Title: Interactions between humans and Panamanian white-faced capuchin monkeys (*Cebus imitator*)

ABSTRACT

Anthropogenic influence is expanding, threatening primate taxa worldwide. With wildlife tourism a burgeoning industry, understanding human-primate interactions is key in avoiding primate defaunation. We observed interactions between humans and a group of wild Panamanian white-faced capuchin monkeys (*Cebus imitator*) at Curú Wildlife Refuge, Costa Rica, in June and July, 2019, and compared our findings with findings for the same group in May-Oct of 2006 and 2007, when the group received more provisioning. We recorded all occurrences of human-primate interactions in 323 15 min samples over 42 consecutive days. We found that capuchins initiated approximately twice as many interactions as humans did (a significant difference). We also found a strong positive correlation between engaging behaviours exhibited by humans and capuchin agonistic behaviours. Capuchins spent significantly more time engaging in moderate behaviours (snatch food, snatch item, vigilance, vocalisation) and less time not interacting with humans, in the presence of tourists and staff, than in the presence of staff only. Time spent in moderate and intense behaviours (approach, beg, chase, offer, take food, threat) was lower in 2019 than in 2006 and 2007. These findings suggest that reducing engaging behaviours by humans may reduce primate agonistic behaviours, and that human group composition affects human-primate interactions. The reduction in moderate and intense behaviours between studies also suggests that reducing direct provisioning could reduce the frequency and intensity of human-primate interactions in tourist sites.

Keywords: human-animal interaction; provisioning; wildlife tourism; ecotourism; ethnoprimatology

INTRODUCTION

Almost 60% of primate taxa are currently threatened with extinction (Estrada et al. 2017) and anthropogenic influences are the primary cause (Dirzo et al. 2014; Estrada et al. 2017). Wildlife tourism has led to a significant increase in interspecies contact, with observable changes in primate behaviour and ecology (McKinney 2016). The most common change experienced by primates in frequent contact with humans is dietary alteration through provisioning (McLennan et al. 2017). Provisioning can occur directly through feeding stations and hand offerings, or indirectly through accessible rubbish or unattended bags (Becker et al. 2015). Provisioning can lead to long term alteration of primate foraging patterns (Altmann and Muruthi 1988; Suzin et al. 2017; Thatcher et al. 2019; Webb and McCoy 2014), movement patterns (Jones-Engel et al. 2004; Lane et al. 2010; Sabbatini et al. 2006), and group size and aggregation (Becker et al. 2015; Jones-Engel et al. 2004; Lane et al. 2010). Subsidised diets are generally high energy and low fibre (Kurita 2014; Sabbatini et al. 2006), and contain higher starch content, contributing to increased parasitic load in host primates (Thatcher et al. 2018). These dietary changes, along with reduced travel and foraging time (Altmann and Muruthi 1988; Suzin et al. 2017; Thatcher et al. 2019), and increased time feeding and socialising (Thatcher et al. 2019), could also contribute to primate obesity (Lane et al. 2010; Sapolsky 2014).

Provisioning leads to interspecies contact (Fuentes et al. 2008; Sabbatini et al. 2006), and human-primate interactions are common at tourist sites, with some sites encouraging provisioning to guarantee interaction with target species (Jones-Engel et al. 2006). For example, black-striped capuchins (*Sapajus libidinosus*) enter tourist areas to access

anthropogenic food sources (Van Hulle and Vaughan 2009), and Barbary macaques (*Macaca sylvanus*) are less likely to avoid humans when provisioning occurs, implying a cost-benefit trade-off between human interaction and food subsidies (Maréchal et al. 2016b). Food transfer still frequently occurs even when tourist sites prohibit provisioning (Maréchal et al. 2016; Sabbatini et al. 2006).

Direct provisioning can increase animal aggression (Sabbatini et al. 2006), and increase primate habituation to humans, specifically tourists (Lane et al. 2010; Sabbatini et al. 2006). There is a risk of overhabituation, defined as a loss of fear in primates (Kauffman 2014), inclusion of humans in social interactions, and acceptance of humans as a food source (Webb and McCoy 2014). Overhabituated primates can become a threat to human safety and health (Webb and McCoy 2014) and lead to interspecies conflict and persecution (Altmann and Muruthi 1988; Sabbatini et al. 2006). Sudden removal of provisioned resources may also spark interspecies conflict, with aggressive behaviour directed at humans due to provisioning withdrawal (Kauffman 2014; Van Hulle & Vaughan 2009).

Wild primates in contact with tourists display other behavioural modifications including avoidance (Hsu et al. 2009; Maréchal et al. 2016), anxiety (Behie et al. 2010; Maréchal et al. 2011; Muehlenbein et al. 2012; Zhang 2011), and agonism (Jones-Engel et al. 2006; Kauffman 2014; Lane et al. 2010; Matheson et al. 2006). Humans generally initiate more interactions than primates do (Hsu et al. 2009; Sabbatini et al. 2006; Suzin et al. 2017), and humans often fail to change their behaviour in response to primate actions (Sabbatini et al. 2006). Tourist behaviours are typically more intrusive than those of other humans (Behie et al. 2010; Westin 2017), risking chronic activation of stress in primates from repeated exposure to tourists (Muehlenbein et al. 2012). This is a concern, because chronic stress can have long-term effects on health (Maestripieri and Hoffman 2011).

Close human-primate interactions are risky for humans as well. Regardless of the instigator, close human-primate interactions may trigger aggressive behaviours in the primates (Jones-Engel et al. 2006; Lane et al. 2010; Sabbatini et al. 2006). This can result in human injury from bites and scratches (Jones-Engel et al. 2006; Lane et al. 2010), with an associated risk of disease transmission (Lane et al. 2010). In Parque Nacional de Brasilia, 17.4% of interactions with black-striped capuchins were categorised as threatening/chasing (Sabbatini et al. 2006), and in Shou-Shan Nature Park, 16.4% of interactions with Formosan rock macaques (*Macaca cyclopis*) were described as human-monkey conflict (Hsu et al. 2009). Provisioning increases the frequency and length of aggressive behaviours (Hsu et al. 2009), with food related aggression linked to food abundance and number of potential feeding sites (Vogel and Janson 2007).

Known as particularly gregarious (Fragaszy et al. 2004; McKinney 2014; Rose et al. 2003), white-faced capuchins (*Cebus imitator*) are dietary generalists (Boubli et al. 2012) and occupy relatively large home ranges (Mittermeier et al. 2013), dependent on food resource availability (Campos et al. 2014). They use anthropogenic food resources opportunistically (Kauffman 2014; McKinney 2011). A study of a group of white-faced capuchins at Curú Wildlife Refuge in western Costa Rica found that capuchins instigate more interactions than humans do and initiate more interactions with tourists than mantled howler monkeys (*Alouatta palliata*) do (McKinney 2014). In 2012, this group were observed to visit the tourist area 2-3 times daily, where they were heavily provisioned with anthropogenic food sources by staff (Webb and McCoy 2014). The capuchins initiated more human-primate interactions than humans (McKinney 2014), and tourist numbers did not affect interaction rates with the group of white-faced capuchins at Curú Wildlife Refuge (McKinney 2014).

We explored interactions between humans and primates in the same group of Panamanian white-faced capuchins at Curú Wildlife Refuge in 2019, using the same methods

as the 2006-2007 study. We aimed to investigate whether and how the capuchins' behaviour had changed over time. We examined interactions with monkeys between tourists and staff, and between staff only.

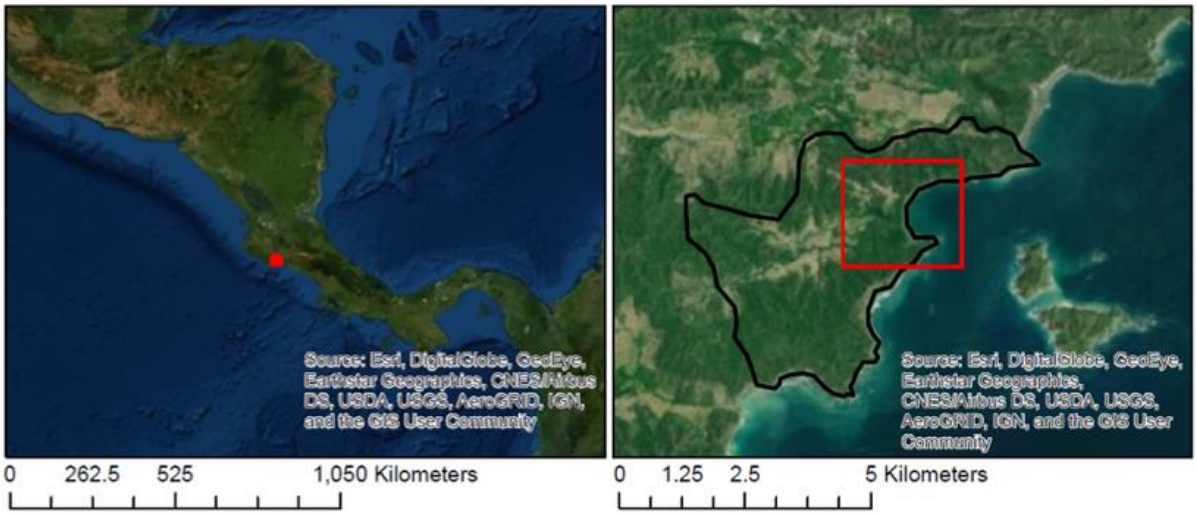
METHODS

Study Site and Population

Curú Wildlife Refuge is a privately managed farm and wildlife refuge, operating on 84 ha of land in northwest Costa Rica (9° 47' 43.69"N, 84° 55' 15.01"W). Curú experiences two seasons annually: wet from May-October and dry from November-April (McKinney et al. 2015). Regional temperatures range from 24.1°C – 29.3°C (median 26.7°C) in June, and 23.9°C – 29.3°C (median 26.6°C) in July, with 82% and 81% humidity, respectively. Mean rainfall is 184.7 mm (June), and 117.1 mm (July), less than experienced in May (201.6 mm), September (224.1 mm) or October (302.7 mm) (Instituto Meteorológico Nacional 2019).

We focused on the group of white-faced capuchins that use the tourist area of the refuge. In previous studies, this group has been referred to as the Banana Gang (McKinney 2010), the Human-Commensal Group (McKinney 2011; McKinney 2014), and the Ceiba Group (Webb and McCoy 2014), though the term 'commensal' is frequently misused in primatology (Marechal and McKinney 2020). During the 2006-2007 study the group was composed of 22 individuals, and during the 2019 study the group was composed of 16 individuals. The group occupy a fragmented habitat of mangroves, plantation, pasture, secondary coconut forests, and deciduous forests, intersected by one main dirt road, eight dirt and boardwalk tourist trails, and several permanent building structures (Figure 1). The activity hub of the tourist area is a boathouse, from which scuba tours depart daily. The surrounding area consists of an administration building and souvenir shop, a dining hall, the landowner's home, a car park, and a picnic area. There are six cabins for tourists and

researchers adjacent to Curú beach, extending from the boathouse to the Quesera trail entrance. The study group is the only group of white-faced capuchins to regularly frequent the cabin and tourist area at this site (McKinney 2011).



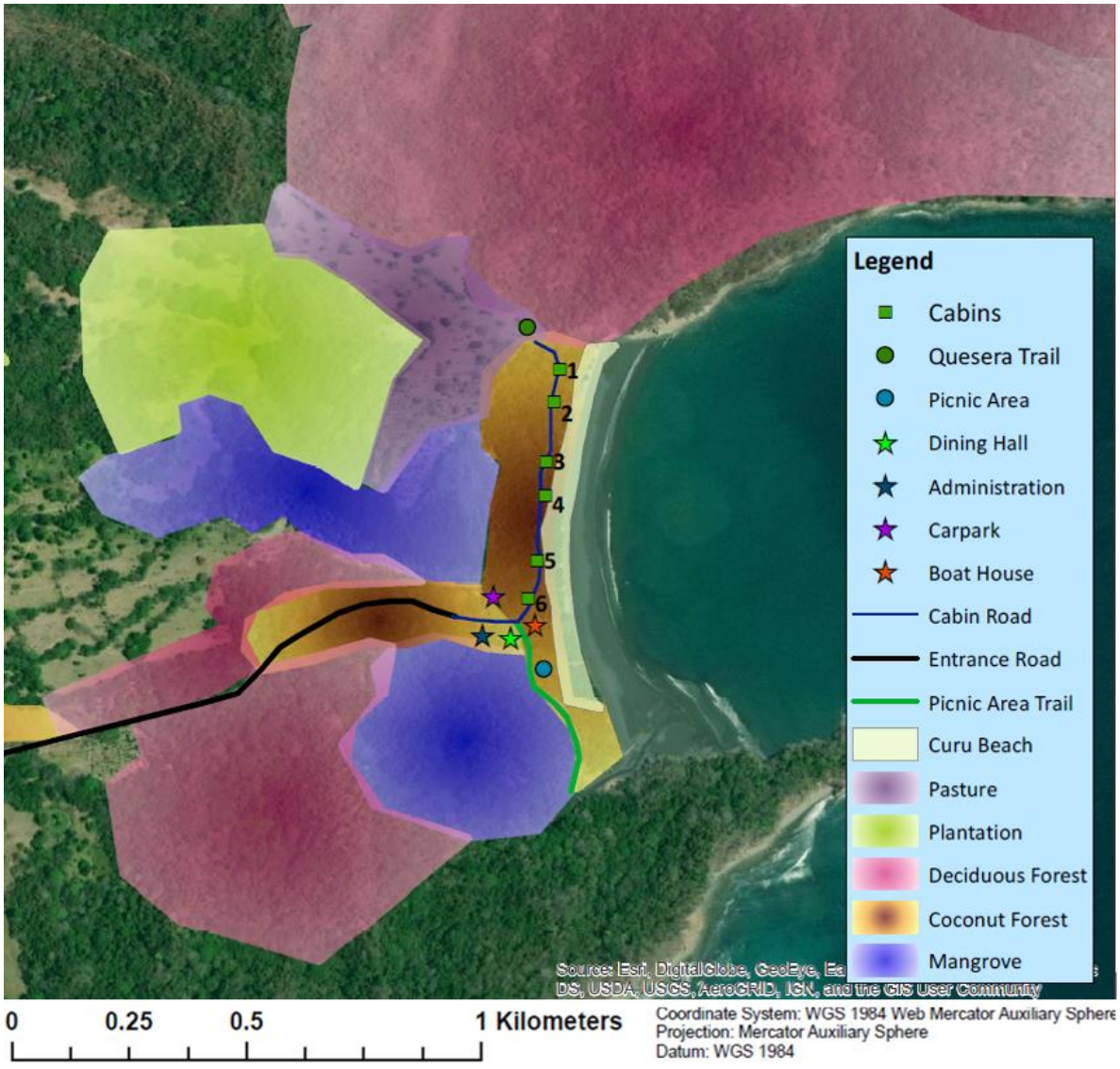


Figure 1. Location of Curú study site in Costa Rica. Top left: Red outline denotes the location of the Curú Wildlife Refuge in Costa Rica, Central America. Top right: Black outline denotes the extent of Curú Wildlife Refuge, and red outline denotes the location of the study site within the refuge. Bottom: key points of interest in the tourist area of the study site; indicated on the map are estimates of the habitat types observed to be used by white-faced capuchins in 2019.

On the anthropogenic influence scale (McKinney 2015), the group is classified as (E) mixed use landscape (protected but with agricultural or extraction activities); (G) diet with

regular scavenged or provisioned human foods; (F) daily human contact with researchers and tourists, comprising moderate interactions such as occasional provisioning; and (C) absence of human predation and indigenous predator population reduced, but new or domesticated predators present. We based classifications on NM's observations at the end of the 2019 study.

The group are habituated to human presence, defined as tolerance of observers with no overt signals of stress or avoidance behaviour (Williamson and Feistner 2003). While this group were provisioned in the past (Webb and McCoy 2014; McKinney 2010), during the 2019 study, staff did not directly provision the white-faced capuchins. However, provisions for local white tailed deer (*Odocoileus virginianus*) were unmonitored and accessible to the group, as was food from unsecured rubbish bins adjacent to the tourist cabins. Common indirect provisions included coconut, watermelon, pineapple, banana, and assorted green vegetables, while provisions accessed via the cabin bins included fruit, rubbish, and processed foods like pizza. Provisioning by tourists is actively discouraged through signs, but still occurred infrequently throughout the 2019 study, consisting of assorted fruit, tortilla chips, and other processed food.

Tourists are free to explore the refuge unguided. The majority of tourists at Curú visit for the day only, and most move quickly through the study area to access activities such as snorkelling and kayaking, or to enjoy leisure time in the picnic area or at the beach.

Data Collection

NM collected data on 42 consecutive days in June and July 2019, from 0500 h to 1700 h daily, dividing data collection across three periods 05:00–08:59 h (31%), 09:00–12:59 h (35%) and 13:00-17:00 h (34%). We recorded data in 15 min samples. We recorded the number of tourists, staff members and white-faced capuchins present at the start of each

164 sample. We collected data via whole-group all-occurrence sampling (Altmann 1974),
165 recording the frequency and duration of human-primate interactions and whether each
166 interaction was initiated by white-faced capuchins or humans. We identified behaviours using
167 an ethogram adapted from McKinney (2010) to facilitate comparison between the two studies
168 (Table 1). We did not formally assess inter-observer reliability, but we used the same data
169 sheet format and TM was available for queries during NM's time in the field. We categorised
170 behaviours as mild, moderate, and intense. We defined mild behaviours as 'no direct
171 engagement' (foraging, run); moderate behaviours as 'low level engagement' (snatch food,
172 snatch item, vigilance, vocalisation); and intense behaviours as 'active engagement' (chase,
173 threat, take food, beg, approach, offer). We defined engaging behaviours exhibited by
174 humans as offer, approach, chase, and vocalisation, and capuchin agonistic behaviours as
175 threat, run, chase, and vocalisation. When the capuchins engaged in more than one behaviour
176 at a time, we recorded the majority group behaviour.
177

Table 1. Ethogram used to study human-primate interactions in white-faced capuchins at Curú Wildlife Refuge, Costa Rica, 2019, adapted from McKinney (2010). *The behaviour "snatch" was referred to as "steal" in the original ethogram.

Category	Behaviour	Description
Mild	Run	Rapid directed movement by monkey
		Rapid directed movement by human
	Forage	Monkey searches for food items, ingesting as each is discovered; often from an anthropogenic source, such as bins and in the boathouse

Moderate	Snatch* food	Monkey grabs food from trash bin, table, porch, or backpack
	Snatch item	Monkey grabs non-food item from person, bag, house, or bin
	Vigilance	Monkey observes humans and social or environmental surroundings
	Vocalisation	Monkey makes noises that appear to be directed toward humans; excludes contact calls and food calls
		Human makes noises to monkeys
Intense	Approach	Monkey moves to within 1 m of human
		Human moves to within 1 m of monkey
	Beg	Monkey waits for food from humans, with hand outstretched
	Chase	Monkey pursues human
		Human pursues monkey
	Offer	Human extends a hand toward monkey with or without provisioning
	Take Food	Monkey accepts food humans offered by hand, threw, or left
	Threat	Monkey branch bounces, bares teeth, directs stare, or breaks branches
		Human shouts, stomps, waves arms, or otherwise threatens monkeys
Not interacting	Not interacting	Monkeys and humans do not engage in behaviours with each other

178

179 **Data Analysis**

We compared the 2019 data (for June and July, the mini-dry season) with data from the entire rainy period of 2006 and 2007 (May-October). To check that this comparison was appropriate, we compared data collected during the months of June and July in 2006 and 2007 (N = 97) and data collected during the remaining rainy season months in 2006 and 2007 (May, August, September, and October) (N = 133). We found no significant difference in the number of humans present per 15 min sample (Mann Whitney: U = 5889.5, P = 0.03, N = 230).

The distribution of time spent in mild, moderate, and intense behaviours per 15 min sample was not normal, so we used non-parametric methods to explore our data. We used the Chi Square Goodness of Fit to test whether humans or capuchins were more likely to initiate interactions, comparing the observed number of interactions initiated by each species per 15 min sample with the expected value of 50%. We used Spearman's rho to test for significant correlations between the number of engaging behaviours shown by humans and the number of capuchin agonistic responses per 15 min sample. We used Mann Whitney U tests to compare the time (s) per 15 min sample capuchins spent not interacting, in moderate interactions, and in intense interactions with tourists and staff vs. staff only. We also used Mann Whitney U tests to compare time (s) per 15 min sample spent in moderate and intense interactions in 2006-2007 vs. in 2019. We focused on moderate and intense behaviours because they indicate higher levels of engagement between humans and capuchins than mild behaviours do.

We performed all statistical analysis in SPSS v. 26 (IBM Corp 2019). We set confidence intervals at 95% and $a = 0.05$. We corrected all Mann Whitney U tests for ties.

Ethical Note

The 2006-2007 study was approved by the IACUC board of The Ohio State University. The 2019 study was conducted under the approval of the University of South Wales research student protocol. The project complies with the IPS code of best practices for field primatology and with Costa Rican law, and a research permit was obtained from the National System of Conservation Areas (SINAC), via the Costa Rican Ministry of Environment and Energy.

Data Availability Statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

RESULTS

The 2006-2007 study data consists of 230 15 min samples. We recorded 1160 discrete behaviours in 57.3 h of observation. We classified 58% of these observations as no interaction between monkeys and humans. Excluding these observations, the most common behaviours recorded in 2006-2007 were white-faced capuchin vigilance, threat, and take food (Table 2). By comparison, the 2019 data set comprises 323 15 min samples. We recorded 2089 discrete behaviours in 80.8 h of observation. We classified 49% of these observations as no interaction between monkeys and humans. Excluding these observations, the most common behaviours in 2019 were white-faced capuchin vigilance and snatch food, and human vocalisation (Table 2).

Table 2. Number and duration of behaviours shown by humans and white-faced capuchins at Curú Wildlife Refuge, Costa Rica, in May-Oct 2006 and 2007, and June-July 2019.

Behaviour	2006 and 2007	2019

	***N* discrete instances**	**Mean duration (s)**	**SD**	**% of all behaviours observed (excluding no interaction)**	***N* discrete instances**	**Mean duration (s)**	**SD**	**% of all behaviours observed (excluding no interaction)**
Monkey run	0	0	0	0	56	9	11.3	5.3
Human run	0	0	0	0	3	2	0.6	0.3
Forage	2	31	1.4	0.4	67	26	19.1	6.3
Snatch food	9	131	104.8	1.8	182	24	33.7	17.2
Snatch item	1	11	-	0.2	8	8	6.5	0.8
Monkey vigilance	217	35	69.9	44.1	439	15	30.5	41.5
Monkey vocalisation	24	52	181.6	4.9	7	19	23.0	0.7
Human vocalisation	7	39	39.7	1.4	168	30	66.6	15.9
Monkey approach	1	10	-	0.2	5	11	8.9	0.5
Human approach	4	112	94.1	0.8	21	14	24.9	2.0
Beg	17	205	251.2	3.5	0	0	0	0

Monkey chase	0	0	0	0	1	6	-	0.1
Human chase	4	11	9.2	0.8	1	9	-	0.1
Offer	0	0	0	0	24	11	6.8	2.3
Take food	97	125	223.1	19.7	17	41	65.0	1.6
Monkey threat	108	43	105.8	22.0	59	15	24.9	5.6
Human threat	1	101	-	0.2	0	0	0	0
No interaction	668	263	291.8	0	1031	262	310.7	0
Total	1160	-	-	-	2089	-	-	-

Data regarding the number of white-faced capuchins present per 15 minute sample are not available for the 2006 and 2007 study, but the mean number of humans present was 6 (range: 1–28). In 2019, the mean number of white-faced capuchins present per 15 minute sample was 7 (range: 1–16), and the mean number of humans present was 3 (range: 1–29). Overall, 75% of human-primate interactions occurred in the presence of eight or fewer humans for 2006 and 2007, and three or fewer for 2019 (Figure 2). In 2019, capuchins initiated approximately twice as many interactions than humans (capuchins 695, 65.7%, humans 363, 34.3%) and this difference was significantly different to chance (Chi-squared test for goodness of fit: $\chi 2 = 104.181$, $P < 0.001$, $N = 1058$).

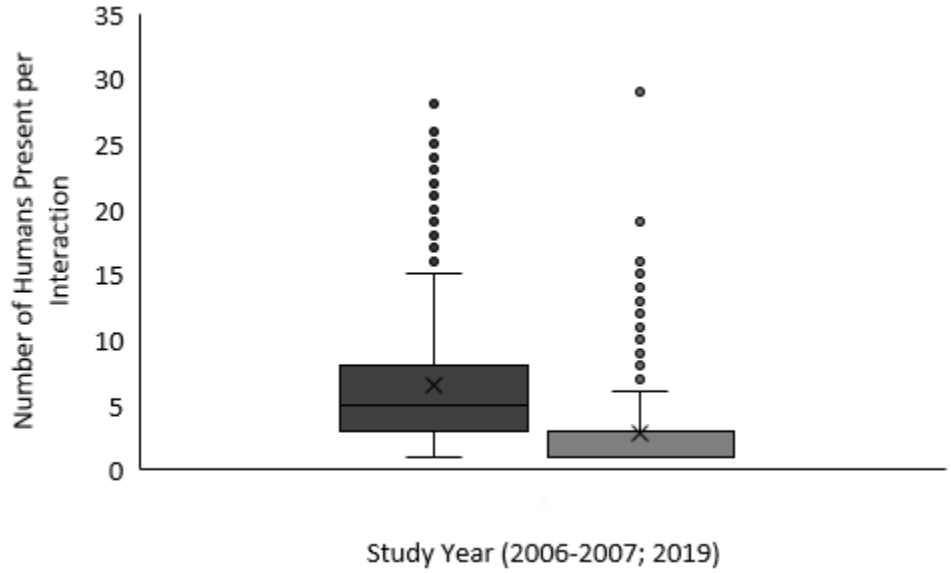
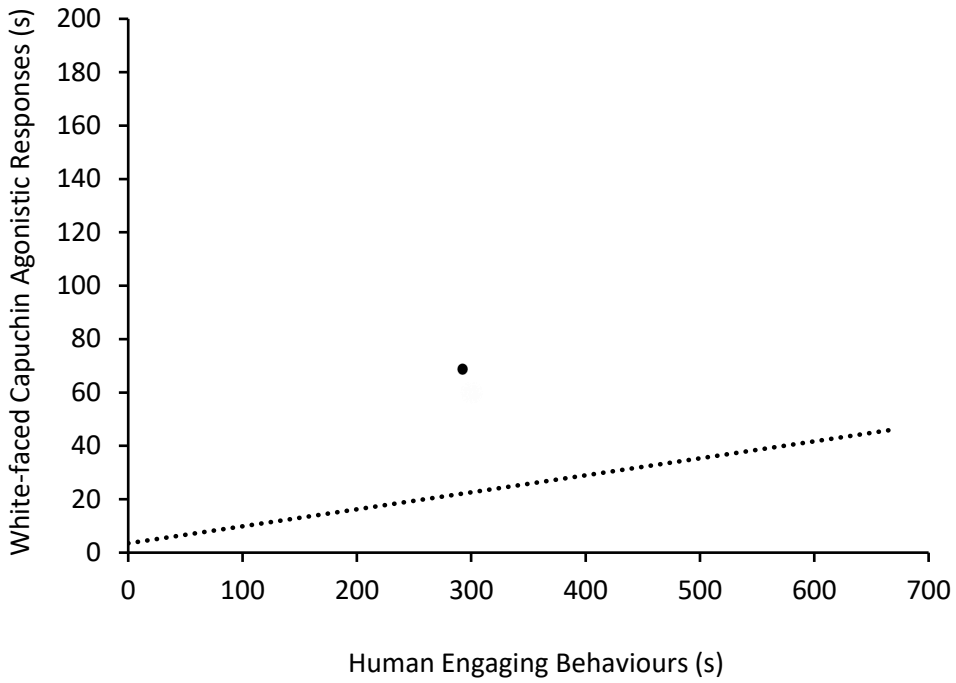


Figure 2. Number of humans present per 15 min sample of human-white-faced capuchin monkey interactions at Curú Wildlife Refuge, Costa Rica, in May-Oct 2006 and 2007 and June-July 2019. 'x' marks the mean, boxes the interquartile range, whiskers the extreme upper and lower values, dots the outliers.

The time humans spent in engaging behaviours was moderately and positively correlated with the time capuchins spent in agonistic behaviours per sample (Spearman's: $\rho = 0.545$, $P < 0.001$, $N = 323$; Fig 3).



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247 **Figure 3.** Relationship between the time spent in engaging behaviours exhibited by humans,
248 and time spent in agonistic behaviours by capuchins per sample, at Curú Wildlife Refuge,
249 Costa Rica, June-July 2019. The line of best fit illustrates a positive linear relationship
250 (Spearman's: $\rho = 0.545$, $P < 0.001$).

251

252 Capuchins spent significantly more time in moderate behaviours in the presence of
253 tourists and staff (N = 436) than staff only (N = 368) (Mann Whitney: U = 60896, $P < 0.001$,
254 N = 804; Fig 4). There was no significant difference in the time spent in intense behaviours in
255 the presence of tourists and staff (N = 100), or staff only (N = 28) (U = 1253, P = 0.395, N =
256 128; Fig 4).

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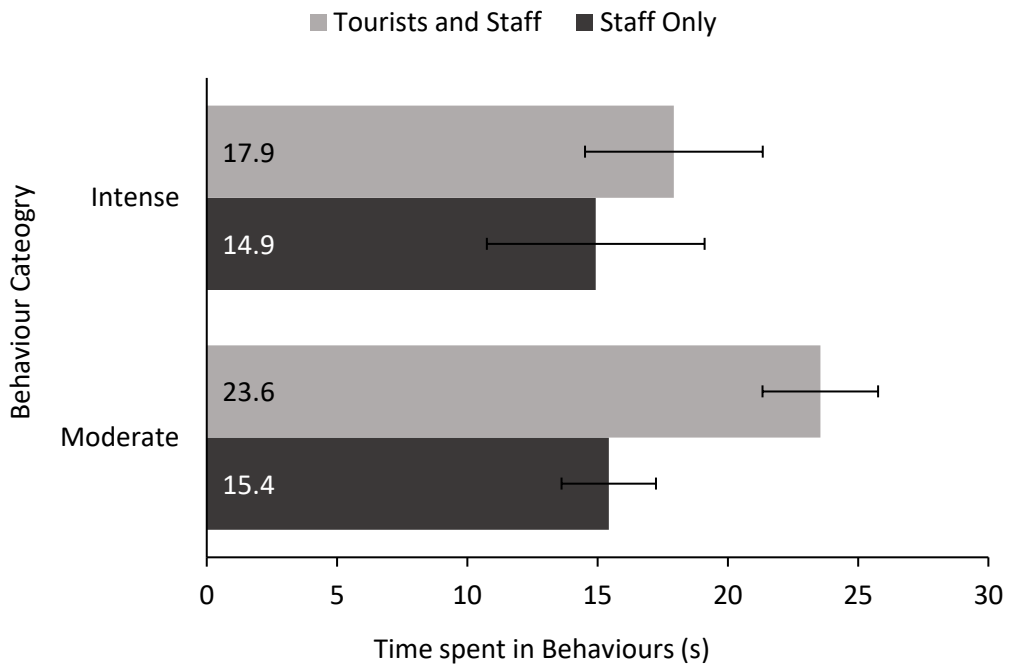

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259 **Figure 4.** Mean +/- standard error time white-faced capuchins spent engaged in intense and
260 moderate interactions with tourists and staff, and staff only, at Curú Wildlife Refuge, Costa
261 Rica, June-July, 2019.

262

263 Capuchins spent significantly more time interacting with humans in the presence of
264 tourists and staff (N = 435) than in the presence of staff only (N = 596) (Mann Whitney: U =
265 68842.500, P < 0.001, N = 1031; Fig 5).

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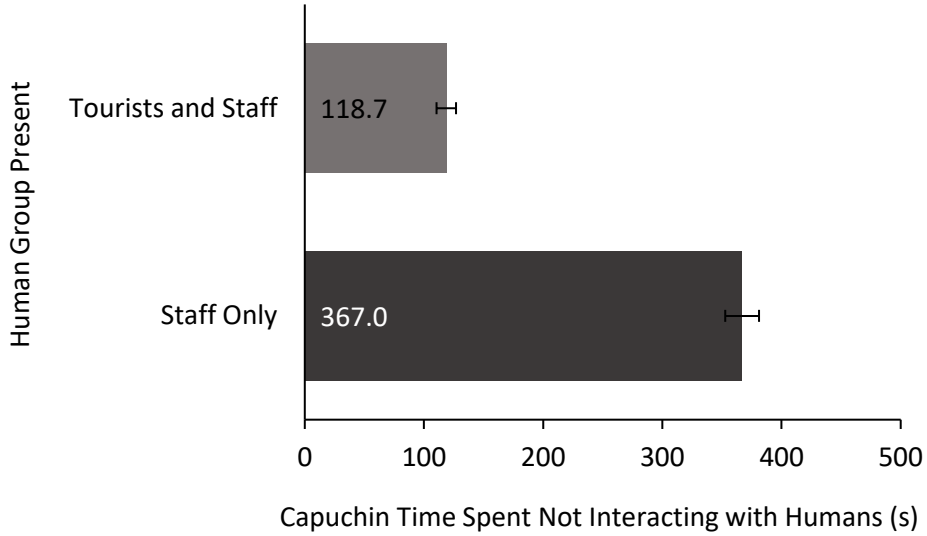
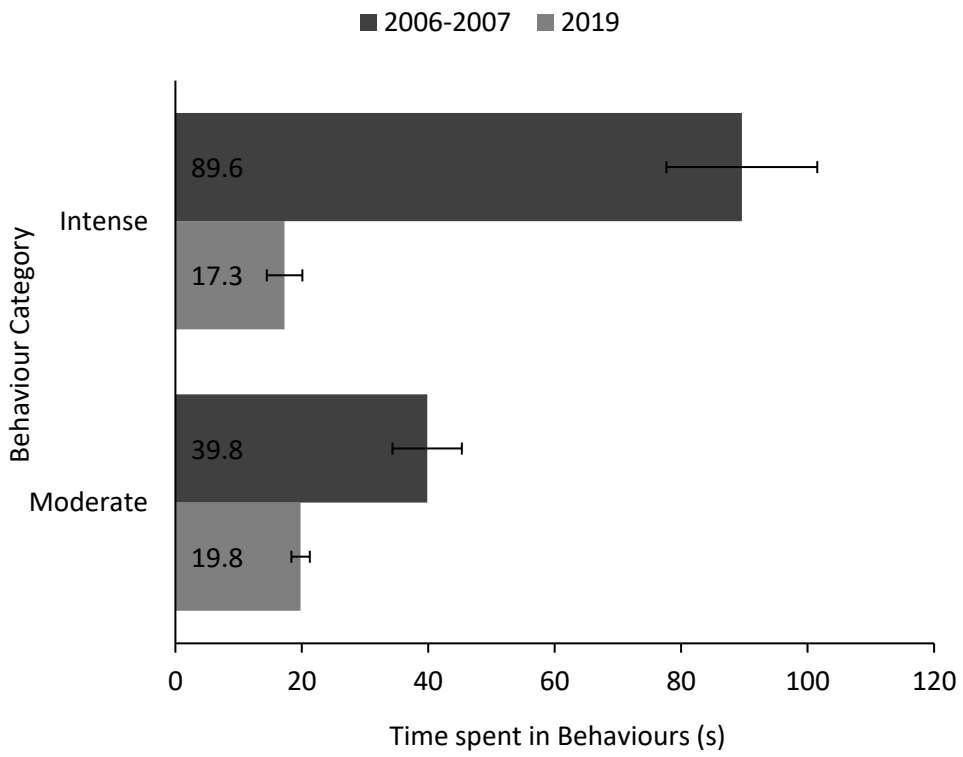


Figure 5. Mean +/- standard error time white-faced capuchins spent not interacting with humans in the presence of tourists and staff, and staff only, at Curú Wildlife Refuge, Costa Rica, June-July, 2019.

Capuchins spent significantly more time in moderate interactions with humans in 2006 and 2007 (N = 258) than in 2019 (N = 809) (Mann Whitney: $U = 78037$, $P < 0.001$, $N = 1067$; Fig 6). Capuchins also spent significantly more time in intense interactions with humans in 2006 and 2007 (N = 232) than in 2019 (N = 128) ($U = 10477$, $P < 0.001$, $N = 360$; Fig 6).



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279 **Figure 6.** Mean +/- standard error time white-faced capuchins spent engaged in intense and
280 moderate interactions with humans at Curú Wildlife Refuge, Costa Rica, in May-Oct 2006
281 and 2007, and June-July 2019.

282

283 **DISCUSSION**

284 In the 2019 study, white-faced capuchins initiated significantly more interactions than
285 humans, consistent with the results of our 2006-2007 study on this group (McKinney 2014),
286 where humans initiated 184 (37.4%) of the 492 interactions recorded, and capuchins initiated
287 308 (62.6%). This differs from the wider literature on primates, where more interactions are
288 initiated by humans (Hsu et al. 2009; Sabbatini et al. 2006; Suzin et al. 2017). In both our
289 2006-2007 and 2019 studies, the majority of tourists did not directly provision the capuchins,
290 and white-faced capuchins initiated the majority of interactions.

291 In our 2006-2007 study, the capuchins were directly provisioned by staff and visited
292 the tourist area twice daily (McKinney 2010). In 2012, they were heavily provisioned by staff

and visited the tourist area 2-3 times daily (Webb and McCoy 2014). In contrast, in 2019, we did not observe direct provisioning by staff and the capuchins only visited the tourist area on average once a day. However, indirect provisioning occurred through access to discarded fruit and vegetables near the boathouse. In both 2006-2007 and 2019, white-faced capuchins frequented the tourist area due to indirect provisioning, similar to other studies in which capuchins repeatedly entered anthropogenic habitats for food (Sabbatini et al. 2006; Van Hulle and Vaughan 2009).

It is illegal to provision wildlife in Costa Rica under the Conservation of Wildlife Act (7317). With specific reference to Curú, we recommend that staff further reduce the indirect provisioning of white-faced capuchins and other wildlife, through gradually reducing the amount of food discarded by the boathouse and building secure waste disposal areas. Reducing indirect provisioning could reduce the frequency and intensity of human-primate interactions for primates living in tourist sites. Previous suggestions for secure garbage bins at Curú have been partially implemented (McKinney 2014), with 2 of 11 garbage bins in the tourist area fortified by metal caging. One garbage bin near the boathouse had been previously secured, but was currently exposed due to erosion, and none of the bins located outside the cabins were secure. These recommendations would help to create a stronger focus on conservation at Curú, and positively influence human attitudes and actions toward white-faced capuchins.

Food is a primary cause of human-primate interactions (Fuentes et al. 2008; Sabbatini et al. 2006), and the study group has been described as more aggressive and direct than other white-faced capuchin groups in Curú Wildlife Refuge which do not have access to anthropogenic food sources (McKinney 2010). The largest difference in capuchin behaviour between our two studies was a decrease in threat behaviours. In the 2006-2007 study, threat behaviours exhibited by capuchins comprised 22% of all behaviours observed, but this figure

was just 5.6% in 2019. Agonistic animal behaviours are often a response to human attempts to engage the target species (Sabbatini et al. 2006). We found that engaging behaviours exhibited by humans were positively correlated with agonistic behaviours by white-faced capuchins. We observed tourists approaching and vocalising to white-faced capuchins, although the latter displayed threat and run behaviours. This is consistent with past research where humans ignored primate fear and threat behaviours and continued to promote interspecies engagement (Maréchal et al. 2017; Sabbatini et al. 2006). The observed decrease in threat, and similar decrease in take food, is possibly due to the reduction in provisioning in 2019, as compared to 2006-2007.

While the frequency of different behaviours between humans and white-faced capuchins at Curú Wildlife Refuge changed between 2006-2007 and 2019, interactions did not intensify. Capuchins spent more time in moderate and intense interactions with humans in 2006-2007 than in 2019. This difference may be due to the reduced direct provisioning observed in 2019, as compared to 2006-2007. However, there are individual differences in primate responses to provisioning (Marty et al. 2020), and the behavioural differences between 2006-2007 and 2019 could also be due to variation in white-faced capuchin group composition. Capuchins spent significantly more time engaged in moderate behaviours and more time interacting with humans in the presence of tourists and staff, than in the presence of staff only. Our findings support previous research suggesting that that tourists are more intrusive in their behaviours than other human groups (Behie et al. 2010; Westin 2017). However, we did not observe a significant difference in the time capuchins spent in intense behaviours when tourists and staff were present, and when only staff were present.

Wildlife tourism of is one of the fastest growing industries in the world (Kauffman 2014), with significant potential for conservation, but hinges on reduced direct and indirect provisioning and moderation of tourist behaviours. Our findings support research suggesting

that tourists are more intrusive than staff (Behie et al. 2010; Westin 2017), and suggest that reducing engaging behaviours by humans may reduce agonistic responses by capuchins. We also show that reducing direct and indirect provisioning could reduce the frequency and intensity of human-primate interactions for primates living in tourist sites. Humans bear the responsibility to reduce anthropogenic pressure on the environment (Sabbatini et al. 2006). Interaction with habituated primates in the absence of provisioning may promote peaceful interspecies coexistence (Hsu et al. 2009), and become a positive driver for conservation, globally.

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