

1 Loud speech at a Peruvian tourist site triggers flight in pygmy marmosets (*Cebuella*  
2 *pygmaea*) and any speech reduces time spent feeding and resting, and increases alert  
3 behavior.

4 Short Title: Pygmy marmosets and tourist noise

5

6 Rebecca L Sheehan<sup>1</sup>, and Sarah Papworth\*<sup>1</sup>

7

8 <sup>1</sup> Royal Holloway, University of London

9

10 \*Author for correspondence: Sarah Papworth, School of Biological Sciences, Royal  
11 Holloway, Egham, Surrey, TW20 0EX

12

13 **Abstract**

14 While potentially beneficial in terms of raising awareness and conservation  
15 funding, tourist-visitation of wild primates can have negative impacts on visited  
16 groups. Tourism-generated noise is a relatively understudied facet of ecotourism  
17 research, and the effects of tourist generated noise on free-ranging, wild primates has  
18 never previously been explored. This study investigates the behavioral responses of  
19 ten groups of pygmy marmosets (*Cebuella pygmaea*) to human speech. Through the  
20 use of a manipulative playback study using recorded human speech, we show that

21 pygmy marmosets within the Tamshiyacu-Tahuayo Reserve, Peru, are significantly less  
22 visible and often move completely out of sight after louder playbacks. Although no  
23 consistent differences were found in other behaviors with playback duration and  
24 volume, playbacks of human speech tended to increase the amount of time individuals  
25 were alert, and decrease feeding and resting behaviors, whereas these effects were  
26 not found in response to playbacks of white noise. Our results demonstrate that  
27 tourist-generated noise can alter the behavior of visited primates, and identifies the  
28 particular effect of noise volume on primate visibility. As all trials in this study took  
29 place near a marmoset group's feeding tree, moving out of sight from the visible study  
30 area is the most energetically costly behavior observed, and also has a negative effect  
31 on visitor enjoyment as it limits the time that they are able to view the target species.  
32 As this response was never observed (nor was any other consistent behavior change)  
33 in control trials where the marmosets were exposed to human presence but not to  
34 speech, this study suggests that negative tourist impacts can be reduced by  
35 encouraging tourists to refrain from speaking in the presence of visited primate  
36 groups.

37

38 **Keywords:** acoustic disturbance, ecotourism, flight initiation, pygmy marmoset

39

#### 40 **Research Highlights**

- 41 • Wild pygmy marmosets at an ecotourism and research site moved away from,  
42 and were less visible after, playbacks of human speech.

- 43       • This effect of reduced visibility and movement away increased as playback  
44       volume increased.
- 45       • Playbacks of human speech were linked to reduced time feeding and resting,  
46       and an increase in alert behaviors by pygmy marmosets.

47

## 48   **1. Introduction**

49       Since its advent in the 1980s (Fennell, 2001) ecotourism has developed into an  
50       industry catering for over 8 billion visitors worldwide each year (Balmford et al., 2015)  
51       and represents a vital source of revenue for a number countries (e.g. Kirkby et al.  
52       2010; Tumusiime & Svarstad 2011). Despite the potential conservation benefits  
53       associated with ecotourism, namely increased funding (Buckley, Morrison, & Castley,  
54       2016) and protection (Robbins et al., 2011), a review by (Kruger, 2005) concluded that  
55       over a third of ecotourism projects are ecologically unsustainable. Ecotourism projects  
56       may be unsustainable for a number of reasons, including negative impacts on flagship  
57       species. These impacts may be apparent at the population level, such as changes in  
58       group movement (Aguilar-Melo et al., 2013; Cunha, 2010; Sibbald, Hooper, Mcleod, &  
59       Gordon, 2011) and population declines (McClung, Seddon, Massaro, & Setiawan, 2004;  
60       Watson, Bolton, & Monaghan, 2014), or at the individual level, causing behavioral  
61       (Meissner et al., 2015; Shutt et al., 2014), physiological (Behie, Pavelka, & Chapman,  
62       2010; Zwijacz-Kozica et al., 2013) and morphological (Borg et al., 2015; Maréchal,  
63       Semple, Majolo, & Maclarnon, 2016) changes.

64           The negative effects of tourism on target species can arise due to a number of  
65 different factors, including the total number of tourists, their proximity and their  
66 behavior. High tourist numbers can lead to over-visitation (where sites operate at a  
67 higher capacity than is deemed sustainable) and accelerated environmental  
68 degradation (Shepard, 2002). Higher tourist numbers have been linked to elevated  
69 levels of anxiety in Barbary macaques (*Macaca sylvana*) (Maréchal et al., 2011),  
70 increased infant-directed aggression in Tibetan macaques (*Macaca thibetana*)  
71 (Huangshan, Berman, Li, & Ogawa, 2007), and decreased intra-group socialization in  
72 Mexican mantled howlers (*Alouatta palliata mexicana*) (Aguilar-Melo et al., 2013).  
73 Increased tourist proximity is directly correlated with the risk of disease transmission  
74 in great-apes (Woodford, Butynski, & Karesh, 2002). It is also linked to aggression  
75 levels (Klailova, Hodgkinson, & Lee, 2010) and elevated fecal glucocorticoid levels  
76 (Shutt et al., 2014), an indicator of physiological stress, in western lowland gorillas  
77 (*Gorilla gorilla*). Aside from the effects of tourist proximity, the interactions that take  
78 place between animals and tourists can be harmful – a possibility that many tourists  
79 don't consider (Grossberg, Treves, & Naughton-Treves, 2003). For example, tourists  
80 attempt to provoke a response from black howler monkeys (*Alouatta pigra*), it causes  
81 the female, juvenile and infant howler monkeys move higher into the canopy, while  
82 sub-adult and adult males approach the humans and/or roar (Grossberg et al., 2003).

83           As negative effects on target species are linked to long-term unsustainability of  
84 ecotourism sites, it is important to reduce these negative effects. While reducing  
85 tourist numbers could create adverse economic outcomes, reducing tourist proximity  
86 and changing their behavior does not have to impact revenues. For example, following

87 guidelines issued by the IUCN, all great-ape tracking companies claiming to implement  
88 'best practice' must enforce a minimum approach distance of 7 meters on all their  
89 tours (Macfie & Williamson, 2010). This regulation is industry-wide and as such,  
90 protects great-apes at all 'best-practice' ecotourism sites.

91         One aspect of tourist-behavior that is seldom regulated is noise generation, but  
92 there is observational evidence which suggests that noise associated with ecotourism  
93 disturbs primates (e.g.. de La Torre et al. 2000; Leason & Macgregor 2014). The  
94 frequency of threat behaviors by Tibetan macaques increases with the decibel level of  
95 the tourist viewing platform at Mt. Huangshan, China (Ruesto, Sheeran, Matheson, Li,  
96 & Wagner, 2010). Boat noise is linked to increased levels of fecal testosterone in male  
97 golden mantled howler monkeys (*Alouatta palliata palliata*) and spider monkeys  
98 (*Ateles geoffroyi ornatus*) suggesting that acoustic disturbance provokes an  
99 (energetically costly) aggressive response in these species (Vanlangendonck, Nuñez,  
100 Chaves, & Gutiérrez-Espeleta, 2015). This is supported by anecdotal observations that  
101 male howlers roar when boats pass with their motor on, but not when the motor is  
102 turned off (Vanlangendonck et al., 2015).

103         Decreases in tourism-related noise may enhance visitor experience either by  
104 leading to increased detection rates (Karp & Guevara, 2011) or reducing the likelihood  
105 that animals will flee from tourists (Kinnaird & Brien, 1996). Following a 60 decibel  
106 playback of human conversation, detection of rainforest birds falls by 39% (Karp &  
107 Guevara, 2011). This pattern was documented both in an intact area of protected  
108 forest and the area immediately surrounding an ecotourism lodge, indicating birds do

109 not habituate to the noise of human conversation (Karp & Guevara, 2011). Similarly,  
110 hoatzins (*Opisthocomus hoazin*) habituate to silent approaches by canoe but continue  
111 to flee from 'noisy' approaches conducted with a conversational playback after 10  
112 weeks of trials (Karp & Root, 2009).

113 In spite of the potentially negative effects for visited species and tourists,  
114 tourist-generated noise remains a relatively understudied aspect of the sustainable  
115 ecotourism debate. Thus far, there have been no manipulative studies investigating  
116 the effects of tourist-generated noise on wild, visited primates. Through the use of a  
117 playback experiment using recordings of human speech, this study provides the first  
118 assessment of primate behavioral responses to human speech. Specifically, we  
119 investigate whether there is a significant change in the behavior of pygmy marmosets  
120 (*Cebuella pygmaea*) following playbacks of human speech, and whether this response  
121 is stronger following louder and/or longer playbacks. We hypothesize that the  
122 following behavioral responses will be seen following playbacks of human speech: 1)  
123 pygmy marmosets will alter their behavior following playbacks, spending more time  
124 vigilant, alert and engaging in self-directed behaviors, and less time engaged in  
125 feeding, resting, social and calling behaviors; 2) individuals will move away from the  
126 playback source, either by hiding and decreasing their visibility, or by completely  
127 leaving the area. It is predicted that these effects will be stronger following louder and  
128 longer playbacks.

## 129 **2 Methods**

### 130 **2.1 Study site**

131 This research was carried out between March and May 2017, in the north-  
132 western tropical rainforest of the Area de Conservacion Regional Comunal de  
133 Tamshiyacu-Tahuayo (ACRCTT) (4.293519°S 73.236237°W). Designated in 1991,  
134 ACRCTT was Peru's first state reserve and covers 4,200 km<sup>2</sup>. Hunting is strictly  
135 regulated in ACRCTT and capture of primates forbidden. Annual precipitation ranges  
136 from 2.4 to 3.0 meters per year (Myster, 2015) and the site is subject to annual  
137 monomodal flooding (Kvist & Nebel, 2001). The study area is located on the  
138 blackwater Tahuayo River and its tributaries - the water contains tannins leached from  
139 litter leading to acidity and reduced nutrients (Myster, 2015). The study site was  
140 flooded for the duration of fieldwork.

141 Only one tour operator, Amazonia Expeditions, has accommodation within the  
142 reserve. This study focusses on the areas surrounding Amazonia Expeditions' facilities  
143 on the Tahuayo River: a main lodge operating since 1995 (henceforth referred to as  
144 'main lodge'), close to El Chino village, visited by all guests, and the Tahuayo River  
145 Amazon Research Center (henceforth referred to as 'research center') which tourists  
146 may choose to visit during longer stays. Most tourists stay for 7 nights, though there is  
147 seasonal fluctuation in total visitor numbers with a peak during July and August.  
148 Footfall and capacity are much lower at the research center.

## 149 **2.2 Study species**

150 Pygmy marmosets (*Cebuella pygmaea*) are the world's smallest monkey and  
151 are distributed across the western Amazon, inhabiting lowland evergreen forests close  
152 to rivers, usually on floodplains (Soini, 1982). Historically pygmy marmoset populations

153 have been shown to be severely affected by live capture, noise pollution and habitat  
154 destruction (de la Torre, Yépez, & Snowdon, 2009). They are gum specialists,  
155 morphologically and behaviorally adapted for exudate feeding, but also eat fruit and  
156 insects (Jackson, 2011; Soini, 1982; Yépez, de la Torre, & Snowdon, 2005). They live in  
157 small, co-operatively breeding groups: a breeding female, her offspring from up to four  
158 successive litters, her mate and 1-2 additional adults (Soini, 1982). Home ranges are  
159 typically small (0.1-0.5 hectares) and centered around one or two feeding trees (de La  
160 Torre et al., 2000). The territoriality and specific feeding behavior of pygmy marmosets  
161 make them ideally suited to the experimental set up used in this study. Unhabituated  
162 groups can be reliably located and distinguished, ensuring appropriate rest periods can  
163 be left between playbacks of the different conditions and reducing the potential for  
164 stress from repeated playbacks to the same individuals. Sixteen marmoset groups  
165 were located in the area (Figure 1). The minimum distance between two marmoset  
166 groups was 255 meters. Three sightings of lone marmosets were documented  
167 although no feeding trees were discovered in these locations.

### 168 **2.3 Experimental stimuli**

169 Ten men and ten women were recorded speaking alone for two minutes. All  
170 participants were volunteers, and the majority Royal Holloway University of London  
171 students and faculty. Recordings were conducted using a Sennheiser ME-66 Short-Gun  
172 Microphone linked to a Marantz PMD661 Field Recorder. Background noise was  
173 removed in Audacity and tracks were randomly allocated to treatments before being  
174 cropped to the correct length in PRAAT. Six treatments were used: 60 seconds



175 playbacks of human voices at 30db, 60db and 78db (equivalent to human's whispering,  
176 speaking and raised voices (Lane, Catania, & Stevens, 1961), 120 seconds of a human  
177 voice at 60db, 15 seconds of a human voice at 60db and a 60 second control playback  
178 of white noise at 0db. Playbacks were conducted using a MiPro MA-303SB speaker and  
179 an Apple iPod Nano. Volume was controlled using pre-marked points on the speaker  
180 dial which generated playbacks that averaged 30db, 60db and 78db (when measured  
181 using a decibel meter at 1m) across three randomly selected playback tracks. Average  
182 ambient volume in the flooded jungle was  $47.762 \pm SD 0.985$  decibels (42 measures  
183 across 6 locations).

#### 184 **2.4 Data collection**

185 Known pygmy marmoset feeding trees were approached by boat, with the  
186 motor turned off at least 100m away. The boat was then paddled to the feeding tree  
187 until there was a good view of the feeding tree and surrounding branches. Once a  
188 marmoset was sighted, the equipment was quietly set up. There was then a five  
189 minute rest period before the experiment commenced to decrease the influence of  
190 the disruption of the boat arriving or marmoset detection of researchers.

191 During each experiment, a focal individual was video recorded using a Nikon  
192 D5200 SLR with a 55-300mm lens for 2 minutes prior to commencement of playback,  
193 and two minutes following the commencement of playback. Acoustic behavior was  
194 recorded using a Sennheiser ME-66 Short-Gun Microphone linked to a Marantz  
195 PMD661 Field Recorder. Recordings did not require the individual to be on the feeding  
196 tree, only that they were visible and did not disappear from view for longer than 20

197 seconds during the two minutes of recording prior to a playback. After each trial, a  
198 laser range finder was used to measure the distance from the speaker to the location  
199 of the marmoset at the commencement of playback. Marmosets were an average of  
200 8.82m from the playback source (min = 4.3m, max = 13.7m).

201 Each of the six treatments were conducted with each of 10 marmoset groups.  
202 Focal individuals were all adults but there was no way to discern whether the same  
203 individual was being recorded each time. The order of treatments was randomized for  
204 each group. Trials were conducted between 0630 and 1730, half in the morning and  
205 half in the afternoon. If no individuals were sighted, minimum time to return to return  
206 to the tree to check again was 2 hours. If individuals were sighted but no playback  
207 made, a playback trial could be attempted again after 6 hours. Following a successful  
208 trial with a playback, another trial was not attempted with the same group for a  
209 minimum of 72 hours.

## 210 **2.5 Data analysis**

211 Behavioral responses were retrospectively analyzed from the videos using  
212 CowLog 2.2 (Hänninen & Pastell, 2009). Behaviors were grouped into six types:  
213 feeding, resting, alert, moving, social (grooming, play and calling), self-grooming,  
214 scratching and vigilance (see ethogram, supplementary materials). The 'unknown'  
215 vigilance category (when vigilance could not be observed as an individual's head was  
216 out of view) was removed before calculating percentage of time allocated to the  
217 remaining vigilance categories. Time allocations for behaviors were converted to  
218 percentage of visible time in two minutes and compared before and after

219 commencement of the playback. If an individual remained out of sight for >20 seconds  
220 they were considered 'absent'. Individuals could also be obscured (e.g. only partially  
221 visible), and these categories were combined to classify individuals as 'out of view'.  
222 When individuals moved completely out of sight after the playback commenced, the  
223 study area continued to be observed for up to 20 minutes until a marmoset was  
224 sighted again, and this was recorded as the 'returned' time. It was not possible to  
225 distinguish whether this was the same marmoset. If a marmoset was not observed  
226 within 20 minutes, the trial ended and was classified as 'not returned'.

227 Pygmy marmosets have three main call types that are identifiable by ear, and  
228 used to maintain group contact. The frequency of these lie outside the auditory  
229 sensitivity of their main predators (Snowdon & Hodun, 1981). After increasing the  
230 scale peak by 0.4, spectrograms were used to view recordings in PRAAT (Boersma &  
231 Weenink, 2018) and allow visual and auditory identification of calls. Presence or  
232 absence of vocalizations before and after the start of the playback in each trial was  
233 recorded.

234 Data was analyzed using RStudio Version 1.0.143 (R Core Development Team,  
235 2018). The difference in behavior between the first two minutes and last two minutes  
236 of experiments were used as the response variable. Mixed-effects linear models  
237 (LMERs) from the package lme4 (Bates, Mächler, Bolker, & Walker, 2015) were used to  
238 test for differences in time visible and percentage time allocated to different behaviors  
239 and vigilance categories before and after the playback. A binomial generalized mixed-  
240 effects linear model (GLMER) was used to investigate differences between

241 experiments in whether the focal individuals moved completely out of sight, and for  
242 changes in calling behavior. In all analyses, group was included as a random variable.  
243 The effect of the explanatory variables playback volume (in dB, 0 dB assigned for silent  
244 playbacks of white noise), playback duration (in seconds, 0 seconds assigned for silent  
245 playbacks of white noise) and the confounding variable distance between playback and  
246 focal individual (m) were tested using the Anova function in the car package (Fox &  
247 Weisberg, 2011). Playback distance was included as a confounding variable to control  
248 for potential variations in playback amplitudes across experiments. In analysis of  
249 change in calling behavior, whether calling was recorded before the playback start  
250 (binary variable, yes/no) was also included as a confounding variable. Conditional  $R^2$   
251 (fixed effects) and marginal  $R^2$  (random and fixed effects) were calculated using the  
252 r.squaredGLMM function from the MuMin package (Barton, 2018).

## 253 **2.6. Ethical Statement**

254 This research was conducted under the authority of Amazonia Expeditions  
255 Research Center, Peru, therefore no permit was required. The research adhered to the  
256 American Society of Primatologists' Principles for the Ethical Treatment of Primates  
257 and ethical approval was granted by the Royal Holloway Research Ethics Committee.

258

## 259 **3. Results**

### 260 **3.1 Overview**

261 In total 94 trials were attempted across 12 groups: 67 were successful. Trials  
262 were unsuccessful for a number of reasons: the focal individual moving out of sight  
263 before playback (N = 14) and human interference (tourist presence or boat noise, N =  
264 6) were the main issues. Trials were also abandoned due to weather conditions (N = 3),  
265 equipment malfunctions (N = 3) and the arrival of a habituated woolly monkey (N = 1).  
266 The analyses below are based on the ten groups where a full set of six trials were  
267 conducted: six groups at the main lodge and four at the research center. For these ten  
268 groups, 60 trials were completed in 83 attempts.

### 269 **3.2 Visibility and absence from view**

270 Overall, individuals were classified as out of view for  $3.18 \pm \text{SD}6.05$  seconds in  
271 the first two minutes of the experiment and  $23.29 \pm \text{SD}28.70$  seconds in the last two  
272 minutes. In control experiments, there was no consistent difference in time the focal  
273 individual was in view in the final two minutes of the experiment compared to the first  
274 two minutes (Table 1). In experiments with playbacks, focal individual were in view for  
275 less time in the final two minutes of the experiment, with an average decrease in view  
276 of  $-27.1$  (95%CI  $-37.1, -17.0$ ) seconds. Individuals were less visible after playbacks at  
277 louder volumes and were predicted to spend  $-0.7$  (95% CI  $-1.0, -0.3$ ) fewer seconds in  
278 sight for each 1dB increase in volume (Figure 2,  $\chi^2 = 15.656$ ,  $p < 0.001$ ), but there was  
279 no effect of playback duration or distance from the focal individual to playback source  
280 (LMER: conditional  $R^2 = 0.18$ , marginal  $R^2 = 0.34$ , Duration  $\chi^2 = 2.353$ ,  $p = 0.125$ ;  
281 Distance  $\chi^2 = 0.001$ ,  $p = 0.976$ ).

282 Focal individuals moved completely out of sight in 18/60 trials but never during  
283 control trials (Figure 3, N = 10). Average time to move out of sight following  
284 commencement of playback was  $61.6 \pm \text{SD } 31.4$  seconds (N = 18, range = 17-112  
285 seconds). There were differences between conditions in the probability the focal  
286 individual was visible at the end of the experiment (GLMER: conditional  $R^2 = 0.51$ ,  
287 marginal  $R^2 = 0.39$ ). Mirroring the results on visible time, as the volume increased, the  
288 probability that the focal individual moved completely out of sight increased ( $\chi^2 =$   
289  $6.849$ ,  $P = 0.009$ ), but there was no effect of playback duration ( $\chi^2 = 0.353$ ,  $P = 0.552$ )  
290 or distance between the playback source and the focal individual ( $\chi^2 = 1.513$ ,  $P =$   
291  $0.219$ ).

292 Individuals that moved completely out of sight returned in 9/18 trials, an  
293 average of  $372.4 \pm \text{SD } 231.4$  seconds (N =9, range = 44 s – 782 s) after they  
294 disappeared from view. In three trials where fled individuals were deemed to have  
295 returned, more than one individual fled the area during the trial and therefore it was  
296 not possible to be certain that it was the focal individual that returned. Although three  
297 individuals from groups near the research center returned to view after fleeing, and  
298 eight individuals returned into view at the main lodge groups, there was no significant  
299 difference (Pearson's chi-squared test:  $N_{\text{main lodge}} = 8$ ,  $N_{\text{research center}} = 10$ ,  $\chi^2 = 2.025$ ,  $df =$   
300  $1$ ,  $P=0.155$ ).

### 301 **3.3 Feeding, resting and alert behaviors**

302 During the experiments, pygmy marmosets fed an average of  $30.9 \pm \text{SD } 34.8$  %  
303 of visible time. In experiments with no playback, there was no consistent difference in

304 the amount of time the focal individual spend feeding in the final two minutes of the  
305 experiment compared to the first two minutes (Table 1). In experiments with  
306 playbacks, time spend feeding decreased by an average of -16.4 (95% CI -24.2, -8.6)  
307 percent of visible time. There was no evidence for significant effect of playback  
308 volume, duration or distance on the change in visible time spent feeding (LMER,  
309 conditional  $R^2 = 0.10$ , marginal  $R^2 = 0.10$ , Volume  $\chi^2 = 2.104$ ,  $p = 0.147$ ; Duration  $\chi^2 =$   
310  $1.209$ ,  $p = 0.272$ ; Distance  $\chi^2 = 0.026$ ,  $p = 0.872$ , Table 1).

311 During the experiments, pygmy marmosets rested an average of  $39.7 \pm SD 35.8\%$   
312 of visible time. For experiments without playbacks there was no consistent difference  
313 in the amount of time the focal individual spend resting in the final two minutes of the  
314 experiment compared to the first two minutes (Table 1). In experiments with  
315 playbacks, resting decreased by -11.7 (95% CI -20.68, -2.9) % of visible time. There was  
316 weak evidence that percentage of visible time resting decreased by -0.3 (95% CI -0.6,  
317 0.0) % for each 1dB increase in volume ( $\chi^2 = 3.012$ ,  $p = 0.083$ ). There was no evidence  
318 for significant effect of playback duration or distance on the change in time spent  
319 resting (LMER: conditional  $R^2 = 0.05$ , marginal  $R^2 = 0.06$ , Duration  $\chi^2 = 1.15$ ,  $p = 0.28$ ;  
320 Distance  $\chi^2 = 0.218$ ,  $p = 0.640$ , Table 1).

321 During the experiments, pygmy marmosets were alert an average of  $4.9 \pm SD$   
322  $8.6\%$  of visible time. For control treatments there was no consistent difference in the  
323 amount of time the focal individual spent alert in the final two minutes of the  
324 experiment compared to the first two minutes (Table 1). In experiments with  
325 playbacks, alert behavior increased by 3.8 (95% CI 0.6, 7.0) % of visible time. There was

326 no evidence for effects of volume, duration, or distance in the change in time spent  
327 alert (LMER: conditional  $R^2 = 0.03$ , marginal  $R^2 = 0.03$ , Volume  $\chi^2 = 0.070$ ,  $p = 0.792$ ;  
328 Duration  $\chi^2 = 0.200$ ,  $p = 0.070$ ; Distance  $\chi^2 = 1.625$ ,  $p = 0.202$ ).

### 329 **3.4 Vigilance**

330 During the experiments, pygmy marmosets spent more time directing vigilance  
331 at other objects than directing vigilance at the playback (general vigilance  
332  $67.5 \pm SD 23.9\%$  of visible time; playback-directed vigilance  $4.7 \pm SD 7.5\%$  of visible time).  
333 There was no consistent difference before and after the playback in the amount of  
334 playback-directed or general vigilance in either control playbacks or playbacks of  
335 human voices (Table 1). There was also no evidence for significant effect of volume,  
336 duration or distance on the change in general or playback-directed vigilance (Playback  
337 directed vigilance, LMER: conditional  $R^2 = 0.01$ , marginal  $R^2 = 0.01$ , Volume  $\chi^2 = 0.287$ ,  
338  $p = 0.592$ ; Duration  $\chi^2 = 0.039$ ,  $p = 0.843$ ; Distance  $\chi^2 = 0.204$ ,  $p = 0.652$ . General  
339 vigilance, LMER: conditional  $R^2 = 0.03$ , marginal  $R^2 = 0.03$ , Volume  $\chi^2 = 0.022$ ,  $p = 0.883$ ;  
340 Duration  $\chi^2 = 0.801$ ,  $p = 0.371$ ; Distance  $\chi^2 = 0.981$ ,  $p = 0.322$ ).

### 341 **3.5 Social and self-directed behaviors**

342 Social behavior was only observed in 8 trials (all of playbacks of human speech)  
343 across 7 groups. In these 8 trials, there was no evidence for consistent changes in  
344 percentage of observed time engaged in social behavior (change of -2.4 percent of  
345 visible time, 95%CI -6.9, 2.1). Social behavior was observed across all playback  
346 experiment conditions but never observed in control experiments. Self-directed  
347 behavior was observed in 19 trials across 8 groups. Although self-directed behavior



348 was observed across all experimental condition, it was only observed twice in control  
349 experiments. There was no evidence for consistent changes in percentage of observed  
350 time engaged in self-directed behavior in response to playbacks of human speech  
351 (change of -1.7 percent of visible time, -8.4, 6.1, n=17).

### 352 **3.6 Vocalizations**

353 In most trials (n=48) there was no change in calling behavior before and after  
354 playback: marmosets were silent both before and after playback in 37 trials, and called  
355 both before and after the playback in 11 trails. Changes in calling behavior were  
356 observed in both control (2 of 10 trials) and playback trials (10 of 50 trials, observed in  
357 all conditions). There was no evidence for a change in calling behavior with playback  
358 volume, duration or distance (GLMER: conditional  $R^2 = 0.15$ , marginal  $R^2 = 0.12$ ,  
359 Volume  $\chi^2 = 0.140$ ,  $p = 0.709$ ; Duration  $\chi^2 = 0.054$ ,  $p = 0.816$ ; Distance  $\chi^2 = 1.798$ ,  $p =$   
360  $0.180$ ; Calling before playback [binary y/n]  $\chi^2 = 2.589$ ,  $p = 0.108$ ).

361

## 362 **4 Discussion**

363 This study demonstrates a link between loud human speech and individuals  
364 leaving the visible study area. As all trials took place near a marmoset group's feeding  
365 tree, flight from the visible study area is deemed to be the most costly behavior  
366 observed. Locomotion itself can have high energetic costs (Steudel-Numbers, 2003)  
367 while movement away from the feeding tree interferes with energetic intake. Further  
368 effects of acoustic disturbance include a decrease in feeding and resting, and an

369 increase in alert behavior after any playback of human speech. All of these behavioral  
370 changes have the potential to impact marmoset fitness.

#### 371 **4.1 Absence and visibility**

372 Many animals react to human presence by displaying anti-predator behaviors  
373 such as flight initiation (Knight, 2009; Smith et al., 2017). Although primates have  
374 previously been recorded to move away from observers at tourist visited sites  
375 (Hodgkinson, Kirkby, & Milner-Gulland, 2014), this study is the first time that the role  
376 of human speech has been experimentally demonstrated to increase the likelihood of  
377 movement away from observers at a tourism site. Due to the design of this study, it  
378 was not possible to conclude individuals fled the area after playbacks, but target  
379 individuals were more likely to be absent from sight following playbacks of human  
380 speech, whereas they remained visible at the end of control trials. This difference  
381 suggests that moving out of sight is a direct response to the noise generated by the  
382 playbacks and not the presence of a boat and researchers. This is supported by the lack  
383 of evidence across all analyses for an effect of distance between the boat and the focal  
384 individuals. As well as leaving the vicinity of the playback source, individuals were less  
385 likely to be visible to the researcher following louder playbacks in comparison to  
386 control trials. Individuals obscured themselves by moving higher up the tree, around  
387 the tree or into more leafy areas. Previous research on pygmy marmosets did not find  
388 a relationship between tourist pressure and visibility(de La Torre et al., 2000), but the  
389 importance of noise, rather than simply presence, is consistent with a previous study in

390 which hoatzins habituated to silent canoe approaches but not acoustic playbacks (Karp  
391 & Root, 2009).

#### 392 **4.2 Feeding, resting and alert behaviors**

393 Although individuals did not appear to alter their vigilance behaviors, they did  
394 decrease the percentage of time spent feeding and resting, and become more alert  
395 when the trial included a playback of human speech. The reduction in feeding and  
396 resting may be as individuals moved on to other branches away, from the main trunk  
397 of their feeding tree (pers. ob.). This possibility is potentially collaborated by the weak  
398 evidence for a decrease in resting as playback volume increased, mirroring the  
399 decrease in visibility and movement out of sight with louder playbacks. A reduction in  
400 feeding behaviors in response to tourist presence has also been documented in other  
401 species, including western lowland gorillas (Klailova et al., 2010; Shutt et al., 2014) and  
402 red deer (*Cervus elaphus*) (Sibbald et al., 2011). This behavioral change can impact  
403 fitness impact as a reduction in time spent feeding may reduce energetic intake.

#### 404 **4.3 Other behaviors**

405 We found no evidence that any of the other behaviors measured changed in  
406 response to the playbacks. The lack of evidence for a change in playback-directed  
407 vigilance is surprising, as the pygmy marmosets did respond to human speech in other  
408 ways. The distracted-prey hypothesis stipulates that, as attention is finite,  
409 anthropogenic disturbance may distract individuals and interfere with their capacity  
410 for predator detection (Chan & Blumstein, 2011). This study did not find either an  
411 increase in playback-directed vigilance, or a decrease in general vigilance, which would

412 have been consistent with the distracted-prey hypothesis. However, these results  
413 could be confounded as focal individuals were less visible after playbacks. It was  
414 assumed that individuals allocated the same proportion of time to each behavior when  
415 out of view as when in view, but this may not be the case. When out of view,  
416 individuals will not always be able to see the playback source or researchers, altering  
417 their vigilance responses.

418         Contrary to predictions, there was also no significant change in time allocated  
419 to self-directed behaviors, social behaviors or calling, and these behaviors were rarely  
420 observed. Self-scratching is an indicator of anxiety (Maréchal et al., 2011) and would  
421 therefore be expected to increase if individuals are stressed by the playbacks. Previous  
422 research on the pygmy marmoset suggested that human disturbance decreased vocal  
423 behavior (de La Torre et al., 2000). However, the evidence from this study suggests  
424 that individuals might respond to human conversation by moving away, rather than  
425 changing their calling behavior or engaging in displacement behaviors such as self-  
426 scratching.

#### 427 **4.4 Effects on tourists**

428         In addition to the impacts on pygmy marmosets, this study demonstrates that  
429 acoustic disturbance may be detrimental to tourist enjoyment. Tourists value  
430 guaranteed encounters and proximity (Bach & Burton, 2017) however we find that  
431 human speech (and therefore tourist speech) can cause animals to hide from view and  
432 even flee the area. Individuals moved out of sight after as little as 17 seconds of human  
433 speech, and once gone the average time to return (if they returned at all) was over 6

434 minutes. This has the potential to impact the tourist viewing experience as it restricts  
435 the amount of time that they can view the marmosets. When there is no acoustic  
436 disturbance, individuals remained in the area when boats were as close as 5.8 meters.

#### 437 **4.5 Recommendations**

438 This study demonstrates that human speech causes changes in pygmy  
439 marmoset behavior in a way that may be detrimental to both primate welfare and  
440 tourist enjoyment. Currently, there is limited regulation in place for primate tourism. In  
441 2010, the IUCN released best-practice guidelines for great-ape tourism (Macfie &  
442 Williamson, 2010) but these do not contain any reference to tourism-generated noise,  
443 and do not cover primate species other than the great apes. Further research is likely  
444 required before official guidelines can be put in place, as these should consider both  
445 species-specific responses and other ways which the presence of tourists may affect  
446 primates, e.g. disease transmission (Muehlenbein & Wallis, 2014). However, based on  
447 the research documented in this study we would recommend that, at least for pygmy  
448 marmosets, ecotourism operators should take steps to reduce acoustic disturbance  
449 during tours.

450 As tourist conversation is generated by individual tourists, educating tourists  
451 could have a strong positive effect. This approach has been shown to be successful in  
452 multiple tourism contexts. For example, informing visitors of the negative link between  
453 tourist-boat proximity and stress in Humboldt penguins (*Spheniscus humboldti*) led to  
454 visitors selecting tour options that reduced negative welfare effects (Vásquez Lavín,  
455 Gelcich, Paz Lerdón, & Montealegre Bustos, 2016). Similar results have been found for

456 dolphin tourism (Bach & Burton, 2017; Filby, Stockin, & Scarpaci, 2015), and notably  
457 visitors are willing to accept management regulations that are detrimental to their  
458 own experience if it means safeguarding dolphin welfare (Bach & Burton, 2017). Given  
459 these previous positive results, informing tourists that talking disturbs primates and  
460 may cause them to move out of sight (especially if they speak loudly) may be enough  
461 to encourage tourists to remain quiet when viewing primates. If talking is absolutely  
462 necessary, whispering (at a volume under 30db) is less likely to cause individuals to  
463 move out of sight.

464 This study did not test whether pygmy marmosets were able to habituate to  
465 acoustic disturbance. A study investigating whether habituation can ameliorate the  
466 behavioral changes reported here would provide useful recommendations for the  
467 pattern of visits which would reduce disturbance at a population level. If pygmy  
468 marmosets do habituate to acoustic disturbance then guides can minimize disturbance  
469 and maximize the tourist experience by taking tourists to frequently-visited groups. In  
470 contrast, if habituation is not observed, spreading tourist visits over multiple groups  
471 would mean each group is disturbed less frequently.

472 In conclusion, the behavioral changes documented in this study highlight the  
473 need for tour operators and tourists to consider the impact noise may have on visited  
474 species. In particular, human speech, and particularly loud speech, changes pygmy  
475 marmoset behavior in ways which are undesirable for both primate welfare and  
476 visiting tourists. Fortunately however, as these responses were not observed in control

477 trials, this study suggests this effect can be reduced by encouraging tourists to refrain  
478 from speaking in the presence of visited primate groups.

#### 479 **5. Acknowledgements**

480 We thank Paul Beaver and Amazonia Expeditions for granting permission to conduct  
481 research in the ACRCTT, and providing logistical support for the duration of the  
482 fieldwork period. We thank all of the staff at Tahuayo lodge for their hospitality and  
483 help locating primate groups, in particular Claudio, Nixon and Melissa for their  
484 assistance as motoristas and trainee guides. Finally, a special mention goes to Andy  
485 Bicerra as my lead guide and provider of local scientific knowledge during the  
486 fieldwork phase.

#### 487 **6. References**

488 Aguilar-Melo, A. R., Andresen, E., Cristóbal-Azkarate, J., Arroyo-Rodríguez, V., Chavira,  
489 R., Schondube, J., ... Cuarón, A. D. (2013). Behavioral and Physiological Responses  
490 to Subgroup Size and Number of People in Howler Monkeys Inhabiting a Forest  
491 Fragment Used for Nature-Based Tourism. *American Journal of Primatology*, *75*,  
492 1108–1116.

493 Bach, L., & Burton, M. (2017). Proximity and animal welfare in the context of tourist  
494 interactions with habituated dolphins. *Journal of Sustainable Tourism*, *25*(2), 181–  
495 197.

496 Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., ...  
497 Manica, A. (2015). Walk on the Wild Side: Estimating the Global Magnitude of

- 498 Visits to Protected Areas. *PLoS Biology*, 13(2), e100207.
- 499 Barton, K. (2018). MuMIn: Multi-Model Inference. *R Package Version 1.42.1*.
- 500 Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting Linear Mixed-  
501 Effects Models using lme4. *Journal of Statistical Software*, 67, 1–48.
- 502 Behie, A. M., Pavelka, M. S. M., & Chapman, C. A. (2010). Sources of Variation in Fecal  
503 Cortisol Levels in Howler Monkeys in Belize. *American Journal of Primatology*, 72,  
504 600–606.
- 505 Boersma, P., & Weenink, D. (2018). Praat: doing phonetics by computer. Retrieved  
506 from <http://www.fon.hum.uva.nl/praat/>
- 507 Borg, C., Majolo, B., Qarro, M., Semple, S., Borg, C., Majolo, B., & Qarro, M. (2015). A  
508 Comparison of Body Size, Coat Condition and Endoparasite Diversity of Wild  
509 Barbary Macaques Exposed to Different Levels of Tourism. *Anthrozoös*, 27(1), 49–  
510 63.
- 511 Buckley, R. C., Morrison, C., & Castley, J. G. (2016). Net Effects of Ecotourism on  
512 Threatened Species Survival. *PLoS ONE*, 11(2), e1047988.
- 513 Chan, A. A. Y., & Blumstein, D. T. (2011). Attention, noise, and implications for wildlife  
514 conservation and management. *Applied Animal Behaviour Science*, 131, 1–7.
- 515 Cunha, A. (2010). Negative effects of tourism in a Brazilian Atlantic forest National  
516 Park. *Journal for Nature Conservation*, 18, 291–295.
- 517 de La Torre, S., Snowdon, C. T., & Bejarano, M. (2000). Effects of human activities on



- 518 wild pygmy marmosets in Ecuadorian Amazonia. *Biological Conservation*, 94, 153–  
519 163.
- 520 de la Torre, S., Yépez, P., & Snowdon, C. T. (2009). Conservation Status of Pygmy  
521 Marmosets (*Cebuella pygmaea*) in Ecuador. In S. M. Ford, L. M. Poter, & L. C.  
522 Davis (Eds.), *The smallest anthropoids* (pp. 451–464).
- 523 Fennell, D. A. (2001). A Content Analysis of Ecotourism Definitions. *Current Issues in*  
524 *Tourism*, 4(5), 403–421.
- 525 Filby, N. E., Stockin, K. A., & Scarpaci, C. (2015). Social science as a vehicle to improve  
526 dolphin-swim tour operation compliance? *Marine Policy*, 51, 40–47.
- 527 Fox, J., & Weisberg, S. (2011). *A {R} Companion to Applied Regression, Second Edition*.  
528 Thousand Oaks, CA: Sage.
- 529 Grossberg, R., Treves, A., & Naughton-Treves, L. (2003). The incidental ecotourist:  
530 measuring visitor impacts on endangered howler monkeys at a Belizean  
531 archaeological site. *Environmental Conservation*, 30(1), 40–51.
- 532 Hänninen, L., & Pastell, M. (2009). CowLog: Open-source software for coding behaviors  
533 from digital video. *Behavior Research Methods*, 41(2), 472–476.
- 534 Hodgkinson, C., Kirkby, C., & Milner-Gulland, E. (2014). The impact of tourist group size  
535 and frequency on Neotropical primate behaviour in Tambopata, Peru. In A. E.  
536 Russon & J. Wallis (Eds.), *Primate Tourism: A Tool for Conservation?* (pp. 215–  
537 229). Cambridge, UK: Cambridge University Press.
- 538 Huangshan, M., Berman, C. M., Li, J., & Ogawa, H. (2007). Primate Tourism, Range

- 539       Restriction, and Infant Risk Among *Macaca thibetana*. *International Journal of*  
540       *Primatology*, 28, 1123–1141.
- 541       Jackson, C. P. (2011). The positional behavior of pygmy marmosets (*Cebuella pygmaea*)  
542       in northwestern Bolivia. *Primates*, 52, 171–178.
- 543       Karp, D. S., & Guevara, R. (2011). Conversational Noise Reduction as a Win-Win for  
544       Ecotourists and Rain Forest Birds in Peru. *Biotropica*, 43(1), 122–130.
- 545       Karp, D. S., & Root, T. L. (2009). Sound the stressor: how hoatzins (*Opisthocomus*  
546       *hoazin*) react to ecotourist conversation. *Biodiversity Conservation*, 18, 3733–  
547       3742.
- 548       Kinnaird, M. F., & Brien, T. G. O. (1996). Ecotourism in the Tangkoko DuaSudara Nature  
549       Reserve: opening Pandora’s box? *Oryx*, 30(1), 65–73.
- 550       Kirkby, C. A., Giudice-Granados, R., Day, B., Turner, K., Velarde-Andrade, L. M., Duenas-  
551       Duenas, A., ... Yu, D. W. (2010). The Market Triumph of Ecotourism: An Economic  
552       Investigation of the Private and Social Benefits of Competing Land Uses in the  
553       Peruvian Amazon. *PLoS ONE*, 5(9), e13015. 5
- 554       Klailova, M., Hodgkinson, C., & Lee, P. C. (2010). Behavioral responses of one western  
555       lowland gorilla (*Gorilla gorilla gorilla*) group at Bai Hokou, Central African  
556       Republic, to tourists, researchers and trackers. *American Journal of Primatology*,  
557       72(10), 897–906.
- 558       Knight, J. (2009). Making Wildlife Viewable: Habituation and Attraction. *Society and*  
559       *Animals*, 17, 167–184.

- 560 Kruger, O. (2005). The role of ecotourism in conservation: panacea or Pandora's box ?  
561 *Biodiversity and Conservation*, 14, 579–600.
- 562 Kvist, L. P., & Nebel, G. (2001). A review of Peruvian flood plain forests: ecosystems,  
563 inhabitants and resource use. *Forest Ecology and Management*, 150, 3–26.
- 564 Lane, H. L., Catania, A. C., & Stevens, S. S. (1961). Voice level: autophonic scale,  
565 perceived loudness, and effects of sidetone. *Journal of the Acoustical Society of*  
566 *America*, 33(2), 160–167.
- 567 Leason, H. C., & Macgregor, O. J. (2014). Proboscis monkey tourism: can we make it  
568 “ecotourism”? In A. E. Russon & J. Wallis (Eds.), *Primate Tourism: A Tool for*  
569 *Conservation?* (pp. 56–75). Cambridge, UK: Cambridge University Press.
- 570 Macfie, E. J., & Williamson, E. A. (2010). *Best Practice Guidelines for Great Ape*  
571 *Tourism*. Gland, Switzerland: IUCN/SSC Primate Specialist Group (PSG).
- 572 Maréchal, L., Semple, S., Majolo, B., & Maclarnon, A. (2016). Assessing the Effects of  
573 Tourist Provisioning on the Health of Wild Barbary Macaques in Morocco. *PloS*  
574 *One*, 11(5), e1055920. h
- 575 Maréchal, L., Semple, S., Majolo, B., Qarro, M., Heistermann, M., & Maclarnon, A.  
576 (2011). Impacts of tourism on anxiety and physiological stress levels in wild male  
577 Barbary macaques. *Biological Conservation*, 144, 2188–2193.  
578 <http://doi.org/10.1016/j.biocon.2011.05.010>
- 579 McClung, M. R., Seddon, P. J., Massaro, M., & Setiawan, A. N. (2004). Nature-based  
580 tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: does

- 581 unregulated visitor access affect fledging weight and juvenile survival? *Biological*  
582 *Conservation*, 119, 279–285.
- 583 Meissner, A. M., Christiansen, F., Martinez, E., Matthew, D., Pawley, M., Orams, M. B.,  
584 & Stockin, K. A. (2015). Behavioural Effects of Tourism on Oceanic Common  
585 Dolphins, *Delphinus* sp., in New Zealand: The Effects of Markov Analysis Variations  
586 and Current Tour Operator Compliance with Regulations. *PloS One*, 10(1),  
587 e0116962.
- 588 Muehlenbein, M. P., & Wallis, J. (2014). Considering risks of pathogen transmission  
589 associated with primate-based tourism. In A. Russon & J. Wallis (Eds.), *Primate*  
590 *Tourism: A Tool for Conservation?* (pp. 278–291). Cambridge, UK: Cambridge  
591 University Press.
- 592 Myster, R. W. (2015). Flooding × tree fall gap interactive effects on blackwater forest  
593 floristics and physical structure in the Peruvian Amazon. *Journal of Plant*  
594 *Interactions*, 10(1), 126–131.
- 595 R Core Development Team. (2018). R: A Language and Environment for Statistical  
596 Computing.
- 597 Robbins, M. M., Gray, M., Fawcett, K. A., Nutter, F. B., Uwingeli, P., Kagoda, E., ...  
598 Robbins, A. M. (2011). Extreme Conservation Leads to Recovery of the Virunga  
599 Mountain Gorillas. *PloS One*, 6(6), e19788.
- 600 Ruesto, L. A., Sheeran, L. K., Matheson, M. D., Li, J.-H., & Wagner, R. S. (2010). Tourist  
601 Behavior and Decibel Levels Correlate with Threat Frequency in Tibetan

- 602 Macaques (*Macaca thibetana*) at Mt. Huangshan, China. *Primate Conservation*,  
603 25, 99–104.
- 604 Shepard, G. H. (2002). Primates in Matsigenka subsistence and world view. In A.  
605 Fuentes & L. Wolfe (Eds.), *Primates Face to Face: The conservation implications of*  
606 *human-nonhuman primate interconnections* (pp. 101–136). Cambridge:  
607 Cambridge University Press.
- 608 Shutt, K., Heistermann, M., Kasim, A., Todd, A., Kalousova, B., Profosouva, I., ...  
609 Setchell, J. M. (2014). Effects of habituation , research and ecotourism on faecal  
610 glucocorticoid metabolites in wild western lowland gorillas: Implications for  
611 conservation management. *Biological Conservation*, 172, 72–79.
- 612 Sibbald, A. M., Hooper, R. J., Mcleod, J. E., & Gordon, I. J. (2011). Responses of red deer  
613 (*Cervus elaphus*) to regular disturbance by hill walkers. *European Journal of*  
614 *Wildlife Research*, 57, 817–825.
- 615 Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., &  
616 Wilmers, C. C. (2017). Fear of the human ‘super predator’ reduces feeding time in  
617 large carnivores. *Proceedings of the Royal Society B: Biological Sciences*,  
618 284(1857), 20170433.
- 619 Snowdon, C. T., & Hodun, A. (1981). Acoustic Adaptations in Pygmy Marmoset Contact  
620 Calls: Locational Cues Vary with Distances between Conspecifics. *Behavioral*  
621 *Ecology and Sociobiology*, 9(4), 295–300.
- 622 Soini, P. (1982). Ecology and population dynamics of the pygmy marmoset, *Cebuella*

- 623         *pygmaea*. *Folia Primatologica*, 39, 1–21.
- 624     Steudel-Numbers, K. L. (2003). The energetic cost of locomotion: humans and primates  
625         compared to generalized endotherms. *Journal of Human Evolution*, 44, 255–262.
- 626     Tumusiime, D. M., & Svarstad, H. (2011). A Local Counter-Narrative on the  
627         Conservation of Mountain Gorillas. *Forum for Development Studies*, 38(3), 239–  
628         265.
- 629     Vanlangendonck, N., Nuñez, G., Chaves, A., & Gutiérrez-Espeleta, G. A. (2015). New  
630         Route of Investigation for Understanding the Impact of Human Activities on the  
631         Physiology of Non-Human Primates. *Journal of Primatology*, 4(1), 123.
- 632     Vásquez Lavín, F., Gelcich, S., Paz Lerdón, X., & Montealegre Bustos, F. (2016). The role  
633         of information in changing tourists behavioral preferences at the Humboldt  
634         penguin reserve in northern Chile. *Ocean and Coastal Management*, 125, 63–69. 3
- 635     Watson, H., Bolton, M., & Monaghan, P. (2014). Out of sight but not out of harm's way:  
636         Human disturbance reduces reproductive success of a cavity-nesting seabird.  
637         *Biological Conservation*, 174, 127–133.  
638         <http://doi.org/10.1016/j.biocon.2014.03.020>
- 639     Woodford, M. H., Butynski, T. M., & Karesh, W. B. (2002). Habituating the great apes:  
640         the disease risks. *Oryx*, 36(2), 153–160.
- 641     Yépez, P., de la Torre, S., & Snowdon, C. T. (2005). Interpopulation Differences in  
642         Exudate Feeding of Pygmy Marmosets in Ecuadorian Amazonia. *American Journal*  
643         *of Primatology*, 66, 145–158.

644 Zwijacz-Kozica, T., Selva, N., Barja, I., Silván, G., Martínez-Fernández, L., Illera, J. C., &  
645 Jodłowski, M. (2013). Concentration of fecal cortisol metabolites in chamois in  
646 relation to tourist pressure in Tatra National Park (South Poland). *Acta*  
647 *Theriologica*, 58, 215–222.

Author copy

648 Table 1: Change in behavior after playbacks, and slope estimates for the effect of  
 649 playback volume, duration and distance on changes in behavior. Means and estimates  
 650 where the 95% confidence interval (95% CI) does not include zero are shown in bold.

Behavior	Change and 95% CI after control playbacks (n=10)	Change and 95% CI after playbacks of human voice (n=50)	Volume (slope estimate and 95% CI from LMER)	Duration (slope estimate and 95% CI from LMER)	Distance (slope estimate and 95% CI from LMER)
Out of view (seconds)	0.7 (-7.9,6.4)	<b>-27.1</b> <b>(-37.1,-17.0)</b>	<b>-0.7</b> <b>(-1.0, -0.3)</b>	0.2 (-0.1,0.4)	-0.1 (-4.2,4.0)
Feeding (% of visible time)	0.18 (-16.6,16.9)	<b>-16.4</b> <b>(-24.2,-8.6)</b>	-0.2 (-0.5,0.1)	-0.1 (-0.3,0.1)	0.3 (-3.0,3.5)
Resting (% of visible time)	-0.8 (-12.1,10.5)	<b>-11.7</b> <b>(-20.6,-2.9)</b>	-0.3 (-0.6, 0.0)	0.1 (-0.1,0.3)	0.8 (-2.4,4.0)
Alert (% of visible time)	4.3 (-2.2,10.9)	<b>3.8</b> <b>(0.6,7.0)</b>	0.0 (-0.1,0.1)	0.0 (-0.1,1.1)	-0.9 (-2.2,0.5)
General vigilance (% of visible time)	-1.9 (-14.7,10.9)	3.2 (-3.0,9.3)	0.0 (-0.3, 0.2),	0.1 (-0.1,0.2)	-1.4 (-4.0,1.3)
Playback-directed	-0.3 (-3.7,3.0)	1.3 (-0.9,3.6)	0.0 (-0.1,0.1)	0.0 (-0.1, 0.1)	-0.2 (-0.7,1.2)



vigilance (% of visible time)					
----------------------------------	--	--	--	--	--

651

652

Author copy

653 Figure legends

654 Figure 1: Locations of pygmy marmoset groups close to tourist facilities within the  
655 Tamshiyacu-Tahuayo Reserve. Circles represent groups of pygmy marmosets,  
656 confirmed by sighting of marmosets on a feeding tree. The northern star shows  
657 Amazonia Expeditions' Main lodge, the southern star is the Amazon Research Center  
658 (ARC). Map produced in QGIS 2.18.12, with rivers digitalized from Google Satellite  
659 images © 2017.

660

661 Figure 2: Change in visibility of individual pygmy marmosets in the last two minutes of  
662 experiments compared to the first two minutes, measured in seconds. Experimental  
663 conditions were either silent playbacks of white noise (0dB) or playbacks of human  
664 speech at 30, 60 or 78dB, corresponding to human whispering, talking or a raised  
665 voice. Playbacks at 30 and 78dB were 60 seconds long, playbacks at 60dB varied  
666 between 15 and 120 seconds.

667

668 Figure 3: Status of individual pygmy marmosets at the end of the 4 minute experiment.  
669 Playback conditions consisted of a silent control and pre-recorded human speech  
670 played back at 30db, 60db and 78db. Bar width is proportional to sample size.

671