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Dramatic decline in a titi monkey population after the 2016-2018 sylvatic yellow fever outbreak in Brazil

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1 **Dramatic decline in a titi monkey population**
2 **after the 2016-2018 sylvatic yellow fever outbreak in Brazil**

3
4 **Short title**

5 Titi monkey decline after YF outbreak

6
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34 **Abstract**

35 Platyrrhini are highly vulnerable to the yellow fever (YF) virus. From 2016 to 2018, the
36 Atlantic Forest of southeast Brazil faced its worst sylvatic YF outbreak in about a
37 century, thought to have killed thousands of primates. It is essential to assess the impact
38 of this epidemic on threatened primate assemblages to design effective conservation
39 strategies. In this study, we assessed the impact of the 2016-2018 YF outbreak on a
40 geographically isolated population of Near Threatened black-fronted titi monkeys
41 (*Callicebus nigrifrons*) in two Atlantic Forest patches of the Santuário do Caraça, MG,
42 Brazil. Extensive pre-outbreak monitoring, conducted between 2008 and 2016, revealed
43 that the home range and group sizes of the population remained stable. In 2016, the
44 population size was estimated at 53-57 individuals in 11-12 groups. We conducted
45 monitoring and playback surveys in 2019 and found that the population had decreased
46 by 68% in one forest patch and completely vanished in the other, resulting in a
47 combined decline of 80%. We discuss this severe loss of a previously stable population
48 and conclude that it was highly likely caused by the YF outbreak. The remaining

49 population is at risk of disappearing completely because of its small size and geographic
50 isolation. A systematic population surveys of *C. nigrifrons*, along other sensible
51 Platyrrhini species, is needed to re-evaluate their current conservation status.

52

53 **Keywords**

54 *Callicebus nigrifrons*, Atlantic Forest, demographic changes, playback survey,
55 monitoring, epizootic

56

57 **Research highlights**

58 • Brazil faced one of its worst yellow fever outbreaks from 2016 to 2018, but
59 systematic data on the impact on local primate populations are lacking

60 • We show that a geographically isolated and partially habituated population of
61 black-fronted titi monkeys *Callicebus nigrifrons* have declined by about 80%
62 after the outbreak

63 • Natural demographic fluctuations or ecological changes do not appear to
64 account for the decline, making the YF outbreak the most likely cause

65 • A systematic Platyrrhini survey is needed to re-evaluate the species' current
66 conservation statuses

67

68 **Graphical abstract**



69

70 A juvenile black-fronted titi monkey photographed shortly after the 2016-2018 sylvatic
71 yellow fever outbreak in the Santuário do Caraça, MG, Brazil

72

73 **Introduction**

74 Yellow fever (hereafter YF) is an infectious disease caused by a *Flavivirus* arbovirus
75 that originated in Africa in the last 1,500 years. The virus was probably introduced from
76 Africa to the Americas during the slave trade period about 300-400 years ago (Bryant,
77 Holmes, & Barrett, 2007). In America, the virus is maintained by a sylvatic cycle
78 between Culicidae hematophagous mosquitoes (*Haemagogus* and *Sabethes*) and
79 nonhuman primates (Possas et al., 2018), mostly restricted to the Amazon, Araguaia,
80 and Orinoco river basins (Bryant et al., 2007).

81 These areas are characterized by low altitude and high rainfall, air humidity, ambient
82 temperature and nonhuman primate diversity and density, which create optimal
83 breeding conditions for mosquitoes and explain the regular emergence of YF outbreaks
84 (Almeida et al., 2019b; Childs, Nova, Colvin, & Mordecai, 2019; Hamrick et al., 2017).

85 Nonhuman primates are the main sources of blood for canopy-inhabiting mosquitoes
86 whose activity peaks during the hottest hours of the day, when primates usually rest
87 (Silva et al., 2020). Unlike African primates, which have long been exposed to the virus
88 and are resistant to the disease (Gould, Lamballerie, Zanotto, & Holmes, 2003),
89 Platyrrhini primates experimentally infected by YF-virus showed high, genera-varying
90 susceptibility (Bugher, 1951; Vasconcelos, 2003). Infected Platyrrhini either die rapidly
91 (3-7 days after infection) or develop immunity, suggesting that they can act as virus
92 amplifiers only during short periods (Bicca-Marques & Freitas, 2010; Dietz et al.,
93 2019). When a population is infected, it rapidly declines and the virus disappears from
94 the area (Abreu et al., 2019a; Moreno et al., 2013; Vasconcelos, 2010). This cycle
95 normally resumes when the virus returns to the area, carried by infected vectors or
96 hosts, and finds a renewed, susceptible monkey population. As a result, outbreaks have
97 occurred in the Brazilian endemic areas, particularly in the Amazon, every 7 to 14 years
98 (Câmara, Gomes, Carvalho, & Castello, 2011).

99 Despite their central role in the sylvatic cycle, Platyrrhini are not responsible for the
100 spread of the virus to non-infected areas in fragmented landscapes, as they usually live
101 in restricted home ranges and rarely travel on the ground between habitat patches
102 (Bicca-Marques & Freitas, 2010; Possas et al., 2018; Souza-Alves et al., 2019b). Wind,
103 on the other hand, can carry infected mosquitoes over long distances, potentially
104 spreading the disease (Almeida et al., 2019b; Paiva et al., 2019). Finally, human factors
105 are also responsible for the expansion of outbreaks. Humans become accidental hosts
106 when bitten by infected mosquitoes (Consoli & Oliveira, 1994), which occurrence
107 increases along with the increasing human activity in forest areas. In this respect, habitat
108 fragmentation increases nonhuman primate density in forest patches and proximity

109 between human and wildlife, potentially boosting the transmission rates of the virus
110 (Kaul, Evans, Murdock, & Drake, 2018; Possas et al., 2018). The YF vaccine provides
111 life-long immunity (World Health Organization, 2019), but it only prevents the
112 dissemination of the virus if the population coverage is above 80%, which is rarely the
113 case in Latin America (Shearer et al., 2017). Moreover, most infected humans are
114 asymptomatic or develop mild symptoms (Vasconcelos, 2003). In sum, the spread of
115 the virus is favored by high human population densities, low vaccination coverage and
116 movement of infected people (Childs et al., 2019; Possas et al., 2018).

117 The highly populated regions of southern and southeastern Brazil remained YF-free for
118 decades until near the end of the 20th century, which have led to a vaccine coverage of
119 less than 80% (Shearer et al., 2017). Between 1998 and 2009, YF outbreaks in these
120 regions caused the death of hundreds of humans and thousands of nonhuman primates,
121 especially howler monkeys (Almeida et al., 2012; Bicca-Marques et al., 2017; Freitas &
122 Bicca-Marques, 2011; Holzmann et al., 2010; Moreno et al., 2013; Romano et al., 2014;
123 Souza et al., 2019; Vasconcelos, Rosa, Monteiro, & Cruz, 2001).

124 From 2016 to 2018, Brazil has faced one of its worst YF outbreaks in nearly 80 years,
125 with 2,153 confirmed human cases including 744 deaths (2016-2017: 777 confirmed
126 cases and 261 deaths; 2017-2018: 1,376 confirmed cases and 483 deaths; Ministério da
127 Saúde 2017, 2018). The outbreak continued in winter 2018-2019 in a moderate form (75
128 human cases, 17 deaths; World Health Organization, 2019) and, at the time of this
129 writing (Feb 2021), it is emerging in the state of Rio Grande do Sul (G1 RS, 2021). The
130 2016-2018 YF outbreak extended over 2,000 km and comprised multiple parallel
131 sylvatic cycles (Moreira-Soto et al., 2018) with *Haemagogus janthinomys* and *H.*
132 *leucocelaenus* as main vectors (Abreu et al., 2019b).

133 Atlantic Forest primates were extensively infected during the 2016-2018 outbreak
134 according to governmental authorities. A total of 2,276 epizootics involving mostly
135 *Callithrix*, *Alouatta*, *Sapajus* and *Callicebus* were reported (2016-2017: N = 1,412
136 cases; 2017-2018: 864 cases; Ministério da Saúde, 2017, 2018). Real rates of epizootics
137 were likely much higher, as only 5% of dead monkeys are estimated to be found and
138 registered (Duchiade, 2018). Systematic analysis of the carcasses showed that *Alouatta*
139 and *Callicebus* are highly sensitive to the YF virus (Sacchetto et al., 2020).

140 In the State of Minas Gerais (MG), 80-90% of the Vulnerable *Alouatta guariba*
141 *clamitans*, 10% of the Critically Endangered *Brachyteles hypoxanthus*, 90% of the
142 Critically Endangered *Callithrix flaviceps* and 40-50% of the Near Threatened *Sapajus*
143 *nigrinus* populations of the Reserva Particular do Patrimônio Natural (RPPN) Feliciano
144 Miguel Abdala (also known as “Caratinga”) vanished during the 2016-2017 outbreak,
145 as well as 26% of the *B. hypoxanthus* population of the RPPN Mata do Sossego (Lopes,
146 2017; Possamai, Mendes, & Strier, 2019; Strier et al., 2019). In the neighboring State of
147 Espírito Santo (ES), the disease caused a population decline of 82% for *A. guariba*
148 *clamitans*, 49% for *C. flaviceps* and the Least Concern *Callithrix geoffroyi*, 25% for the
149 Vulnerable *Callicebus personatus*, 23% for *S. nigrinus* and 10-26% for *B. hypoxanthus*
150 (Gontijo, 2019; Strier et al., 2019). Finally, 30% of the Endangered *Leontopithecus*
151 *rosalia* population from the São João river basin (State of Rio de Janeiro [RJ])
152 disappeared after the outbreak (Dietz et al., 2019). In all these reports, the evidence for
153 virus-caused decline is indirect, as population reductions coincided with the presence of
154 the virus in the regions (Dietz et al., 2019; Lopes, 2017; Strier et al., 2019). Population
155 declines at such rates pose a serious threat to species survival with considerable
156 implications for conservation.

157 The purpose of the study is to assess the state of a geographically isolated and partially
158 habituated population of black-fronted titi monkeys (*Callicebus nigrifrons*) in two small
159 Atlantic Forest patches in Brazil before and after the 2016-2018 YF outbreak, and to
160 evaluate the potential impact of the outbreak on population demography. The study
161 population lives in the RPPN Santuário do Caraça, a reserve located in the upper Rio
162 Doce basin, a highly fragmented Atlantic Forest region in MG (Machado & Fonseca,
163 2000). MG was the epicenter of the 2016-2018 YF outbreak, accounting for 46% of the
164 confirmed human cases and 23% of the confirmed nonhuman primate epizootics
165 (Figueiredo et al., 2018; Ministério da Saúde, 2017, 2018). Three of the closest
166 municipalities to the reserve (namely, Santa Bárbara, Catas Altas and Barão de Cocais)
167 recorded at least 21 confirmed human cases and several suspected cases (Secretaria de
168 Estado de Saúde de Minas Gerais, 2018). These three municipalities also reported
169 confirmed and suspected nonhuman primate cases (Sacchetto et al., 2020; Secretaria de
170 Estado de Saúde de Minas Gerais, 2018). The study population comprised the largest
171 habituated population of *C. nigrifrons* (6 groups and ca. 35 individuals, end of 2016) as
172 well as their neighboring non-habituated groups. Although no primate carcass was
173 recovered, local employees reported fewer cues of black-fronted titi monkeys presence
174 after 2016 (choruses, visual encounters), suggesting that groups were affected by the
175 2016-2018 YF outbreak (Duchiade, 2018).

176 To quantify the potential impact of the YF outbreak on the study population, we
177 assessed the stability of the population from 2008 to 2016 and estimated the
178 demographic changes between 2016 and 2019. Given the lack of extreme climatic
179 events and any noticeable change in habitat quality since 2016, we assumed that if the
180 population was stable from 2008 to 2016, any population reduction after 2016 could be

181 reliably assigned to the YF outbreak. However, if the population had been unstable
182 between 2008 and 2016, it would not be possible to infer the YF as the cause of recent
183 population changes.

184

185 **Methods**

186 **Study site**

187 We conducted the study at the RPPN Santuário do Caraça (“Santuário do Caraça”), a
188 private natural heritage reserve of 11,000 ha in the Serra do Espinhaço, MG, Brazil
189 (20°05’S, 43°29’W) ranging from 730 to 2,072 m above sea level. The reserve is
190 composed of transition zones between the Atlantic Forest and the Cerrado (Brazilian
191 savanna) biomes (Brandt & Motta, 2002; Paz, 1998; Talamoni, Amaro, Cordeiro-
192 Júnior, & Maciel, 2014). Specifically, three main floristic formations structure the
193 reserve’s landscape: the grasslands (*campo limpo*), outcrop fields (*campo rupestre*) and
194 the forests (riverine forest, riparian forest, cloud forest and hillside forest) (Província
195 Brasileira da Congregação da Missão, 2013). The climate is tropical, characterized by a
196 rainy and hot season (October to March, mean monthly rainfall \pm s.d. = 224.6 \pm 76.2
197 mm, mean temperature \pm s.d. = 18.2 \pm 0.7°C) and a dry and colder season (April to
198 September, mean monthly rainfall \pm s.d. = 43.5 \pm 27.3 mm, mean temperature \pm s.d. =
199 15.0 \pm 1.4°C) under the strong influence of the altitudinal gradient (Fick & Hijmans,
200 2017; Moreira & Pereira, 2004).

201 The central part of the reserve (mean elevation: 1,300 m) includes two forest patches of
202 interest for this study, the Tanque Grande forest patch and the Cascatinha forest patch,
203 located 1 km apart from each other (Jarvis, Reuter, Nelson, & Guevara, 2008).
204 Cascatinha is a hillside forest patch of about 32 ha bounded by a river on its southern

205 part and surrounded by grasslands and rocky outcrops on its other parts, preventing any
206 connection to other forested areas. Tanque Grande is a hillside forest patch of about 60
207 ha bounded by human settlements (road, hotel complex) on its northern part, grasslands
208 and a lake on its western part, and surrounded by grasslands and rocky outcrops on its
209 other parts. It can be connected to the core forest of the reserve via a corridor in the
210 south, which can potentially be crossed by titi monkeys, but which does not constitute a
211 suitable habitat for the species because it is a transition zone between grasslands and
212 forests.

213 The Santuário do Caraça is a tourist attraction that receives 60,000-70,000 visitors each
214 year. Human settlements are restricted to an asphalt road, a farm/hotel complex at the
215 entrance of the reserve and a monastery/hotel complex in the core of the reserve, which
216 allow visitors to spend several days on site. Visitors are required to stay on pre-
217 established trails when walking through the natural areas, and to not interact (e.g., feed,
218 touch) with the wildlife, including primates. Hunting is forbidden and there is no recent
219 record of poaching (Província Brasileira da Congregação da Missão, 2013; pers. obs.).
220 From the 28th of November 2018 to the 8th of March 2019, visitors were required to
221 present a valid certificate of YF vaccination to access the reserve.

222 The sanctuary is a conservation hotspot for the local fauna (Talamoni et al., 2014). Five
223 primate species inhabit the reserve: *C. nigrifrons*, *S. nigritus*, *A. guariba clamitans*,
224 *Callithrix penicillata* and *C. geoffroyi* (Berthet, 2018). Gene flow with populations
225 outside of the reserve is restricted because the area is mostly surrounded by high
226 mountains (1,200-2,700 m) with few trees. Fragmentation has recently been aggravated
227 by the intensification of mining activities, land artificialization and intensive forestry on
228 the reserve's border (Província Brasileira da Congregação da Missão, 2013).

229

230 **Study species**

231 Black-fronted titi monkeys are small (1.0-1.5 kg) diurnal primates (Bicca-Marques &
232 Heymann, 2013) endemic to the Atlantic Forest (states of MG, ES, RJ and São Paulo
233 [SP]). They are classified as IUCN Near Threatened because their populations have
234 declined by more than 20% due to habitat loss and forest fragmentation over the past 24
235 years (Jerusalinksy, Melo, Mittermeier, Quadros, & Rylands, 2020). They live in groups
236 of two to six individuals, composed of a life-long monogamous adult pair and their
237 offspring, on a territory of about 20 ha (21-48 ha, Bicca-Marques & Heymann, 2013; 8-
238 28 ha, Caselli, Mennill, Bicca-Marques, & Setz, 2014). The group jointly defends the
239 territorial resources with loud call displays (solos, duets and choruses, Caselli et al.,
240 2014).

241 Black-fronted titi monkeys are mainly frugivorous but also consume insects, seeds and
242 leaves (Bicca-Marques & Heymann, 2013; Caselli & Setz, 2011; Santos, Galvão, &
243 Young, 2012). They are arboreal and spend most of their time in the lower and
244 intermediate canopy of small fruit trees (10-30 m high) to feed or rest during hot hours
245 (Bicca-Marques & Heymann, 2013; Gestich, Caselli, & Setz, 2014; Trevelin, Port-
246 Carvalho, Silveira, & Morell, 2007). They occasionally descend to the forest floor to
247 forage, travel and play (Souza-Alves et al., 2019b).

248 Mated females give birth to one young per year between July and January (Bicca-
249 Marques & Heymann, 2013; Di Bitetti & Janson, 2000; Souza-Alves, Caselli, Gestich,
250 & Nagy-Reis, 2019a; Valeggia, Mendoza, Fernandez-Duque, Mason, & Lasley, 1999).

251 Young adults of both sexes disperse when they reach 3 years of age (Bicca-Marques &
252 Heymann, 2013). The mechanisms involved in the establishment of new territories

253 remain unknown. A pair of collared titi monkeys *Cheracebus torquatus* has been
254 observed shifting their home range to open space for their offspring (Easley & Kinzey,
255 1986) and a mated back-fronted titi monkey adult was reported being evicted from its
256 group by a new individual (Cäsar, 2011). Individuals live up to 12 years in captivity
257 (Rowe, 1996).

258 The study population is composed of four habituated groups of black-fronted titi
259 monkeys living in the Tanque Grande forest patch, two habituated groups living in the
260 Cascatinha forest patch, and their neighbors (i.e., the non-habituated groups whose
261 home ranges overlap with those of the habituated groups). We began the habituation
262 process in 2004 (Berthet, 2018; Cäsar, 2011) and monitored the habituated groups
263 extensively between 2008 and 2010 and between 2014 and 2016.

264 There were other non-habituated black-fronted titi monkey groups in the reserve, but we
265 focused on the habituated ones and their neighbors, for which we have reliable long-
266 term data.

267

268 **Demography, density and spatial distribution**

269 Pre-outbreak monitoring (2008-2010 and 2014-2016)

270 We monitored five groups (A, D, M, P and R groups) for 1,295 h over 15 months
271 between 2008 and 2010 (July-December 2008, May-October 2009, May-July 2010). We
272 habituated the remaining (S) group in 2014 and monitored all six groups for 1,714 h
273 over 17 months between 2014 and 2016 (October-December 2014, April-June 2015,
274 October 2015-August 2016).

275 We located the groups at dawn (around 06:00 am) by acoustic cues, and monitored them
276 continuously until i) we lost them, ii) they settled in a sleeping tree, iii) we completed a

277 behavioral experiment, or iv) after 6 h of monitoring (see Berthet, 2018; Cäsar, 2011 for
278 more details). We georeferenced the position of the estimated center of the group every
279 5 min (2008-2010) or every 10 min (2014-2016) using a handheld Garmin GPSMAP
280 60CSx GPS. We opportunistically recorded encounters with neighboring non-
281 habituated groups.

282 We also opportunistically recorded births, deaths and long-lasting disappearances. We
283 considered that disappearances of unmated individuals older than 30 months were most
284 likely due to dispersion, while disappearances of mated adults were most likely due to
285 death (Bicca-Marques & Heymann, 2013; Bossuyt, 2002; Cäsar, 2011; Dolotovskaya,
286 Roos, & Heymann, 2020). Disappearances of individuals younger than 30 months were
287 also most likely due to death, as they are too young to disperse or to survive solitarily
288 (Cäsar, 2011).

289 We monitored each habituated group during at least two days per month between 2008
290 and 2010 and during at least four days per month between 2014 and 2016. Individuals
291 were reliably identified and recognized using a combination of physical cues, such as
292 body size, tail features, color variations and stains, scars, and facial features (Fig. S1).

293

294 Post-outbreak survey (2019)

295 We recorded data during four consecutive weeks between August and September 2019.
296 We conducted an intensive monitoring session (about 90 h) throughout the study using
297 a procedure similar to that described earlier. Whenever possible, we identified
298 individuals from the 2016 habituated population using the aforementioned physical
299 features. We also recorded the reactions to the presence of human observers (from less
300 tolerant to most tolerant: flight, display, avoidance, curiosity, ignore), as a cue of the

301 habituation stage of the individuals (Williamson & Feistner, 2011). Finally, we
302 georeferenced the position of the estimated center of the group every 10 min using a
303 handheld Garmin GPSMAP 60CSx GPS.

304 Given that we did not monitor the groups between 2016 and 2019 and that some
305 individuals were not habituated, contact time did not exceed 4 h per day for two main
306 reasons. First, most non-habituated individuals regularly fled, and it was not always
307 possible to find them back. Second, the goal of our study was to survey the remaining
308 groups instead of to (re-)habituate them: we avoided to follow groups containing non-
309 habituated individuals (i.e., individuals displaying avoidance, flight behaviors;
310 Williamson & Feistner, 2011) for long periods of time to minimize unnecessary harmful
311 levels of stress (Fedigan, 2010).

312

313 *Post-outbreak playback experiments (2019)*

314 We applied a playback method (Gestich, Caselli, Nagy-Reis, Setz, & Cunha, 2016) to
315 locate black-fronted titi monkey groups. This method relies on the territorial behavior of
316 titi monkeys: broadcasted duets of unknown individuals simulate the presence of
317 potential competitors in or close to the territory. Resident groups respond to the
318 playbacks with duets (usually with the participation of the mated pair) or choruses (the
319 adult pair and/or older offspring) to defend their territory's resources against potential
320 intruders (Caselli, Mennill, Gestich, Setz, & Bicca-Marques, 2015). Estimating
321 population densities using playback methods has been shown to be extremely reliable
322 for black-fronted titi monkeys, with a rate of group detection close to 100% (Gestich et
323 al., 2016).

324 We broadcasted duets from one resident group of each forest patch into the other forest
325 patch to stimulate an intrusion by an unknown couple and trigger vocal responses by
326 residents (Caselli et al., 2015). We used 1-min-long samples extracted from four duets
327 from P and S groups recorded in 2016 in which both mates were calling. We normalized
328 sequences at -1 dB and broadcasted them using an Anchor An-30 (Anchor, Carlsbad,
329 CA) loudspeaker (frequency response range: 100–15,000 Hz, output power: 30 W,
330 Maximum SPL at 1 m: 100 dB), which covers the frequency spectrum of black-fronted
331 titi monkeys' vocalizations and reaches the same levels of the natural emissions of
332 duets. We held the speaker at a height of 2 m and directed it to four directions separated
333 by an angle of 90° for 15 s each to cover a circular area in 1 min.

334 We determined a 200-m playback circumference (i.e., the distance at which the
335 broadcasted duets could be heard) during pilot trials in a forest patch that was not
336 occupied by titi monkeys. We conducted the playback trials in the maximum area
337 occupied by the habituated groups, i.e., the sum of the area occupied by each group
338 from 2008 to 2010 and from 2014 to 2016. We conducted 14 playback trials at 180-m
339 intervals to fully cover the area of interest (Fig. 1).

340 We played two sequences at 5-min intervals per trial in the morning (Gestich et al.,
341 2016) and alternated recordings to avoid habituation to the stimuli. We registered the
342 responses of neighboring groups during the first 5 min after each playback sequence. A
343 trial lasted 12 min (1 min stimulus followed by 5-min waiting period, followed by 1 min
344 stimulus then 5-min waiting period). We estimated the distance of all vocal responses to
345 the playback stimuli and registered their direction in relation to the location of the
346 playback with a compass. When a responding group approached the speaker and was in
347 sight, we did not play the second stimulus to avoid a reduction in responsiveness in

348 future trials. We conducted playback experiments for four days (two consecutive days
349 in the Cascatinha forest patch and two consecutive days in the Tanque Grande forest
350 patch) for at most 4 h per day (Gestich et al., 2016) (See Supplementary Material).

351 We later plotted all location records on the home range map and clustered vocal
352 responses according to the spatial and temporal distance between the responses. We
353 registered clusters as belonging to the same group unless we had evidence that they
354 were distinct groups (Gestich et al., 2016).

355

356 **Estimation of population changes**

357 *Demography*

358 To estimate the population stability between 2008 and 2016, the size of each habituated
359 group in summer (between July and October, depending on data availability) was
360 extracted for the two pre-outbreak monitoring periods. We calculated each group's
361 2008-2010 and 2014-2016 mean size and we used a two-tailed Wilcoxon paired signed-
362 rank test to test whether the mean group sizes varied between the two monitoring
363 periods.

364 To estimate the population changes between 2016 and 2019, we assessed the size of the
365 habituated groups in 2016 and in 2019 based on the monitoring, survey and playback
366 data. We assessed the presence and location of neighboring groups based on anecdotal
367 encounters and playback results. Since we did not know the exact composition of the
368 neighboring groups, we assigned them a hypothetical size of four individuals because
369 black-fronted titi monkey groups are usually composed of one mated pair and one to
370 three offspring (Bicca-Marques & Heymann, 2013).

371

372 Home ranges

373 We used the estimated home ranges as another proxy of the changes in the black-
374 fronted titi monkey population. Given the stability and high territorialism of titi monkey
375 groups (Bicca-Marques & Heymann, 2013; Caselli et al., 2014), home ranges usually
376 remain constant over the years. To estimate the stability of the groups before 2016, we
377 compared the home range size and location of each habituated group between 2008-
378 2010 and 2014-2016: if the population was stable (i.e., well established home ranges, no
379 disappearance of a group or establishment of a new one) then home ranges of the
380 habituated groups should remain constant between the two monitoring periods prior to
381 2016.

382 To this end, we georeferenced the home ranges of the habituated groups using GPS data
383 collected in 2008-2010 and 2014-2016. Due to logistic issues, some of the 2008-2010
384 GPS data were lost, so associated home ranges were drawn using the remaining GPS
385 data, which probably underestimated their real size (see Table 1). We mapped the
386 borders using characteristic hull polygons (Downs & Horner, 2009). While the home
387 range is usually measured as the smallest area in which animals spend 95% of their
388 time, we decided to use 100% of the collected GPS points to remain conservative. We
389 estimated the size of each home range in 2008-2010 and in 2014-2016, and compared
390 them using a two-tailed Wilcoxon paired signed-rank test. We also calculated the
391 proportion of overlap between the two periods (i.e., the proportion of the 2008-2010
392 home range that was still used by the same group in 2014-2016). Finally, we used
393 opportunistic encounters with neighbors to identify the home range borders shared with
394 non-habituated groups in 2008-2010 and 2014-2016.

395 We also used the home range data to estimate changes in the population between 2016
396 and 2019. We hypothesized that if, in 2019, a black-fronted titi monkey group occupied
397 an area located in the 2016 home range of another group, then the latter had probably
398 disappeared from the area between 2016 and 2019.

399 Mapping and calculations were conducted in QGIS 3.8.2 (QGIS Development Team,
400 2009) with the concave hull add-on (Detlev, 2019) and statistical analyses were
401 conducted in R 4.0.0 (R Core Team, 2020).

402

403 **Data availability statement**

404 The data supporting the findings of this study are available from the corresponding
405 author upon request.

406

407 **Ethics statement**

408 The research reported in this article was conducted in compliance with all relevant local
409 and international laws. The 2008-2010 data collection was approved by the University
410 of St Andrews Psychology Ethics Board, the 2014-2016 data collection was approved
411 by the ethical committee CEUA/UNIFAL (number 665/2015) and the 2019 data
412 collection was approved by the CEUA/PUCRS (number 9438).

413

414 **Results**

415 **Pre-outbreak monitoring (2008-2010 and 2014-2016)**

416 *Demography*

417 The size of habituated groups was stable prior to the outbreak (Fig. S2): mean group
418 size did not significantly vary between 2008-2010 and 2014-2016 ($W = 1$, p -value =

419 0.125) (Table 1). In August 2016, the habituated population comprised six groups (33
420 individuals): four groups in Tanque Grande (21 individuals) and two groups in
421 Cascatinha (12 individuals). They were neighbors of five or six non-habituated groups:
422 four groups in Tanque Grande and one or two groups in Cascatinha (Fig. 2). Overall, we
423 found that 11 to 12 groups inhabited the two studied forest patches by the end of 2016.
424 The characteristics of the demographic events confirm that the dispersal of young adults
425 and the death of young individuals were the main causes of disappearance, while the
426 disappearance of mated adults was rare (one observation, i.e., 7% of the total
427 disappearances, see Table 2).

428

429 Home ranges

430 The size of the habituated groups' estimated home ranges tended to increase between
431 the two pre-outbreak monitoring periods, although the difference was not significant:
432 home ranges varied from 4.5-6.2 ha in 2008-2010 (mean \pm s.d. = 5.1 ± 0.8 ha) to 6.3-7.9
433 ha in 2014-2016 (mean \pm s.d. = 7.1 ± 0.7 ha; $V = 0$, p-value = 0.058) (Table 1). Each
434 group's home range in 2008-2010 was still mostly occupied by the same group in 2014-
435 2016 (overlap = 82-97 %, mean \pm s.d. = 89 ± 6 %, Table 1, Fig. 2).

436

437 **Post-outbreak period: 2019**

438 Survey

439 During the 90-h survey, we did not find any sign of the presence of titi monkey groups
440 in the Cascatinha forest patch (no encounter, no duet). In the Tanque Grande forest, we
441 found evidence of the presence of at least three groups. We encountered one of these
442 groups on several occasions, and we heard several duets emitted by this group and at

443 least two other groups, both located outside of the home ranges of the 2016 habituated
444 groups (i.e., two non-habituated groups).

445 The group that we encountered (later referred to as the ‘partially habituated group’) was
446 composed of three individuals. The mated male was the resident adult male of the R
447 group from 2008 to 2016, easily recognizable by its specific physical features.
448 Moreover, this individual ignored our presence in 2019, which is congruent with the
449 fact that the adult male of the R group was one of the most habituated individuals of the
450 2016 titi population. The mated female was born in the A group in 2014, also easily
451 recognizable by her physical traits. This individual exhibited intermediate-tolerance
452 behaviors (avoidance, curiosity) in our presence, suggesting that she was still in the
453 habituation process, a conclusion congruent with the fact that she was only monitored
454 for two years before 2016. The last individual was a juvenile estimated to have been
455 born by the end of 2017 based on observations of its size and behavior (e.g., play,
456 exploration, no participation in territorial defense). The juvenile was not habituated to
457 human presence (flight, avoidance, curiosity). The group ranged in an area previously
458 occupied by the A, D, R and S groups (Fig. 3).

459

460 *Playback experiments*

461 We recorded no response to the five playback trials conducted in the Cascatinha forest
462 patch, but recorded 20 vocal responses to the nine playback trials conducted in the
463 Tanque Grande forest patch (Table S1). The responding individuals were the partially
464 habituated group monitored during the survey, two non-habituated groups whose duets
465 were heard during the monitoring, and a supposedly solitary individual who emitted
466 solos (Fig. 4).

467 One of the non-habituated groups was sighted once and immediately lost, while the
468 other non-habituated group and the solitary individual were never sighted. We did not
469 find any evidence of the presence of other habituated groups during the 4-week survey
470 (no duets nor direct observations).

471

472 Impact of the YF outbreak on the titi monkey population

473 In 2016, we estimated the size of the Cascatinha population at 16-20 individuals (12
474 habituated and 4-8 non-habituated individuals) and the 2016 Tanque Grande population
475 at 37 individuals (21 habituated and 16 non-habituated individuals), i.e., a population of
476 53-57 individuals in the two forest patches. In 2019, we estimated the Cascatinha
477 population at zero, and the Tanque population at 12 individuals (three individuals in the
478 partially habituated groups, one solitary individual and two unknown groups) (Fig. S2).
479 Therefore, we estimate the Cascatinha population to have declined by 100% and the
480 Tanque Grande population to have declined by 68% between 2016 and 2019. Overall,
481 we estimate the black-fronted titi population to have declined by about 80% between
482 2016 and 2019 in the two forest patches (from a total of 53-57 individuals in 2016 to 12
483 individuals in 2019).

484

485 **Discussion**

486 We found that the home ranges and the size of the habituated black-fronted titi monkey
487 groups of the Santuário do Caraça did not markedly vary from 2008 to 2016. The size of
488 the estimated home range tended to increase between 2008-2010 and 2014-2016, and
489 the 2008-2010 home ranges were almost entirely occupied in 2014-2016 by the same
490 groups (mean overlap of around 90%). We believe that the variation trend of the home

491 ranges' size is better explained by differences in sampling effort (given the loss of some
492 2008-2010 GPS data, Table 1) rather than true home ranges variations. The stability of
493 the two forest patches' groups size and home ranges is compatible with the conclusion
494 that populations were stable in both forest patches in 2008-2016.

495 After the 2016-2018 sylvatic YF outbreak, we did not find any black-fronted titi
496 monkey in the Cascatinha forest patch, and we found only three groups and one likely
497 solitary individual in the Tanque Grande forest patch (ca. 12 individuals). One of the
498 remaining groups is composed of the former resident male of the R group, which now
499 occupies an area greatly overlapping the 2008-2016 home range of at least two other
500 groups (D and S group). Given titi monkeys' strong site fidelity and high territoriality
501 (Bicca-Marques & Heymann, 2013; Caselli et al., 2015), the death of D and S group
502 members is the most likely explanation for the changes in home ranges' occupation.

503 We are confident that our combination of a 90-h survey and playback experiments
504 provided reliable data on the occurrence of these shy, but highly vocal platyrrhines
505 (Bicca-Marques & Heymann, 2013). First, playback surveys have an accuracy close to
506 100% to estimate the presence of black-fronted titi monkey groups (Gestich et al.,
507 2016). Second, the two researchers conducting the survey had an excellent knowledge
508 of the habituated black-fronted titi monkey groups from 2016 and their behavior and
509 ecology (home range, regular paths, feeding and sleeping sites, activity budget).
510 Moreover, in 2016, all habituated groups were duetting/chorusing almost every day, and
511 up to nine times per day (unpublished data). It is therefore very unlikely that our 90-h
512 effort over a four-week survey (combined with our presence in the forest patches
513 during/around the playback experiments) was insufficient to detect the titi monkeys.
514 Third, the survey results corroborate those from the playback experiments. In

515 conclusion, it is unlikely that the combination of the two methods failed to detect other
516 titi monkey groups in the Tanque Grande and Cascatinha forest patches. Although we
517 may have missed solitary individuals, which can be argued to be less responsive to
518 intruders' duets than resident groups, the three responses of one solitary to our playback
519 trials (Table S1) does not support this hypothesis. Irrespective of the presence of some
520 undetected solitary individuals, we are certain that most groups disappeared from the
521 forest patches between 2016 and 2019.

522 It is unlikely that natural demographic oscillations could account for the observed
523 overall decline, given the aforementioned long-term population and home range
524 stability of titi monkey species (Bicca-Marques & Heymann, 2013; Easley & Kinzey,
525 1986; Gestich et al., 2016; Müller, 1995), which were confirmed by the pre-outbreak
526 monitoring. Although young adults of both sexes disperse when they reach adulthood
527 (Bossuyt, 2002; Dolotovskaya et al., 2020), resident adults rarely disappear from their
528 home ranges (Bicca-Marques & Heymann, 2013, this study).

529 The hypothesis of major ecological changes either causing the death of the resident
530 groups or forcing them to leave the area is also not supported by the available evidence.
531 No forest fire occurred in the reserve between 2008 and 2019 (INPE, 2011; pers. obs.)
532 and long-term meteorological data do not reveal unusual climatic events (e.g., drought,
533 extreme flooding or extreme temperature variations) between September 2016 and
534 September 2019 (Fig. S3) that could have led to dramatic food shortage. Additionally,
535 black-fronted titi monkeys are not targeted by the illegal pet trade or hunting
536 (Jerusalinksy et al., 2020), and activities detrimental to local wildlife are forbidden
537 within the RPPN Santuário do Caraça by the Sistema Nacional de Unidades de
538 Conservação (SNUC) law, which is locally enforced by forest guards. No logging,

539 deforestation, or poaching was recorded in the Cascatinha or Tanque Grande forest
540 patches between 2016 and 2019 (Abreu A., pers. com.).

541 Contrary to these unlikely hypotheses, the short-term disappearance of a large part of
542 the black-fronted titi monkey population during a YF outbreak can be explained by the
543 high vulnerability of *Callicebus* species to the virus (Sacchetto et al., 2020).
544 Furthermore, the mean home ranges size of the habituated groups in 2016 was smaller
545 than in other populations (7 ha vs 20 ha, Bicca-Marques & Heymann, 2013; Caselli et
546 al., 2014), suggesting a high titi monkey density that may have also facilitated the
547 spread of the YF virus (Possas et al., 2018). Therefore, although we do not have
548 uncontested evidence of the role of YF in the documented dramatic population
549 collapse, this is by far the strongest hypothesis.

550 The fact that no primate carcass was reported by the reserve workers and visitors does
551 not provide a strong argument against the YF hypothesis, as the likelihood of finding a
552 dead small animal is low: it is estimated that only 5% of the monkeys (including species
553 much larger than titi monkeys such as howler monkeys) that die of YF in the interior of
554 forests are recorded (Duchiade, 2018). First, a monkey carcass is quickly eaten by the
555 local scavengers, disappearing in <24 h (pers.obs.). Second, only a small proportion of
556 visitors hike in the forests as the majority remains in the farm/hotel/church complexes
557 or walk on trails that do not cross forested areas. Third, visitors crossing forest patches
558 remain on trails that cover only 0.6% of Cascatinha forest and 0.3% of Tanque Grande.
559 Finally, we cannot exclude the possibility that some visitors encountered a carcass but
560 did not report it to local workers and authorities.

561 We focused our study on a small proportion (11-12 groups) of the Santuário do
562 Caraça's black-fronted titi monkey population because we lacked long-term

563 demographic data for other groups. However, we can likely extrapolate our findings to
564 the whole reserve, as there is no reason to believe that the habituated groups and their
565 neighbors would be more sensitive or more exposed to the YF virus than the rest of the
566 population. Additionally, Caraça's employees reported lower rates of titi monkey
567 choruses or sightings in other parts of the reserve. Therefore, we suspect that the YF
568 outbreak not only affected the Cascatinha and Tanque Grande's population, but also
569 impacted other groups of black-fronted titi monkeys at the Santuário do Caraça. Further
570 investigation is needed to estimate the current state of the remaining Caraça population.
571 Despite the legal protection provided by the reserve, the surviving black-fronted titi
572 monkey population may disappear in the medium- to long-term. Even if the remaining
573 adult individuals are resistant to the YF virus and can pass this trait to descendants
574 (Almeida et al., 2019a), the population is small and geographically isolated from other
575 populations due to the reserve's topography, habitat fragmentation and the intensive
576 human activities in the surrounding areas. These conditions increase the population's
577 vulnerability to stochastic events, such as genetic drift and inbreeding, random
578 demographic variations, natural catastrophes, other disease outbreaks and climatic
579 events (Costa, Fernandes, Hilário, Gonçalves, & Souza, 2012).

580 This prospect is worrisome at the species level. Black-fronted titi monkey populations
581 have experienced declines over the last decades (more than 20% in the past 24 years,
582 Jerusalinsky et al., 2020), mainly due to the degradation of the Atlantic Forest (Ribeiro,
583 Metzger, Martensen, Ponzoni, & Hirota, 2009). Titi monkeys can live in primary and
584 secondary forests (Trevelin et al., 2007) with high and closed canopy (Sales, Hayward,
585 & Passamani, 2016), which enables them to occur in small forest patches embedded in

586 agricultural landscapes (Ribeiro et al., 2009). The inevitable proximity to humans and
587 domestic animals in these landscapes increases the chances of pathogens transmission.
588 The resurgence of similar deadly outbreaks is a severe threat to the local fauna. Brazil is
589 the world's richest country in primate diversity, but 48% of its primate species have
590 declining populations because of habitat loss and fragmentation, hunting, infectious
591 diseases and climate change (Estrada et al., 2018). This YF outbreak worsened the
592 conservation status of most nonhuman primates of southeastern Brazil. Given the
593 absence of accurate pre-outbreak demographic data for most species, reported figures
594 are likely underestimating the damage. Populations of *A. guariba clamitans*, *B.*
595 *hypoxantus*, *C. personatus*, *S. nigritus*, *C. flaviceps*, *C. geoffroyi* and *L. rosalia* (Dietz et
596 al., 2019; Gontijo, 2019; Lopes, 2017; Possamai et al., 2019; Strier et al., 2019) in
597 addition to *Callicebus nigrifrons* (this study) have suffered dramatic losses. The risk of
598 the YF virus remaining in the same region for three transmission seasons or longer
599 (Abreu et al., 2019a), re-emerging and causing further population declines is real.
600 In the light of such a demographic decline in the Santuário do Caraça's population, we
601 highlight the emergency of surveying other, less protected populations of black-fronted
602 titi monkeys, but also other Platyrrhini species, to re-evaluate the conservation status of
603 impacted species and take appropriate measures to protect them. At a broader scale, we
604 call for action, and advise local health and environmental authorities to hear scientists
605 (Abreu et al., 2019a; e.g., Bicca-Marques & Freitas, 2010; Cupertino et al., 2019;
606 Gouveia et al., 2016; Kaul et al., 2018; Oliveira Figueiredo et al., 2020; Possas et al.,
607 2018; Possas, Martins, Oliveira, & Homma, 2017) and to adopt sound conservation and
608 sanitary strategies (e.g. continuous active surveillance of wildlife reserves, regular
609 monitoring of key primate populations, extensive vaccination of vulnerable human

610 populations, communication and awareness campaigns, restriction of wildlife reserves
611 to unvaccinated visitors) to avoid future dramatic outbreaks that can lead to the local or
612 regional extirpation of sensitive species.

613

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638

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936

937 **Tables**

938

939 Table 1. Size and monitoring effort of six habituated titi monkey groups during the
 940 2008-2010 and 2014-2016 surveys. Group mean sizes were calculated using the group
 941 sizes recorded in summer (July-October). The 2008-2010 monitoring effort comprises
 942 the total monitoring effort (i.e., time spent monitoring the groups) and the monitoring
 943 effort from which GPS data were extracted to draw home ranges. Home range sizes are
 944 estimated using 100% characteristic hull polygons (Downs & Horner, 2009). Overlaps
 945 are calculated as proportion of the 2008-2010 home range that was still occupied by the
 946 same group in 2014-2016.

947

			2008-2010			2014-2016		
Forest	Group	Habituation	# Individuals	Home	Monitoring	# Individuals	Home	Monitoring
				range	effort (h)		# remaining from	
			size (ha)	[GPS	2010]	(ha)	[overlap in]
				monitoring		[overlap in	%]	
				(h)]		%]		
	A	2008	5-7 (mean = 6)	5.7	324 [60]	6 (mean = 5.6) [1]	7.7 [97]	225
Tanque	D	2004	2-4 (mean = 2.6)	4.5	322 [42]	4-5 (mean = 4.6) [2]	7.5 [82]	197
Grande	R	2004	2-4 (mean = 3.3)	4.8	347 [60]	4-6 (mean = 5) [1]	6.6 [85]	261
	S	2015	-	-		4-5 (mean = 4.3)	6.5	425
Cascatinha	M	2009	4-5 (mean = 5)	6.2	144 [44]	5-6 (mean = 5.6) [2]	7.9 [89]	269
	P	2008	3-5 (mean = 4)	4.5	158 [60]	4-5 (mean = 5.3) [2]	6.3 [93]	335

948

949

950 Table 2. Likely causes of disappearance of individuals and their age-class, during the
 951 2008-2010 and 2016-2016 surveys (Berthet, 2018; Cäsar, 2011).

	Mated adult (>30 months)	Unmated adult (> 30 months)	Subadult (18-30 months)	Infant (< 6 months)
Confirmed death		1†		
Supposed death	1		1	8
Supposed dispersion		4		
Total	1	5	1	8

952 † The carcass was found by researchers.
 953

954 **Figure legends**

955

956 Fig. 1. Distribution of playback trials in the home ranges of the habituated titi monkey
957 groups in the Tanque Grande (west) and Cascatinha (east) forest patches.

958

959 Fig. 2. Home ranges of habituated titi monkey groups from (A) 2008 to 2010 and (B)
960 2014 to 2016. The S group was habituated in 2014. Home range borders in bold are
961 shared with at least one non-habituated group. In 2016, four habituated groups and four
962 non-habituated groups inhabited the Tanque Grande forest patch (west), and two
963 habituated groups and one-two non-habituated groups inhabited the Cascatinha forest
964 patch (east).

965

966 Fig. 3. Spatial occupation of the surviving partially habituated group (pink dots) during
967 the 2019 survey. The group used an area occupied by the A, D, R, and S groups in
968 2008-2016.

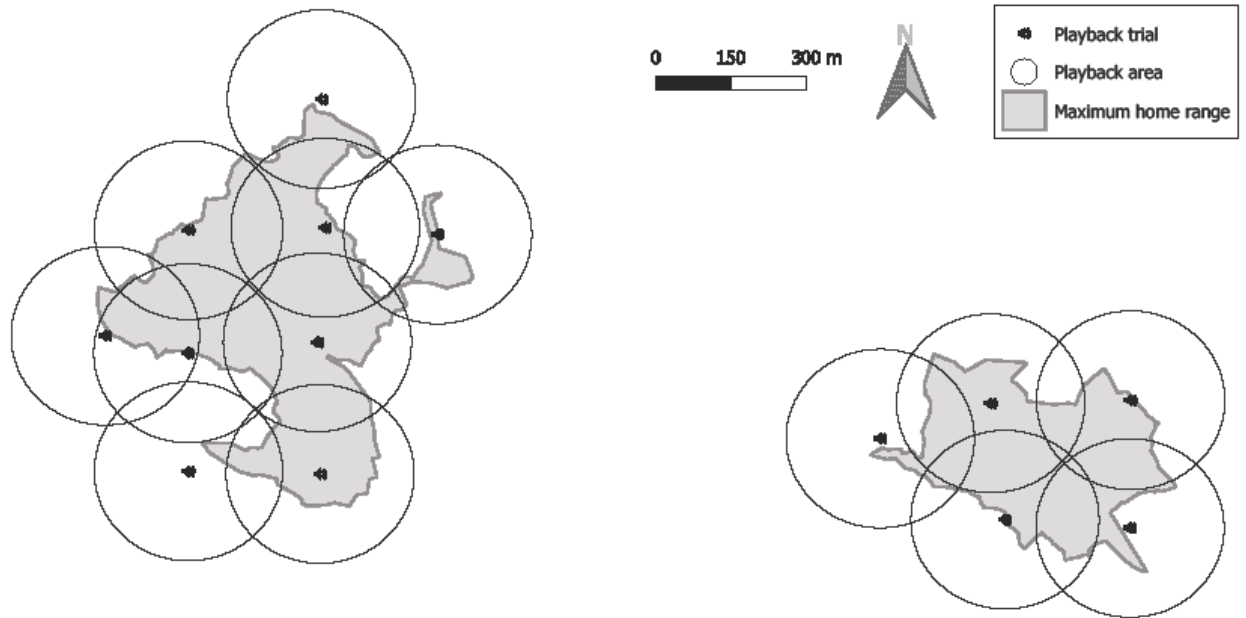
969

970 Fig. 4. Vocal responses to playbacks by a partially habituated group, a supposedly
971 solitary individual and two non-habituated groups in 2019.

972

973 **Figures**

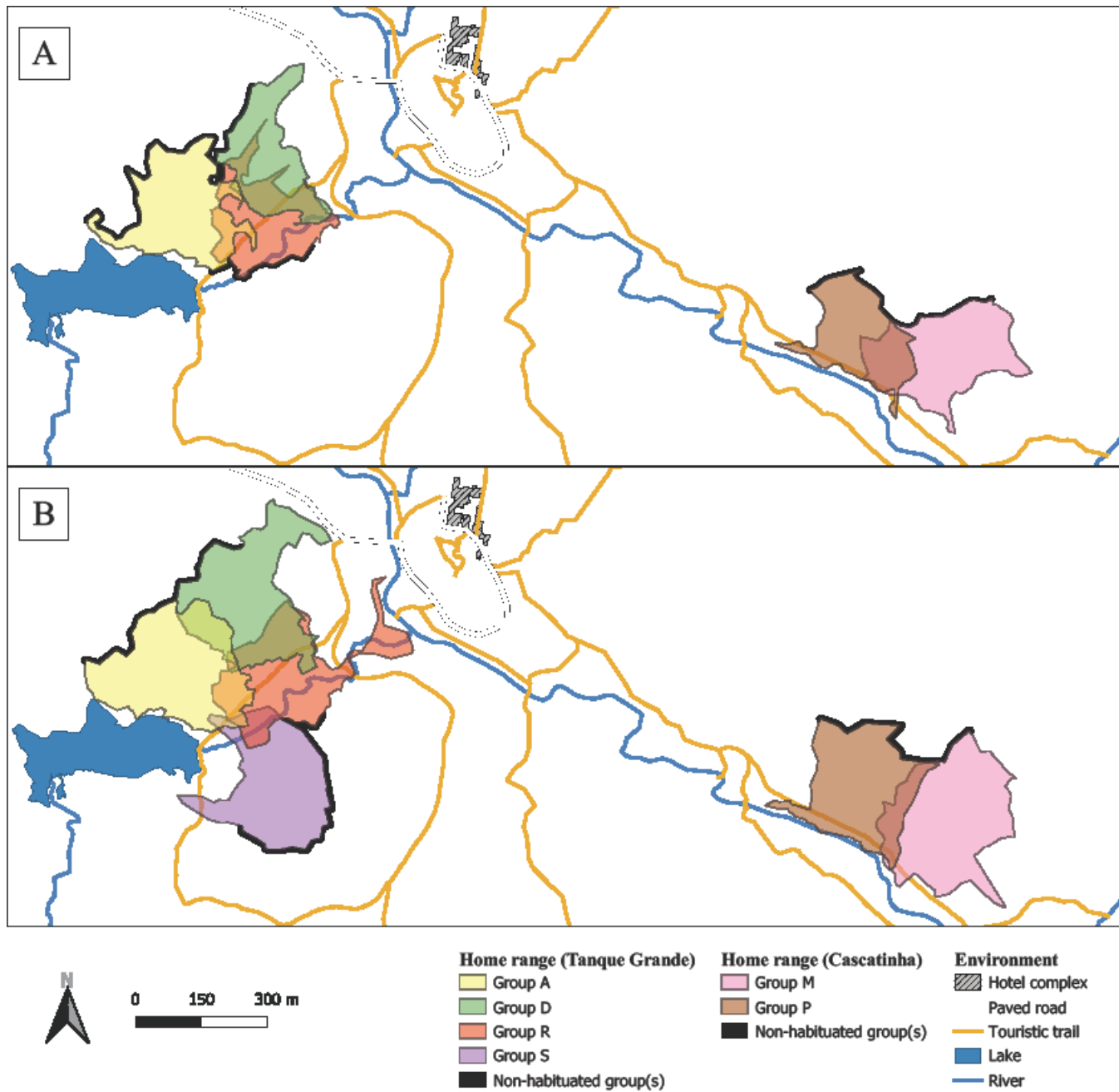
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978 groups in the Tanque Grande (west) and Cascatinha (east) forest patches.

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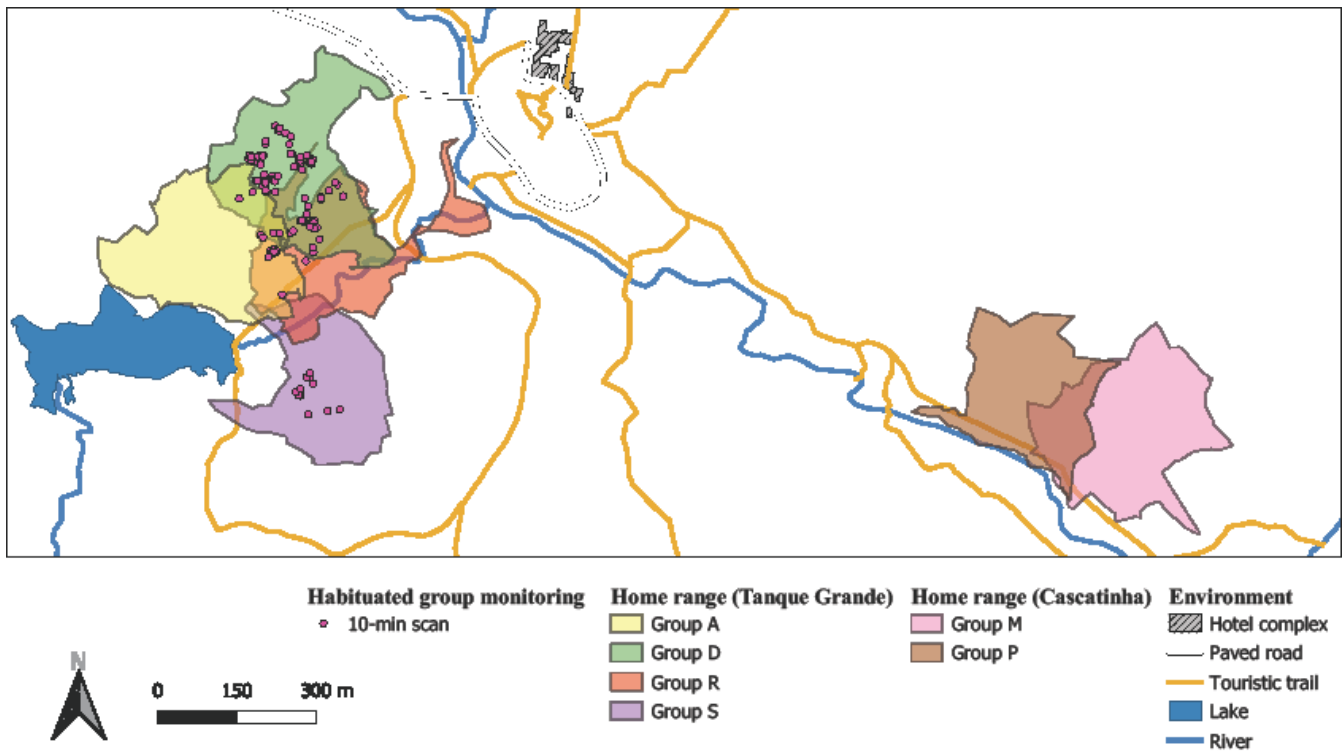


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986 habituated groups and one-two non-habituated groups inhabited the Cascatinha forest
987 patch (east).

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991 Fig. 3. Spatial occupation of the surviving partially habituated group (pink dots) during

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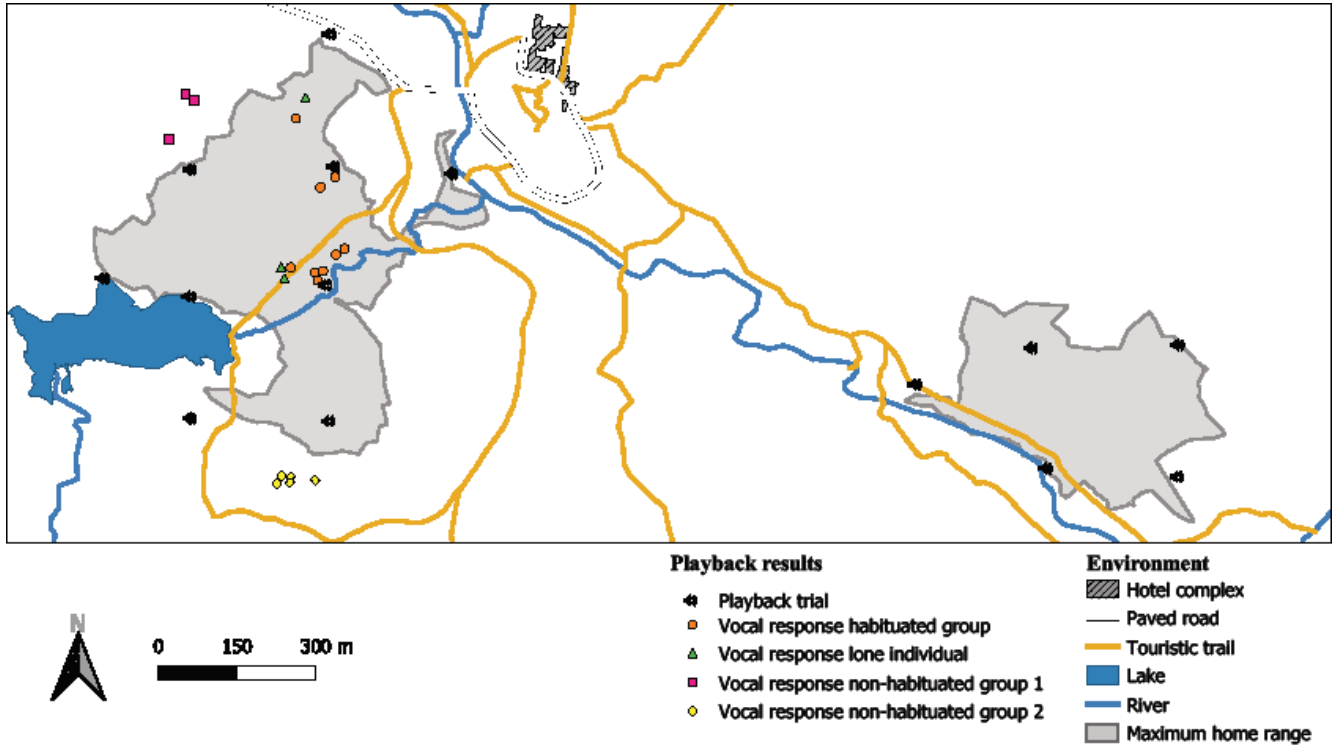
993 2008-2016.

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1000 Fig. 4. Vocal responses to playbacks by a partially habituated group, a supposedly
1001 solitary individual and two non-habituated groups in 2019.

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