

## RESEARCH ARTICLE

Activity Budget, Diet, and Habitat Use in the Critically Endangered Ka'apor Capuchin Monkey (*Cebus kaapori*) in Pará State, Brazil: A Preliminary Comparison to Other Capuchin MonkeysS. G. DE OLIVEIRA<sup>1</sup>, JESSICA W. LYNCH ALFARO<sup>2,3\*</sup>, AND LIZA M. VEIGA<sup>4</sup><sup>1</sup>Curso de Pós-Graduação de Zoologia, Universidade Federal do Pará / Museu Paraense Emílio Goeldi, Belém, Pará, Brazil<sup>2</sup>Institute for Society and Genetics, University of California-Los Angeles, Los Angeles, California<sup>3</sup>Department of Anthropology, University of California-Los Angeles, Los Angeles, California<sup>4</sup>Departamento de Mastozoologia, Universidade Federal do Pará / Museu Paraense Emílio Goeldi, Belém, Pará, Brazil

The Ka'apor capuchin, *Cebus kaapori*, is perhaps the most endangered primate of the Brazilian Amazon. Endemic to a region with extreme intensification of habitat-degrading activities, it survives in remnant populations in a completely fragmented landscape. Before now, the only data available were isolated observations of feeding, locality records, and information on population densities and group size obtained during census. Here we present the first data on the activity budget, diet, and daily path length of the species, and compare our preliminary results with those for other capuchin monkeys. A group of nine Ka'apor capuchins was monitored over a period of four months during the dry season in the Goianésia do Pará municipality, Pará, Brazil. We used instantaneous scan sampling ( $n = 4,647$  scans) to construct an activity budget for the monkeys, and we identified the plants in their diet to species level ( $n = 41$  plant taxa), allowing us to compare dietary overlap with other gracile capuchin species, as well as with the robust capuchin (*Sapajus* spp.), a potential competitor present throughout the range of the Ka'apor capuchin. Like other species of gracile capuchins, *C. kaapori* was highly frugivorous, with the vast majority of the feeding records of arils and fruit pulp (74%), supplemented by arthropods (13%) and seeds (10%), although diet composition was highly variable across months. The group used a total area of 62.4 ha during the study period, and average daily path length was 2,173 m ( $\pm 400$  m), with the entire home range utilized in every month of the study. We found significant overlap in the diet of the Ka'apor capuchin and *Sapajus*, highlighting the urgency to increase knowledge of the ecological needs of *C. kaapori* and understand synergistic effects of sympatry with competitive species, increasing forest fragmentation, and widespread human impact on *C. kaapori* sustainability. *Am. J. Primatol.*

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**Key words:** dietary overlap; gracile capuchin monkey; *Sapajus*; conservation biology; behavioral ecology

## INTRODUCTION

Gracile or untufted capuchin monkeys, *Cebus*, are highly frugivorous but include a broad range of foods within their diet, such as insects, flowers, eggs, small vertebrates, and nectar [Chapman, 1988; Fragaszy et al., 2004; Peres, 1994; Robinson, 1986; Rose, 1998; Terborgh, 1983]. The behavioral ecology of gracile capuchins has been well studied in Panama and Costa Rica [*Cebus capucinus*: Oppenheimer, 1969; Perry, 2008; Perry et al., 2003], the Venezuelan llanos [*Cebus olivaceus*; de Ruiter, 1986; Miller, 1996; Robinson, 1986], and western Amazonia [*C. albifrons* sensu lato: Defler, 1979; Janson, 1986; Matthews, 2009; Terborgh, 1983]. However, little is known about gracile capuchins in Brazil. The least known species is eastern Amazonian *Cebus kaapori*, with a disjunct distribution from all other gracile capuchins. In this

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study, we provide the first ecological and behavioral data for a group of wild Ka'apor capuchin monkeys.

*C. kaapori* is one of the most recently described primates, discovered in 1992 by Queiroz. Its geographic distribution is quite small for Amazonian primates [Carvalho et al., 1999] and it is extremely rare, with low population densities across its range [Lopes & Ferrari, 1996]. Endemic to the states of Maranhão and Pará in Brazil [Kierulff & de Oliveira, 2008], it is categorized as critically endangered by IUCN [Kierulff & de Oliveira, 2008] and recently has been listed as one of the top 25 most endangered primates [Mittermeier et al., 2012]. The Ka'apor capuchin lives in the Amazonian region with the highest human population density and highest level of deforestation and environmental degradation. Current threats include cattle ranches, soy plantations, and the continued construction of large hydroelectric dams. This study took place in Pará state, in the area of influence of the Tucuruí Hydroelectric Dam, one of the largest hydroelectric projects in Brazil. The dam was constructed in 1984 in the Tocantins River, flooding an area of approximately 2,247 km<sup>2</sup> [Fearnside, 1997]. The closing of the gates of the reservoir resulted in the formation of about 1,600 islands with areas from 1 to 1,000 ha [Veiga, 2006]. The principal ecological outcome of this mega-project has been the degradation of surrounding forest and aquatic ecosystems [Fearnside, 1997].

Most taxonomic studies have placed *C. kaapori* within its own species [Groves, 2001, 2005; Silva, 2001], although others consider it a subspecies of *C. olivaceus* [Harada & Ferrari, 1996]. Many morphological characteristics unite it with *C. olivaceus* [Queiroz, 1992], but others such as cranial measurements suggest it is more similar to *C. albifrons* sensu lato [Masterson, 1995] (note that the most recent taxonomic review of capuchins has separated *C. albifrons* into nine species [Rylands et al., 2013]—here and throughout the text we use *C. albifrons* in the broad sense). In this study, we provisionally consider *C. kaapori* as a species, but expect that its behavioral ecology will be most similar to *C. olivaceus*, based on morphological similarity and shared evolutionary history, and to *C. albifrons*, because of morphological and ecological similarity. Previous studies of *C. albifrons* have focused on populations in the western Amazonian rainforest [Defler, 1979; Janson, 1986; Matthews, 2009; Terborgh, 1983], whereas the two study sites with long-term data for *C. olivaceus* are from drier Llanos habitats [de Ruiter, 1986; Fragaszy & Boinski, 1995; Fragaszy et al., 1990; Miller, 1996; O'Brien & Robinson, 1993; Robinson, 1986], so the habitat type for the present study is much more similar to that for the *C. albifrons* studies. However, this is the first study of the behavioral ecology of gracile capuchins both for eastern Amazonia and for Brazil, and so the most ecologically similar and geographi-

cally proximate capuchin studies are with robust capuchins, *Sapajus apella apella* [Sampaio, 2004; Spironello, 1991; Zhang, 1995].

Up until 2001, *C. kaapori* had been observed in the wild only in *terra firme* forest, in primary forest with low levels of degradation [Carvalho et al., 1999; Lopes & Ferrari, 1993; Queiroz, 1992; Silva, 2001]. Queiroz [1992] suggested that the species distribution extended from Amazon rainforest to the palm forest in northeast Maranhão, owing to *C. kaapori*'s ability to exploit palm fruits as food. In fact, the habitat preference for this species is not yet known. Recently, Cunha et al. [2007] found a population of *C. kaapori* on the right bank of the Tocantins River, slightly extending its distribution to the south; this is the population studied here (see Fig. 1). The northern, eastern, and southern distributional limits are still unknown for *C. kaapori*, in part because it is so rare even within its known range that it is difficult to determine with confidence where that range ends [see, e.g., Ferrari & de Souza, 1994].

Ka'apor capuchins have been observed in mixed groups in association with robust capuchins [*S. apella*: Lopes & Ferrari, 1996; Silva & Cerqueira, 1998]. Robust capuchins are frugivores of similar body size to *C. kaapori* and can be considered potential competitors for resources. In his census work, Oswaldo de Carvalho, Jr. (personal communication) found an inverse relationship between the abundance of *C. kaapori* and the presence of *S. apella*, perhaps due to competitive exclusion. Here we compare the plant species and dietary items utilized by *C. kaapori* to those known to be used by *Sapajus* species, as well as activity budget, feeding



Fig. 1. Map of South America, with inlay map of the distribution of *Cebus kaapori* (Source: IUCN, Red List, 2010) in eastern Brazil, in the states of Maranhão and Pará. The blue star indicates the study location in the area of influence of the Tucuruí Hydroelectric Dam.

tree height, and DBH for feeding trees, to assess evidence for dietary and spatial overlap and potential for resource competition. We also compare diet and activity budget of *C. kaapori* to that reported for other gracile capuchin species (*Cebus*), with the caveat that our data are preliminary as they were collected in the dry season only.

*C. kaapori* is confined to a totally fragmented landscape, resulting in high risk of extinction. Until now, the only published data available for this species is on presence of groups and group size, based on census data. Here we present the first ecological and behavioral data for the species. We aim to understand how critically endangered *C. kaapori* compares in activity budget, diet, and spatial use to other capuchin species, and to determine how variable *C. kaapori* behavior is across months. If morphology drives capuchin diet and use of space, we would expect *C. kaapori* to be most similar to *C. olivaceus* and possibly *C. albifrons* in activity budget, diet, and use of space, and less like *C. capucinus* or *Sapajus* species. However, if ecology is the main driver of capuchin diet, we might expect *C. kaapori* to have more in common with other Amazonian *Cebus* and *Sapajus*, in comparison to *Cebus* from the Llanos or *Sapajus* from the Atlantic Forest or Cerrado.

## METHODS

### Study Site and Study Group

The study area is in the Goianésia do Pará municipality in Pará State, Brazil (S 04°08'29.8" W 049°30'43.8"), in the eastern Amazonian "arc of deforestation." The study site is within the area of influence of the Tucuruí Hydroelectric Dam, on the right bank of the Tocantins River (Fig. 1). This study took place across two adjacent forest fragments, together covering over 50 ha within a highly fragmented human-modified forest landscape.

The predominant vegetation in this region is open ombrophylic forest. However, the study area fragments are mostly composed of secondary vegetation, with a high proportion of lianas and shrubby vegetation, in part due to intentional burning in November and December 2009. The study area also includes açai palm forest, primary forest, and riparian forest. Temperature in this area ranges daily from about 35°C in the daytime to 17°C at night, with little variation across the year. The dry season occurs from June to November, and the rainy season from December to April, with a transitional month in May.

We habituated the study group of *C. kaapori* from November 2009 to May 2010. Systematic behavioral data for the study were collected during the dry season between June and September 2010, with limited additional data collected on capuchin plant use in October and November 2010. At the beginning of the habituation period, the study group was

composed of six individuals, including two adult males, two adult females, a juvenile male, and a sixth individual of unknown sex/age class. In January and February 2010, there were two births, and one more individual of unknown sex/age class was observed in September 2010. This study was conducted with institutional approval, adhered to the legal requirements of Brazil, and adhered to the American Society of Primatologists' principles for the ethical treatment of primates. No primates were manipulated in the study.

### Behavioral Sampling and Feeding Resource Identification

Behavioral data were collected on the study group on 25 days across 4 months, with 4 days of data collection in June and 7 days each in July, August and September 2010. The study group was followed from the moment they left the sleeping tree in the morning until they arrived at the sleeping tree at the end of the day.

Instantaneous scan sampling [Altmann, 1974] was performed for 5 min at every 10-min interval. This methodology allowed the calculation of the frequency of each behavioral category. During each scan for each individual we registered activity performed and height from the ground. Activities included: locomotion, foraging, feeding, social interaction, resting/standing still, and other. *Locomotion* was scored if the subject performed any directional movement, either alone or with other individuals, including walking, jumping, galloping, climbing, descending, or running, whether within a tree, across trees, or on the ground. *Foraging* was scored if the individual was engaged in a manual search for vegetable matter, among leaves or mature fruits; a manual search for animal matter, manipulating items such as sticks and leaves; or a visual search for food. *Feeding* was scored if the subject was licking, biting, chewing, drinking or ingesting dietary items. *Standing still/resting* was scored if the individual remained inactive, sitting, lying down, or standing on all four feet, without performing any other apparent activity. *Social interactions* included several subcategories. *Grooming* was scored for the manipulation of hair on a conspecific with hands or mouth. *Vocalizations* were scored for any emission of vocal sound directed at the group, at a conspecific, or another nearby animal such as a predator. *Aggression* was scored for behaviors directed at conspecifics such as hitting, biting, grabbing, or pursuing the other animal in a threatening way that caused the other individual to vocalize. *Interspecific interactions* were scored for any behavioral interaction between the subject and another animal species. *Breaking branches* was scored if the individual repeatedly broke branches in a display. Behaviors categorized as "other" included self-grooming and cleaning, drinking

water, urinating, and defecating. We also collected ad libitum data on infrequent behaviors between scan samples.

If an individual was feeding on plant material during a scan sample, we collected data on species consumed, plant part, and maturity of the item. Height from the ground was coded into the following classes: ground = 0 m, near ground > 0–5 m, above ground = 5–10 m, understory = 10–15 m, subcanopy = 15–20 m, canopy = 20–35 m. All the trees and vines that were used as feeding resources were marked with numbered tags, and for trees, the diameter at chest height was measured and the height estimated. Samples of leaves, fruit and flowers of the trees and vines that were used as resources were collected for subsequent identification to the species level. Arthropods were also identified to the species level when possible. We collected ad libitum data on food processing.

The location of the group was recorded at 15-min intervals throughout each daily follow using a *Garmin GPS*. The projection used was “BR UTM,” under the specifications of the Brazilian Army DSG.

## Data Analysis

Activity budget was estimated using the frequency method [Oates, 1977], in which the contribution of each behavioral category is estimated by the number of occurrences in each scan ( $i = n_i/N \times 100$ , where  $n_i$  = number of scans collected for behavior  $i$ ,  $N$  = total scans collected during the study). The proportion of plant species in the diet, the proportion of different food types, and the proportion of activity spent at different forest heights were estimated in the same way. The data were compared across months to identify temporal differences. To calculate an overall dry season profile for activity budget and to control for bias from uneven sampling across months, we took the mean of mean monthly percentages of time spent in each activity.

To quantify the home range a  $50 \times 50$  m grid was superimposed on a satellite image of the study area, and GPS points were plotted on the image using the GPS Trackmaker Professional software, version 4. We calculated monthly and total area use to establish group movement and home range for July, August, and September. The GPS points at 15-min sampling intervals for each day were connected in a straight line to calculate the daily path length distance. The error for GPS location data was  $\sim 3$  m, as most of the area was not densely covered or closed canopy. This GPS error could inadvertently add distance to the daily path length calculations, while the straight line between 15-min interval sample locations could underestimate actual path length. We performed a Kruskal–Wallis test comparing daily travel distances across July, August, and September, to determine if daily travel distance varied by month. We considered a  $P$ -value less than 0.05 as statistically significant.

## RESULTS

### Activity Budget

We logged a total of 288 observation hours of the study group and 4,647 behavioral scan entries to determine dry season activity budget (Fig. 2). Locomotion was the most frequent behavior, at 47.4% of total scans ( $n = 2,203$ ), followed by feeding (24.0% of the total scans,  $n = 1,116$ ) and foraging (15.3%,  $n = 712$ ). Other activities were less frequent: standing still/resting (9.3%,  $n = 434$ ), social interactions (3.4%,  $n = 156$ ), with “other” activities occurring about 0.5% ( $n = 26$ ) of the time. Within social interactions, time dedicated to different activities included, in descending order: grooming, vocalizing, aggression, interspecific interactions, and branch shaking at the researcher.

Interspecific interactions included agonistic behavior toward the howler monkey, *Alouatta belzebul*, and also toward the squirrel monkey, *Saimiri sciureus* (probably *S. sciureus collinsi* at this site

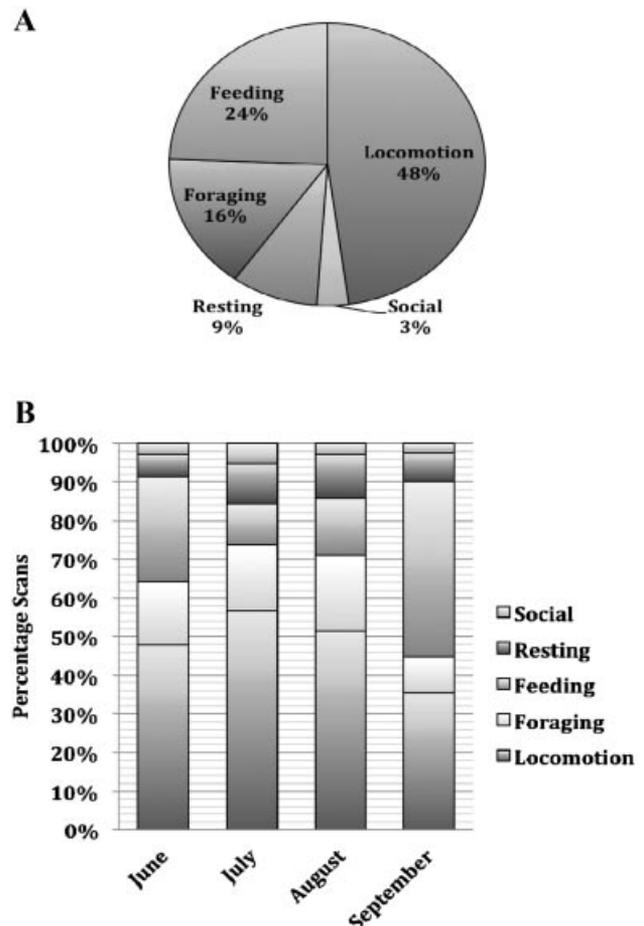


Fig. 2. Dry season activity budget for *Cebus kaapori* group (A) across the study, averaged across months; and (B) activity budget by scans per month for June, July, August, and September 2012. The “Other” category amounted to less than 0.5% of the activity budget and is excluded from the figure.

[Rylands et al., 2013]). In one incident, the squirrel monkeys and capuchins were feeding in the same *Inga alba* trees, and a capuchin monkey was aggressive towards a squirrel monkey in the context of competition for caterpillars as feeding resources. Ka'apor capuchins never participated in feeding or traveling associations with other primates in the study, and they seemed to avoid direct contact with robust capuchin monkeys, *Sapajus apella*. The two capuchin monkey species sometimes would come into proximity with one another but never directly crossed paths nor mixed together when traveling. The *Sapajus* group that overlapped in home range with the *C. kaapori* group had approximately 10 individuals, and stayed within the closed-canopy forest.

### Feeding Behavior and Diet Composition

*C. kaapori* showed a strong preference for fruit (74.1% of feeding scans), including the aril of immature fruit (50.9% of total feeding scans,  $n = 568$ ) and fruit pulp (23.2%,  $n = 259$ ). Lepidopteran caterpillars and other arthropods were consumed in 12.6% of feeding scans ( $n = 141$ ), and endocarp or seeds in 10.2% ( $n = 114$ ). Flowers, leaves, branches, honeycomb, wasp nests, snails, a rodent and unidentified items made up a small proportion of feeding scans (3%). As scan samples can result in a sampling bias that overrepresents clumped group feeding, we performed a complementary analysis to compare the proportion of plant taxa from which Ka'apor capuchins consumed different plant parts: fruit/aril (24/41 identified taxa), seeds/endocarp (12/41), flowers (4/41), leaves (1/41), and structural plant parts (1/41).

Diet was most diverse in July and August (Fig. 3). In June, 91.8% ( $n = 123$ ) of the feeding entries were of caterpillars, order Lepidoptera, from within the new leaves of the plant *I. alba*. In contrast, in September,

monkeys fed largely on the green pulp of the same tree species (*I. alba*), for 87.8% ( $n = 563$ ) of feeding entries for this month.

The species of plants consumed by the monkeys are listed in Table I. The most used plant families were Euphorbiaceae ( $n = 4$  species), Fabaceae ( $n = 4$ ), Arecaceae ( $n = 4$ ), and Salicaceae ( $n = 3$ ). The monkeys showed a consistent preference for seven plant species (in descending order of use): *I. alba*, *Bellucia grossularioides*, *Attalea maripa*, *Alchorneopsis floribunda*, *Gustavia augusta*, *Apeiba burchellii*, and *Bactris maraja*, each consumed in July, August, and September. Of the preferred species, *G. augusta* and *I. alba* were among the ten most common tree species based on transect data at the T4 trail in the Tucuruí Reservoir [Veiga, 2006], about 10 km from the *C. kaapori* study site, and *Bellucia grossularioides* was one of 10 most common species on a nearby island, Ilha do João [Veiga, 2006], but the other four species most frequently consumed by *C. kaapori* in this study were not common at either of these two nearby locations [Veiga, 2006]. *A. maripa* is abundant in highly disturbed Amazonian forests, and *A. burchellii* is often found in secondary forests.

In terms of food processing, Ka'apor capuchins accessed endocarp or seeds by using their hands to hit the following fruits against tree branches: *Theobroma speciosum* (cacao or cocoa), *G. augusta* (genipuarana) and *Sloanea grandiflora* (urucurana). Within the palm family (Arecaceae), for *Euterpe oleracea* (açai), the monkeys gnawed on the endocarp surrounding the seed. For *A. maripa* (inajá), they pulled off the husk (exocarp) with their teeth, and ate the endocarp that either came off with the husk or still surrounded the nut. For *B. maraja* (mombaca) the monkeys fed on the flowers, and used hands and mouth to open the fruit to eat the endocarp; however, only a few monkeys braved the thorns to access the base of the youngest and softest leaves that they pulled out from deep in the middle of the crown of the plant. For *Socratea exorrhiza* (paxiúba) monkeys bit into the fruit to suck out the juice, but they did not eat any of the other plant parts.

Non-plant items used as feeding resources are listed in descending frequency, with number of scans and percentage of total diet: Caterpillar ( $n = 123$ , 11%), ant ( $n = 10$ , 0.9%), unidentified insect ( $n = 5$ , 0.4%), wasp's nest ( $n = 2$ , 0.2%), snail ( $n = 2$ , 0.2%), unidentified rodent ( $n = 1$ , 0.1%), unidentified spider ( $n = 1$ , 0.1%), honeycomb ( $n = 1$ , 0.1%), water from tree hole ( $n = 1$ , 0.1%). Lepidopteran caterpillars were the invertebrates consumed most frequently in scan samples. Capuchins also ate snails of the genus *Corona*. Ant species consumed included *Creमतogaster tenuicula* and *C. brasilienses*, from the group Limata; *Dolichoderus bidens*; *Daceton armigerum*; *Cephalotis atratus*; and *Pheidole* sp. The monkeys also ate an *Apis mellifera* beehive. The group foraged

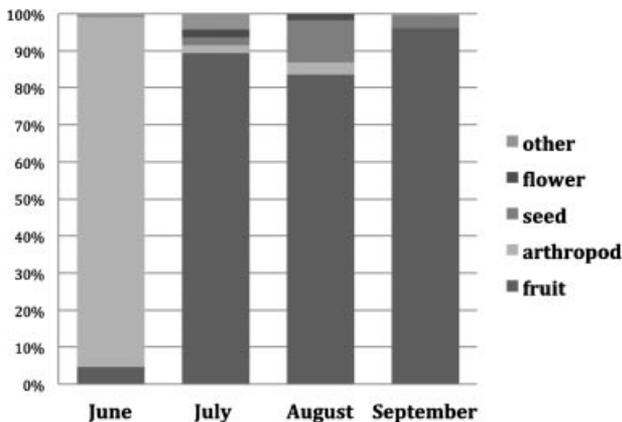


Fig. 3. Proportion of different types of food in the diet for *C. kaapori* during each month of the study: June, July, August, and September 2010.

**TABLE I. List of Plant Species Used by the *Cebus kaapori* Group Between June and September 2010, With Frequency of Observation of Use During Scan Sampling and Plant Part Consumed**

Taxa	Family	Pop name	No. scans	% Scans	Plant part(s)
<i>Inga alba</i> (Scu.) Willd.	Fabaceae	Ingá vermelho	567	50.81	Aril
<i>Bellucia grossularioides</i> (L.) Triana	Melastomataceae	Muúba	186	16.67	Ripe fruit
<i>Attalea maripa</i> (Aubl.) Mart.	Areaceae	Inajá	45	4.03	Endocarp ( $n=42$ ), ripe fruit ( $n=1$ ), husk ( $n=2$ )
<i>Alchorneopsis floribunda</i> Müll. Arg.	Euphorbiaceae	Falsa najarána	34	3.05	Immature fruit
<i>Gustavia augusta</i> L.	Lecythidaceae	Genipuarána	26	2.33	Seed
<i>Apeiba burchellii</i> Sprague	Malvaceae	Pente-de-macaco	18	1.61	Seed
<i>Baccharis maraja</i> Mart.	Areaceae	Mombaca	17	1.52	Flower ( $n=16$ ), seed ( $n=1$ )
<i>Socratea exorrhiza</i> (Mart.) H. Wendl.	Areaceae	Paxiúba	11	0.99	Liquid endocarp
<i>Zanthoxylum rhoifolium</i> Lam.	Rutaceae	Tamanqueira	9	0.81	Ripe fruit
<i>Casearia javitensis</i> H.H.K.	Salicaceae	Falsa copiuba	8	0.72	Ripe fruit
<i>Passiflora coccinea</i> Aubl.	Passifloraceae	Maracujá-de-cobra	6	0.54	Seed and endocarp
<i>Phytolacca rivinoides</i> Kunth et. Bouche	Phyllacaceae	Carirú-de-anta	6	0.54	Fruit
<i>Doloiacarpus major</i> J.F.Gmel ssp. <i>major</i>	Dilleniaceae	Cipó ameixa	4	0.36	Endocarp
<i>Theobroma speciosum</i> Willd. ex Spreng.	Sterculiaceae	Cacau jacaré	3	0.27	Endocarp
<i>Miconia kaplerii</i> Naudin	Melastomataceae	Tinteiro branco	3	0.27	Ripe fruit
<i>Aparisthium cordatum</i> (Juss.) Baill	Euphorbiaceae	Pau-de-facho	1	0.09	Fruit
<i>Banara guianensis</i> Aubl.	Salicaceae	Lacre branco	1	0.09	Fruit
<i>Byrsonima chrysophylla</i> Kunth	Malpighiaceae	Murici	1	0.09	Fruit
<i>Cayaponia</i> sp. Silva Manso	Cucurbitaceae	Gorgão da mata	1	0.09	Fruit
<i>Cordia scabrifolia</i> A.DC.	Boraginaceae	Frejó	1	0.09	Fruit
<i>Cordia bicolor</i> DC.	Boraginaceae	Promombaca	1	0.09	Immature fruit
<i>Dalechampia tiliifolia</i> L.	Euphorbiaceae	Cipó urtiga	1	0.09	Fruit
<i>Dimorphandra gardneriana</i> Tulasne	Fabaceae	Fava de viado	1	0.09	Leaf bud
<i>Eschweileira coriacea</i> (A. DC.) Mart. ex Beg.	Lecythidaceae	Mata mata branco	1	0.09	Flower
<i>Euterpe oleracea</i> Mart.	Areaceae	Açaí	1	0.09	Fruit
<i>Gnetum urens</i> (Aubl.) BL.	Gnetaceae	Pingo-pingo	1	0.09	Fruit
<i>Inga auristellae</i> Herms	Fabaceae	Ingá	1	0.09	Aril
<i>Ipomoea pecora</i> Meisn	Convolvulaceae	Cipó batatarána	1	0.09	Ovary of flower
<i>Iryanthera</i> sp. (A. DC.) Warb	Myristicaceae	Ucúba	1	0.09	Endocarp
<i>Jacaranda copaia</i> (Aubl.) D. Don	Bignoniaceae	Pará-pará	1	0.09	Gall on tree
<i>Laetia procera</i> (Poepp.) Eichler	Salicaceae	Pau jacaré	1	0.09	Seed and endocarp
<i>Paullinia pinnata</i> L.	Sapindaceae	Cipó abóbora	1	0.09	Fruit
<i>Perebea guianensis</i> Aubl. <i>Guianensis</i>	Moraceae	Falsa genipuarána	1	0.09	Green branch pith
<i>Sloanea grandiflora</i> A. E. Sm.	Elaeocarpaceae	Urucurana	1	0.09	Seed
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	Tatapirica	1	0.09	Fruit
<i>Theobroma guianensis</i> (Aubl.) Gmel.	Sterculiaceae	Capuai or cupuí	1	0.09	Fruit
<i>Alexa grandiflora</i> Ducke, <i>Alexa</i> spp.	Fabaceae	Melancieira	0	*	Flower
<i>Doloiacarpus major</i> J Gmelin	Dilleniaceae	Cipó de fogo	0	*	Seed
<i>Ficus cabollina</i> Standley	Moraceae	Figueira mata pau	0	*	Fruit
<i>Hyeronima laxiflora</i> (Tul.) M.Arg.	Euphorbiaceae	Tinteiro do brejo/margonçalo	0	*	Fruit
<i>Pourouma</i> sp. Aubl.	Urticaceae	Embaubão	0	*	Fruit
Not identified	—	—	6	—	—

Note: Percentage of scan samples for feeding on each item is compared to the total number of feeding scan samples in the study. Asterisks indicate plant species that were observed being eaten by the monkeys outside of the scan sampling effort, in October and November 2010.

in the wasp nests of the nocturnal *Apoica pallida*, probably for honey and larvae, as well as in nests of Epiponini wasps (most likely *Polybia* sp.). The only observation of *C. kaapori* vertebrate prey consumption was of a rodent (species unidentified). The monkeys were also observed to drink water from tree holes.

The capuchins' most common foraging behavior for invertebrates was to glean insects from either the new leaves of *I. alba* trees or from dry leaves, after opening up the leaves with their hands. A few times monkeys were observed breaking and opening dry branches or sticks with teeth and hands to access ants. They also frequently searched through ant nests made of leaves in the forest canopy. The monkeys hit snail shells very hard against tree branches to crack them open and access the animal inside.

### Dietary Overlap

A comparison of the plants consumed by our *C. kaapori* group with those reported to be consumed by other *Cebus* and *Sapajus* species revealed that the highest dietary overlap for *C. kaapori* at both the plant genus level (81% of genera by *C. kaapori*) and species level (45% of identified species) was with *Sapajus* (all *Sapajus* species combined: Table II). High dietary overlap at the genus level between *C. kaapori* and *Cebus* species at other field sites was also apparent (for all *Cebus* species combined, there was 65% dietary overlap with *C. kaapori* at the genus level, and 18% overlap at the species level). Somewhat surprisingly, within gracile capuchins, the species with the most dietary overlap to *C. kaapori* was *C. capucinus*, which has been reported to consume 46% of the plant items consumed by *C. kaapori* at the genus level, and 13% at the species level. It is important to note that dietary overlap values are not corrected by research effort, so that overlap is likely biased toward the well-studied capuchins (i.e., *Sapajus* spp. and *C. capucinus*).

In this study, five genera of plants were eaten by *C. kaapori* that to our knowledge never have been reported before as part of the diet of wild capuchin monkeys. These include fruits from *Alchorneopsis floribunda* (Euphorbiaceae), *Aparisthium cordatum* (Euphorbiaceae), *Gnetum urens* (Gnetaceae), *Phytolacca rivinoides* (Phytolaccaceae), and leaves from *Dimorphandra gardneriana* (Fabaceae).

### Substrate Use

The home range included trees up to 35 m in height. When comparing tree height for all feeding trees used by capuchins in the study ( $n = 260$ ), capuchins fed most often in trees from 16 to 20 m tall (45.8% of scans), or in trees from 6 to 10 m tall (19.6% of scans). They preferred feeding trees of relatively wide diameter at breast height, with most

feeding scans recorded in trees from 20 to 30 cm DBH. Only 1% ( $n = 12$ ) of feeding scans occurred on the ground. Overall, when comparing across all activity types ( $n = 4,647$  scan entries) for the percentage of scans registered for each height category, monkeys most frequently used the intermediate forest levels, between 5 and 20 m (78% of scans). However, all levels of the forest were utilized by the capuchins, from the ground to the canopy.

### Daily Path Length and Home Range

Across the study period, the mean daily travel distance was 2,173 m ( $\pm 400$  m). By month, mean daily distance traveled was 2,174 m in July, 2,378 m in August, and 1,968 m in September. There was no significant difference in daily travel distance among months of the study (KW = 1.963,  $df = 2$ ,  $P = 0.375$ ). The shortest recorded daily travel distance was 1,297 m and the longest was 2,913 m.

Based on our assessment of quadrant use from the GPS data, the group used approximately 62.4 ha during the study period. This included both the forest fragments and adjacent degraded and human-impacted land. The capuchin study group used all types of forest available in the area, including secondary forest, primary *terra firme* forest, and flooded areas dominated by açai palms. In fact, we found that the monkeys used almost all quadrants of the home range every month.

### DISCUSSION

A selected comparison of activity budgets across capuchin populations is provided in Table III. The relative decrease in time spent resting, socializing, and feeding, and concomitant increase in locomotion compared to other gracile capuchins may signal dietary stress in the *C. kaapori* population. The *C. kaapori* activity budget is more similar to that for Amazonian *Sapajus*, but the time spent in locomotion is high even compared to the nearby Tucuquí population of *S. apella* [Sampaio, 2004]. However, it is important to note that different studies have collected activity budget data using different methods, and so they may not be directly comparable (see Table III for details on methodological differences). For example, our method of scan sampling may overrepresent readily visible, social activities like feeding and underrepresent solitary or less conspicuous behaviors, like resting; while annual averages may not adequately represent dry season activity budgets. More studies using uniform methods across species and populations are urgently needed.

Queiroz [1992] suggested that *C. kaapori* may have converged with *S. apella* to significantly supplement fleshy fruit with palm nuts, and perhaps seeds and structural plant parts. Here we found *C.*

TABLE II. Comparison of Plant Use by *Cebus kaapori* in This Study to Other Capuchin Monkey Species From the Literature

Taxon	Family	<i>Cebus kaapori</i> (this study)	<i>Cebus albifrons</i>	<i>Cebus olivaceus</i>	<i>Cebus capucinus</i>	All <i>Cebus</i> (excluding <i>C. kaapori</i> )	All <i>Sapajus</i>
<i>Tapirira guianensis</i>	Anacardiaceae	FR					<b>S, FS (1)</b>
<i>Attalea maripa</i>	Areaceae	EN				<b>S, UNK (1)</b>	<b>S, FS (1)</b>
<i>Baccharis maraja</i>	Areaceae	FL, SD	<b>S, UNK (1)</b>		G, FS, SH (1)	G, FS, SH (1)	<b>S, FS (7)</b>
<i>Euterpe oleracea</i>	Areaceae	FR	G, FS (1)			G, FS (1)	<b>S, FL, FS (1)</b>
<i>Socratea exorrhiza</i>	Areaceae	EN					<b>S, FS (1)</b>
<i>Jacaranda copaia</i>	Bignoniaceae	GL			<b>S, FS (1)</b>	<b>S, FS (1)</b>	<b>S, FS (1)</b>
<i>Cordia bicolor</i>	Boraginaceae	FR		G, FS (1)	<b>S, FS (1)</b>	<b>S, FS (1)</b>	G, FS (1)
<i>Cordia scabrifolia</i>	Boraginaceae	FR		G, FS (1)	G, FS (1)	G, FS (1)	G, FS (1)
<i>Ipomoea pecora</i>	Convolvulaceae	FL				G, FS (1)	G, NC, FL (3)
<i>Cayaponia</i> sp.	Cucurbitaceae	FR	G, FS (1)			G, FS (1)	G, FS (1)
<i>Dolichocarpus major</i>	Dilleniaceae	SD			<b>S, FS (1)</b>	<b>S, FS (1)</b>	
<i>Dolichocarpus mojov</i>	Dilleniaceae	EN			G, FS (1)	G, FS (1)	
<i>Sloanea grandiflora</i>	Elaeocarpaceae	SD	G, FS (1)		G, FS (1)	G, FS (1)	G, FS, LV (1)
<i>Alchorneopsis floribunda</i>	Euphorbiaceae	FR					
<i>Aparisthium cordatum</i>	Euphorbiaceae	FR				G, FS (1)	
<i>Dalechampia tiliacifolia</i>	Euphorbiaceae	FR				<b>S, FS (1)</b>	G, FS (1)
<i>Hyeronima laxiflora</i>	Euphorbiaceae	FR		G, FS (1)	<b>S, FS (1)</b>	<b>S, FS (1)</b>	<b>S, FL (2)</b>
<i>Alexa grandiflora</i>	Fabaceae	FL					
<i>Dimorphandra gardneriana</i>	Fabaceae	LV					
<i>Inga alba</i>	Fabaceae	AR	<b>S, FS (1)</b>			S, FS (1)	<b>S, FS (1)</b>
<i>Inga auristellae</i>	Fabaceae	AR			G, FS (1)	G, FS (1)	
<i>Gnetum urens</i>	Gnetaceae	FR			G, FS (1)	G, FS (1)	
<i>Gustavia augusta</i>	Lecythidaceae	SD			G, FS, SH (1)	G, FS, SH (1)	<b>S, FL, FS (1)</b>
<i>Eschweleira coriacea</i>	Lecythidaceae	FL	G, FR (5)			G, FR (5)	<b>S, FS (1)</b>
<i>Byronima chrysophylla</i>	Malpighiaceae	FR			G, FS (1)	G, FS (1)	G, FR, SD, LV (2)
<i>Apeiba burchellii</i>	Malvaceae	SD				G, FR (2)	
<i>Bellucia grossularioides</i>	Melastomataceae	FR	G, FR (5)			G, FR (5)	<b>S, FR (2)</b>
<i>Miconia kaplerii</i>	Melastomataceae	FR	G, FS (1)		G, FS (1)	G, FS (1)	G, FS (1)
<i>Ficus cabollina</i>	Moraceae	FR	G, FS (1)		G, FS (1)	G, FS (1)	G, FS (1)
<i>Perebea guianensis</i>	Moraceae	GB					<b>S, FS (1)</b>
<i>Iryanthera</i> sp.	Myristicaceae	EN			G, UNK (1)	G, UNK (1)	G, FS (1)
<i>Passiflora coccinea</i>	Passifloraceae	SD, EN	G, FR (5)	G, FS (1)	G, FS (1)	G, FS (1)	<b>S, FL, FS (1)</b>
<i>Phytolacca rivinoides</i>	Phytolaccaceae	FR					
<i>Zanthoxylum rhoifolium</i>	Rutaceae	FR					
<i>Banara guianensis</i>	Salicaceae	FR			G, FS (1)	G, FS (1)	<b>S, SD, FR (3)</b>
<i>Casearia javitensis</i>	Salicaceae	FR			G, AR/SD (4)	G, AR/SD (4)	G, SH (1)
<i>Laetia procera</i>	Salicaceae	SD, EN					G, FR (3)
<i>Paulinia pinata</i>	Sapindaceae	FR	G, FS (1)	G, FS (1)	<b>S, FS (1)</b>	<b>S, FS (1)</b>	<b>S, AR (6)</b>
<i>Theobroma guianensis</i>	Sterculiaceae	FR	G, FS (1)			G, FS (1)	G, FS (1)
<i>Theobroma speciosum</i>	Sterculiaceae	EN	G, FS (1)			G, FS (1)	G, FS (1)
<i>Pourouma</i> sp.	Urticaceae	FR	G, FS (1)		G, FS (1)	G, FS (1)	G, FS (1)

Note: G = same plant, genus; S = same plant, species, shown in bold typeface; AR = aril; EN = endocarp; FL = flower; FR = fruit; FS = fruit and/or seeds; GB = green branch; GL = gall on tree; LV = leaves; MD = medulla; ME = mesocarp; NC = nectar; SD = seeds; SH = shoots; UNK = unknown. (1) Fragaszy et al. [2004], see Appendix 1, p. 285 for extensive review of plant use by capuchins; (2) Stampaio [2004]; (3) de Freitas et al. [2008]; (4) Buckley [1983]; (5) Defler [1979]; (6) Galetti and Pedroni [1994]; (7) Mendes Pontes [1997].

TABLE III. Activity Budgets for Some Capuchin Monkey Populations Across Habitat Types

Habitat	Eastern Amazon	Western Amazon	Llanos (Venezuela)	Llanos (Venezuela)	Dry tropical forest (Central America)	Dry tropical forest (Central America)
<i>Cebus</i>						
Location	Tucuruí, Brazil	Tiputini, Ecuador	Hato Masaguaral	Hato Piñero	Santa Rosa, Costa Rica	Curú, Costa Rica
Species	<i>C. kaapori</i>	<i>C. albifrons</i>	<i>C. olivaceus</i>	<i>C. olivaceus</i>	<i>C. capucinus</i>	<i>C. capucinus</i>
Season	Dry season (Jun–Sep)	All year <sup>a</sup>	All year	All year	All year	All year
Citation	This study	Matthews [2009]	(no seasonal info) <sup>b</sup> Fragaszy [1990] <sup>b</sup>	(no seasonal info) Miller [1997] <sup>c</sup>	(no seasonal info) Rose [1994] <sup>d</sup>	(no seasonal info) McKinney [2011]
Method	Mean monthly percentage from scan sampling	Group activity 5-sec scan at 20 min intervals	Instantaneous 5-sec sample within focal individual follows every 15 sec	30 sec samples for each adult female every 1/2 hr	Adult focal data in 10-min continuous-time sessions	20-min interval focal animal follows with sample every 1 min
Locomotion	48	25	20	37	17–18	22
Social	3	4	9	2	3–8	33
Rest	9	5	22	25	15–23	24
Forage/feed	40	66	49	36	50–58	21
<i>Sapajus</i>						
Habitat	Eastern Amazon	Guianas	Western Amazon	Cerrado/Caatinga	Atlantic Forest	
Location	Tucuruí, Brazil	Nouragues, French Guiana	Tinigua, Colombia	Boa Vista, Piauí	Carlos Botelho, São Paulo	
Species	<i>S. apella</i>	<i>S. apella</i>	<i>S. macrocephalus</i>	<i>S. libidinosus</i>	<i>S. nigritus</i>	
Season	Dry season (Jun–Nov)	Dry season (Aug–Nov)	Times of fruit scarcity	All year (no seasonal info)	All year (no seasonal info)	
Citation	Sampaio [2004]	Zhang [1995] <sup>e</sup>	Stevenson et al. [2000]	Izar et al. [2012]	Izar et al. [2012]	
Method	Scan sampling	15-min scan total proportion/month	Focal sampling and instantaneous scans	10-min scan sampling	5-min scan sampling	
Locomotion	40	22–30	26	32 ± 11	36 ± 11	
Social	3	4 to 12	3	4 ± 1 <sup>f</sup>	2 ± 3 <sup>f</sup>	
Rest	4	4 to 10	5	8 ± 5	4 ± 4	
Forage/feed	50	45–68	66	46 ± 7	58 ± 12	

<sup>a</sup>No consistent dry season at this site.<sup>b</sup>Scanning behavior subsumed into foraging category; resting did not include standing still (see Robinson [1986] for monthly activity budgets at same site).<sup>c</sup>Miller's category "moving and foraging" (22% of time) is included here within locomotion.<sup>d</sup>Percentages estimated from graph; scanning included under foraging.<sup>e</sup>Percentages estimated from graph; social includes social interactions, scanning, and interspecific interactions.<sup>f</sup>Social value is from Izar et al. [2012] category "others."

*kaapori* to be strongly frugivorous (74% of feeding scans were fruit), with seeds and endocarp also providing important contributions to the diet (10% of feeding scans and 11 out of 41 plants used were for seeds or endocarp). However, structural plant parts did not form a part of the Ka'apor capuchin diet. Robust capuchins, *S. apella* at Germoplasma Island, also in the area of influence of the Tucuruí Dam, spent 17% of feeding time on structural plant parts in the dry season [Sampaio, 2004], but this type of food was almost never eaten by Ka'apor capuchins at Tucuruí in our study. Arthropods were also a more important part of the diet for *Sapajus* (32% of feeding scans) [Sampaio, 2004] compared to *C. kaapori* (13% of feeding scans) in this region. These key dietary differences found between *Sapajus* and *Cebus* in the same local area during the dry season mirror differences reported in sympatric *Sapajus* and *Cebus* at Manu, Peru [Terborgh, 1983] and suggest some morphological or physiological constraints on diet breadth or preference between the two genera of monkeys.

Terborgh [1983] suggests that the most important plant families for neotropical primates are Moraceae, Annonaceae, and Arecaceae, with *Inga* also of special importance within Fabaceae. In contrast, in the Llanos habitat, *C. olivaceus* shows a preference, in terms of number of species used and percentage of scans for feeding, for the following plant families: Moraceae, Sterculiaceae, Rubiaceae, Boraginaceae, Annonaceae, Verbenaceae, Rutaceae, and Sapindaceae [Robinson, 1986]. For Amazonian *S. apella* near Manaus, Brazil, the most important plant families in terms of time spent feeding were Arecaceae, Sapotaceae, Euphorbiaceae, Moraceae, and Goupiaceae [Spironello, 1991], and for *S. apella* in Tucuruí, near the *C. kaapori* field site, the most commonly used families were Arecaceae, Fabaceae, Anacardiaceae, and Malpighiaceae [Sampaio, 2004]. In this study, the Ka'apor capuchin spent the most time feeding on Fabaceae, Melastomataceae, Arecaceae, Euphorbiaceae, Lecythidaceae, and Malvaceae, with no overlap to *C. olivaceus* preferred plant families but with Fabaceae and Arecaceae in common with Terborgh [1983], Sampaio [2004], and Spironello [1991], and Euphorbiaceae also in common with Spironello's [1991] Amazonian *Sapajus* study. This highlights ecology as a main driver, rather than morphology or phylogenetic constraint, for capuchin plant family preference in a given habitat.

We found that dietary overlap was significant between *C. kaapori* and *Sapajus* spp. when we compared genera and species of plants consumed by *C. kaapori* in this study to those reported in the literature for other capuchins. At Manu National Park in Coshu Cashu, Peru, the only long-term study site with ecological data for both *Sapajus* and *Cebus*, Terborgh [1983] found a wide overlap in diet

between the two species, with 45 of the 70 plant food items eaten by *Cebus* also consumed by *Sapajus*. Mendes Pontes [1997] also reported 67% overlap in plant resources between *C. olivaceus* and *S. apella* on Maracá Island, Roraima, Brazil. Further studies are urgently needed to understand dietary overlap and both indirect and direct competition with *S. apella*, a robust capuchin species sympatric with *C. kaapori* throughout its range, to understand how interactions between these two capuchin species may affect extinction probability for the Ka'apor capuchin in the increasingly degraded and human altered habitat.

In terms of non-plant items, *C. kaapori* included caterpillars, ants, other insects, wasp's nests, snails, and spiders in their diet. Snails, wasp's nests, caterpillars, grasshoppers, and ants were the most important invertebrate prey items for *C. olivaceus* at Hato Masaguaral [Fragaszy & Boinski, 1995], and *C. albifrons* in Peru preferred these invertebrates in descending order: ants; grasshoppers and katydids; wasp larvae; Lepidoptera pupa; caterpillars; spiders and spiders' nests [Terborgh, 1983]. *Sapajus* species have also been recorded eating all the general categories of arthropods described in this study [Freitas et al., 2008; Gomez-Posada, 2012; Izawa, 1979; Izawa and Mizuno, 1977; Sampaio, 2004; Stevenson et al., 2000]. All capuchins appear to have a similar dietary niche in terms of invertebrate prey preferences.

Vertebrate prey items were rare for *C. kaapori* (less than 0.1% of feeding records), even lower than the frequency for vertebrate prey in *C. olivaceus* [Robinson, 1986] and *C. albifrons* [Terborgh, 1983]. Vertebrate prey can be more important for *C. capucinus*, forming up to 2.5% of the diet [Chapman & Fedigan, 1990]. Vertebrate prey items consumed in other studies of gracile capuchins include: frogs, lizards, iguanas, bird nestlings and eggs, bats, anteaters, coati nestlings, squirrels, mice, and other rodents [Fragaszy & Boinski, 1995; Perry & Rose, 1994; Robinson, 1986; Rose et al., 2003; Terborgh, 1983]. In this study, however, only a rodent (species unidentified) was observed being consumed. More time with Ka'apor capuchins is likely to reveal a broader vertebrate prey list, but a study of *S. apella* in the Tucuruí area also showed a very low rate of vertebrate prey consumption (0.4% of scans) [Sampaio, 2004] in comparison to other *Sapajus* sites [Freitas et al., 2008; Izawa, 1979; Terborgh, 1983], suggesting the possibility of a reduced density of small vertebrates in the hydroelectric dam-affected ecology.

This study took place in the dry season, at a time of year when immature and mature fruits are relatively abundant [Veiga, 2006]. We found that Ka'apor diet was temporally variable, and that on a particular series of days, their diet was highly concentrated on a single source of food (i.e., *I. alba* pods, caterpillars). Monitoring Ka'apor capuchin diet and behavior throughout the year will help

understand how the diet shifts when some of the key resources observed in the Ka'apor capuchin diet in this study are unavailable.

*C. kaapori* used trees of all heights for feeding, but preferred those from 16 to 20 m, in a forest with trees up to 35 m. In comparison, in a forest with trees up to 50 m, preferred feeding tree height for *C. albifrons* in the dry season in Peru is at more than 20 m (87% of time), whereas for *Sapajus* at the same site spend 73% of time in trees of less than 20 m in the dry season [Terborgh, 1983]. Mean diameter at breast height (DBH) for *C. kaapori* feeding trees was 20–30 cm, more similar to the large crown trees preferred by *C. albifrons* in Peru [Terborgh, 1983], rather than the smaller-diameter trees (1–20 cm DBH) Phillips [1995] reported used by *C. capucinus*.

Comparing time spent at different heights in the forest, *C. kaapori* spent 55% of time above 10 m and 44% below. *S. apella* in Tucuruí spent over 80% of time in the dry season below 10 m in the forest [Sampaio, 2004], and similarly *Sapajus libidinosus* in Serra da Capivara spent more than 90% of its time in both dry and wet seasons below 10 m [Moura, 2004]. While all capuchins make use of all levels of forest, it appears there may be some niche stratification with *C. kaapori* spending a higher proportion of time up high.

Mean daily path length was approximately 2,173 m, coincident with that found in other capuchin species, for example  $2,357 \pm 506$  m in *C. capucinus* [Parr et al., 2011], 1,460 m for *C. albifrons* in the dry season [Terborgh, 1983], 2,000–2,500 m in the dry season for *S. apella* [Zhang, 1995], and 2,200 m in the dry season for *S. macrocephalus* [Terborgh, 1983]. In contrast, the home range of the group for the 4 months of the study was only 62 ha, surprisingly small for gracile capuchins. Home ranges for *C. olivaceus* are estimated at 200–300 ha [Robinson, 1986] and for *C. albifrons* 110–240 ha [Defler, 1979; Matthews, 2009; Terborgh, 1983], but only 80–90 ha in some *Sapajus* populations (see review in Matthews [2009] for all capuchins). The small home range size found for *C. kaapori* is probably related to the boundaries on travel imposed by the intense fragmentation of the habitat in the study site. However, the short length of the study may underestimate the total home range for the group. For example, the 10-week study on *C. capucinus* by Baldwin and Baldwin [1997] estimated home range as 32–40 ha, but longer studies have shown a much wider range, from 26 to 440 ha, for the home range for *C. capucinus* [Buckley, 1983; McKinney, 2010; Rose, 1998; Vogel, 2005; Vogel and Janson, 2007].

In our study, the nearest suitable forest fragment for *C. kaapori* habitation was 400 m away from the fragments within the group's home range. At the end of the study (late September), the monkeys in our group disappeared from the fragments in the study area. Later, after many days searching, we found only four individuals from the previous group of nine

traveling together in the fragment. The others may have gotten separated from this subgroup across different fragments, or perhaps the missing monkeys were shot by hunters. This highlights the urgency for conservation action for *C. kaapori*.

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