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Interactions Between Humans and Panamanian White-Faced Capuchin Monkeys (*Cebus imitator*)

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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–October 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 behaviors exhibited by humans and capuchin agonistic behaviors. Capuchins spent significantly more time engaging in moderate behaviors (snatch food, snatch item, vigilance, vocalization) 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 behaviors (approach, beg, chase, offer, take food, threat) was lower in 2019 than in 2006 and 2007. These findings suggest that reducing engaging behaviors by humans may reduce primate agonistic behaviors, and that human group composition affects human–primate interactions. The reduction in moderate and intense behaviors between studies also suggests that reducing direct provisioning could reduce the frequency and intensity of human–primate interactions in tourist sites.

Keywords Ecotourism · Ethnoprimatology · Human–animal interaction · Provisioning · Wildlife tourism

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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 behavior 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). Subsidized diets are generally high energy and low fiber (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 socializing (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 tradeoff between human interaction and food subsidies (Maréchal, MacLarnon, *et al.* 2016). Food transfer still frequently occurs even when tourist sites prohibit provisioning (Maréchal, Semple, *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 behavior directed at humans due to provisioning withdrawal (Kauffman 2014; Van Hulle and Vaughan 2009).

Wild primates in contact with tourists display other behavioral modifications including avoidance (Hsu *et al.* 2009; Maréchal, Semple, *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 behavior in response to primate actions (Sabbatini *et al.* 2006). Tourist behaviors 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 behaviors 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 categorized 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 behaviors (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' behavior 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 to October and dry from November to April (McKinney *et al.* 2015). Regional temperatures range from 24.1°C to 29.3°C (median 26.7°C) in June and 23.9°C to 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 2014), and the Ceiba Group (Webb and McCoy 2014), though the term "commensal" is frequently misused in primatology (Maréchal 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 (Fig. 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).

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 behavior (Williamson and Fiestner 2003). While this group were provisioned in the past (McKinney 2010; Webb and McCoy 2014), 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 05:00 h to 17:00 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 sample. We collected data via whole-group all-occurrence sampling (Altmann 1974), recording the frequency and duration of human–primate interactions

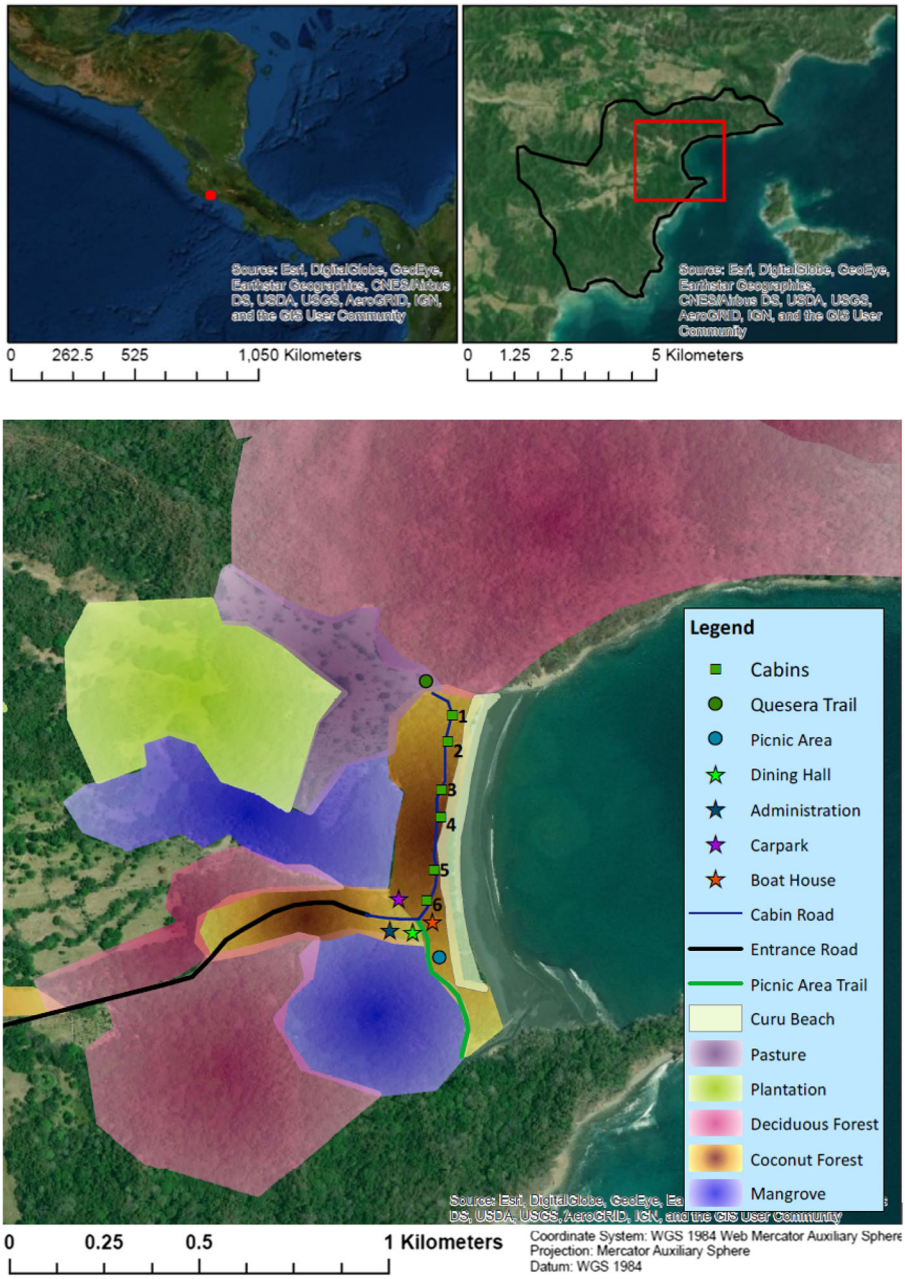

Fig. 1 Location of Curú study site in Costa Rica. (Top left) Red outline denotes the location of the Curú Wildlife Refuge in Costa Rica, Central America. (Top right) Black outline denotes the extent of Curú Wildlife Refuge, and red outline denotes the location of the study site within the refuge. (Bottom) 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.

and whether each interaction was initiated by white-faced capuchins or humans. We identified behaviors using an ethogram adapted from McKinney (2010) to facilitate comparison between the two studies (Table I). We did not formally assess inter-observer reliability, but we used the same data sheet format and TM was available for queries during NM's time in the field. We categorized behaviors as mild, moderate, and intense. We defined mild behaviors as "no direct engagement" (foraging, run); moderate behaviors as "low-level engagement" (snatch food, snatch item, vigilance, vocalization); and intense behaviors as "active engagement" (chase, threat, take food, beg, approach, offer). We defined engaging behaviors exhibited by humans as offer, approach, chase, and vocalization, and capuchin agonistic behaviors as threat, run, chase, and vocalization. When the capuchins engaged in more than one behavior at a time, we recorded the majority group behavior.

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

Table I Ethogram used to study human–primate interactions in white-faced capuchins at Curú Wildlife Refuge, Costa Rica, 2019

Category	Behavior	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[a] food	Monkey grabs food from trash bin, table, porch, or backpack.
	Snatch item	Monkey grabs nonfood item from person, bag, house, or bin.
	Vigilance	Monkey observes humans and social or environmental surroundings.
	Vocalization	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 behaviors with each other.

Adapted from McKinney (2010)

[a] The behavior "snatch" was referred to as "steal" in the original ethogram

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 behaviors per 15-min sample was not normal, so we used nonparametric 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 ρ to test for significant correlations between the number of engaging behaviors 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 behaviors because they indicate higher levels of engagement between humans and capuchins than mild behaviors do.

We performed all statistical analysis in SPSS v. 26 (IBM Corp. 2019). We set confidence intervals at 95% and $\alpha = 0.05$. 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. The authors declare that they have no conflict of interest.

Data Availability The data sets generated during and/or analyzed 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 behaviors 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 behaviors recorded in 2006–2007 were white-faced capuchin vigilance, threat, and take food (Table II). By comparison, the 2019 data set comprises 323 15-min samples. We recorded 2089 discrete behaviors 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 behaviors in 2019 were white-faced capuchin vigilance and snatch food, and human vocalization (Table II).

Table II Number and duration of behaviors shown by humans and white-faced capuchins at Curú Wildlife Refuge, Costa Rica, in May–October 2006 and 2007, and June–July 2019

Behavior	2006 and 2007				2019			
	N discrete instances	Mean duration (s)	SD	% of all behaviors observed (excluding no interaction)	*N* discrete instances	Mean duration (s)	SD	% of all behaviors 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 vocalization	24	52	181.6	4.9	7	19	23.0	0.7
Human vocalization	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	—	—	—

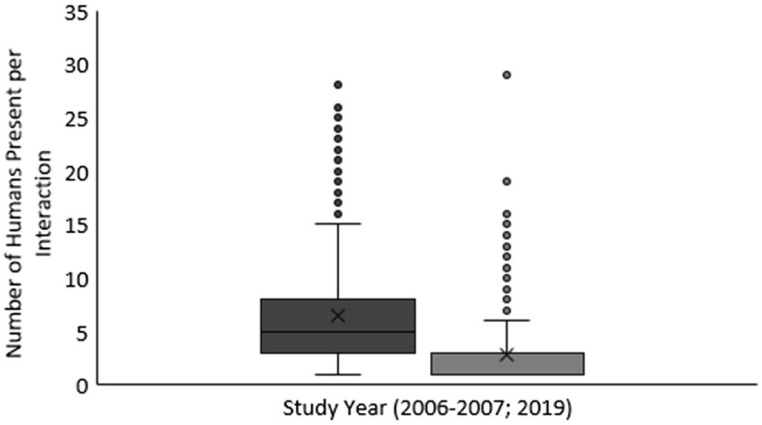

Fig. 2 Number of humans present per 15-min sample of human–white-faced capuchin monkey interactions at Curú Wildlife Refuge, Costa Rica, in May–October 2006 and 2007 and June–July 2019. An x marks the mean, boxes the interquartile range, whiskers the extreme upper and lower values, and dots the outliers.

Data regarding the number of white-faced capuchins present per 15-min 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-min 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 (Fig. 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 from chance (chi-squared test for goodness of fit: $\chi^2 = 104.181$, $P < 0.001$, $N = 1058$).

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

Capuchins spent significantly more time in moderate behaviors in the presence of tourists and staff ($N = 436$) than staff only ($N = 368$) (Mann–Whitney: $U = 60{,}896$, $P <$

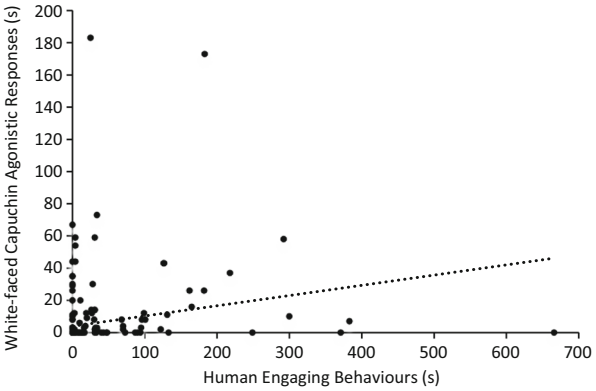

Fig. 3 Relationship between the time spent in engaging behaviors exhibited by humans, and time spent in agonistic behaviors by capuchins per sample, at Curú Wildlife Refuge, Costa Rica, June–July 2019. The line of best fit illustrates a positive linear relationship (Spearman's: $\rho = 0.545$, $P < 0.001$).

0.001, $N = 804$; Fig. 4). There was no significant difference in the time spent in intense behaviors in the presence of tourists and staff ($N = 100$), or staff only ($N = 28$) ($U = 1253$, $P = 0.395$, $N = 128$; Fig. 4).

Capuchins spent significantly more time interacting with humans in the presence of tourists and staff ($N = 435$) than in the presence of staff only ($N = 596$) (Mann–Whitney: $U = 68{,}842.500$, $P < 0.001$, $N = 1031$; Fig. 5).

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).

Discussion

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

In our 2006–2007 study, the capuchins were directly provisioned by staff and visited the tourist area twice daily (McKinney 2010). In 2012, they were heavily provisioned by staff and visited the tourist area two or three times daily (Webb and McCoy 2014). In contrast, in 2019, we did not observe direct provisioning by staff and the capuchins visited the tourist area on average only 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

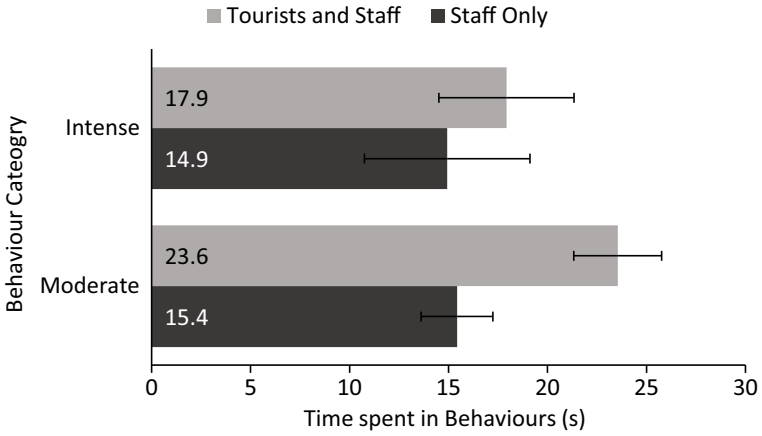

Fig. 4 Mean ± standard error time white-faced capuchins spent engaged in intense and moderate interactions with tourists and staff, and staff only, at Curú Wildlife Refuge, Costa Rica, June–July, 2019.

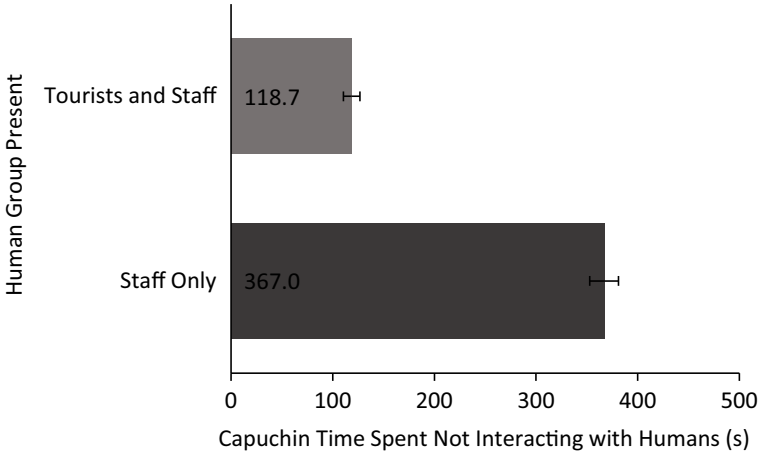

Fig. 5 Mean ± standard error time white-faced capuchins spent not interacting with humans in the presence of tourists and staff, and staff only, at Curú Wildlife Refuge, Costa Rica, June–July, 2019.

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

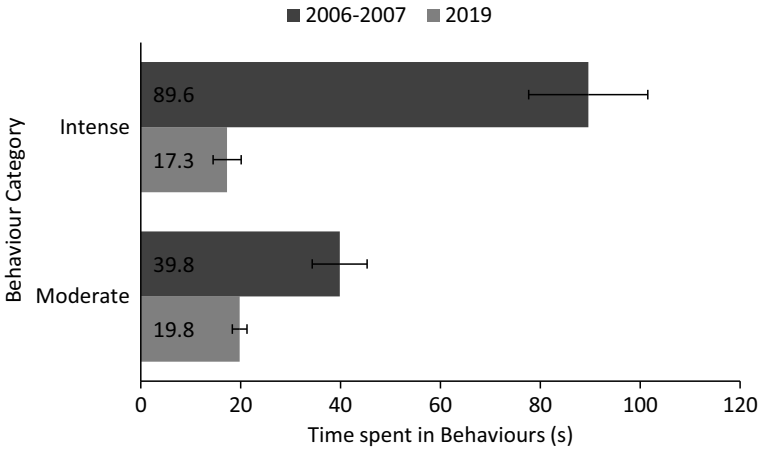

Fig. 6 Mean ± standard error time white-faced capuchins spent engaged in intense and moderate interactions with humans at Curú Wildlife Refuge, Costa Rica, in May–October 2006 and 2007, and June–July 2019.

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 that do not have access to anthropogenic food sources (McKinney 2010). The largest difference in capuchin behavior between our two studies was a decrease in threat behaviors. In the 2006–2007 study, threat behaviors exhibited by capuchins comprised 22% of all behaviors observed, but this figure was just 5.6% in 2019. Agonistic animal behaviors are often a response to human attempts to engage the target species (Sabbatini *et al.* 2006). We found that engaging behaviors exhibited by humans were positively correlated with agonistic behaviors by white-faced capuchins. We observed tourists approaching and vocalizing to white-faced capuchins, although the latter displayed threat and run behaviors. This is consistent with past research in which humans ignored primate fear and threat behaviors 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 behaviors 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 behavioral 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 behaviors 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 behaviors 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 behaviors 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 behaviors. Our findings support research suggesting that tourists are more intrusive than staff (Behie *et al.* 2010; Westin 2017) and suggest that reducing engaging behaviors 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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Author contributions TM conceived and designed the research protocol. NLM conducted fieldwork in 2019, TM conducted fieldwork in 2006 and 2007. NLM and TM analysed the data, and wrote the manuscipt.

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