Articles

HUMAN-MONKEY INTERACTION DYNAMICS AND THEIR DIETARY IMPACTS ON CENTRAL AMERICAN WHITE-FACED CAPUCHINS *(CEBUS IMITATOR)* AT MANUEL ANTONIO NATIONAL PARK, COSTA RICA

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Abstract

Wild capuchin monkeys are highly adaptable to anthropogenic environments. We assessed how the interaction dynamics between humans and three groups of Panamanian white-faced capuchin monkeys (*Cebus imitator*) in Manuel Antonio National Park, the most visited national park of Costa Rica, affected the feeding behavior and diet of these animals in 2008-2009. On average, individual monkeys acquired 2.4 human food items per focal hour during peak hours of park visitation by humans. Although human visitors directly and indirectly provisioned monkeys in the park, 71 % of monkeys' acquisition of human food items were a result of monkey-initiated interactions (MIIs) rather than human-initiated interactions (HIIs), and adult male monkeys were the most frequent initiators (with 157 adult male MIIs in the study period, compared to 33 initiated by adult females and 84 by juveniles). Adult male monkeys were also the most likely to make direct contact with humans to grab food (35 of 50 direct grabs of food from humans were by adult male monkeys). Adult females acquired food from humans through HIIs at about the same rate as adult males in their group. Secondary acquisition of human food from other monkeys accounted for about one-third of all events of monkey acquisition of human food, and juvenile monkeys had higher median hourly rates than adults in their group to acquire human food through secondary acquisition. Humans frequently offered fruit when provisioning (61.4 % of provisioning events), but monkeys actively acquired fruit, meat, candy, condiments, chips, crackers and dairy items, and only 36.5 % of MIIs were to acquire fruit. Our results suggest that in parks where humans have frequent contact with capuchin monkeys, park regulations should not only prohibit direct provisioning, but require visitors not to bring food into parks. Stronger measures such as fines or park expulsion for those interacting with monkeys might be more effective, and environmental education is necessary as a strategy to inform visitors what to expect from the monkeys and how to avoid accidental provisioning.

Keywords: Ethnoprimatology, tourism, anthropogenic diet, *Cebus capucinus*, gracile capuchin monkeys

Resumen

Los monos capuchinos silvestres son altamente adaptables a los ambientes antropogénicos. Evaluamos cómo la dinámica de interacción entre los humanos y tres grupos de monos capuchinos cariblancos panameños (*Cebus imitator*) en el Parque Nacional Manuel Antonio, el parque nacional más visitado de Costa Rica, afectó el comportamiento alimentario y la dieta de estos animales en 2008-2009. En promedio, los monos individuales adquirieron 2.4 alimentos de humanos por hora focal durante las horas pico de la visita de humanos al parque. Aunque los visitantes humanos aprovisionaron directa e indirectamente a los monos en el parque, el 71 % de la adquisición de ítems alimentarios de humanos por parte de los monos fue el resultado de interacciones iniciadas por los monos (MII) más que de interacciones iniciadas por los humanos (HII), y los monos machos adultos fueron los iniciadores más frecuentes (con 157 MII machos adultos en el período de estudio, en comparación con 33 iniciados por hembras adultas y 84 por juveniles). Los monos machos adultos fueron también los que más probabilidades tenían de entrar en contacto directo con los seres humanos para tomar alimentos (35 de las 50 tomas directas de alimentos de los seres humanos fueron realizadas por monos machos adultos). Las hembras adultas adquirieron comida de los humanos a través de las HIIs en aproximadamente la misma proporción que los machos adultos de su grupo. La adquisición secundaria de alimentos de otros monos representó alrededor de un tercio de todos los casos de adquisición de alimentos de humanos por parte de los monos, y los monos jóvenes tuvieron tasas horarias medias más altas que los adultos de su grupo para adquirir alimentos de humanos a través de la adquisición secundaria. Los humanos frecuentemente ofrecían fruta al aprovisionarles (61,4 % de los eventos de aprovisionamiento), pero los monos adquirían activamente fruta,

carne, dulces, condimentos, patatas fritas, galletas y productos lácteos, y sólo el 36,5 % de los MII fueron para adquirir fruta. Nuestros resultados sugieren que en los parques donde los humanos tienen contacto frecuente con los monos capuchinos, las regulaciones de los parques no sólo deberían prohibir el aprovisionamiento directo, sino también exigir a los visitantes que no traigan comida a los parques. Medidas más estrictas, como multas o expulsión del parque para quienes interactúen con monos, podrían ser más eficaces, y la educación ambiental es necesaria como una estrategia para informar a los visitantes sobre lo que deben esperar de los monos y cómo evitar el aprovisionamiento accidental.

Palabras Clave: Etnoprimatología, turismo, dieta antropogénica, *Cebus capucinus*, monos capuchinos gráciles

Introduction

Capuchin monkeys (*Cebus* and *Sapajus*) are found throughout most of Central and South America. They are highly adaptable to anthropogenic environments and populations can persist alongside humans. As monkeys become more habituated to human food through mechanisms such as crop-foraging or provisioning by humans in parks, human-monkey conflict can escalate due to the combination of increased human presence and increasingly habituated monkeys' bold and direct foraging for human food, together putting both species at risk for injury and disease transmission, as well as for diet-related health consequences in monkeys.

At the time of our study, in the late 2000s, Costa Rica was home to a flourishing ecotourism industry, associated with increased development and habitat fragmentation around primate habitats (Broadbent et al., 2012). Central American white-faced capuchin monkeys (*Cebus imitator*) experienced intense contact with humans and access to human food at Manuel Antonio National Park (MANP). Tourist groups brought large amounts of food into the park to consume at the beach or picnic tables, so capuchins had access to a wide variety of human foods in addition to their natural diet. Previous studies about capuchin use of human resources found they will consume diverse human foods, from fruit to cooked foods, condiments, sweets and dairy products (Sabbatini et al., 2006, 2008; McKinney, 2011; Campbell, 2013). At MANP, Kaufman (2014) calculated that already in 1998, a capuchin group with high exposure to human visitors spent 46 % of its feeding time eating human-resourced foods. However, Kaufman (2014) also noted that capuchins got much of their human food by actively searching through garbage and grabbing food from picnic tables or out of backpacks, rather than from provisioning initiated by humans.

Our study examined which particular human-possessed food resources were acquired by three capuchin groups in MANP in 2008-2009, as well as how often and through what means. We were particularly interested to understand whether monkeys most often initiated interactions involving food with humans, or if it was humans that initiated provisioning of the monkeys. We also aimed to determine what percentage of food-related human-monkey interactions involved physical contact.

While there is an increasing amount of research on the impact of anthropogenic disturbances on primate diet and behavior, many studies of provisioned, semi-provisioned, human-commensal and human-sympatric primates define the categories of primate overlap and interaction in diverse ways (Sabbatini et al., 2006, 2008; McKinney, 2011; Campbell, 2013). A bidirectional approach to categorizing inter-primate interactions adds additional granularity to our understanding of the complex motivations and variations in the way that human and non-human primates engage with each other around food resources in a natural area. In order to understand the human-monkey dynamics of food transfer at MANP, we collected data on human-initiated versus monkey-initiated interactions.

Human-initiated interactions (HIIs) involve humans selecting food for the monkeys to consume based on previous impressions about the diets of "monkeys" as well as what is available to feed the monkeys, while monkey-initiated interactions (MIIs) involve capuchin individuals making diet choices based on the availability of human and natural food items, as well as their own behavioral ecology and diet preferences. A study of black capuchins (*Sapajus nigritus*) in Brazil showed that most interactions between humans and monkeys were HIIs (Fahy, 2013). In contrast in Curú Wildlife Refuge, Costa Rica, nearly all of the interactions that white-faced capuchin monkeys had with humans were MIIs (McKinney, 2014).

Sabbatini and colleagues (2006) performed a survey of visitors at a national park in Brazil where bearded capuchin monkeys (*Sapajus libidinosus*) utilized human foods. From a total of 300 respondents, 64.7 % thought capuchin monkeys had strictly vegetarian diets (Sabbatini et al., 2016). Additionally, when respondents were given a list of potential foods for capuchins and asked to select those that capuchins consume, fruit was the most common food category chosen (45 %), followed by leaves (28 %; Sabbatini et al., 2016). In another study of *Sapajus* sp. in a park in the urban matrix of Foz de Iguaçu, respondents who visited the park reported that they gave the monkeys fruits or cultivated items over 90 % of the time, rather than processed foods, although respondents also mentioned that other people gave a somewhat higher percentage of processed foods, with fruit still as the majority (Suzin, 2015). These findings led to our hypothesis that HIIs would involve fruit at significantly higher rates than other foods.

While capuchin diets do contain a high percentage of fruit, they also contain much more protein and fat than the diets of frugivorous and folivorous primates, due to capuchins' consumption of insects and vertebrate prey (Hladik et al., 1971; Fragaszy et al., 2004). We predicted that human foods with higher protein and fat content would be obtained more frequently by MIIs than by HIIs, as capuchins are likely to prefer these foods while human visitors to the park are unlikely to consider them potential food for monkeys.

Capuchin monkey sex, age, and group characteristics all may affect the frequency and type of acquisition of human food. Studies of white-faced capuchin foraging behavior suggest that adult male capuchin monkeys may show higher rates of MII acquisition behaviors as well as a higher rate of direct contact interactions with humans compared to adult capuchin females. At Santa Rosa National Park, Costa Rica, adult male *Cebus imitator* displayed foraging patterns that involved more opportunistic and higher-risk foraging strategies compared to adult females (Rose, 1994). Adult males have reduced vulnerability to predators compared to female capuchins, due to significant sexual dimorphism (Rose, 1994). Direct contact interactions are high risk interactions for monkeys as they involve extreme proximity to humans, a potential predator and disease carrier. In areas with low human impact, female capuchins rely on a low-risk, stable diet consisting of foraging behaviors that limit exposure to predators and spend less time than males on the ground (Rose, 1994). A study of *Cebus imitator* in Cahuita National Park in Costa Rica where monkeys have access to human food showed that 100 % of monkey-initiated human food acquisitions were by adult males, and that all of these MIIs were agonistic (Campbell, 2013).

Juvenile capuchins may be more likely to obtain human resources via secondary acquisition than adults, because juveniles often show more interest in other monkeys' food than adults do (Visalberghi et al., 1998), with the majority of the food interest directed towards adult capuchins rather than other juveniles (Fragaszy et al., 2004; Agostini and Visalberghi, 2005). Juvenile capuchins exhibit greater levels of begging and receive more food via tolerated food transfer than adults (Perry and Rose, 1994).

Monkeys' proactive human food acquisition behavior may vary based on amount of exposure to humans, with capuchin groups that range most often in areas with high human presence more likely to actively acquire food. Here we compare human-resourced food acquisition rates for three different groups of capuchin monkeys with different degrees of exposure to humans. The aim of this study was to investigate the influence of human presence and food-provisioning on the feeding behavior of capuchins in MANP. Specifically, we studied the behavior of three capuchin groups with different levels of interaction with MANP's visitors to assess: (i) the types of human-capuchin interactions observed related to human food acquisition, (ii) frequency of HIIs compared to MIIs, and whether interactions included direct or indirect contact between monkeys and humans; (iii) the influence of age, sex and group categories on the frequency of interactions and the proportion of interaction types.

Methods

Study site

This study was carried out during a 15-month period (February-August 2008 and January-August 2009) in MANP, Puntarenas province, Central Pacific coast, Costa Rica (Table 1). This park is not only Costa Rica's smallest national park in terms of the land area (1,625 terrestrial ha according to SINAC, Sistema Nacional de Areas de Conservación, in Costa Rica), but it is also the most heavily visited national park in Costa Rica (ICT, 2017), and at the time of the study was receiving between 400 to 1000, or more, human visitors per day; in 2011, MANP had over 300,000 visitors (ICT, 2017) and by 2018 this had increased to over 500,000 visitors annually (ICT, 2017). MANP is home to howler monkeys *Alouatta palliata*, squirrel monkeys *Saimiri oerstedii citrinellus*, and white-faced capuchin monkeys *Cebus imitator* (sensu Rylands et al., 2013; formerly called *Cebus capucinus* or *Cebus capucinus imitator)*, and many tourists visit this park to see these primates, although according to a survey of visitors, primates are not the main draw, and could in fact be detractors from visiting the park due to negative monkey-human interactions (Kaufman, 2014).

Capuchin study groups

We collected behavioral data on three *Cebus imitator* groups exposed to varying levels of interaction with humans (Table 1). The high-interaction group HI was composed of 15 individuals that had near daily high-proximity and food-related interactions with hundreds of national and international visitors. The foraging area of HI included a mangrove lagoon, wet tropical forest, the volunteer bunk house and park ranger house and the two most popular beaches in the park (Manuel Antonio and Playa Dos). Facilities included a large picnic area, benches, individual picnic tables outside of the picnic area, and trash cans. The HI group spent several hours almost every day along Manuel Antonio Beach, the picnic areas, and the beach trail, which were often occupied by hundreds of humans.

The low-interaction groups L1 and L2 were composed of 12 and 15 individuals, respectively (Table 1); they each had occasional food-related interactions with smaller numbers of visitors. The foraging area of L1 included a hilly peninsula at the end of the two aforementioned beaches and their steep cliffs, and a loop trail around the perimeter of the peninsula. There were no trash cans or picnic tables in the L1 territory. The ranging area of L2 included part of the mangrove lagoon, an extensive wet tropical forest away from hiking trails and development, as well as the main

trail into the park, two side trails, the houses of volunteers and park rangers, and a small side beach often populated by visitors. There were no picnic tables or trash cans in the territory of L2, but this group occasionally visited the Manuel Antonio beach into HI territory with access to trash cans.

Table 1. Capuchin monkey study group compositions by age-sex classes for focal animal sampling at MANP. Infants were not included as focal subjects and so not included here.

	Adult Males	Adult Females	Juveniles
HI	4	3	8
L1	3	3	6
L2	6	4	5

Capuchins were identified individually using facial features, hair color and length, scars, birthmarks, and body size. Using body size, genital traits, and behavior we classified the focal individuals in three main age-sex classes: adult males, adult females, and juveniles. Due to the difficulty in sexing juvenile capuchin monkeys (Carosi et al., 2020), they have not been separated by sex in our analyses. Infants were not included in the study as focal subjects because they did not forage on their own or interact with humans.

Behavioral data collection

Due to park regulations, researchers only had access to MANP during 'open hours', 9 a.m. to 4 p.m., except for Mondays, when the park was closed to visitors, but the researchers were allowed to visit during the same hours. This meant that researchers would have to find the monkey groups each day, often with help from park guides or rangers. Some areas of the park were inaccessible due to the lagoon and surrounding vegetation. For this reason, data collection was biased towards afternoon hours.

Behavioral data were collected by author M.S. and field assistants between 9 a.m. to 4 p.m., upon finding the groups for the day, using 10-min focal animal sampling at 15-min intervals (Altmann, 1974), collected specifically when the monkeys were in general proximity to humans, in order to capture human-monkey interactions. Focal animal samples alternated through individuals in different age-sex categories. Within each focal sample *ad libitum* data were collected on all social, human interaction, and human resource acquisition behaviors. Focal samples were discarded if the individual was not visible for more than two scan samples. Inter-observer reliability between the primary investigator (M.S.) and field assistants was tested by performing simultaneous focal samples on the same animal and determining a percentage of discrepancies based on total discrepancies observed and total behaviors recorded.

Human resource acquisition bouts were categorized in the following ways, based on observational data collected *ad libitum* during the early days of the study prior to the onset systematic focal animal follow data collection:

Monkey-Initiated Interactions (MIIs)

Direct Grab: the taking of human resources directly from a person or from a bag/object being held or worn by a person. This included grabbing food items out of a person's hand, grabbing plastic bags containing food out of a person's hand, charging a person with a threat face until a food item was dropped due to fear and then collecting the food item, jumping on a backpack that was being worn, or otherwise directly removing a human resource from a person who was not offering the food item to the monkey at that time.

Indirect Grab: the taking of human resources from a person when the resources were not in the person's direct possession. This included taking items from unattended backpacks or off of unattended towels, or from tables when the food was not in someone's personal possession. This also included grabbing food items out of trash bags on someone's towel. To be classified as an indirect grab, it needed to be clear that the human possessor of the food did not put the food out intentionally for the monkey to take, indicated by surprise or anger when the monkey obtained the food, or an attempt to discourage the monkey from eating or taking the food.

Human-Initiated Interactions (HIIs)

Direct Provisioning: the food item was given directly by a human to a monkey, through hand-to-hand or hand-to-mouth provisioning. To be considered direct provisioning, it must be clear that the human offered the food to the monkeys and was not simply holding food they intended to consume themselves. To be counted as direct provisioning the monkey had to accept the offered food item and taste, lick, bite or consume the food item.

Indirect Provisioning: the food item was offered from a human to a monkey by the human placing it in close proximity to a monkey or monkeys. This often consisted of humans setting pieces of food on a branch, table, or trash can surrounded by monkeys, or throwing a food item towards the group of monkeys. It could be distinguished from indirect grabs in that the provisioner did not express surprise or anger at the monkey taking the food, and there were attempts to encourage rather than discourage acquisition and consumption. It had to be clear that the provisioner intended for the monkeys to eat the food, and the monkey had to taste, lick, try or eat the food, to be classified as provisioning.

Secondary Acquisition: the acquisition of human food resources by one monkey from another monkey in the group. Secondary acquisition happened when one monkey obtained a food resource via one of the above means, and either tolerated a direct grab of pieces of the food item while still in its possession, or, discarded all or part of that resource allowing other monkeys to indirectly scavenge the remains.

Acquisition of a food item was counted once per focal sample per food type and acquisition method. For example,

being fed or grabbing a bag of cookies was counted as one provisioning incident or one grab regardless of how many cookies are eaten, or if the bag was dropped and picked back up by the same individual. However, a direct grab of a bag of cookies followed by a direct grab of a sandwich during one focal sample would be considered two direct grabs. Also, direct provisioning from a bag of chips followed later by a direct grab of that bag of chips was considered both a direct provisioning and a direct grab.

Data Analyses

Behavioral rates were calculated for each focal individual by taking the total number of times the behavior occurred for that individual divided by the total number of focal 'feeding near human' hours for that individual, calculated through summing 10-minute focal samples. Behavioral rates were calculated for age and sex classes within groups and are presented as medians (Quartile 1 – Quartile 3 (Interquartile range)) with outliers depicted in the figures. Calculations were performed using R software.

Results

Our study included a total of 240 observation days; during the 156 days of quantitative data collection we collected 251.5 focal 'feeding near human' hours across all three groups, with 97.33 focal hours for HI, 83 focal hours for L1, and 71.17 focal hours for L2. A total of 85.83 focal hours of data were collected for adult males (AM), 81.67 for adult females (AF), and 84 for juveniles (JU). Inter-observer reliability was confirmed at more than 95 % between the principal investigator (MS) and each field assistant prior to including any focal follow data from that field assistant in the study.

Types of human food acquired

Human food obtained by monkeys was classified into the following categories (Table 2): fruit, bread, chips, meat, cookies, candy, crackers, dairy, condiments, and 'other', which included coconuts (young green coconuts were sold outside the park for visitors to drink the coconut juice—they had a small hole sliced in the top for a straw; monkeys put their hands into the hole to scrape the meat off the inside of the coconut). Overall, human food items were acquired by monkeys at a rate of 2.4 items per focal hour, but the rate of human food acquisition varied widely by capuchin group: individuals from HI group acquired 4 human food items on average per focal hour, while L1 acquired 1.4 items and L2 acquired 1.2 items per focal hour. An overview of the different types of acquisition that occurred in the study and median individual hourly acquisition rates per group is depicted in Figure 1.

Table 2. Total occurrence of capuchin food acquisition of human food in this study. Numbers indicate total number of times a monkey in a focal animal follow gained possession of a human food resource, including direct or indirect acquisition from humans, as well as secondary acquisition.

Food Type	HI (97.3 hrs)	LO1 (83 hrs)	LO2 (71.2 hrs)	Total (251.5 hrs)
Fruits: bananas, mangos, apples, pineapple	175	78	41	294
Bread: Sliced white bread, baguettes, sometimes with mayonnaise	50	17	18	85
Chips: Tortilla chips, potato chips, cheese puffs	32	8	0	40
Meat: fried chicken, sliced lunch meat, hot dogs	35	3	1	39
Cookies (processed and packaged)	24	5	9	38
Candy: sour gummy candies, caramels, chewy candies	21	3	5	29
Crackers: cheese crackers, soda crackers, wheat crackers	16	2	2	20
Condiments: mayonnaise, ketchup	18	0	1	19
Other: flavored granola bars, cut whole coconut, unknown	11	1	7	19
Dairy: milk, cookie flavored milk, American cheese	7	0	3	10
Total items acquired	389	117	87	593
Mean overall rate of human food item acquisition per focal hour	4	1.4	1.2	2.4

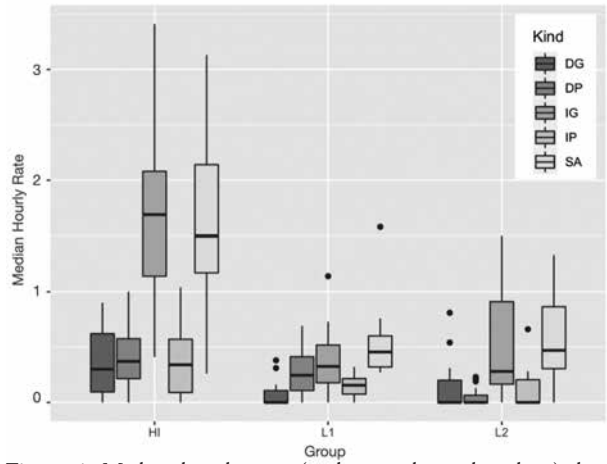

Figure 1. Median hourly rates (with quartiles and outliers) that human food was acquired by individuals during focal follows for each of the three monkey groups in the study (HI, L1, L2), separated by type of food acquisition (from left to right for each group: DG = Direct Grab, DP = Direct Provisioning, IG = Indirect Grab, IP = Indirect Provisioning, SA = Secondary Acquisition).

We expected that humans would be more likely to provision monkeys with fruit compared to non-fruit items. In fact, 70 out of 114 HIIs were with fruit (61.4%), whereas only 100 out of 274 MIIs were for fruit (36.5%). The most common non-fruit food item provisioned by humans to monkeys was bread (21.9% of HII events). In contrast, meat, candy, condiments, and dairy items were rarely or never offered by humans, but all of these were taken on many occasions by monkeys, especially in the HI group.

All three monkey groups accessed both fruit and non-fruit food items from humans, but at different rates. When taking into consideration both primary and secondary acquisition of foods by the monkeys, on average, HI group members acquired fruit in 3.13 bouts per focal hour, and non-fruit at 1.74 bouts per focal hour; L1 accessed fruit at 0.90 and non-fruit at 0.40 bouts per focal hour, and L2 accessed fruit at 0.38 and non-fruit at 0.86 bouts per focal hour. Some individual monkeys' acquisition of human-resourced food items strongly skewed toward fruit, while other monkeys ate far more non-fruit than fruit items from humans, although most monkeys acquired a mix of fruit and non-fruit resources.

For direct contact interactions, 63 of 114 were fruit (55.3%), whereas indirect contact interactions included fruit 107 of 274 times (39.1%). Bread, chips, cookies and crackers were the most common non-fruit items monkeys acquired in indirect interactions. Secondary acquisition of human food from other capuchin monkeys was an important mechanism, accounting for more than one-third of all human-food acquisition events observed (206 out of 593 events). Secondary acquisition was biased slightly toward nonfruit items (89 fruit events, 117 non-fruit events). The preference for secondary acquisition of non-fruit items over fruit items was most marked in the HI adult females, who acquired 23 non-fruit items but only two fruit items from other capuchin monkeys during focal follows in the study.

Resources provisioned to the monkeys through HIIs were always unwrapped or peeled by the humans, and offered ready to eat, while food that was grabbed by monkeys often had to be extracted from a bag, box, backpack or wrapper. Provisioning rarely involved travel on the ground, as food was often placed on trees, branches, tables, or directly into the hand of the monkey. In contrast, in MIIs, monkeys directly approached humans, jumped onto their backs to rummage through backpacks, or went to the ground, for example to grab food from backpacks set on towels at the beach.

One juvenile monkey appeared to use deception to manipulate other group members, so he could grab human food from the ground. He stood on a low branch, looking towards a bag of cheese-flavored tortilla chips on the ground, while five group mates foraged on the ground nearby. He emitted an alarm call and the other monkeys jumped and ran up into the trees, performing vigilant warning behaviors. Immediately the juvenile jumped to the ground, ran to grab the chip bag, and carried it with him into the trees.

Group effects on human food acquisition

The group with the greatest exposure to human visitors (HI) showed the highest number of and the highest relative proportion of MIIs and direct interactions for human food acquisition. Acquisition of human resources by HI group was seen on 81.5% of observation days (note that on Mondays the park was closed to visitors; therefore, the monkeys were acquiring food from humans on almost every day that the park was open). Food acquisition behaviors included charging and threatening humans in possession of food; mobbing picnic tables where food was laid out; jumping onto individuals' backpacks and bags while they were being worn or carried; opening bags, backpacks, or other items on towels left unattended; opening "monkey-proof" trash cans to forage for scraps; picking up leftovers found on the ground; and being fed both by hand by visitors and indirectly by visitors who placed food on branches, tables, or trash can lids in front of monkeys.

In contrast, acquisition of human resources by L1 group was seen on 13.2% of observation days and for L2 group on 12%. The overlap in L1 and HI's home ranges included two smaller side beaches that were frequently populated by human visitors; this area was disputed frequently in intergroup encounters between these two groups. L1 interacted with humans when its ranging patterns crossed the trails on the peninsula several times per day, and occasionally when it traveled to one of the side beaches. On the beaches, L1 monkeys occasionally opened unattended backpacks and bags, and on trails they sometimes grabbed food being consumed by hikers, or they were provisioned by visitors. L2's interactions with humans occurred primarily along the trails, with occasional provisioning and grabbing of bags held by tourists or food carried by tourists, and some incidences of jumping onto worn backpacks, particularly by one young male. When L2 was on the beaches in its home range the monkeys sometimes explored bags, backpacks, and other items on towels that were unattended.

Sex and age differences in human food acquisition

As overall group acquisition rates for human food were significantly different from each other, we kept data separated by group in the subsequent analyses. Within each of the three study groups, on average adult males engaged in a higher median rate of food acquisition from humans and a higher proportion of MIIs to HIIs for primary human food acquisition than did adult females or juveniles (Fig. 2). The majority of adult male utilization of human resources in MANP were the result of grabs and indirect provisioning. Adult males for each group performed more indirect grabs than adult females for that group but, did not successfully acquire significantly more indirect provisioning items compared to adult females in their group. Within groups, on average adult females did not show large differences in

rates of MIIs compared to HIIs, or in indirect versus direct contact interactions. Juveniles in the HI group were more likely to initiate interactions to acquire food and, did so at a median rate of 2.46 times per focal hour, compared to juveniles in the low exposure groups, who performed successful MIIs much less frequently (LO1: 0.16; LO2: 0.30 times per focal hour).

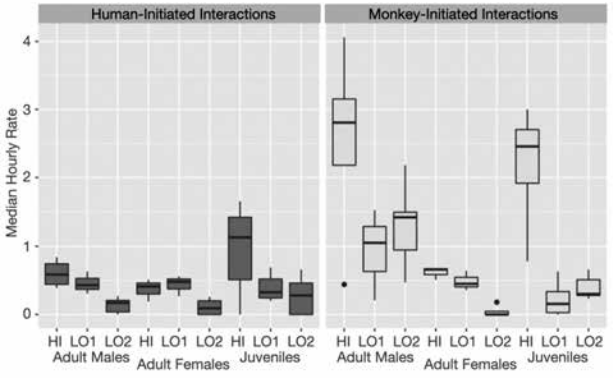

Figure 2. Median hourly rate (with quartiles and outliers) of human-initiated interactions (dark grey boxes) and monkey-initiated interactions (light grey boxes) during focal follows that led to primary monkey acquisition of human food resources, by capuchin age, sex and group membership.

When comparing frequency of interactions with direct versus indirect contact, all age-sex classes in all groups had more indirect interactions than direct interactions with humans. However, the median frequency of both direct contact and indirect contact with humans was significantly higher for adult males and juveniles of the high contact (HI) group compared to other age-sex-group categories (Fig. 3).

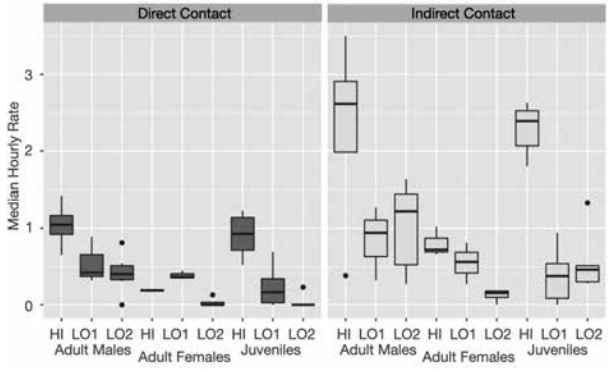

Figure 3. Median hourly rate (with quartiles and outliers) of direct contact (dark grey boxes) and indirect contact (light grey boxes) during focal follows as the means of primary acquisition of human feeding resources, by capuchin age, sex, and group membership.

Secondary acquisition of human food

Secondary acquisition made up a substantial proportion of all human food attained in capuchin monkeys' diet, for all sex-age classes. The HI group had a higher median hourly rate of secondary acquisition per focal hour (1.5 acquisitions) compared to the other two groups (LO1 = 0.46, LO2 = 0.47). In each group juveniles had higher median rates of secondary acquisition of resources than their adult counterparts (Fig. 4).

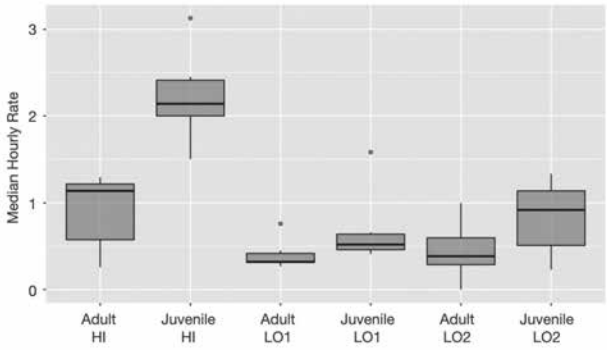

Figure 4. Median hourly rate (with quartiles and outliers) of secondary acquisition of human feeding resources, when one monkey acquires the human resource from another monkey, by capuchin age class and group membership.

Discussion

Understanding how white-faced capuchins utilize human resources is a key step in being able to manage and prevent conflict between humans and monkeys where park visitors have the opportunity to interact with wild monkeys. Preventing escalating monkey-human conflicts over human-sourced food is essential not only to protect the integrity of the local ecosystem and health of the monkey population but to ensure a truly sustainable ecotourism economy (Krüger, 2005; Webb and McCoy, 2014). Our results suggest that monkeys in MANP in our 2008-2009 study period initiated the majority of interactions to access human food. While MANP park regulations at the time focused exclusively on preventing tourists from provisioning the monkeys directly, our findings showed that the primary issue driving capuchin consumption of human food was capuchin access to human food, particularly for adult male and juvenile capuchins. Direct provisioning, although part of the habituation process, represents a relatively less frequent means by which capuchins obtain human resources. It is currently unknown whether indirect access to human food precedes monkey willingness to accept food directly from humans or whether direct feeding by humans is the initial driver toward human-food seeking behaviors in monkeys. However, the indirect access to human food not intentionally facilitated by humans was a large proportion of the human food consumed by monkeys in this park, and reducing that access is essential for managing the monkey consumption of human resources. We suggest that prevention of access to human resources within parks with a high volume of visitors should be expanded beyond regulations restricting direct provisioning, including using more effective monkey-proof trash cans, limiting human food consumption to an enclosed area, or restricting visitors from bringing food into the parks. We also suggest that stronger measures, such as fines or expulsion from park for those interacting with monkeys, might be more effective, and that environmental education is necessary as a strategy to

inform people what to expect from the monkeys and how to avoid accidental provisioning.

In fact, in the years after our study, MANP has enforced stricter regulations, in which visitors are not allowed to bring food in the park, and there are spot inspections to check bags for food at the entrance gate. While this has clearly improved the monkey-human interactions at the park, capuchin monkeys still patrol the beaches looking for food in close contact with humans (JWL, pers. obs.); this suggests that once capuchins are habituated to the possibility of human food as a resource, it is hard to extinguish their interest or habituation to humans.

Adult male capuchin monkeys at MANP initiated more food acquisition interactions and had higher levels of direct contact interactions than adult females in the same group. In white-faced capuchins, males are the dispersing sex, and they often disperse several times during their lifetime, alone or in groups (Jack and Fedigan, 2004; Fedigan and Jack, 2012). This, in combination with males' increasingly aggressive food acquisition techniques, suggests that when habituated males from these groups disperse, they will continue to actively acquire human resources in their new group. Juveniles obtained more of their human resources via secondary acquisition compared to adults, suggesting a route by which dispersing males, who are the most active at grabbing food from humans, will have a significant impact on the diet choices of juveniles in their new groups. The role of social facilitation in the development of capuchin diets means that juvenile capuchins in groups where adult capuchins regularly consume human foods will learn to rely on human foods as a standard part of their diet. This suggests a small window of time for correction and mitigation between the habituation and provisioning of monkeys by humans and the time at which monkey populations view human foods as a central part of their standard diet.

Relatedly, secondary acquisition of human-resourced food occurred in all age-classes and groups in our study. It is important to recognize that human-resourced food items do not only go to the first monkey that acquires them; they also are shared within the capuchin group, potentially affecting diet and health of even those group members that never become strongly habituated to close contact with humans. For example, adult females in the HI group were relatively risk-averse foragers, with lower rates of primary acquisition of human food than adult males or juveniles, but almost all of the food that they acquired secondarily from other group members was non-fruit—in other words, high sugar, high fat content with potential health implications.

Analysis of capuchin groups with different levels of interaction with humans may help researchers understand how acquisition rates change over time as human presence and monkey habituation increase. As expected the group with the highest level of contact with tourists showed a higher proportion of MIIs and direct contact interactions compared to other groups. MIIs with humans may be contingent on high familiarity with and desire for human resources, indicating enough previous exposure to a particular resource so it no longer provokes neophobia, as well as a perceived value which outweighs the opportunity cost of acquisition (Visalberghi et al., 2003; Fragaszy et al., 2004; Agostini and Visalberghi, 2005).

At MANP humans preferentially offered monkeys more 'natural' food items like fruit. However, store-bought fruit often has drastically higher sugar content and lower fiber content than fruits in monkeys' natural diet, such as palm fruit. In addition, monkeys initiated most food interactions and preferred to acquire sugar-dense, salt-dense foods. The types of human foods consumed by the study subjects and the high consumption rate were likely cause of acute health problems such as vomiting and diarrhea observed during the study. The fat, refined sugar, and sodium content of foods such as cookies, candy, potato chips, fried chicken, mayonnaise, and many other foods the capuchins encounter and eat have the potential to cause long-term health problems with reproductive consequences. In addition, the direct contact with humans and increased time spent on the ground retrieving human food may result in higher human-primate disease transmission or parasitic infections. While aggression was not the primary focus of this study, our observations indicated that levels of aggression between monkeys over human food resources was similar to aggression observed over high-fat, high-protein foods in their natural diet, but that human food resulted in intragroup aggression almost daily while high-fat, high-protein natural foods were consumed much less frequently.

Future studies on acquisition of human food by primates should include data regarding all available types of human foods at the study site as well as any incidences of humans unsuccessfully offering food to monkeys in order to better differentiate between opportunistic and preferential foraging. Collecting focal animal data across the waking hours of the primates, not just during visiting hours of parks, or when monkeys were in proximity to humans, would also lead to less biased estimates of human food consumption by primates. Concurrent data collection on natural food item consumption versus human food consumption would also help to distinguish the degree of impact human food had on primate diet in areas where they are exposed to human foods.

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