

1 **TITLE**

2 High density of white-faced capuchins (*Cebus capucinus*) and habitat quality in the

3 Taboga Forest of Costa Rica

4

5 **RUNNING HEAD**

6 Capuchin density in the Taboga Forest

7

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24 **ABSTRACT**

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

46

47 **KEYWORDS**

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

49

50 **RESEARCH HIGHLIGHTS**

51 • Here we introduce a new white-faced capuchin study site in the Taboga Forest,
52 Costa Rica, a fragmented tropical dry forest.

53 • Forest fragments like Taboga may support high primate densities because they
54 provide a mosaic of habitats and key resources.

55

56 **ACKNOWLEDGEMENTS**

57 We are grateful to the following Costa Rican institutions for allowing us to work in the
58 Taboga Forest since 2017: the Ministerio de Ambiente y Energía (MINAE), the
59 Comisión Nacional para la Gestión de la Biodiversidad (CONAGEBIO), and the
60 Universidad Técnica Nacional (UTN). We would also like to thank the following people:
61 Dr. Susan Perry for guidance and support; Courtney Anderson and Jahmaira Archbold
62 for skilled field assistance during our first year; and the students of UTN who assisted
63 with data collection. Finally, we would like acknowledge the University of Michigan for
64 their financial support. The authors have no conflicts of interest to declare.

65

66 INTRODUCTION

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

83

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

89 unprotected and understudied (Dexter et al., 2018). For example, over 90% of the
90 tropical dry forests in North and Central America are vulnerable to anthropogenic
91 disturbance (Miles et al., 2006). However, a variety of primate species are found in
92 tropical dry forests, with some even continuing to flourish in fragments. Most notably,
93 white-faced capuchins (*Cebus capucinus*), howler monkeys (*Alouatta palliata*), and
94 spider monkeys (*Ateles geoffroyi*) are common sympatric species, yet they demonstrate
95 markedly divergent responses to fragmentation and other forms of anthropogenic
96 disturbance (e.g., Williams-Guillén, Hagell, Otterstrom, Spehar, & Gómez, 2013).
97
98 Understanding how different species respond to anthropogenic disturbance has
99 important implications for conservation and reforestation efforts. This is especially true
100 when it comes to tropical dry forests, which were once the predominant forest type on
101 the west coast of Central America (Gillespie, Grijalva, & Farris, 2000). While spider
102 monkeys are rarely found in small fragments (instead requiring large territories to
103 support their frugivorous diet: Williams-Guillén et al., 2013), both capuchins and howlers
104 can thrive there. As large-bodied omnivores, capuchins, in particular, can
105 opportunistically exploit a broad array of plants and animals (Ford & Davis, 1992; Rose,
106 1994; Panger et al., 2002; Perry 2012) and can adapt to anthropogenic disturbances
107 that threaten many other species (i.e., showing neutral or even positive edge effects:
108 Bolt et al., 2018 [*C. capucinus*]; surviving in fragmented habitats: Lins & Ferreira, 2019
109 [*Sapajus flavius*]; Cunha, Vieira, & Grelle, 2006 [*C. sp.*]). However, certain factors may
110 constrain capuchin densities. For example, low capuchin densities in Nicaraguan forest
111 fragments have been attributed to human hunting, poaching, and the pet trade

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

125

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

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

138

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

156

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

163

164 **METHODS**

165 *Study site and subjects*

166 We conducted this study at the Capuchins at Taboga research site, established in June
167 2017 in la Reserva Forestal Taboga (the Taboga Forest Reserve; i.e., Taboga) in
168 Guanacaste province, Costa Rica. The reserve was established in 1978 and contains
169 296 hectares of largely tropical dry forest (~3 x 4 km), representing an important piece
170 of the fragmented biological corridor connecting the Guanacaste Mountains to the
171 Tempisque River Basin (Fig. 1). The Universidad Técnica Nacional (UTN) of Costa Rica
172 operates an experimental farm of 702 hectares that encompasses the reserve along
173 with agricultural land. The UTN farm consists of irrigated land dedicated to the
174 cultivation of sugarcane (100 hectares), rice (30 hectares), and grass for cattle (4.5
175 hectares). There is also a tilapia farm and research center as well as a water research
176 laboratory. As such, Taboga is characterized by distinct forest edges (i.e., farm land and
177 roads) as well as more transitional or “natural” forest edges (i.e., canals and rivers). The
178 reserve is almost exclusively bordered by sugarcane and rice fields, aside from a 2 km
179 perimeter that borders private forested land and 1 km bordering public forested land.

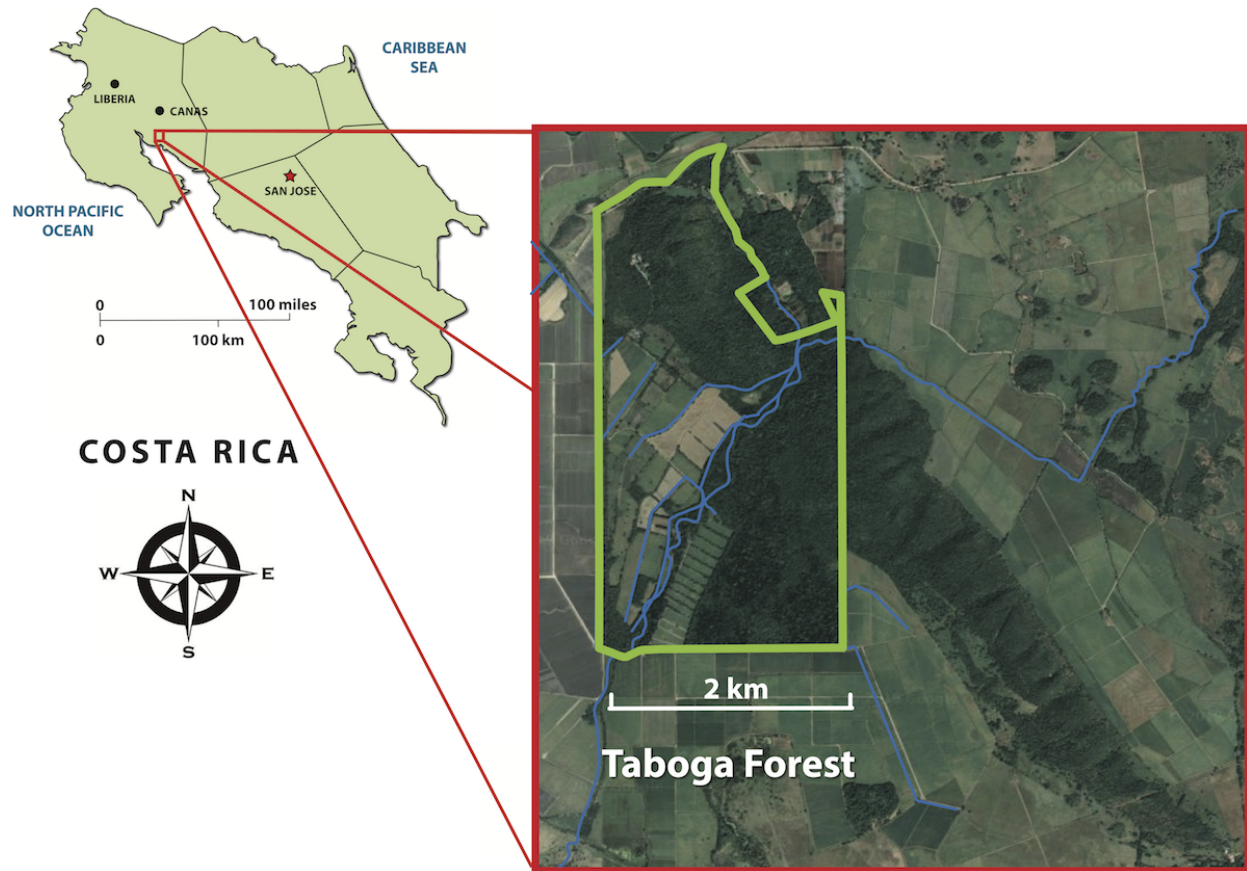


Figure 1. Location of the Taboga Forest in Costa Rica. The official Taboga Forest Reserve boundary is within this larger reserve held by the Universidad Técnica Nacional (see Fig. 3a). However, for simplicity, we refer to this entire area as the Taboga Forest or “Taboga”.

180

181

182 Taboga is largely characterized by seasonally dry tropical forest, a highly threatened

183 ecosystem that features a closed canopy and seasonal deciduousness (Janzen, 1988;

184 Miles et al., 2006). In addition to the dry forest, there are also riparian, semi-deciduous

185 forests around the river and a palm forest dominated by the native species *Attalea*

186 *rostrata*, part of which becomes inundated during the wet season. The area experiences

187 two distinct seasons (Fig. 2): a hot, dry season from Nov-Apr (mean daily maximum

188 temperature = 35.38 °C +/- 0.20 SE; mean daily rainfall = 0.66 mm +/- 0.27 SE) and a

189 cooler wet season from May-Oct (mean daily maximum temperature = 32.57 °C +/- 0.21

190 SE; mean daily rainfall = 8.93 mm +/- 1.09 SE). Mean daily minimum temperatures
191 remain consistent throughout the year (dry season: 26.25 °C +/- 0.10 SE; wet season:
192 25.46 °C +/- 0.11 SE). The river provides fresh water year-round and many of the
193 canals used by the UTN farm for irrigation are consistently full during the dry season
194 (Fig. 3C).

195

196

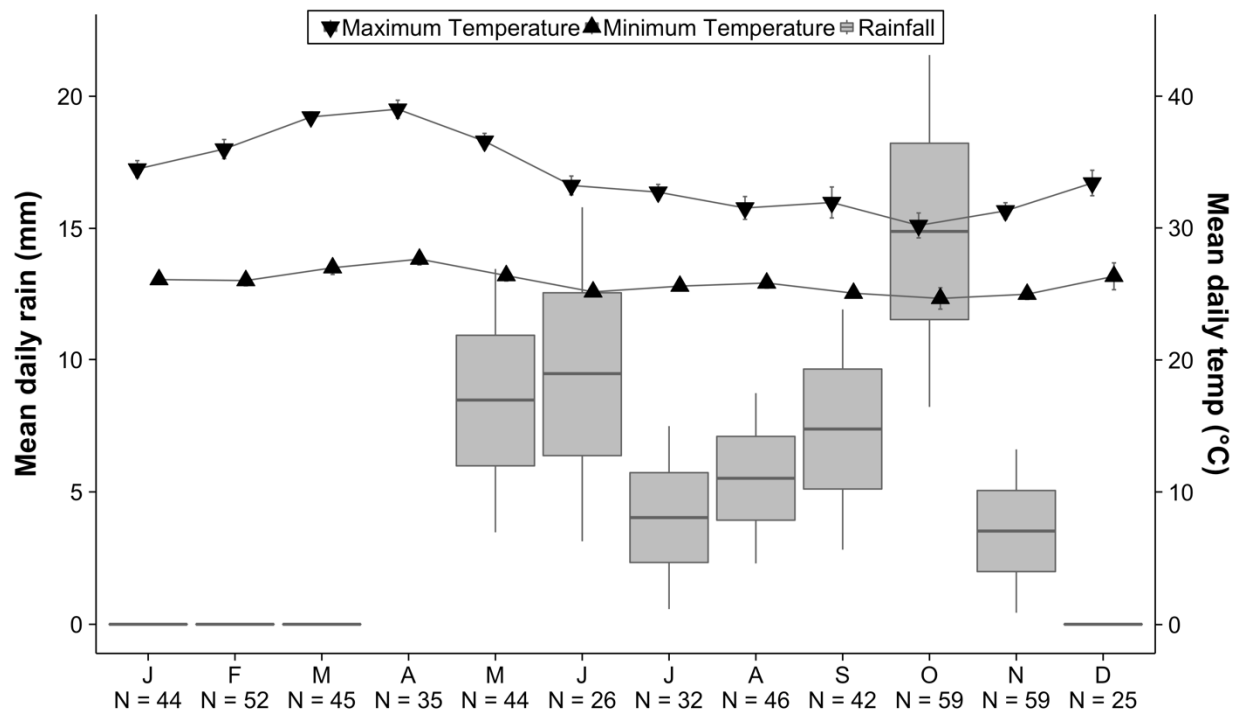


Figure 2. Temperature (black triangles) and rainfall (grey boxes) data from the Taboga Forest from Jul 2017 - May 2019. Numbers along the x-axis indicate the number of days of weather data measured per month.

197

198

199 The Capuchins at Taboga research project (directed by Thore Bergman, Jacinta
200 Beehner, Marcela Benítez, Elizabeth Tinsley Johnson) is focused on the behavioral
201 biology, endocrinology, and cognition of wild white-faced capuchins (*C. capucinus*).
202 Note that the taxonomy of Central American capuchins is in flux and some authors refer
203 to Costa Rican capuchins as *C. capucinus imitator* (Ruiz-Garcia et al., 2012; Lynch
204 Alfaro et al., 2014; Melin et al., 2017; Hogan et al., 2018). However, we prefer the more
205 general name *C. capucinus* because the defining feature of the capuchins first
206 described as “imitator” is a frontal tuft in females, something that is clearly absent in our
207 populations (Thomas, 1903). Our research group has identified at least 12 distinct
208 capuchin groups in the reserve since July 2017. We collect GPS data on group
209 movements and behavioral data on three of these groups (“Tenori”, “Mesas”, and
210 “Palmas”), including regular group scans (all groups) and weekly focal follows of each
211 individual (in Tenori group and some individuals in Mesas group). Whenever possible,
212 groups are followed from their morning sleeping site to their evening sleeping site. The
213 Tenori group is entirely habituated to observers on foot, and the Mesas and Palmas
214 groups are mostly habituated. These three groups range in size from 16 (Mesas) to 17
215 (Tenori) to 36 individuals (Palmas). The breakdown of age / sex categories can be
216 found in Table 1.
217

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:

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

265

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

271

272 *Vegetation survey analyses*

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

280 Second, to test whether canopy cover varied between edge and interior forest and/or if

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

285

286 *Primate survey*

287 Between Feb-Apr 2019, we conducted a primate population survey using 32 line
288 transects comprising pre-existing roads and paths (i.e., along canals or firebreaks) and
289 a network of trails created by the project (19 cut trails total, each at least 0.2 km apart;
290 Fig. 3b). Transect lengths ranged from 0.2 km to 2.2 km and we walked most transects
291 twice (once in the morning between 6:00-10:00 and once in the afternoon between
292 14:00-16:00), each time in an alternate cardinal direction, for a total of 55 km in
293 transects. Three transects were only walked once due to lack of maintenance.
294 Transects were not surveyed when it was raining.

295

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

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

305

306 *Primate survey analyses*

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

316

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

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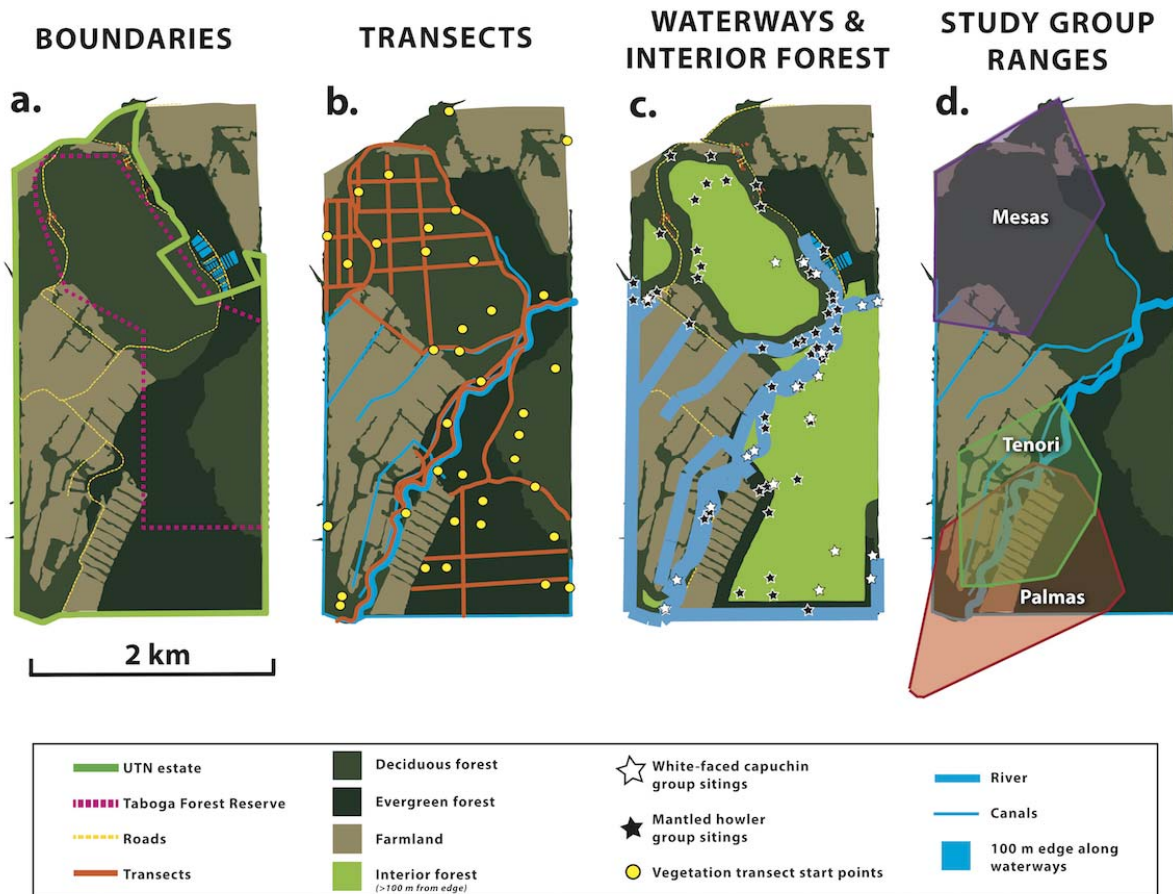


Figure 3a-d. Maps of (a) the UTN Estate and the Taboga Forest Reserve (together, the “Taboga Forest”), with overlays displaying: (b) both primate and vegetation transect locations, (c) 0.1 km buffer zones for forest edges and year-round water sources, and (d) home ranges for three groups of wild white-faced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

321

322

323 RESULTS

324 *Capuchin density and home range size*

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

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

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

337

338 With respect to our habituated groups, Tenori had the smallest range size (60.5 ha,
339 70% of which was “edge” habitat) in comparison with Mesas (129.4 ha, 60% edge) and
340 Palmas (102.1 ha, 57% edge) groups (Fig. 3d). We do not yet have accurate estimates
341 of how much our capuchin groups overlap. We will soon have data from another group
342 (Escameka group) that overlaps with the Mesas group, providing us with two points of
343 overlap (Tenori and Palmas groups, and Mesas and Escameka groups).

344

345

346 **Table 2.** Group size and density comparison for this (“Taboga”) and other white-faced
347 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

348

349

350 *Vegetation survey*

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

362 0.132; Table 3), mean tree density ($U = 234.5$, $p = 0.36$; Table 3), or Shannon's
 363 Diversity Index ($U = 153$, $p = 0.20$; Table 3).

364

365 **Table 3.** Mean \pm standard error of vegetation measures in the edge and interior of all
 366 trees, monkey food trees, and indicator tree species. Bold indicates significant
 367 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

368

369

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

378

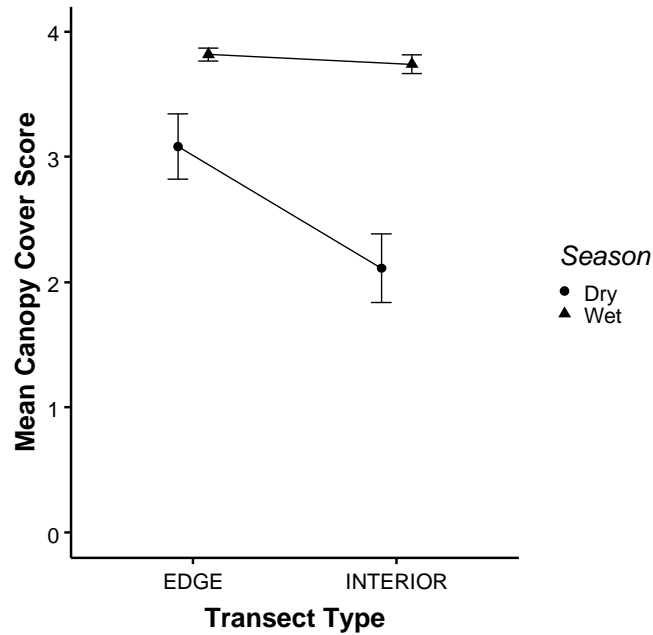


Figure 4. Mean canopy cover score (\pm standard error) across season and transect type.

379

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

390 As predicted, capuchin group encounters were higher near permanent water sources
391 (i.e., the river or large canals: 0.78 groups/km; CI: 1.42, 4.41) compared to farther from
392 water (0.15 groups/km; CI: -4.41, -1.42; $p = 1.73 \times 10^{-4}$; Fig. 5b). Contrary to our
393 predictions, however, howler group encounter rates were also significantly higher near
394 water sources (1.69 groups/km; CI: 0.42, 1.72) compared to farther from water (0.57
395 groups/km; CI: -1.72, -0.42; $p = 1.24 \times 10^{-3}$; Fig. 5d).
396

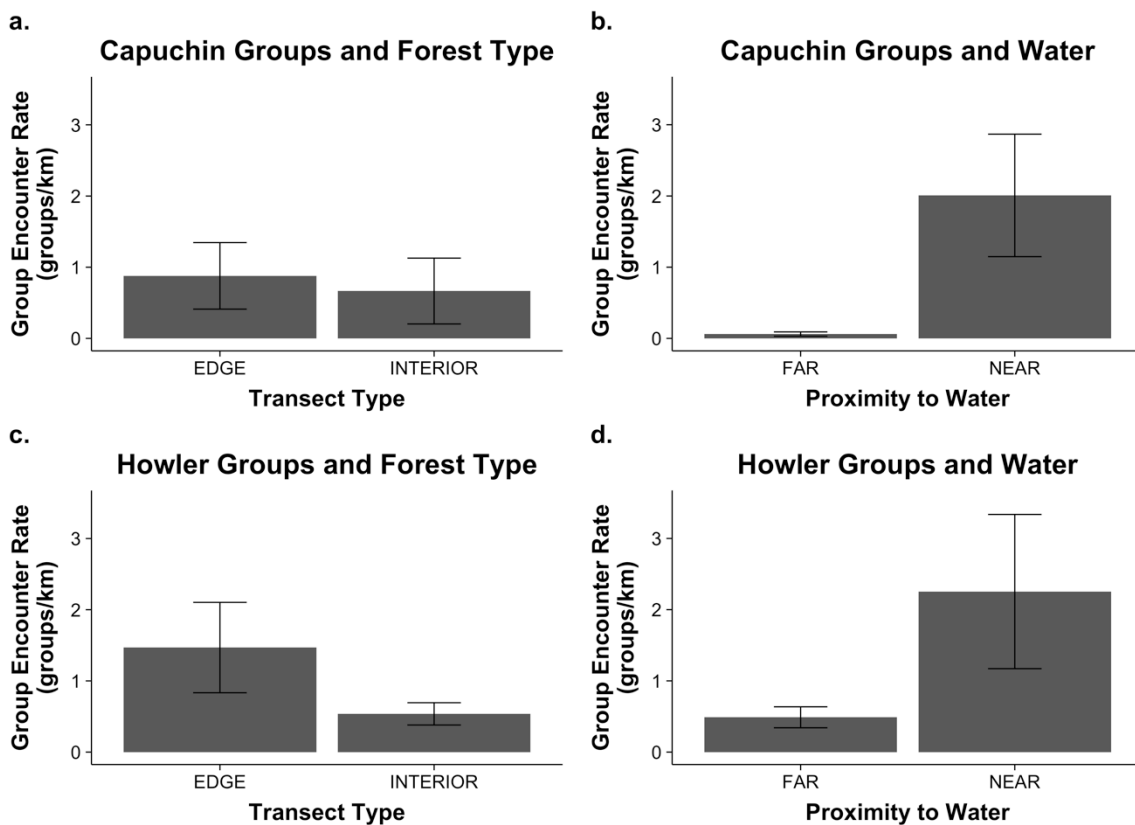


Figure 5a-d. Mean group encounter rate (groups/km walked \pm standard error) by forest type in Taboga. **(a)** capuchin groups in edge and interior forest; **(b)** capuchin groups near (<0.01 km) or far (>0.01 km) from a permanent water source; **(c)** howler groups in edge and interior forest; **(d)**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

397

398

399 **DISCUSSION**

400 The Taboga Forest of Costa Rica has one of the highest densities of white-faced
401 capuchins thus far recorded. Here, we asked whether specific features of the forest
402 might allow these capuchins to survive and reproduce at such high densities. Our
403 results suggest that the presence of reliable year-round water sources is critical for
404 capuchins (and possibly for howlers) living in a seasonally dry habitat. For example,
405 capuchins in Santa Rosa National Park (another tropical dry forest in Costa Rica) rely
406 on a limited number of water holes during the dry season, and access to these water
407 holes is thought to be the primary constraint on the capuchin population (Fedigan &
408 Jack, 2001; Fedigan, Rose, & Avila, 1996, 1998). In contrast, Taboga has two types of
409 year-round water supply: the river and a system of canals. We did not test whether
410 forest characteristics varied significantly according to distance from water sources.
411 However, because the canals have cement bottoms, we think that it is unlikely that the
412 canals impact the surrounding flora all that much. We will implement future studies to
413 test how forest characteristics vary with proximity to the river (and the associated
414 riparian/semi-deciduous forest type). For example, riparian forests may contain certain
415 fruiting trees central to the capuchin diet, overall larger trees due to year-round water
416 supply, and/or year-round canopy cover. Our results also suggest that howlers at
417 Taboga may be more dependent on permanent water sources than at other sites, as
418 they were also frequently found near permanent water sources. However, this may have
419 more to do with the forest subtype near the river (i.e., evergreen and riparian) than the
420 need to drink water daily (Fedigan & Jack, 2001).
421

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

442

443 Together, our data suggest that the difference between edge and interior forest at

444 Taboga is less than that from other sites (e.g., Arroyo-Rodríguez & Mandujano, 2009;

445 Bolt et al., 2018; Harris, 1988; Lehman, Rajaonson, & Day, 2006; Saunders, Hobbs, &
446 Margules, 1991). This may be because the initial anthropogenic disturbance (i.e.,
447 creation of pastures and croplands around the reserve) happened some time ago and
448 the forest is actually in the intermediate stages of regeneration (Kalacska et al., 2004).
449 Three lines of evidence support this hypothesis. First, both edge and interior forest at
450 Taboga exhibit high species richness and diversity, which also characterize
451 intermediate tropical dry forest succession at nearby Santa Rosa (Kalacska et al.,
452 2004). Second, tree species that characterize the first stage of tropical dry forest
453 succession (of which many remain through stages 2 & 3) are well-established in the
454 forest edge. Specifically, these trees had a significantly higher mean DBH in edge forest
455 compared to interior forest. Third, the early stages of dry forest succession are
456 characterized by a high percentage of deciduous trees (Kalacska et al., 2004). Yet, we
457 found that the edge forest in Taboga was semi-evergreen throughout the dry season.
458 This, of course, raises the question of why the interior forest is more deciduous. It may
459 be that the Taboga Forest is small enough that it lacks a true “interior” (Banks-Leite,
460 Ewers, & Metzger, 2010), and therefore the entire forest represents different stages of
461 regeneration. Alternatively, much of the interior forest is also more elevated and may
462 lack year-round water sources. Finally, flood-irrigation of agricultural land during the dry
463 season might spill-over into edge forests, thus allowing for year-round canopy
464 maintenance.

465

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

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

484

485 The abundance of the capuchins in Taboga has important implications for conservation
486 efforts. For certain species, the size and disturbance of a forest fragment may matter
487 less than the composition and availability of key resources, like above-ground water.
488 Our analysis here adds to our understanding of factors that influence primate
489 abundance, and also establishes Taboga as critical case study in tropical dry forest
490 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.

502

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