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**

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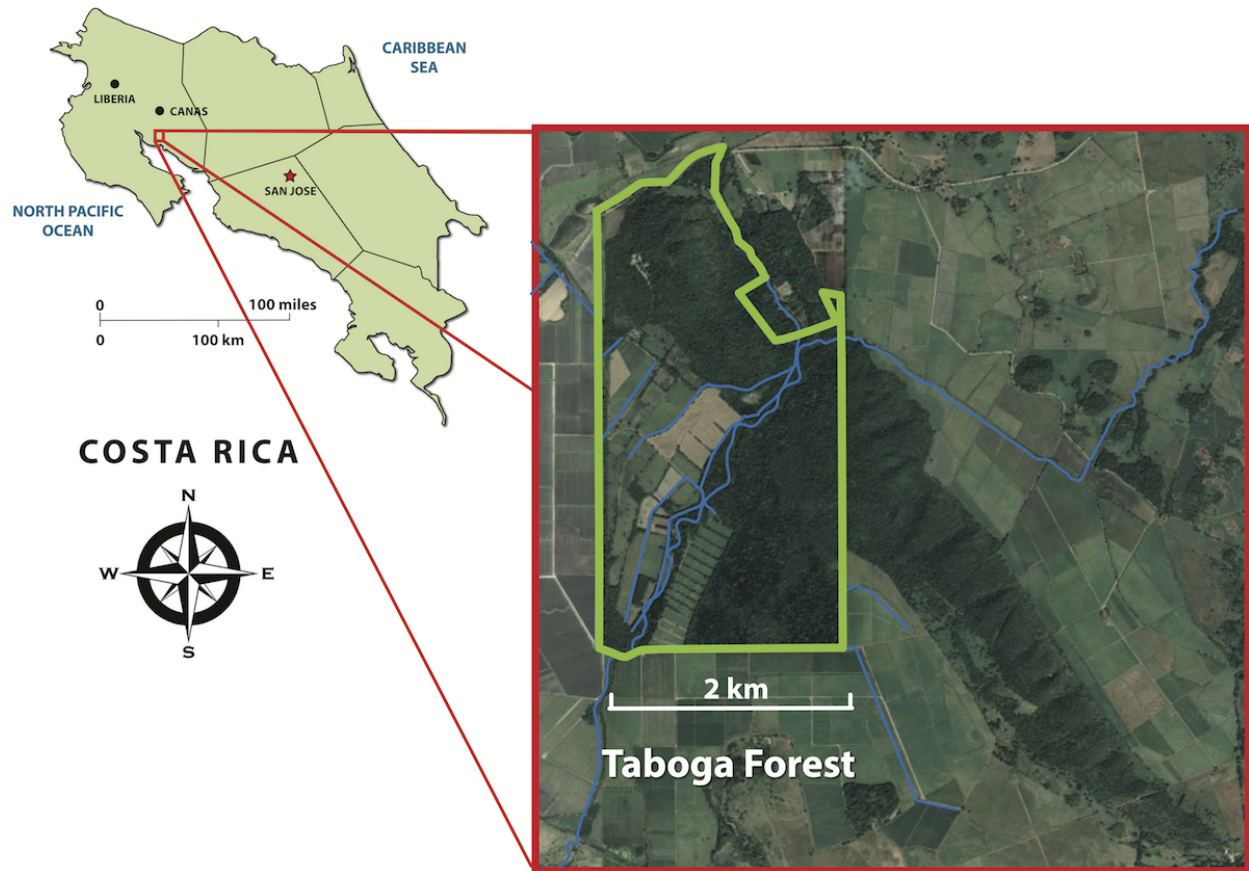
Figure 1. Location of the Taboga Forest in Costa Rica. The official Taboga Forest Reserve boundary is within this larger reserve held by the Universidad Técnica Nacional (see Fig. 3a). However, for simplicity, we refer to this entire area as the Taboga Forest or "Taboga".

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

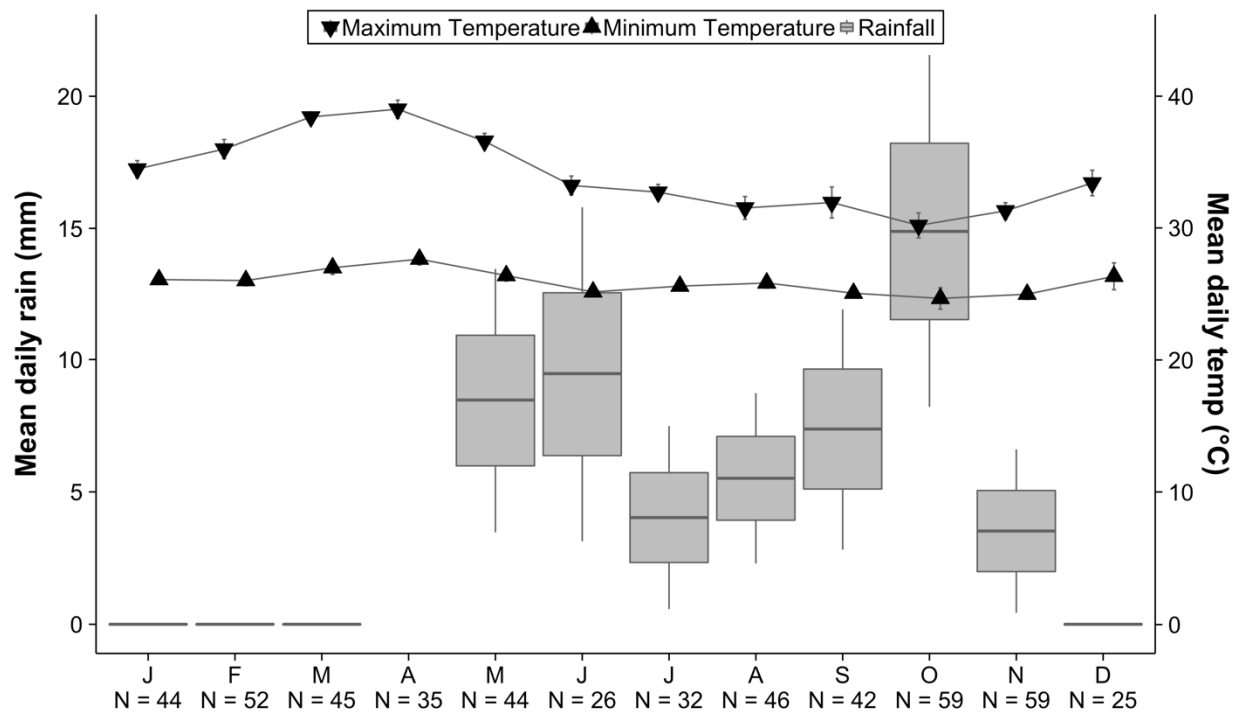194   (Fig. 3C).

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 & Leasor, 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

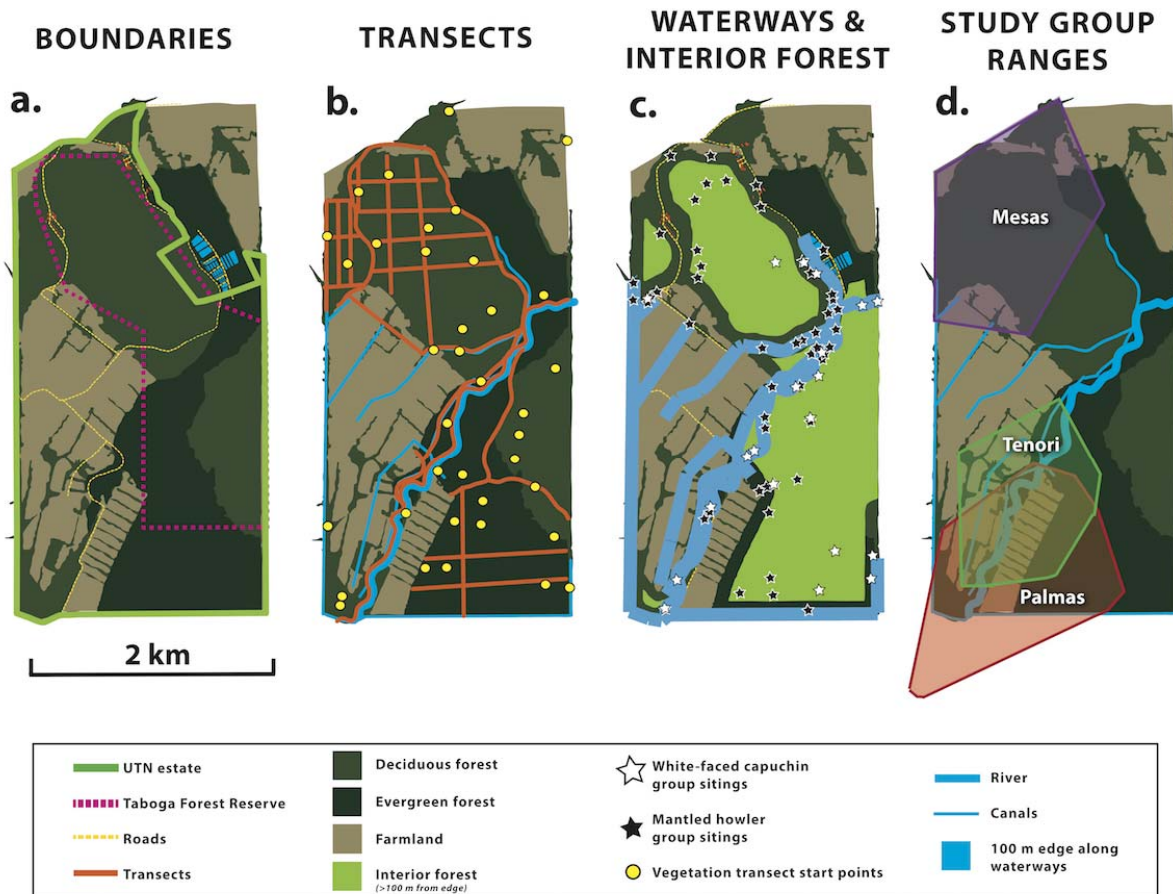319   package (Wickham, 2009).

320

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 ± 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 ± 1.31	14.30 ± 1.72	12.85 ± 1.31	15.23 ± 1.96	**16.21 ± 1.55**	**11.30 ± 1.72 ***
Density (trees/m2)	0.13 ± 0.01	0.15 ± 0.03	0.08 ± 0.01	0.07 ± 0.04	0.03 ± 0.01	0.08 ± 0.03
Richness	12.30 ± 1.01	11.15 ± 1.23	7.40 ± 0.61	6.90 ± 1.50	3.00 ± 0.61	4.45 ± 0.72
Diversity index (H)	2.10 ± 0.11	1.89 ± 0.14	1.65 ± 0.12	1.34 ± 0.13	0.67 ± 0.15	0.99 ± 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.
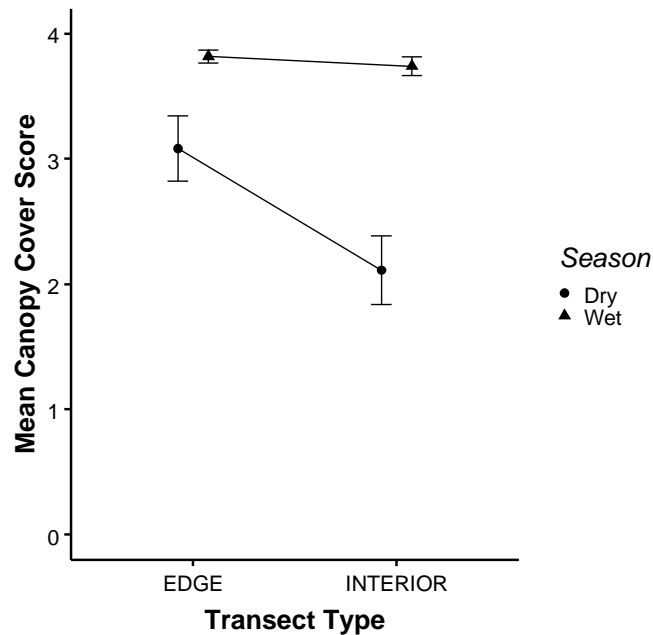
378

Figure 4. Mean canopy cover score (± 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 x 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 x 10-3; Fig. 5d).

396

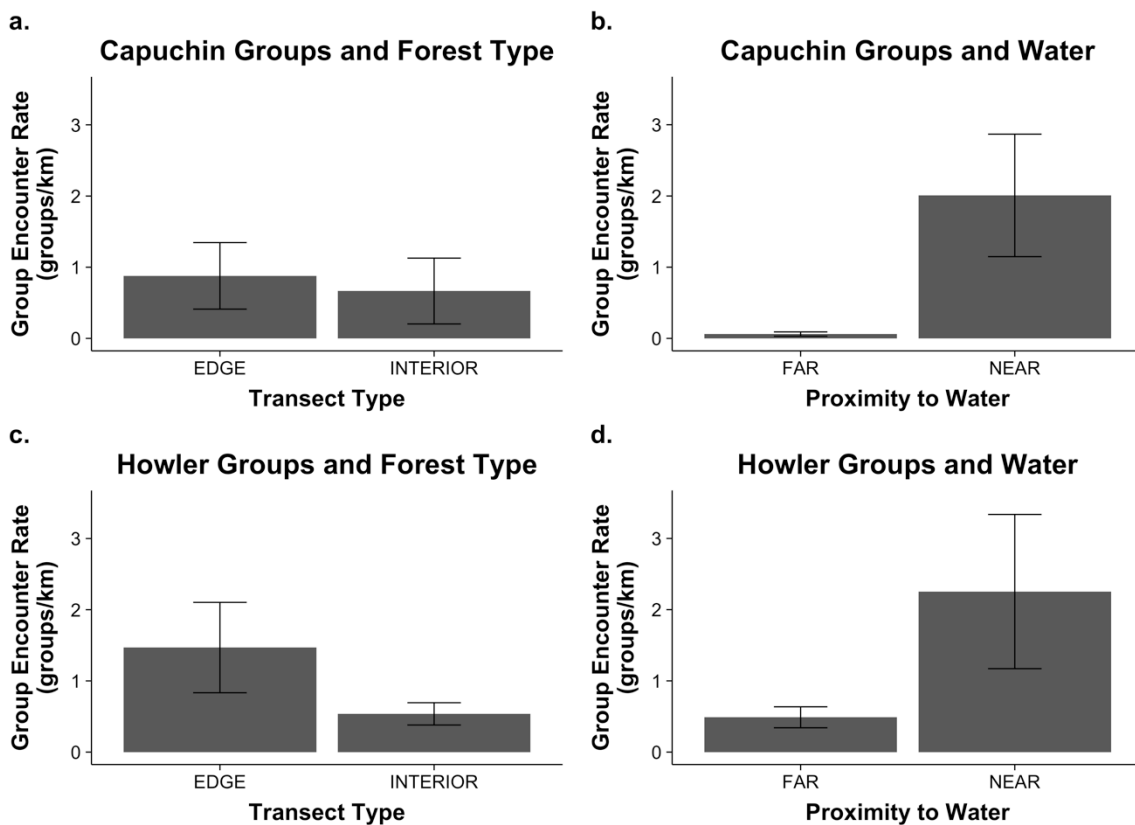
Figure 5a-d. Mean group encounter rate (groups/km walked ± standard error) by forest type in Taboga. **(a)** capuchin groups in edge and interior forest; **(b)** capuchin groups near (<0.01 km) or far (>0.01 km) from a permanent water source; **(c)** howler groups in edge and interior forest; **(d)**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