 95–
660 114.

661 RStudio Team. (2016). RStudio: Integrated Development Environment for R. Retrieved
662 from <http://www.rstudio.com/>

663 Ruiz-Garcia, M., Castillo, M.I., Ledezma, A., Leguizamon, N., Sánchez, R., Chinchilla,
664 M., Gutierrez-Espeleta, G. A. (2012). Molecular systematics and phylogeography
665 of *Cebus capucinus* (Cebidae, Primates) in Colombia and Costa Rica by means
666 of the mitochondrial COII gene. *American Journal of Primatology*, 74(4):366-80.

667 Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological Consequences of
668 Ecosystem Fragmentation: A Review. *Conservation Biology*, 5:18–32.
669 <https://doi.org/10.1111/j.1523-1739.1991.tb00384.x>

670 Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*.
671 Urbana, IL. University of Illinois Press.

672 Spellerberg, I. F. (2005). *Monitoring Ecological Change*. Cambridge University Press.

673 Thomas, O. (1903). New mammals from Chiriqui. *Journal of Natural History*, 11(64):
674 376-382.

675 Vogel, E. R. (2004). The ecological basis of aggression in white-faced capuchin
676 monkeys, *Cebus capucinus*, in a Costa Rican dry forest. (Doctoral dissertation).
677 Stony Brook University, NY.

678 Wickham, H. (2009). ggplot2: Elegant Graphics for Data Analysis. Retrieved from
679 <http://ggplot2.org>

680 Williams-Guillén, K., Hagell, S., Otterstrom, S., Spehar, S., & Gómez, C. (2013).
681 Primate populations in fragmented tropical dry forest landscapes in Southwestern
682 Nicaragua. In L. Barrett (Ed.), *Primates in Fragments* (105–120). New York, NY:
683 Springer.