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ORIGINAL ARTICLE

# Foraging strategies of black-fronted titi monkeys (*Callicebus nigrifrons*) in relation to food availability in a seasonal tropical forest

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**Abstract** Many primates have to cope with a temporal scarcity in food availability that shapes their foraging strategies. Here we investigated the changes in diet, activity, and ranging behavior of a group of black-fronted titi monkeys (*Callicebus nigrifrons*) according to the availability of the main high-nutritional-density item in their diet and the foraging strategy adopted when this food is scarce. We monitored one habituated group using instantaneous scan sampling over 1 year (533 h of observation, 61 days) in a seasonal tropical forest fragment (245 ha). We simultaneously collected data on food availability with fruit traps. The titi monkeys consumed fleshy fruits, the main high-nutritional-density item of their diet, in accordance with its availability, and the availability of this item modulated the ingestion of vegetative plant parts, a relatively low-nutritional-density food. During high fleshy fruit availability, the titi monkeys consumed more fleshy fruits, flowers, and invertebrates. They also traveled more, but concentrated their activity in a central area of their home range. Conversely, during fleshy fruit scarcity, they increased the breadth of their diet, switching to one richer in seeds and vegetative plant parts, and with greater plant diversity. At the same time, they reduced most energy-demanding activities, traveling less and over shorter distances, but using their home range more broadly. Corroborating the optimal foraging theory, titi monkeys altered foraging strategies according to temporal food fluctuations and responded to low fleshy fruit availability by changing their diet, activity, and ranging behavior. The adoption of a low-cost/low-yield strategy allowed us to classify them as energy minimizers.

**Keywords** Feeding ecology · Seasonality · Diet · Space use · Activity pattern · Optimal foraging theory

## Introduction

Optimal foraging theory suggests that animals optimize their energy yield while foraging (MacArthur and Pianka 1966; Pyke et al. 1977). The relationship between energy gained while feeding ("benefits") and energy expended to acquire and process the food ("costs") usually defines the foraging strategies of animals (Norberg 1977; Krebs and Davies 1993). Whether a food item should be consumed is independent of its abundance, and depends only on the abundance of the higher-rank food (Pyke et al. 1977; e.g. Harrison 1984). As the abundance of a preferred food type increases, the number of food types included in the optimal diet will shrink (Pyke et al. 1977). Therefore, because the availability of most resources varies in time, seasonality tends to influence the food choice of animals (Garber 1987; Hemingway and Bynum 2005).

Seasonality in resource production has lead to the evolution of morphological, behavioral, and physiological adaptations in consumers (van Schaik et al. 1993). Resource availability can affect diet, ranging, and behavior

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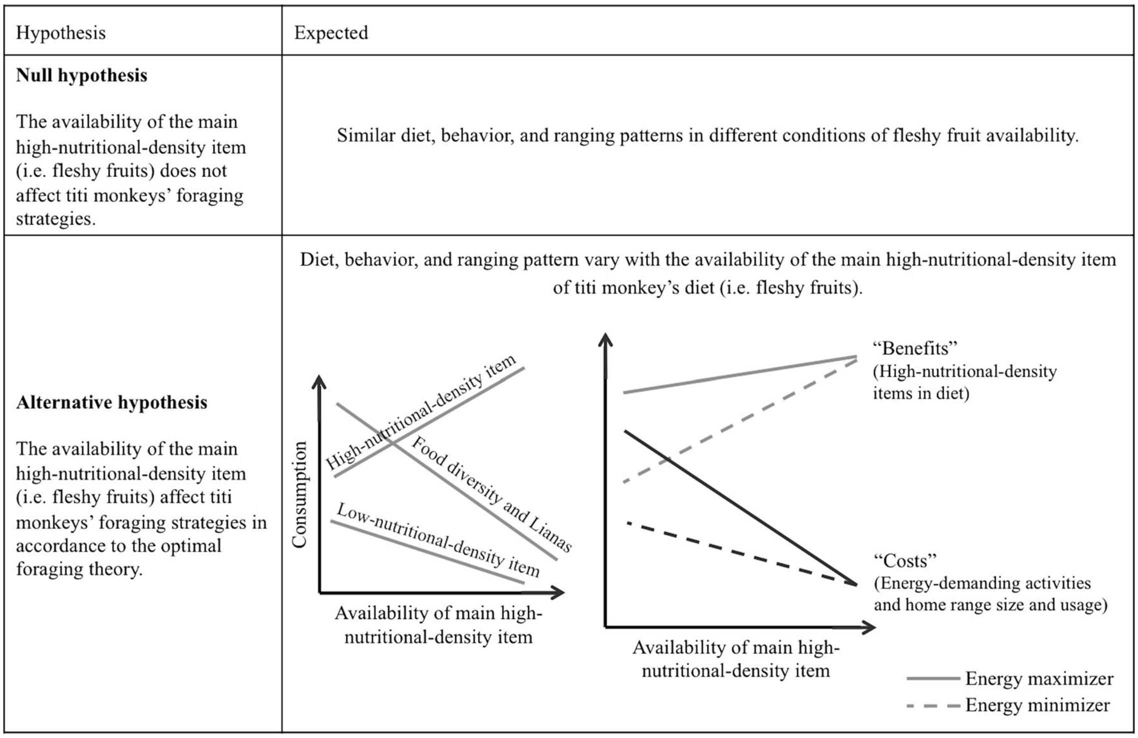
of primates (Hemingway and Bynum 2005). During low resource availability, for instance, primates can respond with dietary changes, increasing or decreasing their dietary breadth (e.g. *Pithecia chrysocephala*, Setz 1993; *Cercopithecus doggetti*, Kaplin et al. 1998; *Callicebus nigrifrons*, Caselli and Setz 2011; *Macaca silenus*, Santhosh et al. 2015) and/or switching food types or plant species ingested (e.g. *Alouatta seniculus*, *Lagothrix lagotricha cana*, *Pithecia albicans*, *Saguinus* sp., *Sapajus apella*, Peres 1994; *Callicebus melanochir*, Müller 1996). Some species rely on fallback foods, which are resources that become particularly important when preferred foods are scarce (Marshall et al. 2009; Lambert 2011). Fallback foods can be either resources of lower-nutritional-density (lower inherent energy yield) that are abundant in the habitat but require more processing time (e.g. vegetative plant parts), or resources of higher-nutritional-density (greater inherent energy yield) that are more difficult to find and are typically mechanically protected (longer handling time; e.g. seeds; Lambert 2011).

Primates can also respond to food availability with behavioral and ranging changes. The amount of time traveling and travel distances, two potential measures of energy expenditure (Krebs and Davies 1993), can vary according to the foraging strategy of the species. Energy minimizers (Schoener 1971) feed on alternative abundant items and reduce the energy expended foraging, conserving energy during lean seasons (low-cost/low-yield strategy; e.g. *Colobus polykomos*, Dasilva 1992; *Ateles chamek*, Wallace 2005; *Callicebus melanochir*, Heiduck 2013). Contrarily, energy maximizers (Schoener 1971) spend more time and energy searching for food, maintaining a similar energy intake across seasons (high-cost/high-yield strategy; e.g. *Gorilla beringei*, Vedder 1984; Rothman et al. 2008). Analogously, since home ranges can be a function of the availability and distribution of resources, limited by the costs of resource acquisition, home range usage can also be related to these two strategies regarding optimal use of energy (Mitchell and Powell 2004). Similar to energy maximizers, resource maximizers use the highest resource/area ratio possible, whereas area minimizers, similar to energy minimizers, use the minimum area needed to obtain the lowest resource value required for survival and reproduction (Mitchell and Powell 2004). Aside from altering home range size and usage (e.g. *Sapajus apella*, Zhang 1995), primates may also rely on a specific microhabitat within their home range (e.g. *Gorilla beringei*, Vedder 1984; *Ateles paniscus chamek*, *Cebus albifrons unicolor*, *Saimiri* sp., Peres 1994), or may even switch habitat types (e.g. *Lagothrix lagotricha*, Defler 1996; *Alouatta seniculus*, Palacios and Rodriguez 2001; *Ateles chamek*, Wallace 2006).

Small-bodied frugivores (<1.5 kg) are more likely to be susceptible to environmental variations such as food fluctuations, since small-bodied animals are highly vulnerable to seasonality (Lindstedt and Boyce 1985), and in addition, frugivores depend on a seasonally fluctuating resource (van Schaik et al. 1993). Titi monkeys (33 species recently divided into three genera: *Callicebus*, *Cheracebus*, and *Plecturocebus*; Byrne et al. 2016) are highly frugivorous small-bodied primates (Easley 1982; Müller 1996; Caselli and Setz 2011; Souza-Alves et al. 2011; Kulp and Heymann 2015) from a poorly studied but diverse and widespread New World clade, many of which live in seasonal environments (especially members of the genus *Callicebus*). Therefore, they represent a good model to study the relationship between food availability and the foraging and behavioral strategies of frugivorous primates. To investigate these relationships, we studied a group of black-fronted titi monkeys (*Callicebus nigrifrons*) in a seasonal environment.

It is already known that *Callicebus nigrifrons* is behaviorally flexible and can alter its diet and activity pattern between seasons (Caselli and Setz 2011), but the effects of food availability on other aspects of the species' foraging behavior is still unknown. Here, we investigate how temporal variations in food may affect the diet and activity patterns of black-fronted titi monkeys (*Callicebus nigrifrons*). We also evaluate for the first time the ranging behavior of a group and assess their foraging strategies under differing availability of fleshy fruits (the main high-nutritional-density item of their diet). First, we tested how monthly availability of different foods influenced the consumption of each food item. Based on a previous study (Caselli and Setz 2011), and on the provisions of optimal foraging theory (Pyke et al. 1977; Harrison 1984), we predicted that only the consumption of the main high-nutritional-density item of their diet (i.e. fleshy fruits) would be positively linked to availability, and its availability would negatively affect the consumption of a relatively lower-nutritional-density food item (i.e. vegetative plant parts). In addition, we expected that in periods when fleshy fruits were in short supply, the titi monkeys would use a broader set of foods, increasing food diversity (Pyke et al. 1977) and diet niche width. We also predicted that during these periods, growth forms displaying alternative periodicity in their phenology (i.e. that produce fruits when most plants do not; e.g. lianas at our study site; Garcia et al. 2014) would be of high importance in their diet. Second, we investigated which type of foraging strategy (high-cost/high-yield or low-cost/low-yield) titi monkeys adopt when fleshy fruits (their preferred high-nutritional-density item) is scarce. We predicted that if titi monkeys were energy maximizers and adopted a high-cost/high-yield strategy, they would increase energy-consuming activities and possibly increase home range size and usage (resource



| Hypothesis | Expected |
|---|---|
| **Null hypothesis**<br>The availability of the main high-nutritional-density item (i.e. fleshy fruits) does not affect titi monkeys' foraging strategies. | Similar diet, behavior, and ranging patterns in different conditions of fleshy fruit availability. |
| **Alternative hypothesis**<br>The availability of the main high-nutritional-density item (i.e. fleshy fruits) affect titi monkeys' foraging strategies in accordance to the optimal foraging theory. | Diet, behavior, and ranging pattern vary with the availability of the main high-nutritional-density item of titi monkey's diet (i.e. fleshy fruits). |

**Fig. 1** Study hypotheses for the influence of fleshy fruit availability on the foraging strategies of a group of frugivorous primates (titi monkeys, *Callicebus nigrifrons*)

maximization) in order to maintain a high consumption of fleshy fruit. In contrast, we expected that if they were energy minimizers and adopted a low-cost/low-yield strategy, the titis would consume fewer fleshy fruits but more alternative items, and would reduce energy-consuming activities and home range size and usage (area-minimization; see Fig. 1 for hypotheses schema).

## Methods

### Study site

The study was carried out at Ribeirão Cachoeira, a 245 ha Atlantic Forest remnant (22°50′S, 46°55′W) located in an environmental protection area in Campinas, State of São Paulo, southeastern Brazil. The forest vegetation is classified as seasonal semi-deciduous (Santos 1998), and is characterized by seasonal variations in fruit availability (Garcia et al. 2014). The climate is mild rainy, with a wet and warm season from October through March and a dry and colder season from April through September (Santos 1998; Fig. 2). The mean temperature is around 22 °C, and annual precipitation about 1424 mm, including the year during which we conducted the study (Cepagri 2012; Ciiagro 2016).

### Study group and monitoring

We habituated (from March through May 2010) and monitored (from June 2010 through May 2011) one group of free-ranging black-fronted titi monkeys (*Callicebus nigrifrons*). During the study, the composition of the group varied from three to five individuals. We collected data from dawn to dusk ("complete days") or from the time the group was found until it was lost. Since there are differences in day length between months, we standardized the sampling effort to 45 observation hours per month (±SD 5 h). We sampled a mean of five observation days per month (±SD 1.08 day), in which approximately three observation days (±SD 0.74 day) were "complete days".

We considered only "complete days" ($N = 36$) and days with observation hours ≥90 % of the mean observation hours in "complete days" of the same month ($N = 4$) to estimate daily path length and traveling speed ($N = 40$ days in total). For all other analyses, we used data from "complete days" ($N = 36$) and days with observation hours ≥50 % of the mean observation hours in "complete days" of the same month ($N = 25$), totaling 533 observation hours and 61 observation days. The sampling effort, observation period, and the distribution of scan samples throughout the day were similar between resource-lean months ($N = 2683$ behavior records; $N = 550$ diet records; approx. 144 obs. hours;

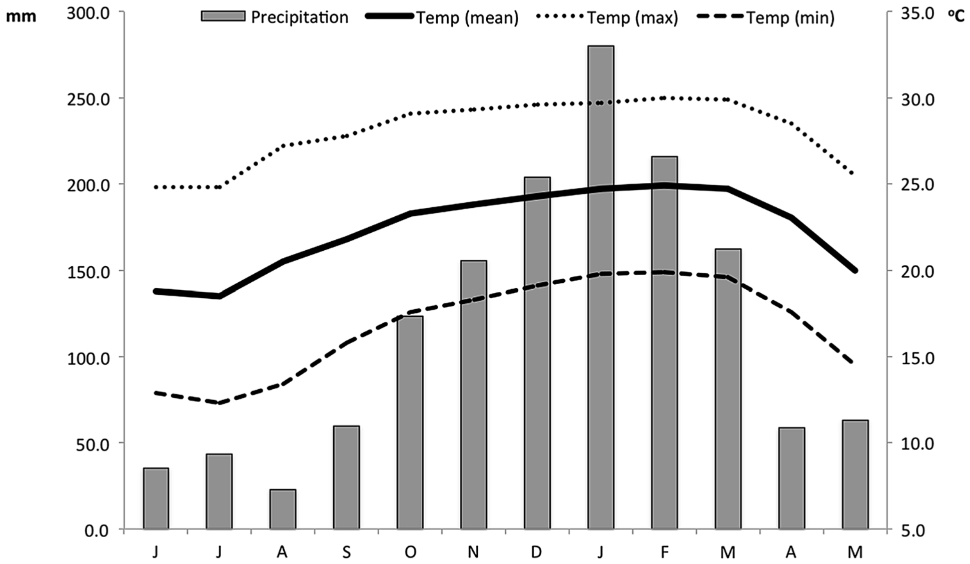


**Fig. 2** Mean monthly temperature and precipitation at Campinas (source: Cepagri Unicamp, based on meteorological data collected between 1988 and 2008)

18 days) and resource-rich months ($N = 2556$ behavior records; $N = 563$ diet records; approx. 125 obs. hours; 14 days), enabling comparisons between them.

### Food resource availability

Temporal variation in fleshy fruit, dry fruit/seed, and flower availability was obtained from 100 rectangular fruit traps (Smythe 1970; each with dimensions of 18.4 × 27.8 cm) distributed along five line transects evenly spaced within the study group's home range. The fruit traps were positioned 20 m apart and 1 m perpendicular to each transect (Terborgh 1983). The total area sampled by the traps (5.12 $m^2$) is equivalent to 0.003 % of the group's home range area, which is in agreement with other studies, which typically use 0.00003–0.017 % (Chapman et al. 1994). We chose to use fruit traps because they allowed us to easily estimate monthly food availability from several growth forms (trees, shrubs, and lianas) simultaneously with the behavioral and diet data collection. This was important, because lianas, for instance, supply a considerable amount of food for titi monkeys (Caselli and Setz 2011; Souza-Alves et al. 2011), and at our study site, can display different periodicity in their phenology compared to other growth forms (Garcia et al. 2014).

Every 15 days we collected all fleshy fruits (fruits with pulp or aril), dry fruits or seeds (fruits without pulp or aril, winged seeds, and capsules), and flowers from the fruit traps and weighed them separately. We did not include seeds from fleshy fruits in our estimate of seed availability because we had evidence of a lack of effective predation of these in titis (1154 of 1195 ingested fleshy fruit seeds were intact in their feces; $N = 51$ fecal samples collected simultaneously with our data).

Fleshy fruits are the main item in the diet of titi monkeys (Easley 1982; Müller 1996; Caselli and Setz 2011; Souza-Alves et al. 2011). These fruits typically have a high amount of soluble carbohydrates, and so have high-nutritional-density (Garber 1987; Strier 2007; Lambert 2011). Consequently, we used the monthly biomass of fleshy fruits collected in the fruit traps to measure the availability of the main high-nutritional-density item of their diet. In order to investigate titi monkeys' response during lean periods, we determined two periods of contrasting fleshy fruit availability based on the amount of fleshy fruits collected by the traps (Fig. 3). We considered the leanest months to be those in which we collected a biomass of fleshy fruit lower than the lower limit of the 95 % confidence interval (CI), and the richest months as those with a biomass higher than

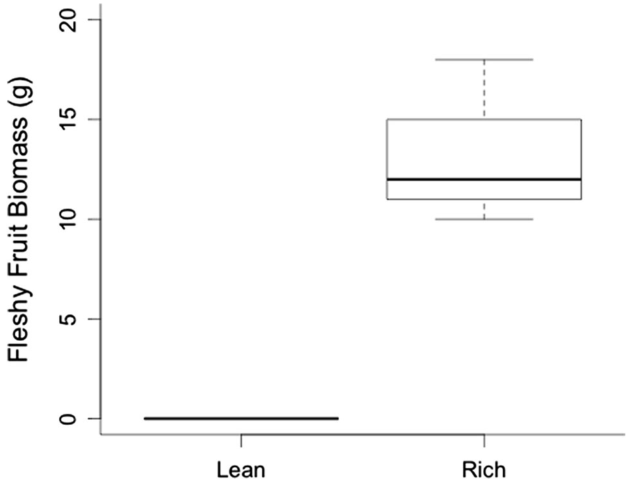


**Fig. 3** Fleshy fruit biomass collected by the fruit traps during the lean and rich months at the study group's home range (located in Ribeirão Cachoeira remnant, southeastern Brazil)

its upper limit. The lean period coincided with the driest months in our study area (mid-dry season: June, July, and August). The richest months were October, December, and April.

### Diet and activity pattern

We recorded the behavior and diet of each visible member of the group with instantaneous scan sampling every 5 min (Altmann 1974). Behaviors were divided into the following: feeding (manipulating, processing, chewing, and swallowing food), resting (standing, sitting, or laying, not performing any activity), traveling/moving, and other activities (vocalizing, playing, and grooming). To determine the diet of the group, we divided the items consumed into fleshy fruits, dry fruits/seeds, vegetative plant parts (leaves and buds/shoots), flowers, and invertebrates. Whenever possible, we also recorded whether the item ingested was from lianas or trees/shrubs. The activity pattern and the composition of the group's diet were estimated by producing estimates per day of the amount of time spent eating each food item or performing each activity, and then calculating the relative frequency of each behavior in the total budget and each item in the total diet. The plants were identified in the field by botanists (see acknowledgments), with the help of a field guide (Ramos 2007), and data from an extensive botanical survey conducted at our study site (Santos 1998). The list of plant species used as food sources by the titi monkeys (Online Resource 1) was obtained using the all-occurrence method (Altmann 1974).

### Space use

We recorded the geographical position of the study group every 10 min with a GPS unit. We also recorded the location of all important feeding sites (those trees/shrubs or lianas/vines in which at least half of the group foraged together during at least 20 min). We calculated the daily path length by adding the distances between consecutive geographical position points using GPS TrackMaker 13.7 software (Ferreira 2010). Traveling speed was obtained by dividing each daily path length by total travel time on that same day.

We calculated the group's home range area with the minimum convex polygon (MCP; Hayne 1949) and adaptive kernel (Worton 1989) methods, using 95 % of the geographical position points. To estimate the utilization distributions (UDs), we used kernelUD with the default method for the estimation of the smoothing parameter (the ad hoc method). A UD describes the collective intensity of use of different areas by group members, giving the probability of relocating the group at any place within its range during a specified time period (Powell 2000; Calenge 2006). We ran these analyses in R software version 3.1.1 (R Development Core Team 2014) using the "adehabitatHR" package (Calenge 2011). To estimate the percentage of monthly home range overlap (from MCP estimates) within each productivity period, we used the package "rgeos" (Bivand et al. 2015).

### Data analysis

We tested the strength of the relationship between monthly food availability (monthly biomass of each item collected; independent variable) and monthly consumption of each food item (dependent variable) using linear regressions for fleshy fruits and dry fruits/seeds, and Spearman rank correlation tests for flowers (since this data did not follow the assumptions of parametric tests). We also investigated the relation between the consumption of a generally lower-nutritional-density food (i.e. vegetative plant parts) and the availability of the main high-nutritional-density item of their diet (i.e. fleshy fruit) using a linear regression. Whenever necessary, we used log or arcsin (for proportions) transformations.

To investigate the foraging strategy of titi monkeys when the main high-nutritional-density item of their diet (i.e. fleshy fruits) was scarce, we compared the potential "costs" and "benefits" between lean and rich periods. We used energy-demanding activities (i.e. travel time, travel speed, and travel distance; Krebs and Davies 1993) as measures of the energetic cost of foraging, and the amount of time feeding on overall high-nutritional-density items (i.e. fleshy fruits, flowers, and seeds; Garber 1987; Strier 2007; Lambert 2011) as a measure of energy gained while feeding ("benefits"; similar to Harrison 1985; Agetsuma 1995; Agetsuma and Noma 1995; Heiduck 2013). We considered fleshy fruits as the main high-nutritional-density item in the titi monkey diet, since these fruits are the major component of their diet with readily available energy (Caselli and Setz 2011), and they also may need less manipulation and processing time than other high-nutritional-density food item, such as seeds (Lambert 2011).

First, we produced estimates per day of diet, activity budget, distances traveled, and traveling speed, and monthly estimates of home range size. We then calculated the absolute difference between the mean of each variable (food item, activity category, daily path length, traveling speed, and home range size) in lean and rich periods, and compared this difference to the distribution of differences expected under the null hypothesis (variables are similar between the two periods) to calculate the associated two-tailed $P$ value. The distribution of the differences expected under the null hypothesis was generated by 1000 randomizations of the values between lean and rich periods

**Table 1** Percentage of feeding samples (±SD) in which each food item was consumed by *Callicebus nigrifrons* during an annual cycle ($N = 61$ obs. days), lean months ($N = 19$ obs. days), and rich months ($N = 14$ obs. days), and observed differences between the two productivity periods, the simulated differences expected under the null hypothesis, and associated $P$ values

| | Item consumption (%) | | | Obs. diff. | Sim. diff. | $P$ |
|---|---|---|---|---|---|---|
| | Annual | Lean | Rich | | | |
| Fleshy fruits | 47 ± 30 | 27 ± 21 | 55 ± 27 | 28 | 8 | <0.01* |
| Seeds and dry fruits | 22 ± 22 | 35 ± 23 | 6 ± 8 | 29 | 7 | <0.01* |
| Vegetative plant parts | 19 ± 16 | 30 ± 20 | 14 ± 10 | 16 | 5 | 0.02* |
| Flowers | 2 ± 6 | <1 ± 2 | 5 ± 12 | 5 | 2 | 0.05* |
| Invertebrates | 10 ± 12 | 7 ± 12 | 19 ± 15 | 12 | 4 | 0.01* |
| Liana items | 51 ± 32 | 72 ± 27 | 54 ± 30 | 18 | 8 | 0.09 |

* $P \leq 0.05$

followed by their comparison (Monte Carlo simulation; Manly 1997). We performed the analysis of each variable separately with R 3.1.1 software (R Development Core Team 2014). We also tested whether dietary plant species diversity, which was calculated with the Shannon diversity index ($H_e'$, based on the number of feeding records for each plant species), was different between the two productivity periods, using a diversity $t$ test in PAST 8.9 software (Hammer et al. 2001).

## Results

### Relation between diet and food availability

Titi monkeys consumed fleshy fruits in proportion to their availability (linear regression: $F = 5.32$, $df = 1$, $R^2 = 0.35$, $P = 0.04$). By contrast, the ingestion of vegetative plant parts, a lower-nutritional-density item, was negatively related to the availability of fleshy fruits (linear regression: $F = 7.37$, $df = 1$, $R^2 = -0.42$, $P = 0.02$). Seeds/dry fruits and flowers were eaten regardless of their availability (linear regression: $F = 0.58$, $df = 1$, $R^2 = 0.06$, $P = 0.46$; and Spearman correlation: $r_s = -0.42$, $N = 12$, $P = 0.18$, respectively).

### Variation in diet, activity pattern, and ranging behavior between months of contrasting fleshy fruit availability

During the months with the lowest fleshy fruit availability (lean months), the titi monkeys consumed more seeds and vegetative plant parts, and a greater diversity of plant species (plant diversity in lean season: $H_e' = 2.6$; plant diversity in rich season: $H_e' = 2.3$; diversity $t$ test: $t = 3.06$, $df = 1019$, $P < 0.01$), while they ingested lower percentages of fleshy fruits, insects, and flowers (Table 1). Liana consumption was similarly high between lean and rich months (accounting for more than 50 % of feeding records; Table 1), and supplied all types of food items (Online Resource 1).

During fleshy fruit scarcity, the group spent less time traveling/moving and distances traveled were shorter, but other activities, traveling speed, and monthly home range size were similar between the two productivity periods (Tables 2, 3). Home range exploitation, however, was more diffuse during the lean months, when the feeding resources (of which 90 % were lianas) were more diffusely spaced throughout the habitat. During this period, there was no overlap between the three monthly home ranges, and titis shifted their core area (i.e. areas more frequently used; Fig. 4). In contrast, during the three rich months, the titi monkeys concentrated their activities near the center of their home range, where one-third of the resources were located, with a monthly overlap of 30 % (Fig. 4).

## Discussion

We have demonstrated the relation between temporal food fluctuations and food consumption by a group of titi monkeys (*Callicebus nigrifrons*), and how they alter their foraging behavior according to the availability of the main high-nutritional-density items of their diet. Corroborating both our first prediction and optimal foraging theory (Pyke et al. 1977; Harrison 1984), the group of titi monkeys consumed only the main high-nutritional-density items of their diet (i.e. fleshy fruits) in accordance with their availability over the course of 1 year, and the availability of this item modulated the consumption of a relatively lower-nutritional-density item, the vegetative plant parts.

The results did not support our prediction that the titi monkeys would rely more on lianas during lean periods. Despite the large number of feeding sites comprising lianas in the lean months, the titi monkeys fed on lianas in high proportions throughout the year. In contrast, the data corroborated the prediction that, in an optimal diet, the inclusion of food types would increase as the abundance of

**Table 2** Percentage of total behavior records spent in each activity (±SD) by *Callicebus nigrifrons* during an annual cycle ($N = 61$ obs. days), lean months ($N = 19$ obs. days), and rich months ($N = 14$ obs. days), and observed differences between the two productivity periods, the simulated differences expected under the null hypothesis, and associated *P* values

| | Activity budget (%) | | | Obs. diff. | Sim. diff. | *P* |
|---|---|---|---|---|---|---|
| | Annual | Lean | Rich | | | |
| Traveling | 21 ± 6 | 19 ± 5 | 24 ± 7 | 5 | 2 | 0.05* |
| Feeding | 31 ± 9 | 28 ± 10 | 29 ± 8 | 1 | 2 | 0.81 |
| Resting | 45 ± 9 | 49 ± 11 | 43 ± 9 | 6 | 3 | 0.08 |
| Other activities | 3 ± 3 | 3 ± 2 | 4 ± 3 | 1 | 1 | 0.34 |

* $P \leq 0.05$

**Table 3** Travel distances (daily path length), traveling speed, and home range size (±SD) of *Callicebus nigrifrons* during an annual cycle ($N = 40$ obs. days), lean months ($N = 11$ obs. days), and rich months ($N = 10$ obs. days), and observed differences between the two productivity periods, the simulated differences expected under the null hypothesis, and associated *P* values

| | Space use | | | Obs. diff. | Sim. diff. | *P* |
|---|---|---|---|---|---|---|
| | Annual | Lean | Rich | | | |
| Travel distances (m) | 1222 ± 530 | 631 ± 376 | 1412 ± 495 | 781 | 218 | <0.01* |
| Travel speed (m/min) | 7 ± 3 | 5 ± 4 | 7 ± 2 | 2 | 1 | 0.09 |
| Home range size (ha; MCP) | 17 | 7 ± 4 | 8 ± 3 | 1 | 3 | 0.89 |

Home range size for the annual cycle was calculated as the total area used during the entire study period, while home range size presented for lean and rich periods are monthly estimates

* $P \leq 0.05$

preferred food types decreased (Pyke et al. 1977). When the availability of fleshy fruits was lowest, the titi monkeys consumed a greater diversity of plant species and increased the ingestion of dry fruits/seeds and vegetative plant parts.

The ability of the group of titi monkeys to increase dietary breadth and switch food items at times of fleshy fruit shortage suggests that they have diet flexibility, which is the most common response to food scarcity in primates (Hemingway and Bynum 2005). Other species of titi monkeys also switch food items, with the exception of *Cheracebus torquatus*, which lives near the equator and exhibits less seasonal variation in food choice (Easley 1982). During fruit availability bottlenecks, *Callicebus melanochir* will feed more on seeds (Heiduck 1997), *C. coimbrai* (Souza-Alves et al. 2011) and *Plecturocebus brunneus* (Wright 1985) on leaves, and *Cheracebus lugens* on seeds and flowers (Palacios et al. 1997). Here, seeds were a prominent fallback food, supporting other findings that titi monkeys may play an important role as seed predators during food scarcity, despite lacking the full range of dental adaptations to seed-eating present in other pitheciines (Heiduck 1997; Palacios et al. 1997; dos Santos et al. 2012; Palacios and Rodriguez 2013). It is important to note, however, that these were generally unripe seeds in hard-husked fruits or ripe seeds from softer fruits (see Online Resource 1). The increased reliance upon seed predation characterizes the evolutionary history of pitheciids (Kay et al. 2013). Titi monkeys (a basal group in the phylogeny of the pitheciines), uakaris, and sakis represent a morphocline of increasingly specialized dental features for sclerocarpic foraging (Kay et al. 2013). In this sense, sclerocarpy may have begun by progressively pushing back the ripeness point at which seeds could be exploited, minimizing the impact of resource bottleneck.

Since unripe seeds usually have elevated concentrations of secondary compounds (Kinzey 1992), by increasing dietary breadth along with seed ingestion, our study group might have lowered the risk of over-ingestion of any given toxin through dietary diversification (Glander 1982; Palminteri et al. 2016). In a proximate scale (i.e. ecological), behavioral flexibility such as the capability to switch the diet and increase seed consumption may be an important adaptive response to seasonal environments, reducing the impact of seasonal fruit shortages (Norconk 2011), since the nutritional composition of seeds consumed by titi monkeys is similar to that of the fleshy fruit parts eaten (Heiduck 1997).

When testing which type of foraging strategy titi monkeys adopt when their main high-nutritional-density item is scarce, we found evidence that they are energy minimizers and adopt a low-cost/low-yield strategy. By switching from a diet of large amounts of fleshy fruits and a moderate amount of invertebrates, to a diet richer in seeds and leaves, the study group might have maintained similar gross

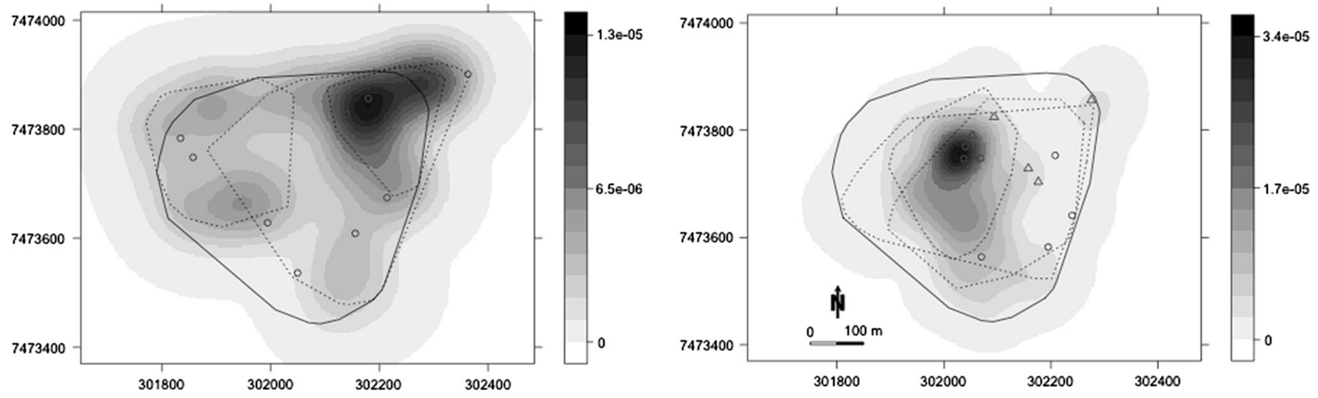


**Fig. 4** Home range of the *Callicebus nigrifrons* study group with monthly used home ranges (95 % MPCs), the utilization distribution (UD) estimates (using the adaptive kernel method), and the location of the most important feeding sources used during lean (*left*) and rich (*right*) months. The UD *grayscale* indicates the probability of finding the group in a particular location, with more frequently used areas in *darker colors*. *Polygon with thicker line* indicates total annual home range; *polygons with dotted lines* indicate monthly home ranges; *triangles* indicate trees, and *circles* indicate lianas

energy intake and nutritional balance between the two periods of contrasting productivity. This is because, in general, seeds are rich in lipids (Kinzey and Norconk 1993), and are therefore an alternative high-nutritional-density food (Lambert 2011), while leaves (especially young leaves) may have a high protein content, similar to invertebrates (Garber 1987; Lambert 2011). But because of the higher expenses associated with extended handling and processing time that results from hard pericarps and higher levels of secondary compounds in seeds and the higher fiber content in leaves (Kinzey and Norconk 1993; Lambert 2011), the energy yield during lean months may have been lower. As a result, the titi monkeys reduced some energy-demanding activities, such as traveling, which was also expected under the optimal foraging theory (MacArthur and Pianka 1966; Pyke et al. 1977).

Typically, when primates increase the consumption of items that require more processing time, they also travel less (e.g. *Sapajus apella*, Zhang 1995; *Pan troglodytes verus*, Doran 1997; *Propithecus verreauxi*, Norscia et al. 2006; *Ateles chamek*, Wallace 2006; *C. melanochir*, Heiduck 2013; *P. brunneus*, Wright 2013). Although in our study the traveling speed was similar between the two productivity periods, travel distances (daily path length) and travel time—two other potential measures of energy expenditure (Krebs and Davies 1993)—were reduced during the lean months. Moreover, despite keeping similar home range sizes, the low degree of monthly home range overlap and the broader utilization distribution during the lean months indicate that the study group used the home range area more diffusely as fleshy fruits became scarce, in addition to using the habitat more efficiently (considering that they were traveling shorter distances per day, and consequently expending less energy). This less concentrated use of their home range during lean months may be related to the distribution of feeding resources, which seems to be more widely spaced in the habitat, or to the increase in diet breadth, since finding a greater diversity of plants may require a more extensive use of the habitat (Palminteri et al. 2016). Although our results suggest a relationship between home range usage and resource distribution, further studies focusing on resource distribution are needed to confirm this spatial use pattern.

Lastly, it is important to note that fruit traps capture only food items fallen from the canopy; therefore, they measure a residual quantity of the available resources (total resource production minus the amount eaten by frugivores), which potentially underestimates resource production (Terborgh 1983). Although this method does not provide an estimate of overall resource abundance, it provides reliable data on seasonal fluctuations in resource availability (Terborgh 1983; Chapman et al. 1994), and so was appropriate for our study.

We conclude that the study group of titi monkeys responds to the availability of the main high-nutritional-density item of its diet (i.e. fleshy fruits) in a manner similar to that predicted by optimal foraging theory (MacArthur and Pianka 1966; Pyke et al. 1977). The titi monkeys displayed foraging behaviors similar to the low-cost/low-yield strategy in response to fleshy fruit scarcity, feeding on alternative items and reducing energy expenditure; this allows us to classify them as energy minimizers (Schoener 1971). Our study also highlights the importance of seeds as fallback foods for titi monkeys, and of lianas and plant species from the families Myrtaceae, Rubiaceae, and Moraceae as important feeding sources for primates in fragmented areas, which should therefore be considered in habitat restoration projects in this part of Brazil.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All research reported in this article was non-invasive, and no experiments were conducted on animals.

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