ZOOLOGIA 36: e30845
ISSN 1984-4689 (online)
zoologia.pensoft.net

ZOOLOGIA
An International Journal for Zoology

RESEARCH ARTICLE

Activity budget and social behavior of urban capuchin monkeys, *Sapajus* sp. (Primates: Cebidae)

Janaína P. Back[1], **Adriane Suzin**[2], **Lucas M. Aguiar**[1]

[1]*Instituto Latino-americano de Ciências da Vida e da Natureza, Universidade Federal da Integração Latino-Americana. Avenida Tarquínio Joslin dos Santos 1000, 85870-901 Foz do Iguaçu, PR, Brazil.*
[2]*Instituto de Biologia, Universidade Federal de Uberlândia. Rua João Naves de Ávila 2121, 38400-902 Uberlândia, MG, Brazil.*
Corresponding author: Janaína P. Back (janainapaulajpb@gmail.com)

http://zoobank.org/07DBD2AF-187E-4CD9-9457-3467CC91D413

ABSTRACT. Constant changes in natural environments impose challenges to wild animal populations, especially those that depend on social life. We gathered data on the activity budget and social interactions of a capuchin monkey (*Sapajus* sp.) group of 17 individuals confined to an urban green area receiving human food supplementation. We observed the capuchins between 7:00 am and 5:00 pm, three days a month, between January 2012 and June 2013 (total of 530 hours of direct observations). We collected 15,208 behavioral records through instantaneous scan sampling and 2,538 events of social interaction in an adapted version of the "all occurrences" method. Activity budget of capuchins was dominated by traveling (42%) and foraging (38%), followed by feeding (10%), social interactions (5%), resting (4%), and others (2%). Except for feeding, the time spent on other activities varied across sex-age classes. Social interactions of capuchins were dominated by affiliative interactions (80%), mainly social play, followed by agonistic (11%) and cooperative (10%) interactions. Sexual interactions were rare (0.4%) and often involved juveniles (45% of the events). Juveniles performed most of the social interactions, followed by the alpha male, and were the main receptors of grooming, food sharing, and agonism. On the other hand, they were the main group involved in allocarrying of infants. Grooming between females and from them to alpha male was infrequent. However, grooming of the alpha male towards the adult females was frequent. We interpreted the deviations in the activity budget and social interactions of the urban capuchins as effects of human food supplementation and restriction on dispersal, illustrating the behavioral ability of capuchin monkeys to adjust their activity in human-altered environments.

KEY WORDS. Anthropic influence, food provisioning, Neotropical primates, urban wildlife.

INTRODUCTION

The growth of human populations and the consequent changes suffered by natural environments have forced populations of nonhuman primates (hereafter "primates") to adapt to the effects of habitat fragmentation. These changes include impacts on matrix permeability, quality and abundance of food resources, demography, sexual partnership, and inter-specific interactions (Sol et al. 2013). Primates can increase their behavioral repertoire in response to new stimuli from the environment. For example: stone handling in *Macaca fuscata* Linnaeus, 1758 (Leca et al. 2008); food extraction abilities in *Macaca radiata* Geoffroy, 1812 (Mangalan and Singh 2013); explore human food resources, and display variations in activity budget and social behavior, *Sapajus libidinosus* Spix, 1823 (Sabbatini et al. 2008), *Cebus capucinus* Linnaeus, 1758 (Mckinney 2011), *Macaca mulatta* Zimmermann, 1780 (Jaman and Huffman 2013), *Pan troglodytes* Blumenbach, 1776 (McLennan 2013, McLennan and Ganzhorn 2017), *Papio hamadryas* Linnaeus, 1758 (Boug et al. 2017). Understanding the extent of these changes in their behavioral repertoire is an important factor to describe how primates adapt to living around human beings.

Forest fragmentation and human interference tend to reduce the risk of predation by natural predators, to limit migration and to introduce high-energy aggregated food resources (Izar et al. 2012, Jaman and Huffman 2013). Anthropic food supplementation can produce different effects on primate behavioral patterns, depending on the amount, quality, and spatial distribution of such resources. For instance, high-energy anthropic food accessible for all individuals can reduce foraging time and increase the time spent socializing and resting: *Chlorocebus pygerythrus* Cuvier, 1821 (Saj et al. 1999), *M. mulatta* (Jaman and Huffman 2013), *Macaca fascicularis* Raffles, 1821 (Sha and Hanya 2013). Alternatively, scarce food supplementation can increase food competition and agonistic interactions (Kamal et al. 1997, El Alami et al. 2012). Finally, the absence of human food resources may force individuals to spend more time spaced apart, reducing social interactions in very small fragments (Jaman and Huffman 2013, Orihuela et al. 2014).

Capuchin monkeys (*Cebus* Erxleben, 1777 and *Sapajus* Kerr, 1792 – Primates: Cebidae) are omnivorous Neotropical primates with flexible social and feeding behavior (Fragaszy et al. 2004). They vary their time budget according to the season, daytime, social status, reproductive condition, sex, and age (Robinson 1984, 1986, Fragaszy et al. 2004, Rímoli et al. 2008). Usually capuchin monkeys spend more time searching for food (traveling and foraging) than resting and socializing (Fragaszy et al. 2004, Rímoli et al. 2008, Tárano and López 2015). Juvenile and adult females tend to spend more time searching for food due to the curiosity and foraging inability of the former, and the energetic requirements of the latter (Robinson 1984, 1986, Strier 2011, Tárano and López 2015). Also, hierarchic conditions imposed on juvenile monkeys force them to explore marginal resources, whereas high-quality foods tend to be consumed by the adults (Janson 1985, Janson and van Schaik 1993). However, feeding tolerance and food sharing towards juvenile can also be observed (Fragaszy et al. 2004).

Robust capuchins (*Sapajus* spp.) live in multi-male, multi-female polygynic groups (3–30 individuals), where females tend to be philopatric and males tend to migrate before reaching sexual maturity (Fragaszy et al. 2004, Carosi et al. 2005, Tiddi et al. 2011, Izar et al. 2012). During estrus, females actively solicit males (proceptivity), whereas the alpha male tends to monopolize copulations (Di Bitetti and Janson 2001, Fragaszy et al. 2004, Carosi et al. 2005), although this could be difficult in large groups (Lynch-Alfaro 2005). Alpha males and dominant females tend to ally with reciprocal benefits, where males secure his reproduction and females get protection against infanticide and invaders (Janson 1984, Di Bitetti 1997, Tiddi et al. 2011). Thus, the social structure of robust capuchins involves hierarchies of dominance among males and females. This produces several kinds of agonistic, affiliative, and cooperative behaviors (Fragaszy et al. 2004, Izar et al. 2006). Philopatric adult females are more commonly involved in grooming relationships, especially among themselves (including reciprocal grooming), and towards the offspring and alpha male (O'Brien 1993, Di Bitetti 1997), although time spent grooming can decrease markedly with aging (Schino and Pinzaglia 2018). Juveniles are the most engaged individuals in social play (Resende and Ottoni 2002, Fragaszy et al. 2004). Capuchin monkeys also cooperate in various ways. For example, juvenile and subadult helpers frequently carry the infants, and adults share food with the young (Perry and Rose 1994, Brosnan 2010, Hattori et al. 2012).

In the municipality of Foz do Iguaçu, southern Brazil, a group of robust capuchins survives confined to a small forest fragment in an urban area, with frequent contact with humans (Aguiar et al. 2014, Suzin et al. 2017). They often receive food supplementation that is offered through direct human-monkey interaction, or through large amounts of food left on a platform (Suzin et al. 2017). In the present study, we describe the activity budget and social interactions of these capuchin monkeys, to assess how they modify their behavior in response to such human interference.

MATERIAL AND METHODS

Study site and subjects

The study group lives in a 3.7 ha forest fragment (25°28' 56.1"S; 54°33'55.9"W; DMS) within the urban matrix of the municipality of Foz do Iguaçu, state of Paraná, southern Brazil. This area is considered as a Municipal Reserve. The vegetation is classified as Seasonal Semi-deciduous Forest, within the Atlantic Forest Domain (Ribeiro et al. 2009). The forest fragment includes both native and exotic fruit trees (such as *Ficus* sp., *Syagrus romanzoffiana* Cham., *Jacaratia spinosa* Aubli., *Morus nigra* L., *Mangifera* sp. L., *Psidium* sp. L., *Eriobotrya japonica* Thunb., *Persea americana* Mil.). The fragment is surrounded by houses and small corn and soy plantations. The climate is classified as humid subtropical (mean temperature 21 °C, ranging from 40 °C in the Summer to 0 °C during Winter), with annual average rainfall of 1,700 mm (Alvares et al. 2013).

The study group comprised 17 individuals: one adult male, five adult females, three subadults, three juvenile, and five infants. These capuchins are confined to this forest fragment because the urban matrix impedes connectivity with other forest patches. Although *Sapajus nigritus* (Goldfuss, 1809) occurs naturally in this region, the coats of individuals in this group are blonder and they resemble *Sapajus cay* (Illiger, 1815). Therefore, they are referred here as *Sapajus* sp. According to local people, these capuchins have been present in the area for about 35 years, and were most likely introduced. They forage on and eat resources of the forest fragment, but also from human dwellings and crops, including human food leftovers (e.g., rice, beans, candy, and soda; Suzin et al. 2017). The city government has been provisioning food (fruits and meat) to the monkeys on a platform three times a week since August 2012, and human visitors frequently feed them as well (0.4 human-monkey interactions/h, in which 58% of the interactions were people feeding the monkeys, Suzin et al. 2017). The bulk of the diet (71% of feeding records) is anthropic food, mainly given by human visitors (44% of feeding records; e.g., fruit, bread, candy, and meat) and by the city government (Suzin et al. 2017). These monkeys, especially juveniles, often forage by manipulating natural (e.g., sticks, hard fruits) and anthropic objects (e.g., cans, plastic bottles; 1 events/h in the group; G.F. Silva unpublished data), including tool use (Aguiar et al. 2014). We did not observe the occurrence of natural predators, human hunting, or other human-monkey conflicts in the area during the study, and such events have not been mentioned in any interviews with local people (Suzin et al. 2017).

Data collection

We habituated the group to the presence of human observers between September and December 2011. Posteriorly, we followed and observed the group between 07:00 am and 5:00 pm, for three days a month, between January 2012 and June 2013. We classified the individuals in sex-age classes (adult male, adult female, juvenile, subadult and infant) according to Izawa (1980). We recorded the individuals' activity within three minutes at every 7-min interval, using the scan sampling method (Altmann 1974), taking care to not capture records from the same individual during each sampling. We distinguished the categories of the activity budget into "foraging" (including visual and/or tactile exploration, capturing and/or handling any object or food item), "traveling", "feeding", "resting", "social interaction" (including only dyadic interactions: affiliative, agonistic, cooperative, and sexual), and "others" (including vigilance, drinking, defecating, urinating, urine washing, and interactions with observers; adapted from Fragaszy et al. 2004).

We used an adapted version of the All Occurrences sampling method (Altmann 1974) to collect data on social interactions, since we were not sure if all individuals of the group were within our sight at any given instant, as required by the method. We collected data for all events of social interactions of the dyads within sight during the followings of the capuchin group. We considered as affiliative interactions grooming and social play, which are associated with the development and maintenance of social bonds (Wilson 2000, Sussman et al. 2005). We considered two degrees of agonistic interactions according to physical contact (Wilson 2000): aggression (pushing, hitting, grabbing, wrestling, biting), and threats (silent or vocalized facial displays, lunging, swiping, bouncing, and chasing) (Leca et al. 2002). We considered sexual interactions as behaviors of female proceptivity, including touching and displays (eyebrow raises, head and body tilts), inspections of genitalia, and copulations (Fragaszy et al. 2004, Carosi et al. 2005, Lynch-Alfaro 2005). We considered cooperative interactions as the alloparental carrying of the young on the back and food sharing, because these behaviors initially impose costs to the initiator, but can promote mutual benefits (by kinship or reciprocity; Davies et al. 2012). We were able to discriminate between parental and alloparental carrying (hereafter "allocarrying") because the infants' maternal relationships were known. Finally, we considered food sharing as all events of one individual collecting or receiving food directly from the hands or the mouth of another monkey (adapted from Hattori et al. 2012).

Data analysis

We estimated the activity budget (e.g., feeding, foraging, traveling, resting, and socializing) for each sex-age class (except for infants, due to their dependence on mothers) through the method of proportions (Fortes and Bicca-Marques 2005). For this estimate, we divided the number of records of each category of behavior per each hour of observation (e.g., 7:00–7:59, 8:00–8:59, ... 16:00–16:59) by the total number of behavioral records, for each sex-age class.

We used a Kruskal-Wallis non-parametric ANOVA to compare the proportion of records of each category of behavior of the activity budget for the sex-age classes, as these behavioral records were not normally distributed. Dunn's post-hoc test was used for the pairwise comparisons of the respective proportions. We analyzed the social interactions through sociometric matrices and the relationships among dyads of sex-age classes were expressed in social webs (Whitehead 2008). We calculated the frequencies of events (in percentage) for each social behavior in each dyad, considering the total number of events of dyads of the respective behavioral category. We used the G-test to test the homogeneity of emissions, receptions and participations (emissions plus receptions) among sex-age classes. For this analysis, we used the proportion (events/number of individuals in each sex-age class) of emission, reception and participation of each sex-age class. The expected frequency of the emissions, receptions, and participation for each class was calculated considering the mean of the events of each direction of behavior divided by the number of individuals in each sex-age class. The infants were excluded as emitters of allocarrying and food sharing, and the adult male, adult females, and subadults were excluded as receivers of allocarrying.

We assessed data normality and homoscedasticity with the Shapiro-Wilk and Levene tests, respectively. All tests were performed using the BIOESTAT 5.3 software package (Ayres et al. 2007), with a significance level of $p \leq 0.05$.

RESULTS

We obtained a total of 15,208 observation records (adult male: n = 1,683; adult females: n = 3,968; juveniles: n = 8,978; subadults: n = 759) in 3,180 scans and 2,538 events of social interactions during 530 hours of direct observation distributed in 53 days of sampling effort.

Activity budget

The activity budget was dominated by traveling (42% of records; n = 6,390) and foraging (38%; n = 5,740), followed by feeding (10%; n = 1,497), social interactions (5%; n = 730), resting (4%; n = 559), and others (2%; n = 359). Except for feeding (H = 2.7916; DF = 3; p = 0.4249; Fig. 1), the time spent in other activities significantly varied across sex-age classes (traveling: H = 25.3850; DF = 3; P<0.0001, foraging: H = 22.8137; DF = 3; $p < 0.0001$; resting: H = 16.8240; DF = 3; $p < 0.0080$; social interaction: H = 20.2731; DF = 3; $p < 0.0001$; Fig. 1). Juveniles rested less than the adult male, although they foraged more than other sex-age class and socialized more than adult females and subadults (Fig. 1). Adult females traveled more than juveniles (Fig. 1).

Social interactions

The most frequent social interactions were affiliative interactions (80% of events; n = 2,023), followed by agonistic (11%; n = 272), cooperative (9%; n = 232), and sexual interactions (0.4%; n = 11). Juveniles were the sex-age class most

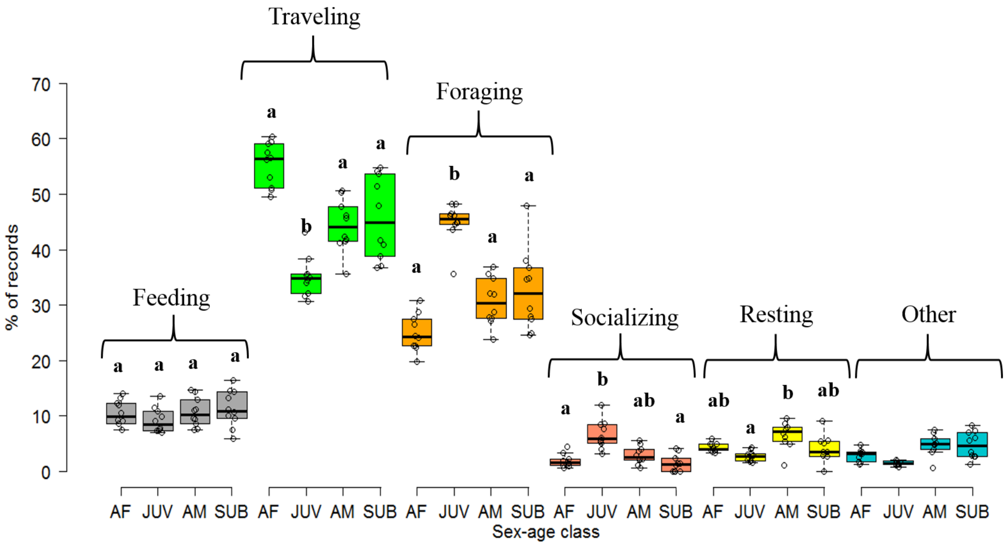


Figure 1. Proportions of records (in percentage) of behavioral categories in the activity budget of sex-age classes of urban capuchin monkeys. Boxes represent the interquartile ranges; horizontal lines within the boxes represent the medians; whiskers indicate minimum and maximum values; circles indicate the proportions of records per hour of observation. Different letters indicate significant differences between sex-age classes. Kruskal-Wallis followed by Dunn's test; $p \leq 0.05$. (AF) adult females, (AM) adult male, (SUB) subadults, (JUV) juveniles.

involved in interactions (732 events/individual), followed by the adult male (441 events/individual), adult females (122 events/individual), infants (63 events/individual), and subadults (54 events/individual).

The most frequent affiliative interactions (4 events/h) consisted of social play (73%; 3 events/h), followed by grooming (27%; 1 event/h). Juveniles comprised the most frequent dyad composition during social play (Fig. 2). Participation and grooming emission by adult females and the grooming reception by juveniles were higher than expected by chance (Table 1, Fig. 3). Reciprocal grooming between adult females was rare (n = 4 events). Adult females were groomed primarily by the adult male, and groomed primarily juveniles (Fig. 3).

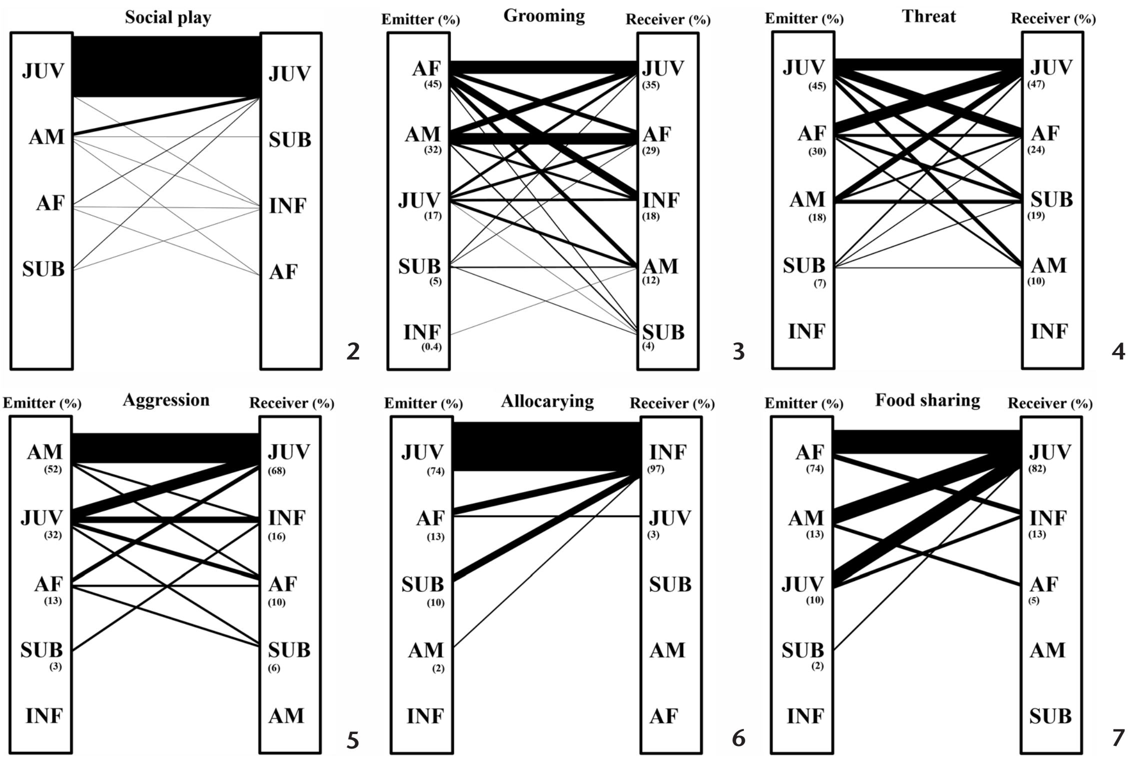
The most frequent agonistic interactions (0.5 events/h) were threats (89%; 0.4 events/h), followed by aggressions (11%; 0.06 events/h). Juveniles were more often involved (emitting plus receiving) in threats than expected by chance (Table 1; Fig. 4). Adult females emitted more and adult male received less threats than expected by chance (Table 1; Fig. 4). The distribution of participations in aggressions among sex-age classes did not differ from expected by chance, but juveniles received more aggressions than expected (Table 1; Fig. 5).

The most frequent cooperative interactions (0.4 events/h) consisted of allocarrying (83%; 0.4 events/h), followed by food sharing (17%; 0.07 events/h). Juveniles and infants participated in allocarrying more than expected by chance (Table 1). Juveniles emitted more, and infants received more allocarrying than expected by chance (Table 1; Fig. 6). Juveniles participated in food sharing more and received four times more shared food than expected by chance (Table 1; Fig. 7). The adult male and adult females were the most frequent sharers with juveniles, though with no statistical significance.

Sexual interactions were infrequent (n = 11; 0.02 events/h), and the adult male participated in 73% of the interactions. Among sexual interactions, we observed six copulations, four sexual displays, and one inspection of genitalia. All sexual displays preceded the observed copulations. The adult male copulated with an adult female (n = 2), with a subadult female (n = 1), and with a juvenile (n = 1). Two copulations involved one juvenile with a subadult female. Inspection of genitalia was done by the adult male towards a subadult female, whereas sexual displays were done mostly towards the adult male from subadult females (n = 2), and from a juvenile (n = 1). A juvenile performed one sexual display towards a subadult female.

DISCUSSION

Overall, the observed urban capuchin monkeys spent almost 80% of time searching for food (traveling plus foraging), and only 10% of time feeding. Except for feeding, the time spent in all other activity groups (foraging, traveling, resting and socializing) varied across sex-age classes. We found that an overwhelming majority of social interactions was affiliative (almost 80% of social interactions), especially juvenile social play. Grooming interactions between females and from them to the alpha male were infrequent. However, grooming of the alpha male towards adult females was frequent. Juveniles were the main receptors of grooming, food sharing and of threats



Figures 2–7. Social webs expressing interactions (in percentage of the total observation records) for each sex-age dyad of urban capuchin monkeys in each social behavior: (2) social play, n = 1,476 events; (3) grooming, n = 547; (4) threat, n = 241; (5) aggression, n = 31; (6) allocarrying, n = 193; (7) food sharing, n = 39. Percentages of emissions and receptions are in decreasing order in all columns, except for social play. Line thickness is proportional to the percentages of interactions of each dyad. (AF) adult females, (JUV) juveniles, (AM) adult male, (SUB) subadults, (INF) infants.

of the adult females and of aggressions of the adult male. On the other hand, the juveniles were the main emitters of the allocarrying for infants. Sexual interactions were infrequent in the group and unusually involved juveniles.

Activity budget

The time spent in traveling and foraging by the observed capuchin monkeys was higher when compared to populations of robust capuchins in larger fragments and continuous forest – *S. nigritus* (Rímoli et al. 2008); and *S. libidinosus* (Sabbatini et al. 2008, Verderane et al. 2013). We believe that the high investment in traveling might be explained by the scattered distribution of food offered by people, their primary food resource, in space and time (Suzin et al. 2017). This has been previously described for long-tailed macaques – *M. fascicularis* (Sha and Hanya 2013). In fact, capuchin-people interactions were frequent in our site, mainly in the context of provisioning (Suzin et al. 2017). However, the high investment in foraging could also be a result of the large amount of objects discarded by humans in the fragment, resulting in a high frequency of manipulation of objects (G.F. Silva unpublished data).

On the other hand, the low feeding rate observed here could be explained by the high energetic content and availability of food offered by people, satisfying individual demands with less effort and a smaller amount than those provided by the forest (Jaman and Huffman 2013). Consequently, the use of the anthropic food can be associated with a decrease in time spent in feeding and increase in resting time, as observed for *Papio cynocephalus* Linnaeus, 1766 (Altmann and Muruthi 1988) and *M. mulatta* (Jaman and Huffman 2013). The capuchins in this study spent less time feeding, but they also spent less time resting, which contrasts with the pattern described above for animals with access to anthropic food. This low investment in rest could be explained by the frequent human stimulus, as also observed in captive gracile capuchins, *Cebus olivaceus* Schomburgk, 1848, by Tárano and López (2015). In our study site, humans frequently use the fragment as path shortcuts and often contact and feed the capuchins (Suzin et al. 2017).

The time spent in social interactions by the study group (almost 5%) is similar to those reported for wild capuchins (3% for *S. cay*: Pinto 2006, 4% for *S. nigritus*: Rímoli et al. 2008, 5% for *S. libidinosus*: Cutrim 2013) than those reported for provisioned

Table 1. Proportions (events/number of individuals in each sex-age class) of emissions, receptions, and participations (emissions plus receptions) observed (in bold) and expected (bottom line) for social interactions within each sex-age class of urban capuchin monkeys. AF = adult females, JUV = juveniles, AM = adult male, SUB = subadults, INF = infants, DF = degrees of freedom.

Behavior	Direction of behavior	Events/number individual of each sex-age class					Test value		
		AF	AM	SUB	JUV	INF	G	DF	p
Grooming	Emission	**49.4**	**177.0**	**9.0**	**31.3**	**0.4**	70.88	4	**<0.0001***
		21.9	109.4	36.5	36.5	21.9			
	Reception	**31.4**	**71.0**	**8.0**	**64.0**	**20.6**	35.24	4	**<0.0001***
		21.9	109.4	36.5	36.5	21.9			
	Participation	**80.8**	**248.0**	**17.0**	**95.3**	**21.0**	60.50	4	**<0.0001***
		43.8	218.8	72.9	72.9	43.8			
Threats	Emission	**14.6**	**44.0**	**5.3**	**36.0**	**0.0**	27.69	4	**<0.0001***
		9.6	48.2	16.1	16.1	9.6			
	Reception	**11.6**	**24.0**	**15.0**	**38.0**	**0.0**	29.55	4	**<0.0001***
		9.6	48.2	16.1	16.1	9.6			
	Participation	**26.2**	**68.0**	**20.3**	**74.0**	**0.0**	51.87	4	**<0.0001***
		19.3	96.4	32.1	32.1	19.3			
Aggression	Emission	**0.8**	**16.0**	**0.3**	**3.3**	**0.0**	8.86	4	0.0645
		1.2	6.2	2.1	2.1	1.2			
	Reception	**0.6**	**0.0**	**0.7**	**7.0**	**1.0**	14.61	4	**0.0056***
		1.2	6.2	2.1	2.1	1.2			
	Participation	**1.4**	**16.0**	**1.0**	**10.3**	**1.0**	5.36	4	0.2519
		2.5	12.4	4.1	4.1	2.5			
Allocarrying	Emission	**5.4**	**4.0**	**6.7**	**47.3**	–	60.84	3	**< 0.0001***
		9.6	48.2	16.1	16.1	–			
	Reception	–	–	–	**2.0**	**37.4**	36.20	1	**< 0.0001***
		–	–	–	32.2	19.3			
	Participation	**5.4**	**4.0**	**6.7**	**49.3**	**37.4**	103.45	4	**< 0.0001***
		15.4	77.2	25.7	25.7	15.4			
Food sharing	Emission	**3.2**	**11.0**	**0.3**	**3.7**	–	5.40	3	0.1463
		1.9	9.7	3.2	3.2	–			
	Reception	**0.4**	**0.0**	**0.0**	**10.7**	**1.0**	19.50	4	**0.0006***
		1.6	7.8	2.6	2.6	1.6			
	Participation	**3.6**	**11.0**	**0.3**	**14.3**	**1.0**	12.96	4	**0.0114***
		3.1	15.6	5.2	5.2	3.1			

Statistically significant differences between observed and expected proportions are indicated by asterisk (*). G-test, $p \leq 0.05$.

capuchins (8% and 10% by *S. libidinosus*: Sabbatini et al. 2008, Sacramento et al. 2017, respectively). We believed that the small amount of time spent in social interactions may be explained by the scattered distribution of people-offered food, which can reflect in decreased proximity between the members of the group, which means fewer opportunities for socialization. The existence of only one adult male and the absence of neighboring groups might also be a factor lowering the amount of social interactions. The low investment in social interactions performed by adult females, when compared to juveniles, may be due to their apparent low cohesiveness (J.P. Back personal observation). This is also probably a result of the scattered distribution of local anthropic food as described above. The low investment in foraging and high investment in traveling (probably to find people with food) support this interpretation. Finally, although juveniles and subadults may have more scarce access to food (Janson and van Schaik 1993), we did not observe significant differences in time spent in feeding among sex-age classes, which could be a result of the availability of abundant and frequent anthropic food supplementation, allowing access to all individuals.

Regarding sex-age classes, juveniles invested more time in foraging and less in traveling than other classes, which is similar to previous observations in gracile capuchins (Robinson 1986). Juvenile capuchins might be foraging more due to their curiosity and lower access to food (Janson and van Schaik 1993, Fragaszy et al. 2004). The high proportion of time invested in social interactions by juveniles may be associated with the high number of young individuals in the group, contributing to increased time spent on social play, as also observed in captive gracile capuchins (Tárano and López 2015).

Social interactions

Social interactions were mostly performed by juveniles, followed by the adult male, indicating their integration in the social structure of this group. On the other hand, subadults were the least frequent participants, probably due to their subordinate status or peripheral position, usual in robust capuchins (Fragaszy et al. 2004, Izar et al. 2006). The overwhelming predominance of positive interactions (90%: affiliative plus cooperative) in this study reflected high tolerance among individuals. This may also be a consequence of the anthropic food supplementation, which allows all individuals in the group to find food, relaxing within-group competition (Altmann and Muruthi 1988, Jaman and Huffman 2013). In addition, the restriction to spatial dispersion imposed by the urban matrix surrounding the forest fragment could increase kinship among these capuchins, contributing to positive interactions (Strier 2011, Davies et al. 2012). Most affiliative interactions consisted of social play, primarily performed by juveniles, as found in other studies (Resende and Ottoni 2002, Fragaszy et al. 2004). We believe the presence of several young immature individuals in the group, which are more socially active (Resende and Ottoni 2002, Fragaszy et al. 2004, Schino and Pinzaglia 2018), may have favored the occurrence of this behavior.

The frequency of grooming behavior found in our study (1 event/h) is similar to the rates observed for wild robust capuchins, with 1 events/h for *Sapajus nigritus* Goldfuss, 1809 (Di Bitetti 1997) to 2 events/h for *Sapajus apella* Linnaeus, 1758 (Izawa 1980), although there were some apparent deviations in grooming patterns for females and the alpha male. For example, adult females groomed less among themselves and reciprocal grooming among females was rare (<0.01 events/h) in comparison to other observations in conserved habitats (O'Brien 1993, Perry 1996, Di Bitetti 1997, Tiddi et al. 2011). The grooming of the adult females to alpha male was also infrequent. Conversely, adult females were mostly groomed by the alpha male. Cases of weak interactions among robust capuchin females have been attributed to females' spatial dispersal (Izar et al. 2012). Because female transfer is unlikely in the study area, the low frequency of interactions among adult females could be associated with the detachment produced by the scattered distribution of anthropic food. However, other factors could be operating, such as age, lack of competing groups in the fragment, and low risk of predation, which may also contribute to lower cohesiveness, restricting opportunities for social interactions among adult females and the dominant male (Janson 1984, Koenig 2002, Strier 2011, Tiddi et al. 2011, Schino and Pinzaglia 2018). On the other hand, the dominant male may still need to secure mating, which would explain the high rates of grooming towards the adult females (Janson 1984, Tiddi et al. 2011). As expected, adult females invested more time grooming the young, probably due to parental and alloparental care (Izawa 1980, Fragaszy et al. 2004). Female grooming towards juveniles could have other functions and express appeasement, due to frequent female agonism towards juveniles, or even a mechanism of reciprocity, because juveniles are the main helpers in the group (see below). Additionally, the fact that there was only one adult male in the group could be leading females to groom juveniles that might be their potential partners in the future.

The rates of agonism observed in our study group (0.5 events/h) was low when compared to other capuchin groups: 1 event/h for *C. capucinus* (Phillips 1995) and for *S. apella* (Ferreira et al. 2008), and again could be a reflect of the daily provisioning that decreased competition for food. The heterogeneous distribution of food provided by humans may contribute to the scattered distribution of foraging individuals, resulting in fewer opportunities for agonist interactions (Janson and Vogel 2006). Threats were much more common than aggressions, probably because aggressions demand a greater amount of energy, and may cause injuries or even death (Strier 2011). As expected from their low social status (Ferreira et al. 2008, Strier 2011), juveniles were the main receivers of threats from adult females and aggression from the dominant male. The agonism among juveniles and adult females can emerge due to their physical and social proximity (Fragaszy et al. 2004), particularly when humans offer food to attract them. Aggressions emitted by the dominant male towards juveniles can emerge not only because of human provisioning but also due to the frequent participation of juveniles in sexual behaviors (Janson 1985), as observed here.

Most cooperative interactions involved juveniles, including allocarrying of infants, their probable siblings or cousins, as well as receiving food from adults, their probable parents, grandparents, or uncles. The allocarrying of infants performed by juveniles not only offers advantages in terms of energetic economy for the parents but can also enhance their own genetic fitness when they care for their kin, as they might be gathering experience to take care of their own offspring in the future (Strier 2011, Davies et al. 2012). Adult capuchins shared food primarily with juveniles (almost 60%), which could also be viewed as a form of parental or alloparental care. Adult food sharing could be also interpreted here as a payoff for the allocarrying of infants performed by juveniles – a mechanism of indirect reciprocal altruism (O'Brien 1993, Davies et al. 2012).

As expected for robust capuchin breeding systems, the dominant male was the preferred partner in sexual interactions (Carosi et al. 2005, Izar et al. 2012). However, sexual interactions observed in this study were rare in comparison to other studies (e.g., Lynch-Alfaro 2005): the proceptivity of females was markedly reduced, and juveniles were frequently involved (45% of the events). It is noted that our sampling effort could disfavor observation of sexual behavior where reproduction is seasonal (e.g., *S. nigritus*: Di Bitetti and Janson 2001). However, because sexual seasonality often follows food resources seasonality, there is a possibility that constant human food provisioning might lead to occurrence of sex and births in our study group throughout the year, as partially supported by the births observed: two during the Winter (one in September 2011 and one in August 2012) and three in the Summer (between December 2012 and

January 2013). We believe the presence of a single adult male in the group and the urban constraints to dispersion from the natal group could favor the engagement of juveniles in sexual interactions. If the supposed increased kinship could be demotivating towards courtship among relatives (Strier 2011, Davies et al. 2012), on the other hand, juveniles may take opportunities that are unlikely to occur outside the natal group.

In conclusion, we found deviations in activity budget and social interactions of capuchins living in the studied small urban fragment, possibly influenced by the availability of anthropic food and the restrictions for dispersion imposed by the urban matrix. However, we cannot rule out the possibility that other factors have shaped the behavior of these animals. Therefore, future studies should investigate specifically the effects of dispersal restriction and food given by people on the behavior, demography and genetics of these animals. Although the disparate high population density (4.9 individuals/hectare; J.P. Back unpublished data) and the annual birth rate (0.7 births/adult/female, J.P. Back unpublished data) similar to those of wild populations in conserved habitats (Di Bitetti and Janson 2001) suggest high-energy input for these urban capuchins, future studies should also investigate the impact of human presence and food on the health and welfare of these monkeys. These kind of studies are very important in Primate Conservation Biology, because we have an urgent demand to understand how primates adapt around human beings, as the contact between human and nonhuman primates are an inescapable aspect today.

ACKNOWLEDGEMENTS

We would like to thank UNILA and Fundação Araucária for the scholarships provided to J.P. Back and A. Suzin, and the City Government of Foz do Iguaçu for the permits to conduct the study. We also thank Alexandre Vogliotti, María Celia Baldovino, Michel V. Garey, José Eduardo Silva Pereira, editors and the anonymous reviewers that provided useful comments on the manuscript.

LITERATURE CITED

Aguiar LM, Cardoso RM, Back JP, Carneiro EC, Suzin A, Ottoni EB (2014) Tool use in urban populations of capuchin monkeys (*Sapajus* spp.). Zoologia 31(5): 516–519. https://doi.org/10.1590/S1984-46702014000500012

Altmann J (1974) Observational study of behavior: Sampling methods. Behaviour 49: 227–267. https://www.jstor.org/stable/4533591

Altmann J, Muruthi P (1988) Differences in daily life between semi-provisioned and wild-feeding baboons. American Journal of Primatology 15(3): 213–221. https://doi.org/10.1002/ajp.1350150304

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Koppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Ayres M, Ayres Jr M, Ayres DL, Santos AS (2007) Bioestat 5.3 – Aplicações estatísticas nas áreas das ciências biomédicas. ONG Mamirauá, Belém, 364 pp.

Boug AM, Islam Z, Iwamoto T, Mori A, Yamane A, Schreier AL (2017) The relationship between artificial food supply and natural food selection in two troops of commensal Hamadryas Baboons *Papio hamadryas* (Mammalia: Primates: Cercopithecidae) in Saudi Arabia. Journal of Threatened Taxa 9: 10741–10756. https://doi.org/10.11609/jott.3348.9.10.10741-10756

Brosnan SF (2010) What do capuchin monkeys tell us about cooperation? In: Forsyth DR, Hoyt CL (Eds) for the greater good of all: perspectives on individualism, society & leadership. New York, Palgrave Macmillan Publishers, 11–28.

Carosi M, Linn GS, Visalberghi E (2005) The sexual behavior and breeding system of tufted capuchin monkeys (*Cebus apella*). Advances in the Study of Behavior 35: 105–149. https://doi.org/10.1016/S0065-3454(05)35003-0

Cutrim FHR (2013) Padrão comportamental e uso de ferramenta em macacos-prego (*Sapajus libininosus*) residentes em manguezal. PhD thesis, São Paulo, Brazil: Universidade de São Paulo. Available online at: http://www.teses.usp.br/teses/disponiveis/47/47132/tde-09012014-163238/pt-br.php

Davies NB, Krebs JR, West SA (2012) An introduction to behavioural ecology. Chichester, Wiley-Blackwell, 416 pp.

Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behavior 54(1): 199–211. https://doi.org/10.1006/anbe.1996.0416

Di Bitetti MS, Janson CH (2001) Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal Primatology 22(2): 127–142. https://doi.org/10.1023/A:1005611228927

El Alami A, Van Lavieren E, Rachida A, Chait A (2012) Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the endangered barbary macaque (*Macaca sylvanus*) in the central high atlas mountains, Morocco. American Journal of Primatology 74(3): 210–216. https://doi.org/10.1002/ajp.21989

Ferreira RG, Lee PC, Izar P (2008) Food competition in a semifree-ranging *Cebus apella* group. Folia Primatologica 79: 463–475. https://doi.org/10.1159/000158525

Fortes VB, Bicca-Marques JC (2005) Ecologia e comportamento de primatas: Métodos de estudo de campo. Caderno La Salle XI, Canoas 2: 207–218.

Fragaszy D, Visalberghi E, Fedigan L (2004) The Complete Capuchin: The Biology of the Genus *Cebus*. New York, Cambridge University Press, 356 pp.

Hattori Y, Leimgruber K, Fujita K, De Waal FBM (2012) Food-related tolerance in capuchin monkeys (*Cebus apella*) varies with knowledge of the partner's previous food-consumption. Behaviour 149(2): 171–185. https://www.jstor.org/stable/41444696

Izar P, Ferreira RG, Sato T (2006) Describing the organization of dominance relationships by dominance-directed tree method. American Journal Primatology 68: 189–207. https://doi.org/10.1002/ajp.20216

Izar P, Verderane MP, Peternelli-Dos-Santos L, Mendonça-Furtado O, Presotto A, Tokuda M, Visalberghi E, Fragaszy D (2012) Flexible and conservative features of social systems in tufted capuchin monkeys: Comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. American Journal Primatology 74: 315–331. https://doi.org/10.1002/ajp.20968

Izawa K (1980) Social behavior of the wild black-capped capuchin (*Cebus apella*). Primates 21(4): 443–467. https://doi.org/10.1007/BF02373834

Jaman MF, Huffman MA (2013) The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. Primates 54(1): 49–59. https://doi.org/10.1007/s10329-012-0330-6

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift für Tierpsychologie 65(3): 177–200. https://doi.org/10.1111/j.1439-0310.1984.tb00098.x

Janson CH (1985) Aggressive and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18(2): 125–138.

Janson CH, van Schaik CP (1993) Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira M, Fairbanks L (Eds) Juvenile Primates. New York, Oxford University Press, 57–73.

Janson CH, Vogel E (2006) Hunger and aggression in capuchin monkeys. In: Hohmann G, Robbins MM, Boesch C (Eds) Feeding Ecology in Apes and other Primates: Ecological, Physiological and Behavioral Aspects. New York, Cambridge University Press, 285–312.

Kamal KB, Boug A, Brain PF (1997) Effects of food provisioning on the behaviour of commensal hamadryas baboons, *Papio hamadryas*, at Al Hada Mountain in western Saudi Arabia. Zoology in the Middle East 14(1): 11–22. https://doi.org/10.1080/09397140.1997.10637699

Koenig A (2002) Competition for resources and its behavioral consequences among female primates. International Journal Primatology 23(4): 759–783. https://doi.org/10.1023/A:1015524931226

Leca JB, Fornasieri I, Petit O (2002) Aggression and reconciliation in *Cebus capucinus*. International Journal Primatology 23(5): 979–998. https://doi.org/10.1023/A:1019641830918

Leca JB, Gunst N, Huffman MA (2008) Food provisioning and stone handling tradition in japanese macaques: A comparative study of ten troops. American Journal Primatology 70(8): 803–813. https://doi.org/10.1002/ajp.20551

Lynch-Alfaro JW (2005) Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). American Journal Primatology 67: 313–328. https://doi.org/10.1002/ajp.20188

Mangalam M, Singh M (2013) Flexibility in food extraction techniques in urban free-ranging bonnet macaques, *Macaca radiata*. PloS ONE 9(3): e91480. https://doi.org/10.1371/journal.pone.0085497

Mckinney T (2011) The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced capuchins (*Cebus capucinus*). American Journal Primatology 73(5): 439–448. https://doi.org/10.1002/ajp.20919

McLennan MR (2013) Diet and feeding ecology of chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest-farm interface. International Journal Primatology 34(3): 585–614. https://doi.org/10.1007/s10764-013-9683-y

McLennan MR, Ganzhorn JU (2017) Nutritional characteristics of wild and cultivated foods for chimpanzees (*Pan troglodytes*) in agricultural landscapes. International Journal of Primatology 38(2): 122–150. https://doi.org/10.1007/s10764-016-9940-y

O'Brien TG (1993) Allogrooming behaviour among adult female wedge-capped capuchin monkeys. Animal Behavior 46(3): 499–510. https://doi.org/10.1006/anbe.1993.1218

Orihuela G, Terborgh J, Ceballos N, Glander K (2014). When top-down becomes bottom up: behaviour of hyperdense howler monkeys (*Alouatta seniculus*) trapped on a 0.6 ha island. PLoS ONE 9(4): e82197. https://doi.org/10.1371/journal.pone.0082197

Perry S (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. American Journal of Primatology 40(2): 167–182. https://doi.org/10.1002/(SICI)1098-2345(1996)40:2<167::AID-AJP4>3.0.CO;2-W

Perry S, Rose L (1994) Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. Primates 35(4): 409–415. https://doi.org/10.1007/BF02381950

Phillips KA (1995) Foraging-related agonism in capuchin monkeys (*Cebus capucinus*). Folia Primatologica 65(3): 159–162. https://doi.org/10.1159/000156882

Pinto MCM (2006) Padrão comportamental de um grupo de macacos-prego (*Cebus apella cay* Illiger, 1815) no Parque Estadual Matas do Segredo, Campo Grande (MS). MSc thesis, Campo Grande, Brazil: Universidade Federal de Mato Grosso do Sul. Available online at: http://repositorio.ufms.br:8080/jspui/handle/123456789/594

Resende BD, Ottoni EB (2002) Brincadeira e aprendizagem do uso de ferramentas em macacos-prego (*Cebus apella*). Estudos de Psicologia 7(1): 173–180. https://doi.org/10.1590/S1413-294X2002000100018

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142(6): 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Rímoli J, Strier KB, Ferrari SF (2008) Seasonal and longitudinal variation in the behavior of free-ranging black tufted capuchins *Cebus nigritus* (Goldfuss, 1809) in a fragment of Atlantic forest in southeastern Brazil. In: Ferrari SF, Rímoli J (Eds) A Primatologia no Brasil 9. Sociedade Brasileira de Primatologia, Pará, 130–146.

Robinson JG (1984) Diurnal variation in foraging diet in the wedge-capped capuchin *Cebus olivaceus*. Folia Primatologica 43(4): 216–228. https://doi.org/10.1159/000156183

Robinson JG (1986) Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. Smithsonian Contributions to Zoology 431: 1–60. https://doi.org/10.5479/si.00810282.431

Sabbatini G, Stammati M, Tavares MCH, Visalberghi E (2008) Behavioral flexibility of a group of bearded capuchin monkeys (*Cebus libidinosus*) in the national park of Brasília (Brazil): Consequences of cohabitation with visitors. Brazilian Journal of Biology 68(4): 685–693. https://doi.org/10.1590/S1519-69842008000400002

Sacramento TS, Mendes FDC, Peres MK, Tavares MCH (2017) Comportamento alimentar e padrão de atividades de macacos (*Sapajus libidinosus*) aprovisionados no Parque Nacional de Brasília, DF. In: Oliveira A, Ferreira R, Luna V (Eds) A Primatologia no Brasil 14. Recife, Sociedade Brasileira de Primatologia, 152–164.

Saj T, Sicotte P, Paterson JD (1999) Influence of human food consumption on the time budget of vervets. International Journal of Primatology 20(6): 974–977. https://doi.org/10.1023/A:1020886820759

Schino G, Pinzaglia M (2018) Age-related changes in the social behavior of tufted capuchin monkeys. American Journal Primatology 80(3): e22746. https://doi.org/10.1002/ajp.22746

Sha JCM, Hanya G (2013) Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*). American Journal Primatology 75(6): 581–592. https://doi.org/10.1002/ajp.22137

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. Animal Behavior 85(5): 1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Strier KB (2011) Primate Behavioral Ecology. New Jersey, Prentice Hall, 408 pp.

Sussman RW, Garber PA, Cheverud JM (2005) Importance of cooperation and affiliation in the evolution of primate sociality. American Journal of Physical Anthropology 128(1): 84–97. https://doi.org/10.1002/ajpa.20196

Suzin A, Back JP, Garey MV, Aguiar LM (2017) The relationship between humans and capuchins (*Sapajus* sp.) in an urban green area in Brazil. International Journal Primatology 38(6): 1058–1071. https://doi.org/10.1007/s10764-017-9996-3

Tárano Z, López MC (2015) Behavioural repertoires and time budgets of semi-free-ranging and captive groups of wedge-capped capuchin monkeys, *Cebus olivaceus*, in zoo exhibits in Venezuela. Folia Primatologica 86(3): 203–222. https://doi.org/10.1159/000381397

Tiddi B, Aureli F, Schino G, Voelkl B (2011) Social relationships between adult females and the alpha male in wild tufted capuchin monkeys. American Journal Primatology 73(8): 812–820. https://doi.org/10.1002/ajp.20939

Verderane MP, Izar P, Visalberghi E, Fragaszy DM (2013). Socioecology of wild bearded capuchin monkeys (*Sapajus libidinosus*): an analysis of social relationships among female primates that use tools in feeding. Behaviour 150(6): 659–689. https://doi.org/10.1163/1568539X-00003076

Whitehead H (2008) Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis. Chicago, University of Chicago Press, 336 pp.

Wilson EO (2000) Sociobiology: The New Synthesis. London, Harvard University Press, 697 pp.

Submitted: October 25, 2018
Accepted: January 26, 2019
Available online: June 4, 2019
Editorial responsibility: Diego Astúa de Moraes

Author Contributions: JPB, AS and LMA contributed equally to this article.

Competing Interests: The authors have declared that no competing interests exist.