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Diet of the Caquetá Titi (*Plecturocebus caquetensis*) in a Disturbed Forest Fragment in Caquetá, Colombia

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Abstract: We report on a year-long study of the diet of a group of the Critically Endangered (CR) *Plecturocebus caquetensis* living in a 23-ha forest fragment, once part of an extensive, closed-canopy, lowland rainforest. We observed the group for 550 hours during the study. We recorded and identified all items eaten and the time invested in all behaviors by all individuals. The monkeys spent 37.7% of their time foraging and eating from a time budget of 41.5% resting, 16.7% locomotion, and 4.1% social behavior. Based on 12,443 minutes of feeding observations, we estimated a diet that consisted of 21% fruits, 21% seeds, 27% immature leaves, 15% arils, mesocarps and exocarps, 7% flowers, 4% mature leaves, 3% arthropods, and 2% stems and roots. The group ate food items of 159 species of plants from 41 families. The 15 most important plant food species were: *Pourouma bicolor* (Urticaceae) 8.3% of the diet; *Socratea exorrhiza* (Arecaceae) 6.7%; *Miconia dolichorrhyncha* (Melastomataceae) 4.4%; *Eschweilera punctata* (Lecythidaceae) 3.8%; *Cydista* sp. (Bignoniaceae) 3.3%; *Cecropia sciadophylla* (Urticaceae) 3%; *Bellucia pentamera* (Melastomaceae) 2.7%; *Helianthostylis sprucei* (Moraceae) 2.7%); *Iryanthera crassifolia* (Myristicaceae) 2.6%; *Virola sebifera* (Myristicaceae) 2.6%; *Siparuna* sp. (Monimiaceae) 2.3%; *Siparuna decipiens* (Monimiaceae) 2.2%; *Soracea muriculata* (Moraceae) 2.2%; *Heteropsis flexuosa* (Araceae) 2.2%; and *Inga leiocalycina* (Fabaceae) 2%. The ten predominant families were Fabaceae (17 spp.), Melastomataceae (11 spp.), Annonaceae (11 spp.), Moraceae (9 spp.), Araceae (9 spp.), Bignoniaceae (8 spp.), Myristicaceae (8 spp.), Lauraceae (7 spp.), Rubiaceae (6 spp.) and Euphorbiaceae (6 spp.). Arthropods eaten were mostly Arachnida and the species of the orders Hymenoptera (especially ants), Diptera, Orthoptera and Lepidoptera, 58.5% of the animal prey feeding records. This is the first detailed information on the ecology of this Critically Endangered titi. The diet is similar to those of other *Plecturocebus* species, especially the most closely related—*P. ornatus* and *P. discolor*.

Key words: Neotropical primate feeding, Pitheciidae, titi monkeys

Resumen: Se realizó un estudio de un año sobre la dieta de un grupo de la especie Críticamente Amenezada (CR) *Plecturocebus caquetensis* que vivía en un fragmento forestal de 23 ha que históricamente formaba parte de un bosque lluvioso de tierras bajas de dosel cerrado. Se realizaron barridos lentos de individuos de un grupo de esta especie, registrando e identificando todos los ítems consumidos (artrópodos identificados a Orden) y el tiempo invertido en todos los comportamientos. Los monos pasaron el 37,7% de su tiempo buscando alimento y comiendo de un presupuesto de tiempo que incluyó 41.5% de descanso, 16,7% de locomoción, 4,1% de comportamientos sociales. La dieta del grupo consistió en 21% de frutas, 21% de semillas, 27% de hojas inmaduras, 15% de arils, 7% de flores, 4% de hojas maduras, 3% de artrópodos y 2% de tallos y raíces, basado en el tiempo gastado comiendo cada artículo. Los primates escogieron 159 especies de plantas de 41 familias y los resultados de su uso se basan en 12,443 minutos de observación durante 550 horas de observación a lo largo del año. Las 15 especies de alimentos vegetales más importantes a partir de minutos de consumo son *Pourouma bicolor* (8,3% de la dieta) (Urticaceae), *Socratea exorrhiza* (6,7%) (Arecaceae), *Miconia dolichorrhyncha* (4,4%) (Melastomataceae), *Eschweilera punctata* (3.8%) (Lecythidaceae), *Cydista* sp. (3,3%) (Bignoniaceae), *Cecropia sciadophylla* (3%) (Urticaceae), *Bellucia pentamera* (2,7%) (Melastomaceae), *Helianthostylis sprucei* (2,7%) (Moraceae), *Iryanthera crassifolia* (2,6%) (Myristicaceae), *Virola sebifera* (2,6%) (Myristicaceae), *Siparuna* sp. (2,3%) (Monimiaceae), *Siparuna decipiens* (2,2%) (Monimiaceae), *Soracea muriculata* (2,2%) (Moraceae), *Heteropsis flexuosa*

(2,2%) (Araceae) e *Inga leiocalycina* (2%) (Fabaceae). Las diez familias más escogidas basadas en el número de especies comidas son Fabaceae (17 especies), Melastomataceae (11 especies), Annonaceae (11 especies), Moraceae (9 especies), Araceae (9 especies), Bignoniaceae), Myristicaceae (8 especies), Lauraceae (7 especies), Rubiaceae (6 especies) y Euphorbiaceae (6 especies). Los artrópodos consumidos fueron principalmente de los siguientes órdenes: Hymenoptera (especialmente hormigas), Araneae, Diptera, Orthoptera y Lepidoptera que reflejan 58.5% de los artrópodos disponibles monitoreados. Los datos representan la primera información detallada sobre la ecología de esta especie de primate en peligro de extinción. La especie es similar a otras especies de *Plecturocebus*, especialmente las especies más relacionadas, *P. ornatus* y *P. discolor*.

Palabras clave: alimentación de primates neotropicales, monos amenazados.

Introduction

Although the recently described *Plecturocebus caquetensis* (Defler, Bueno and García, 2010) is closely related to *P. ornatus* and *P. discolor*, its diet and ecology are as yet mostly undescribed (Hoyos *et al.* 2016). Because the species is Critically Endangered (CR), it is important to fill these gaps in its basic natural history and ecology (Defler and Garcia 2012). Only a few articles have been published on the species, mostly about its conservation and the reasons for its endangered status (Defler *et al.* 2010; Garcia and Defler 2011; García *et al.* 2012; Defler *et al.* 2015).

The reduction and loss of habitat in tropical forests is damaging to tropical ecosystems and primate communities since fragmented forests alter the population dynamics of the fauna and vegetation, and especially affect food sources (Marsh 2003; Marsh and Chapman 2013). The Colombian department of Caquetá is the Amazonian department with the most prevalent cattle-ranching and the most widespread deforestation. The area loses 2,500 ha of forest each year, with annual increases in this forest destruction (Peña-Vanegas *et al.* 2010). Recent research relating fragmentation to primate behavior has demonstrated that fragmentation has direct effects on ecological variables that affect primates—their home range, activity budgets, and diet (Marsh 2003; Arroyo 2007; Carretero-Pinzón 2008; Bouroncle 2009; Wagner *et al.* 2009; Gomez-Posada 2012; Marsh and Chapman 2013). In this way fragmentation is decisive in the decline of primate populations, and *P. caquetensis* is now verging on extinction.

In Colombia, there are three isolated populations of the *Plecturocebus cupreus* superspecies complex (see Mayr 1942, 1970, 1978, to review the concept): the northernmost, *P. ornatus*, is distributed north of the Río Guayabero to the Río Upía in Meta and probably no further east than the Río Meseta; *P. caquetensis* is known from the south of the department of Caquetá between the ríos Orteguaza and Caquetá; and *P. discolor* is found south of the Río Guamués in the department of Putumayo, extending into Ecuador and Peru (Defler 2010). This study provides the first description of the diet of the Critically Endangered (CR) Caquetá titi or macaco del Caquetá (*P. caquetensis*) in a rainforest fragment remaining from a previously widespread, closed-canopy, lowland rainforest.

Methods

Study site

During 2013, we studied the diet and feeding behavior of the Caquetá titi in the municipality of Valparaíso. The study site is a forest fragment of approximately 23 ha (01°04'21.7"N, 75°36'06.7"W, elevation 224 m), about 63 km southeast of Florencia, the capital of the department of Caquetá, and near the village of Playa Rica (Valparaíso), Colombia (Fig. 1). The region was previously covered by a dense, lowland tropical forest, which was colonized from about 50–60 years ago.

Mean precipitation registered in the nearby town of Valparaíso (18 km to the north) based on twenty years of data is 3215.1 mm (monthly max. 669.7 mm, monthly min. 14.7 mm) with an average temperature of 26.2°C (min. 23.8°C, max 28.5°C) (N = 20 years) (IDEAM 2014). For the year 2013, the total annual rainfall was 3535 mm, with May (593.9 mm) and July (518.9 mm) the wettest months. The driest months were January (69.2 mm), October (202.3 mm), November (160.3 mm), and December (88.4 mm) (Fig. 2).

Study group

We made observations on a habituated group composed of an adult male, an adult female, a subadult/young adult male, two juveniles (one male, one female), an infant-yearling, and a newborn, born in October 2013; 6–7 individuals in all during the year. The species usually produces a singleton every year. The newborn was carried constantly by the father. The infant-yearling was the next smallest but was independent. The two juveniles were half-grown (larger than the yearling) and looked to be same age (twins?), and the male "sub-adult" was a lone male that accompanied the group but was peripheral to the mated pair.

Because of the nature of the fragment, dispersion of the "subadult" might have been hampered, but other studies of *Plecturocebus* and *Cheracebus* report a supernumerary adult that is attached to but peripheral to the main group (Defler 2010). Home range was estimated using a system of trails forming 25-m^2 quadrates and cut throughout the area used by the monkeys. The group was observed for 550 hours from January to December 2013. The group lived in the 23-ha forest fragment with two other groups of *Plecturocebus*.

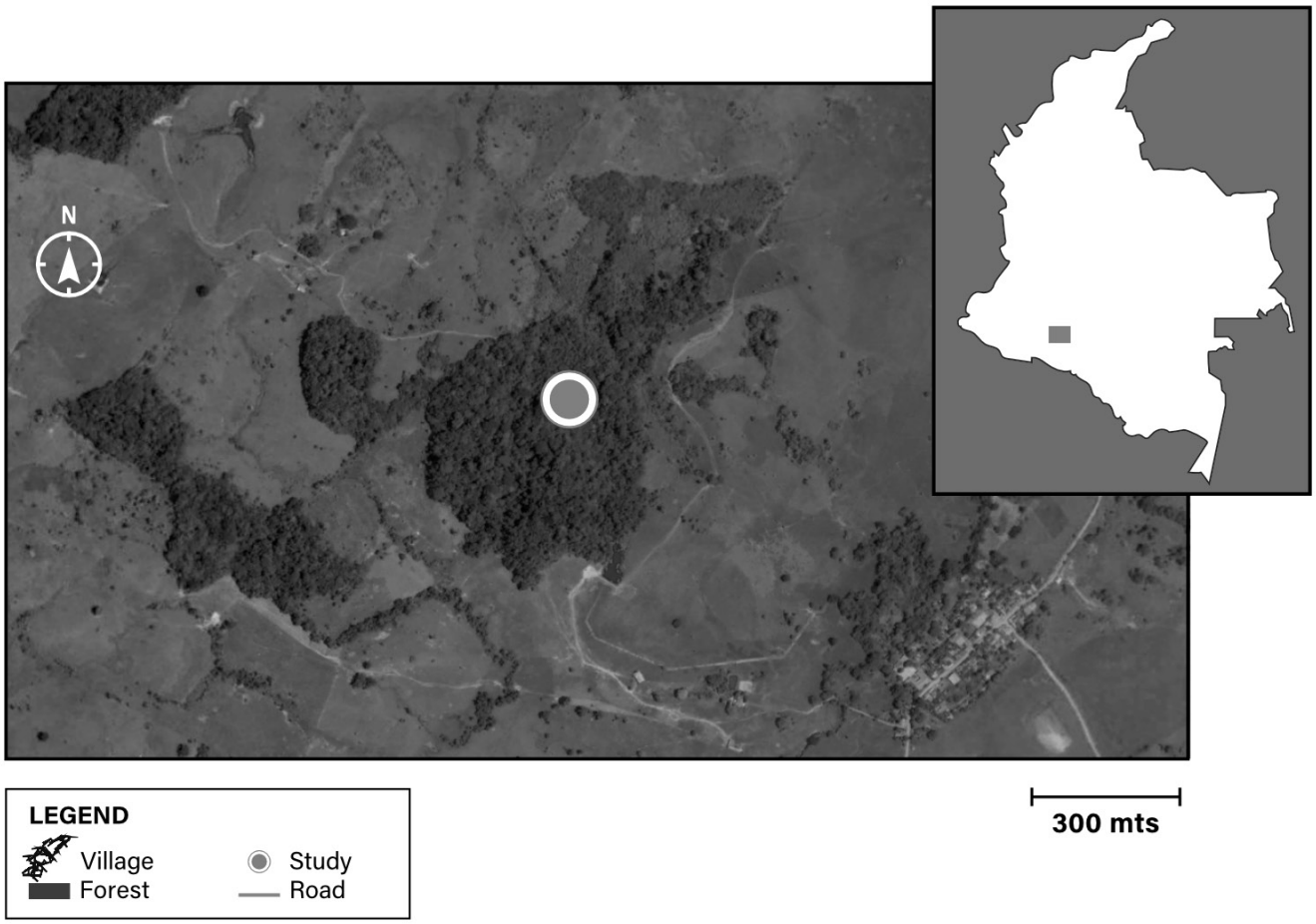

Figure 1. Location of the study area. The village of Playa Rica can be seen in the south-east corner of this image.

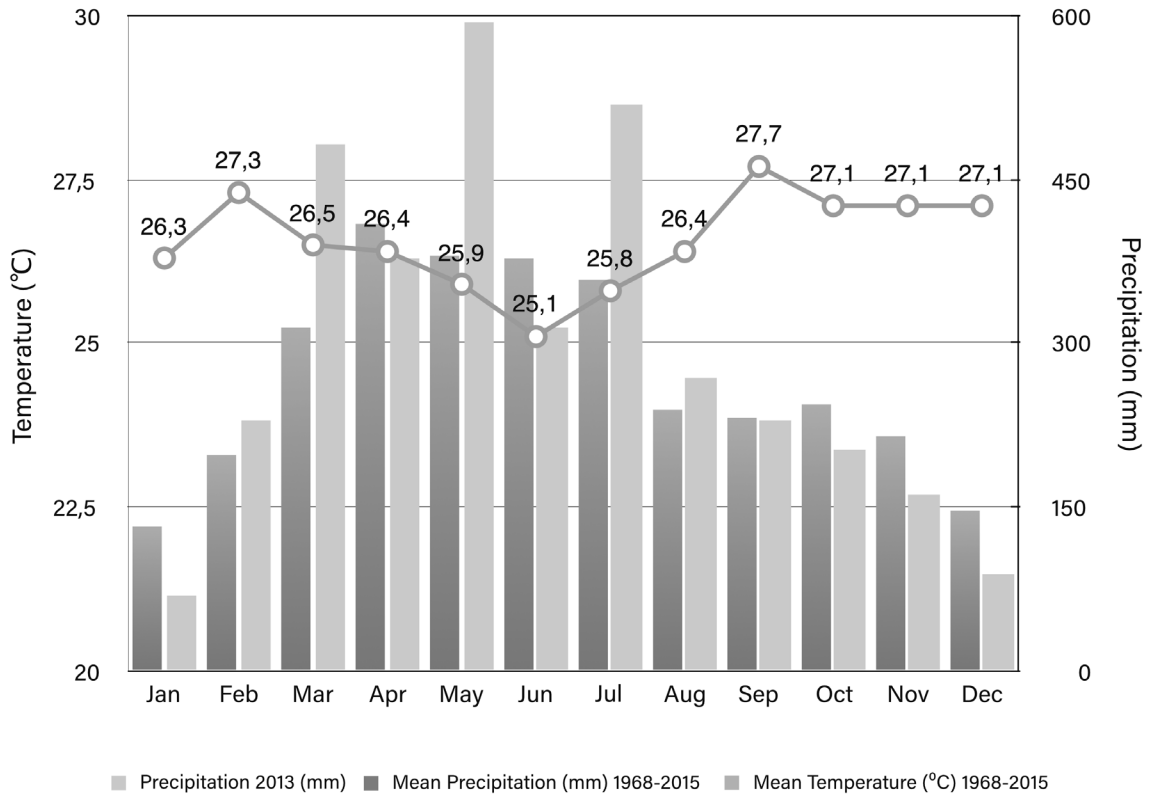

Figure 2. Means for monthly temperature and precipitation from 1994 to 2013. Data from the IDEAM Weather Station at Valparaíso, Caquetá. The dotted line represents the temperature, the bars precipitation.

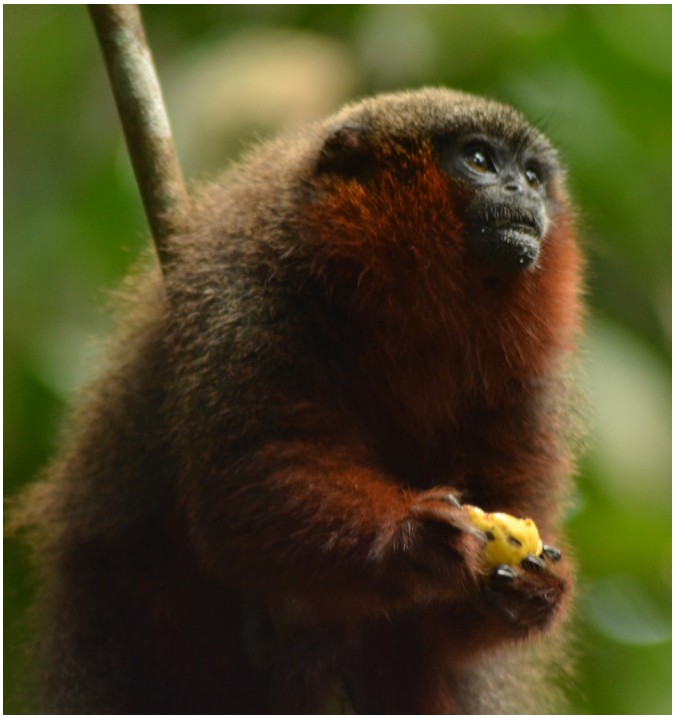

Figure 3. The Caquetá titi, *Plecturocebus caquetensis*. Photo by Adriana Acero-Murcia.

Data collection

Data on the monkeys were collected during the first ten days of each month, from January–December 2013. Much of January–March was dedicated to habituating the group, so the best data were those from April–December. The group was followed from 6 am to 6 pm. Two weeks each month were dedicated to the collection of phenological data and of voucher specimens of plants and arthropods included in their diet.

Data collection – behavior

Data collected during a 10-minute focal period of each animal included the length of time for each behavior of the following categories: resting, locomotion, feeding, sexual behavior, other social behaviors, vocalization and elimination. The time spent in each behavior was summed for each day, then combined by month, and further combined into a total score for each behavior and converted into percentages of the 550 hours of observation. The definitions of each behavior are as follows. Rest – any immobile position, whether standing, sitting, reclining, or suspensory, that did not include obvious interactions with another individual or with an object. Locomotion – any mobile activity, whether walking, running, climbing, jumping, swinging, or brachiating in the same tree or between different trees. Feeding – any handling, ingestion, chewing, or obvious search for foods. Sexual Behaviors – any obvious sexual interest, including nuzzling genitalia and mounting. Other Social Behaviors – any direct interaction between two or more individuals, including playing, grooming, contact, or agonistic (fighting or displacement). Vocalization – any vocalization of the animal. Elimination – urinating and defecating. We scored only the mother´s behaviors, without considering the infant. We did not carry out focal sampling on the dependent infant or first-year infants. We estimated the heights in the trees where all activities occurred, using four height categories: class 1 = 0.5–5 m, class 2 = 6–10 m; class 3 = 11–15 m; class 4 = 16 m and higher.

Data collection – diet

During each 10-minute focal sample, we also recorded the time spent eating each item, the height above ground where the activity occurred, and the DBH of each tree where the activity occurred. Data collection was facilitated by more than one observer (usually two). A feeding bout began at the time the new item was taken up by the monkey until leaving the tree or an interruption of feeding for more than one minute. We counted the number of items eaten by an individual when there was optimal visibility during the 10-minute session in order to calculate food processing times.

We marked all trees in which the monkeys were observed feeding and collected a voucher specimen for identification to genus or species. Plant parts identified were fruits (F), mature leaves (ML), young leaves (YL), seeds (S), mesocarps, arils, exocarps (MAE), flowers (FL), and stems and roots (SR).

Plant phenology

We studied the general phenology of the vegetation by establishing four plots of 25 m^2 and marking (with aluminum tags) and identifying all trees with 5-cm DBH or more and estimating their height. These marked trees were then monitored for phenophases every 15 days. A Shannon index (H) for diversity was calculated for each of the four plots, based on the marked and identified trees, and a mean was calculated for the four plots.

Fruits and flowers were monitored by estimating the number of mature, immature fruits or flowers on a branch and then multiplying the number according to branches bearing fruit. The percentages of immature and mature leaves were estimated comparing them to the entire tree canopy.

Collection of arthropods

To quantify the availability of arthropods in the diet, we set up four quadrates of 5 m^2 to a height of 1.7 m that we examined each month for the presence of arthropods. Arthropods were captured by hand and saved in 70% alcohol for identification to order. The quadrates included four different substrates: lianas, sleeping trees, foraging trees and other areas of activity (including the ground). The capture time in each quadrate was limited to 40 minutes, always between 6 am and 12 noon. All captured arthropods were counted (see Carretero-Pinzón 2008, based on Boinski and Fowler 1989).

We quantified the levels of animal prey foraging that were observed, dividing height above ground into four levels: level 1: 0–5 m; level 2: 6–10 m: level 3: 11–15 m: level 4: above 15 m. The choice of the collection quadrates was based on the fact that the titis spent a great deal of time foraging low in the forest and were frequently even seen on the ground.

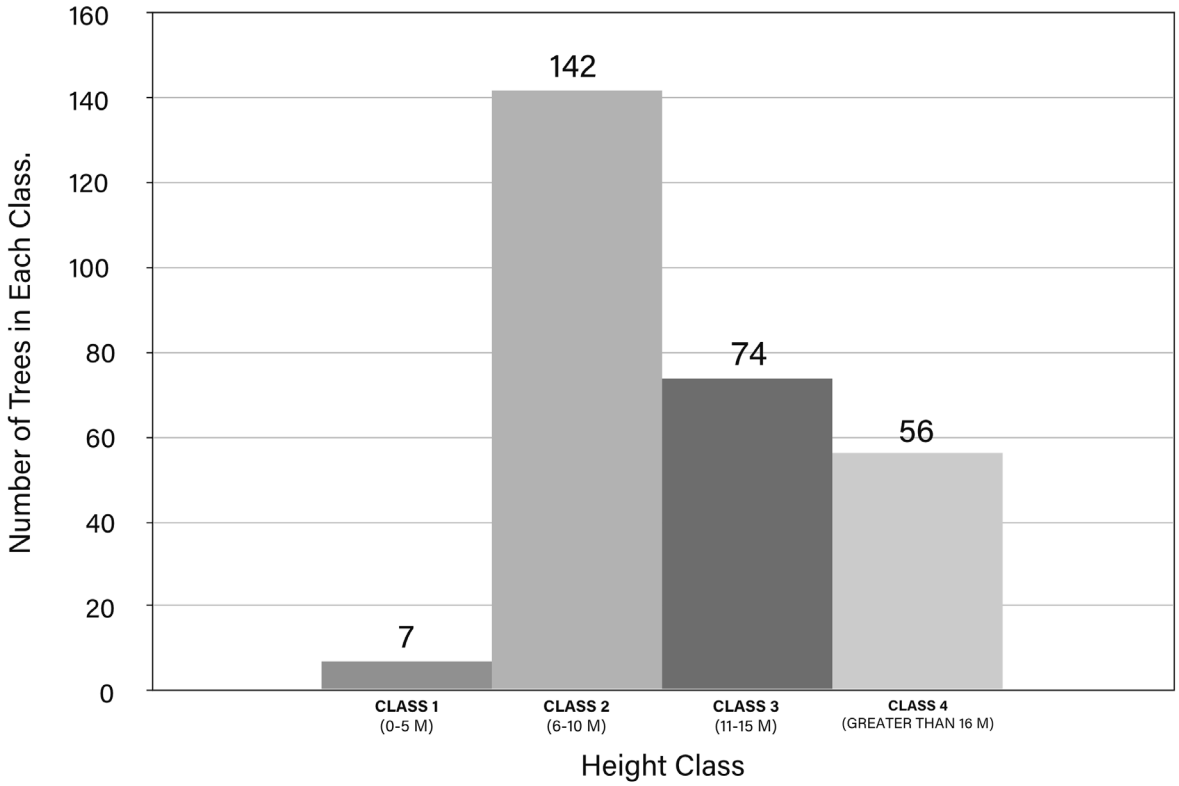

Figure 4. Tree heights in the four plots: height classes are class 1 (0–5 m), class 2 (6–10 m), class 3 (11–15 m), class 4 (greater than 16 m).

Figure 5. Male and infant *Plecturocebus caquetensis* foraging for insects near the ground. Photo by Adriana Acero-Murcia.

Although we attempted to identify the arthropods that the monkeys ate, it was generally impossible; only when parts fell to the ground could we identify the order. It was, however, often possible to score the time dedicated to eating arthropods during each 10-minute focal observation.

Results

Tree heights and diversity

Some trees in the sample reached 35 m, but 51% were between 6 m and 10 m tall, and only 20% of the trees were taller than 16 m (Fig. 4). The Shannon indices for species diversity varied in each plot: 3.57, 3.103, 3.329 and 3.111 for a mean of 3.278 for the four plots. This can be considered a moderate diversity, not particularly high. Diversity in this forest fragment is probably affected by nearby colonists cutting down some of the trees.

Time budget and use of forest strata

Based on 33,000 minutes (550 hours) of observations, the monkeys spent 37.7% of their time foraging for food and eating, 41.5% resting, 16.7% in locomotion, and 4.1% engaged in social behaviors. The majority of their daytime activities were in the sub-canopy and understory, below 15 m (87%). They slept higher up, however, above 16 m from the ground. Twenty-eight percent of their time they were at or below 5 m from the forest floor, and quite often descended to the ground to search for arthropods or to retrieve a fruit (Table 1; Fig. 5).

Plant part of the diet

The appendix lists the 159 species of the 41 families in the diet of the study group, along with the plant part eaten (e.g., fruit, flower, or seed), the number of repeat visits to the species, the number of minutes eating the plant part, and the percentage of total feeding time. The plant parts eaten were from 285 trees, 12 shrubs, 67 vines and lianas, 13 palms, 30 epiphytes, and 12 herbs.

The diet of the study group comprised 21% fruits (mesocarps, exocarps), 21% seeds, 27% immature leaves, 15% arils, 7% flowers, 4% mature leaves, 3% arthropods, and 2% stems and roots (12,443 minutes of observations when the titis were feeding). The 14 most important species in the diet (≥2% of diet) are based on the time that the animals spent eating items from each (Table 2). These fourteen species were also the trees most often visited. The ten plant families most represented in the diet were Leguminosae (16 species), Melastomataceae (11), Annonaceae (11), Moraceae (9), Araceae (9), Bignoniaceae (8), Myristicaceae (8), Lauraceae (7), Rubiaceae (6), and Euphorbiaceae (6).

Table 1. Height above ground where the titis were active.

Level above ground	Percentage of total observations
Level 1 (0–5 m)	28%
Level 2 (6–10 m)	41%
Level 3 (11–15 m)	18 %
Level 4 (above 16 m)	13%

The predominant categories of foods varied during the year (Table 3). In the 22 data collection periods (two periods of five days in each of the 11 months), five species overlapped from one month to the next, resulting in an overlap of 45.5% for the predominant monthly species (an overlap from one month to the next would represent 9.1% for the year, five species overlaps equal $5 \times 9.1 = 45.1\%$).

The indices of fruit consumption (the number of visits to each species, time spent feeding, and fruits ingested per minute) of the species most preferred by the titis—five species of Melastomataceae, one of Loranthaceae, one of Moraceae—are shown in Table 4. The availability of immature and mature fruits was high from December to April and lower from May to November, but we found no correlation with rainfall or with fruit consumption (Fig. 6). The time spent eating fruit did, however, correlate negatively ($r = -0.6077$, $n = 9$, $p = 0.082383$, $p < 0.10$) with time spent resting, and there was a positive correlation ($r = 0.6975$, $n = 9$, $p = 0.036724$, $p < 0.05$) between monthly fruit consumption and the monthly consumption of immature leaves. Seasonality was not evident in the availability of young leaves. Immature leaves were available year-round but, according to our phenological records, there was a peak in availability in April (and probably March, for which data is unavailable but our *ad hoc* observations suggested this was the case) (Fig. 7).

Table 5 shows the species involved and the number of bouts, time spent feeding, and the number of items eaten per minute for immature and mature leaves, seeds, arils, stems and roots, and flowers. The titis ate mature leaves of four species. The consumption of immature leaves was dominated by one species (*Sorocea muriculata*) from the Moraceae family. Indices of seed-eating underline the importance of one family and species (*Pourouma bicolor*: Urticacae), representing about half the seeds chosen, although seeds of seven other species were also eaten. *Pourouma bicolor* was mostly available to the monkeys at the end of the year (December–January), when most *Pourouma* species were in fruit. *Iryanthera crassifolis* (Myristicaceae) was a key species for the consumption of arils (which many classify with fruits). The diet included the stems and roots of just one species of Araceae (*Philodendron deflexum*). Indices of consumption of flowers shows the families Lecythidaceae (two species of *Eschweilera*), Vochysiaceae (*Vochysia laxiflora*), and Bignoniaceae (three unidentified species) to be the most important (Santos *et al.* 2012).

Arthropods

Our monthly capture of arthropod prey items varied throughout the year with the greatest number captured during

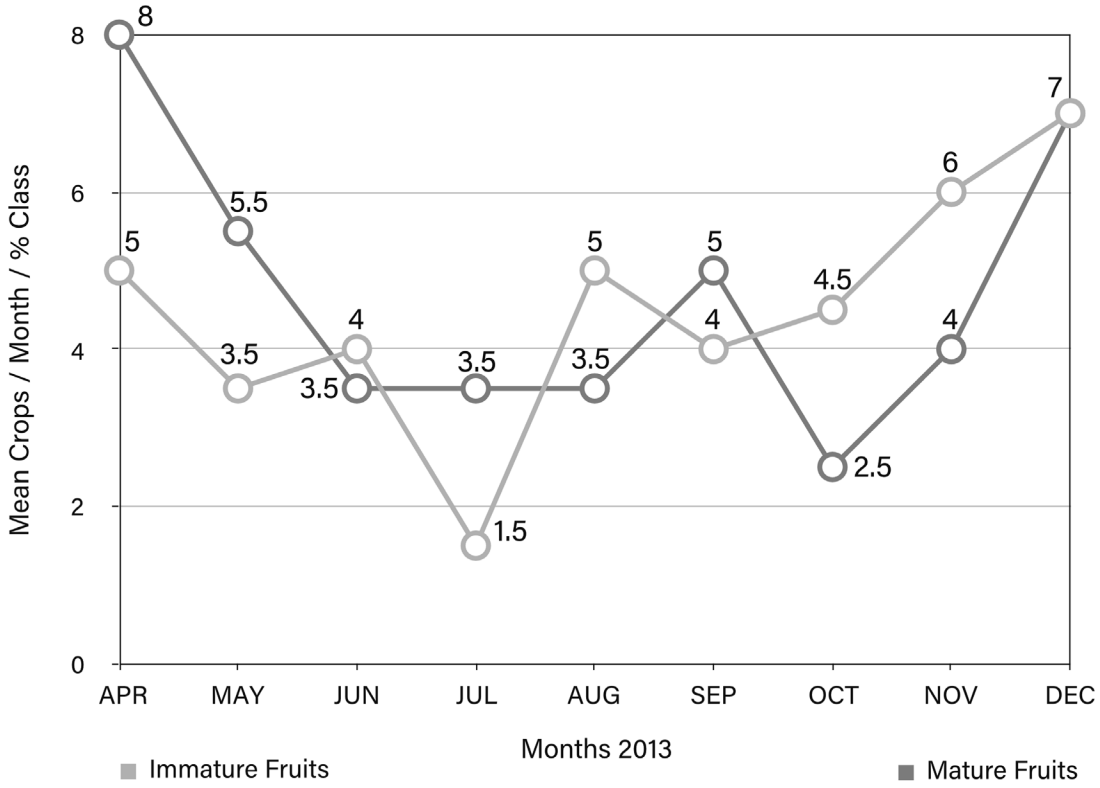

Figure 6. Availability of mature and immature fruit crops during 2013 (April–December).

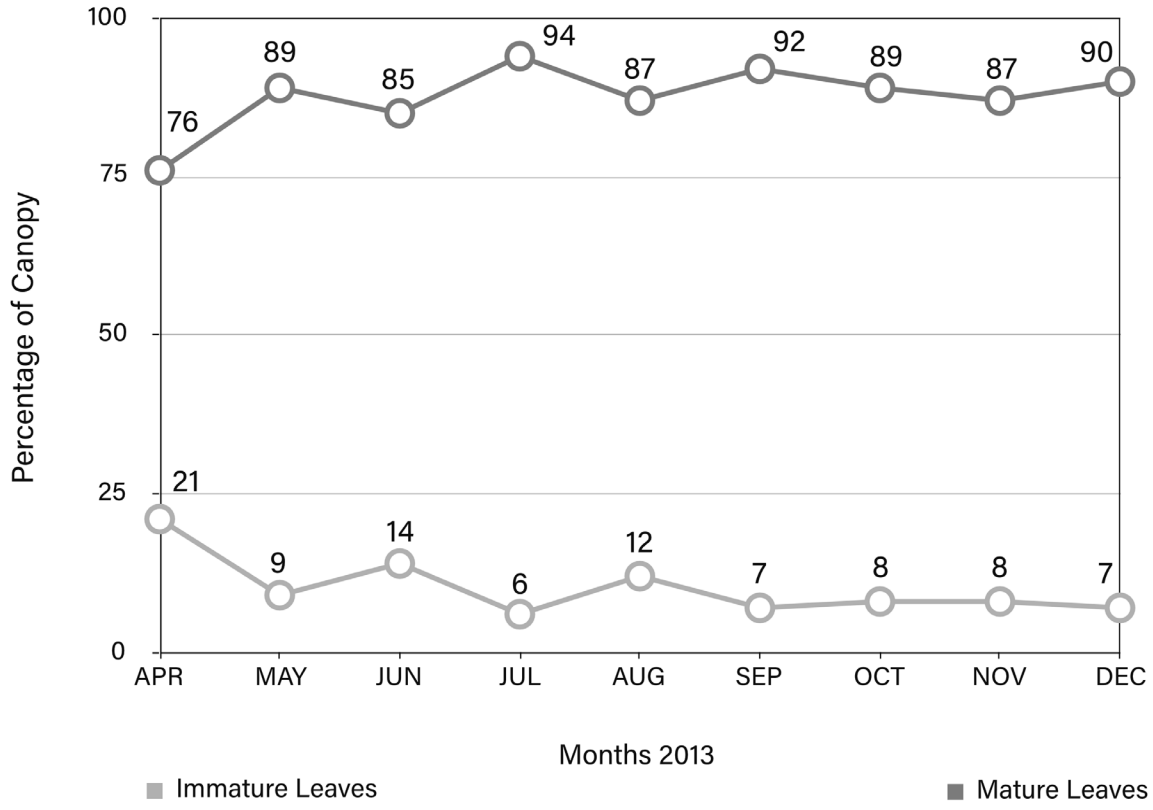

Figure 7. Availability of immature and mature leaves as a percentage of the canopy (April–December 2013) of the 14 most important species of food plants in the study.

March, October and November. Since the majority of feeding took place below 10 m, we feel that our monthly collections of arthropods reflected the available offering. Table 6 lists the arthropods collected by us. It includes 24 orders, broken down into percentages of units (individual arthropods) that were available to the primates.

Of the 24 arthropod orders, eight (those in bold in Table 6) were seen to be eaten by the titi monkeys: Coleoptera; Araneae; Hymenoptera (mostly ants); Lepidoptera; Hemiptera; Orthoptera; Diptera; and Acarina. The titis ate from the most available groups according to our collections. The titis captured their arthropod prey from living and hanging-dead leaves, on the ground, on tree trunks and branches, from the air, and from lianas. It was common for them to spend time on the ground both foraging and playing. The group spent a total of 28% of their time within 5 m of or on the ground.

The titi group's feeding on arthropods varied during the year, but we found no correlation between monthly rainfall during 2013 and our sampling data ($r = -0.2447$, $p \leq 0.0.05$, n.s.), though there was a moderate negative correlation between monthly rainfall and time spent foraging and eating arthropods ($r = -0.6593$, $p \leq 0.05$). Our sampling data also were not correlated with time spent eating ($r = -0.0262$, $p \leq 0.05$, n.s.), and we were unable to reliably distinguish the orders of the arthropods being eaten by the monkeys.

Discussion

The diet described here is similar to those of other titi monkeys that have been studied (*Callicebus* – Müller 1996; Price and Piedade 2001; Caselli and Setz 2011; Trevelin *et al.* 2007; Souza-Alves *et al.* 2011; Santos *et al.* 2012; *Plecturocebus* – Tirado-Herrera and Heymann 2003; Carillo-Bilbao *et al*. 2005; Bicca-Marques and Heymann 2013; Kulp and Heymann 2015; Quintero-Tapia 2017; *Cheracebus* – Kinzey 1977; Kinzey *et al.* 1977; Palacios *et al.* 1997; Palacios and Rodríguez 2013). Titis concentrate mainly on ripe fruits, arthropods and seeds, although earlier studies often did not distinguish seeds from fruits, a semantic confusion that has fortunately now been corrected in recent studies. Currently there are not enough field data to be able to distinguish ecological differences among this recently subdivided genus (Byrne *et al.* 2016), especially since there is considerable variability among groups of the same species. As in other titis, the majority of the diets are made up of plant foods that are supplemented with arthropods and seeds. What is particularly interesting for comparison are the various components of the plant foods and the levels of arthropod consumption, as well as the different levels of importance of eating seeds.

Our study group ate far fewer fruits than many other callicebines. Bicca-Marques and Heymann (2013, p.201) compared eight species and showed values for fruit-eating that varied from 36–86% of the diet, with a mean of 66.6%. Polanco (1992) studied a group of *P. ornatus*, the titi most closely related to *P. caquetensis*, in a pristine rainforest not far north of our study site, and recorded that the 81% of its diet was composed of fruit, considerably more han the 21% that we obtained. But many authors do not distinguish fruits from arils. If we add fruits and arils, the percentage of fleshy tissues is raised to 36% of the diet. The high percentage of leaves consumed by the titis in our study still suggests that fruits and arils are depressed in this diet. Although there are certainly inter-annual differences in crop sizes, we believe that these percentages may be because of depressed fruit production in a distressed habitat. The diet of our study group comprised 21% fruits, 21% seeds, 27% immature leaves, 15% arils, 7% flowers, 4% mature leaves, 3% arthropods, and 2% stems and roots (this last might, at least in part, be a filler to compensate for the lack of fruit). The majority of the data in the above comparison reported leaf consumption below that of our study group (mean = 16.6% leaf consumption reported). The low fruit consumption and high leaf consumption could indicate a sub-optimal habitat for these study animals.

Seeds can make up a substantial contribution of the diet for some species of titis or even for some groups within a species (Heiduck 1997; Palacios *et al.* 1997; Kulp and Heymann 2015; Alvarez and Heymann 2012; Santos *et al.* 2012; Palacios and Rodríguez 2013) (Table 7). In this study we calculated that 15% of the plant species were exploited for seeds, representing 21% of total feeding time, with a preponderance of feeding on three species at the end and beginning of the year: *Pourouma bicolor*, *Bellucia pentamera* (also pulp) and *Siparuna* sp. But at times seeds can become for some species and places almost the entire diet. During the dry season of a bamboo masting year in the Atlantic forest of Brazil, about 90% of the diet for one group of *Callicebus nigrifrons* was of bamboo seeds, while in other groups in the same study during the same period, seeds contributed 72.8%, 46.7% and 59.7% of their diet. There were only 51 plant species in the diet of the *Callicebus nigrifrons* studied by Santos *et al.* (2012); about one-third of the number in our study—159 species. Other studies make no mention of seed predation, but it seems likely that it occurred but was not distinguished from other parts of the fruit (Kinzey 1977, 1981; Kinzey *et al.* 1977; Easley, 1982; Bilbao *et al.* 2005) (Table 2). Caselli and Setz (2011) considered seeds to be a "low-quality" food item, and they lumped seeds in with the category of fruits. The importance of seed consumption among the three genera of titis demonstrates an ecological, evolutionary adaptation related to the rest of the pitheciid radiation, although in the case of the titis (Callicebinae) seed exploitation is less important than among the sakis, bearded sakis, and uakaris (Pitheciinae).

In our study, there were marked changes in the diet during the year, influenced by the availabilty food resources. They fed more on young leaves, seed, and fruits during the rainy season. Food availability was greater at the end of the marked rainy season. Some studies mention that fruit consumption is greater during the dry season than the wet season, and that the contribution of such as seeds is greater in the dry season (Müller 1996; Heiduck 1997; Palacios *et al.* 1997). We believe that the forest fragment where we studied this group

Table 2. The fourteen most important food species based on time eating them and the number of visits to each species, each ≥2% of the diet.

Family	Species	Number of visits	% of diet	Plant part eaten
Urticaceae	*Pourouma bicolor*	124	8.3	Seeds, mesocarp
Arecaceae	*Socratea exorrhiza*	120	6.7	Exocarp, mesocarp
Melastomataceae	*Miconia dolichorrhyncha*	86	4.4	Fruits
Lecythidaceae	*Eschweilera punctata*	58	3.8	Immature leaves
Bignoniaceae	*Cydista* sp.	48	3.3	Seeds
Urticaceae	*Cecropia sciadophylla*	67	3.0	Fruits
Melastomataceae	*Bellucia pentamera*	55	2.7	Seeds
Moraceae	*Helianthostylis sprucei*	56	2.7	Immature leaves
Myristicaceae	*Virola sebifera*	41	2.6	Arils
Myristicaceae	*Iryanthera crassifolia*	31	2.6	Aril
Moraceae	*Soracea muriculata*	41	2.2	Fruits
Monimiaceae	*Siparuna decipiens*	55	2.2	Seeds
Araceae	*Heteropsis flexuosa*	61	2.2	Roots

Table 3. The dietary items most eaten each month. Different monthly observations were separated by 15 days, i.e. the end of one month´s observations was 15 days from the beginning of the next month´s observations. 01=first five days of sample; 02=second five days of sample in each. The two fivc-day samples in each month were separated by two days.

Month	Species	Item eaten
February-01	*Bellucia pentamera*	Seed
February-02	*Bellucia pentamera*	Seed
March-01	*Miconia elata*	Fruit
March-02	*Matisia idroboi*	Leaf
April-01	*Miconia dolichorrhyncha*	Fruit
April-02	*Miconia elata*	Fruit
May-01	*Calyptranthes forsteri*	Fruit
May-02	*Eschweilera* sp.	Hm
June-01	*Siparuna* sp. 2	Fruit
June-02	*Calyptranthes forsteri*	Fruit
July-01	*Cydista* sp.	Seed
July-02	*Miconia dolichorrhyncha*	Fruit
August-01	*Sorocea muriculata*	Leaf
August-02	*Sorocea muriculata*	Leaf
September-01	*Eschweilera punctata*	Aril*
September-02	*Eschweilera punctata*	Leaf
October-01	*Phthirusa pyrifolia*	Fruit
October-02	*Adenocalymma cladotrichum*	Leaf
November-01	*Socratea exorrhiza*	Aril*
November-02	*Socratea exorrhiza*	Aril*
December-01	*Pourouma bicolor*	Seed
December-02	*Pourouma bicolor*	Seed

*Many studies would classify arils as fruits, which technically is incorrect.

Table 4. The seven fruits eaten most by the *Plecturocebus caquetensis* study group.

Family	Species	Nº of visits	Time	No. of fruits eaten/ minute
Melastomataceae	*Miconia dolichorrhyncha*	86	550	8
Melastomataceae	*Miconia tomentosa*	43	241	6
Melastomataceae	*Miconia elata*	25	134	9
Melastomataceae	*Henriettella fascicularis*	24	125	5
Loranthaceae	*Phthirusa pyrifolia*	23	149	5
Moraceae	*Ficus americana andicola*	9	85	5
Melastomataceae	*Miconia napoana*	9	56	9

Table 5. The consumption of mature and immature leaves, seeds, arils, stems and roots and flowers by the *P. caquetensis* study group.

Family	Species	No of visits	Time	No. eaten/minute
Mature leaves				
Lecythidaceae	*Eschweilera* sp.	30	218	1
Fabaceae	*Inga* sp. 2	17	108	1
Rubiaceae	*Psychotria transiens*	5	24	1
Nyctaginaceae	*Neea* sp.	3	15	1
Immature leaves				
Moraceae	*Sorocea muriculata*	41	271	4
Dilleniaceae	*Davilla* sp.	4	12	4
Anacardiaceae	*Tapirira* sp. 1.	3	15	4
Violaceae	Not identified	2	7	4
Seeds				
Urticaceae	*Pourouma bicolor*	124	1038	3
Melastomataceae	*Bellucia pentamera*	55	338	3
Monimiaceae	*Siparuna* sp. 2	47	290	3
Passifloraceae	*Passiflora ambigua*	11	70	7
Monimiaceae	*Siparuna* sp. 1	11	62	3
Araceae	*Monstera adansonii*	7	27	3
Annonaceae	*Cremastosperma microcarpum*	4	28	6
Arils				
Myristicaceae	*Iryanthera crassifolis*	31	155	3
Fabaceae	*Inga* sp. 1	8	57	3
Fabaceae	*Inga* sp. 2	3	10	2
Stems and roots				
Araceae	*Philodendron deflexum*	34	138	1
Flowers				
Lecythidaceae	*Eschweilera punctata*	58	472	1
Lecythidaceae	*Eschweilera* sp.	30	218	2
Vochysiaceae	*Vochysia* aff. *laxiflora*	24	229	1
Bignoniaceae	sp. 1	18	119	1
Myristicaceae	*Virola callophylla*	8	29	1
Annonaceae	*Duguetia* sp. 2	5	33	1
Fabaceae	*Brownea* sp.	4	13	1
Bignoniaceae	sp. 3	3	26	3
Bignoniaceae	sp. 2	3	22	1
Burseraceae	*Protium aracouchini*	3	11	1
Fabaceae	*Inga multijuga*	2	5	1

Table 6. Ranking and total percentages of arthropod orders that were collected each month (total collected during the year = 1108 arthropods). Rank is based on total arthropods collected. The orders we observed to be part of the diet of the titis are in bold.

Rank	Order	% of total units	Rank	Order	% of total units	Rank	Order	% of total units
1	**Coleoptera**	26.8	9	Blattodea	1.1	14	Ephemeroptera	0.2
2	**Araneae**	26.6	10	Isoptera	0.7	14	Tricoptera	0.2
3	**Hymenoptera**	13.8	11	Opiliones	0.6	14	Uropygi	0.2
4	**Lepidoptera**	9.0	12	Diplopoda	0.5	14	Ephemeroptera	0.2
5	**Hemiptera**	7.3	12	Mantodea	0.5	15	Anisoptera	0.1
6	**Orthoptera**	5.6	12	Zygoptera	0.5	15	Heteroptera	0.1
7	**Diptera**	3.5	13	Chilopoda	0.4	15	Plecoptera	0.1
8	**Acarina**	1.8	13	Phasmida	0.4	15	Socoptera	0.1

Table 7. Reports of seed eating in the diets of some titi monkeys *Plecturocebus*, *Cheracebus* and *Callicebus* spp.

Species	% Seeds in the diet	Reference
Plecturocebus caquetensis	21% (12 months)	Acero *et al.* (this study)
Cheracebus lugens	26.9% (12 months)	Palacios *et al*. (1997)*
Cheracebus lugens	48% (12 months)	Palacios and Rodríguez (2013)*
Cheracebus lugens	21.7% "fleshy parts and seeds" (4 months)	Alvarez and Heymann (2012)*
Callicebus coimbrai	4.6% (0–23%; n = 5 months)	Santana (2012)
Callicebus nigrifrons	7.7–90% (12 months; 4 groups; median 10.6–59.7%	Santos *et al*. (2012)
Plecturocebus cupreus	11.4% pulp and seeds (5 months)	Kulp and Heymann (2015)
Callicebus melanochir	26.4%	Heiduck (1997)

*These three studies were of the same habituated group of *Callicebus lugens* in the Estación Biológica Caparú in eastern Colombia.

may not be adequate to the needs of the animals and that the high consumption of leaves reflects this inadequacy. It was a remnant of a previous closed-canopy lowland humid forest, but it is difficult to define the preferred habitat of this primate. Although the known distribution of this species is in a region that was primordialy closed-canopy, moist, tropical forest, the damage to these forests over years of human interventions and destructive activities complicates any useful categorization or definition of its habitat type beyond that of degraded. Since several species of titis have been implicated in a preference for edge habitat, and the closely related *Plecturocebus ornatus* has been found in some forest fragments in very high densities, it is possible that, irrespective of the original habitat preferences of *Plecturocebus caquetensis*, the species' survival in fragments of lowland humid forest that were originally part of an intact, closed canopy forest might favor the continued presence of this species (Wagner *et al.* 2009; Defler and Carretero 2016; Defler and Carretero in press). The dispersal of young is undoubtedly made more difficult because of the treeless expanses between fragments. In some ways the degradation may be beneficial, in others harmful. Their evaluation demands multi-year comparative studies.

It is evident that titis have a degree of flexibility in the exploitation of their resources and that this flexibility allows for their survival under the difficult circumstances of forest fragmentation. However, in the case of *Plecturocebus caquetensis* and other endangered titis, the continued degeneration and loss of their habitat through fragmentation and forest loss will continue to erode populations unless protected areas are established that can allow for the maintenance of their genetic viability in the long-run. Corridors between fragments could ensure the gene flow necessary to maintain genetic diversity, but all of this guarantees a difficult road ahead in attempts to conserve this endangered species.

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Ethical Note

We obtained all permissions and licenses required for this research in Colombia. The animals were observed from appropriate distances and were never manipulated or threatened.

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Appendix

Plant food items eaten by *Plecturocebus caquetensis* at Playa Rica (Valparaíso), Caquetá, Colombia during 2013; Family, Species, number of visits to resource, food item (part) eaten, time recorded eating on the species (minutes), and percent of total diet. [1]Total time recorded feeding – 12,443 minutes.

Family	Scientific name	No. of visits	Food item	Time recorded (minutes)[1]	% of diet[1]
Acanthaceae	*Mendoncia* sp.	6	Fruit	30	0.2
	Mendoncia lindavii	15	Seeds	86	0.7
Achariaceae	*Lindackeria paludosa*	1	Fruit	8	0.06
Anacardiaceae	*Tapirira* sp. 1	3	Young leaves	15	0.1
Annonaceae	*Cremastosperma microcarpum*	4	Seeds	28	0.2
	Duguetia sp. 1	2	Young leaves	8	0.06
	Duguetia sp. 2	5	Flowers	33	0.3
	Guatteria cargadero	7	Young leaves	41	0.3
	Guatteria hyposericea	2	Young leaves	4	0.03
	Guatteria megalophylla	6	Fruit	42	0.3
	Guatteria sp. 1	2	Fruit	3	0.02
	Guatteria sp. 2	20	Mesocarp, arils, exocarp	135	1.1
	Rollinia sp. 1	2	Fruit	7	0.06
	Oxandra xylopioides	1	Fruit	3	0.02
	Unonopsis stipitata	2	Young leaves	3	0.02
Araceae	*Anthurium* sp. 1	10	Young leaves	51	0.4
	Anthurium sp. 2	22	Young leaves	81	0.7
	Heteropsis flexuosa	61	Fruit	271	2.2
	Monstera adansonii	7	Seeds	27	0.2
	Monstera obliqua	5	Fruit	21	0.2
	Monstera sp.	7	Fruit	25	0.2
	Philodendron deflexum	34	Stems, roots	138	1.1
	Syngonium spp.	3	?	15	0.1
	Undet. Species	13	Young leaves	47	0.4
Arecaceae	*Oenocarpus bataua*	22	Mesocarp, arils, exocarp	120	1.0
	Socratea exorrhiza	120	Mesocarp, arils, exocarp	836	6.7
Aristolochiaceae	*Aristolochia pilosa*	3	Young leaves	8	0.06
Bignoniaceae	*Adenocalymma cladotrichum*	20	Young leaves	113	0.9
	Cydista sp.	48	Seeds	410	3.3
	Fridericia schumanniana	1	Young leaves	5	0.04
	Stizophyllum riparium	3	Young leaves	11	0.09
	sp. 1	18	Flowers	119	1.0
	sp. 2	3	Flowers	22	0.2
	sp. 3	3	Flowers	26	0.2
	sp. 4	7	Flowers	47	0.4
Boraginaceae	*Cordia nodosa*	1	Mesocarp, arils, exocarp	2	0.02

Burseraceae	*Crepidospermum rhoifolium*	2	Young leaves	9	0.07
	Protium aracouchini	3	Flowers	11	0.09
	Tetragastris altissima	8	Fruit	52	0.4
Coenogoniaceae	*Coenogonium linkii*	2	?	2	0.02
Combretaceae	sp.	2	Fruit	6	0.05
Costaceae	*Dimerocostus strobilaceus*	1	Fruit	1	0.008
Cucurbitaceae	*Gurania acuminata*	2	Young leaves	5	0.04
	Siolmatra sp.	1	Fruit	4	0.03
Dilleniaceae	*Davilla* sp.	4	Young leaves	12	0.1
Euphorbiaceae	*Alchornea glandulosa*	1	Young leaves	4	0.03
	Alchornea triplinervia	3	Seeds	32	0.3
	Hieronyma oblonga	9	Fruit	43	0.4
	Mabea nitida	8	Young leaves	52	0.4
	Pausandra trianae	2	Seeds	12	0.1
	Pseudosenefeldera inclinata	2	Seeds	6	0.05
Fabaceae	*Brownea ariza*	4	Flowers	13	0.1
	Diplotropis purpurea	5	Young leaves	23	0.2
	Inga acrocephala	23	Fruit	120	1.0
	Inga alba	9	Young leaves	77	0.6
	Inga brachyrhachis	1	Young leaves	5	0.04
	Inga ciliata	7	Young leaves	38	0.3
	Inga cylindrica	3	Young leaves	3	0.02
	Inga edulis	3	Mesocarp, arils, exocarp	10	0.08
	Inga leiocalycina	26	Fruit	243	2.0
	Inga multijuga	2	Young leaves, flowers	5	0.04
	Inga thibaudiana	1	Young leaves	3	0.02
	Inga sp. 1	8	Mesocarp, arils, exocarp	57	0.5
	Inga sp. 2	17	Mature & young leaves	108	0.9
	Inga sp.	1	Young leaves	1	.008
	Macrolobium limbatum	1	Young leaves	5	0.04
	Macrolobium sp.	3	Flowers	5	0.04
	Zygia latifolia	9	Young leaves	29	0.2
Hypericaceae	*Vismia baccifera*	1	Young leaves	3	0.02
	Vismia sp.	1	Fruit	2	0.02
Lauraceae	*Endlicheria pyriformis*	3	Young leaves	7	0.06
	Nectandra longifolia	5	?	19	0.2
	Ocotea javitensis	3	Fruit	7	0.06
	Ocotea longifolia	25	Fruit	220	1.7
	Ocotea sp.	1	Fruit	6	0.05
	Rhodostemonodaphne sp.	8	Fruit	38	0.3
	Unidentified sp.	5	Seeds	31	0.3

Lecythidaceae	*Eschweilera bracteosa*	2	Young leaves	5	0.04
	Eschweilera coriacea	2	Young leaves	9	0.07
	Eschweilera punctata	58	Young leaves	472	3.8
	Eschweilera sp.	30	Mature leaves	218	1.8
	Gustavia sp. 1	1	Young leaves	3	0.02
Loranthaceae	*Oryctanthus alveolatus*	2	Fruit	10	0.08
	Phthirusa pyrifolia	23	Fruit	149	1.2
Malvaceae	*Matisia idroboi*	20	Young leaves	79	0.6
Marcgraviaceae	*Marcgravia macrophylla*	7	Young leaves	45	0.4
	Marcgravia peduncularis	1	Fruit	3	0.02
	Unidentified sp.	3	Young leaves	26	0.2
Melostomataceae	*Bellucia pentamera*	55	Fruit	338	2.7
	Clidemia sp.	4	Fruit	15	0.1
	Conostegia sp.	1	Fruit	1	0.008
	Henriettella fascicularis	24	Fruit	125	1.0
	Miconia dolichorrhyncha	86	Fruit	550	4.4
	Miconia elata	25	Fruit	134	1.1
	Miconia napoana	9	Fruit	56	0.5
	Miconia tomentosa	43	Fruit	241	1.9
	Miconia sp. 1	3	Fruit	26	0.2
	Miconia sp. 2	3	Seeds	4	0.03
	Miconia sp. 3	3	Fruit	16	0.1
Menispermaceae	*Abuta grandifolia*	3	Young leaves	14	0.1
	Curarea toxicofera	5	Young leaves	19	0.2
Monimiaceae	*Siparuna decipiens*	55	Seeds	274	2.2
	Siparuna obstipa	3	Fruit	15	0.1
	Siparuna sp. 1	11	Seeds	62	0.5
	Siparuna sp. 2	47	Seeds	290	2.3
	Unidentified sp.	11	Fruit	64	0.5
Moraceae	*Brosimum* sp. 1	5	Young leaves	24	0.2
	Brosimum sp. 2	2	Fruit	4	0.03
	Ficus americana ssp. *andicola*	9	Fruit	85	0.7
	Ficus sp.	3	Young leaves	14	0.1
	Helianthostylis sprucei	56	Young leaves	336	2.7
	Pseudolmedia laevis	8	Young leaves	64	0.5
	Sorocea affinis	2	Young leaves	4	0.03
	Sorocea muriculata	41	Fruit	271	2.2
	Unidentified sp.	1	Young leaves	8	0.06
Myristicaceae	*Iryanthera crassifolia*	31	Mesocarp, arils, exocarp	325	2.6
	Iryanthera sp.	8	Seeds	64	0.5
	Otoba parvifolia	22	Young leaves	131	1.0

	Virola callophylla	8	Flowers	29	0.2
	Virola pavonis	1	Seeds	7	0.06
	Virola peruviana	3	Mesocarp, arils, exocarp	10	0.08
	Virola sebifera	41	Mesocarp, arils, exocarp	325	2.6
	Virola sp.	3	Seeds	17	0.1
Myrtaceae	*Calyptranthes forsteri*	2	Young leaves	10	0.08
	Unidentified sp.	10	Fruit	70	0.6
Nyctaginaceae	Neea sp.	3	Mature & young leaves	15	0.1
	Species	1	Young leaves	10	0.08
Passifloraceae	*Passiflora ambigua*	11	Seeds	70	0.6
Polypodiaceae	*Microgramma baldwinni*	16	Fruit	61	0.5
Rubiaceae	*Bertiera* sp.	13	Young leaves	59	0.5
	Carapichea dolichophylla	9	Fruit	40	0.3
	Ladenbergia magnifolia	2	Seeds	11	0.09
	Psychotria lupulina	1	Young leaves	6	0.05
	Psychotria transiens	5	Mature leaves	24	0.2
	Unidentified sp.	1	Fruit	2	0.02
Salicaceae	*Casearia* sp. 1	4	Fruit	15	0.1
	Casearia sp. 2	1	Seeds	3	0.02
	Tetrathylacium macrophyllum	9	Seeds	21	0.2
Sapotaceae	*Micropholis guyanensis*	6	Young leaves	24	0.2
	Pouteria sp.	7	Young leaves	57	0.5
Solanaceae	*Cestrum racemosum*	2	Young leaves	8	0.06
	Juanulloa ochracea	15	Fruit	107	0.9
	Lycianthes glandulosa	4	?	20	0.2
	Solanum sp.	8	Seeds	37	0.3
	Tetrathylacium macrophyllum	9	Seeds	21	0.2
Ulmaceae	*Ampelocera* sp.	28	Young leaves	172	1.4
Urticaceae	*Pourouma bicolor*	124	Fruit, seeds	1038	8.3
	Pourouma cecropifolia	1	Young leaves	3	0.02
	Pourouma cucura	7	Young leaves	38	0.3
	Pourouma sp.	7	Mesocarp, arils, exocarp	70	0.6
	Cecropia sciadophylla	67	Seeds	372	3.0
Verbenaceae	*Petrea volubilis*	13	Young leaves	100	0.8
Violaceae	*Rinorea* sp.	2	Fruit	11	0.09
	Unidentified sp.	2	Young leaves	7	0.06
Vochysiaceae	*Vochysia* aff. *laxiflora*	24	Seeds	229	1.8
Undetermined	Unidentified ref. 673	12	Flowers	112	0.9
Undetermined	Morphotype 2	5	Young leaves	45	0.4
Undetermined	Unidentified ref. 434	1	Flowers	10	0.08
Undetermined	Ref. 579	1	Young leaves	6	0.05