

Research Article

Behavior and ecology of the white-footed tamarin (*Saguinus leucopus*) in a fragmented landscape of Colombia: small bodied primates and seed dispersal in Neotropical forests

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Abstract

Tamarins are small-bodied Neotropical primates that mainly feed on ripe fruits and insects, and supplement their diet with plant exudates, nectar, fungi and vertebrate prey. They are important seed dispersers in Neotropical forests as they are able to disperse a large number of small and medium-sized seeds from parental trees. In this paper, we describe the diet of the white-footed tamarin (*Saguinus leucopus*) and its role as seed disperser in a fragmented landscape in Colombia. During a twelve month period, we collected data on activity patterns, ranging behavior and feeding ecology, as well as on habitat-wide forest productivity. *S. leucopus* fed from >95 plant species and spent 17% of their time feeding. We found a positive relationship between fruit consumption and ripe-fruit availability. Dietary diversity increased during periods of fruit scarcity, when the tamarins fed more on insects and exudates. During periods of fruit scarcity, they relied more heavily on the borders of forest fragments and made occasional incursions into adjacent fragments across a matrix of pastures. They used larger areas and had larger overlapping home ranges during periods of fruit scarcity. We recovered at least 44 species of seeds effectively dispersed by tamarins, including small and medium-sized seeds (range <1–26 mm). Seeds were dispersed up to 500m from parent trees across a wide diversity of habitat types. This study provides further evidence on the important role small-bodied frugivorous primates play in the recovery of forest connectivity and in the maintenance of tropical forest diversity in human-impacted landscapes.

Keywords: Seed dispersal, fragmentation, primate behavioral ecology

Received: 28 March 2016; **Accepted** 6 May 2016; **Published:** 27 June 2016

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Cite this paper as: de Luna, A. G., García-Morera, Y. and Link, A. 2016 Behavior and ecology of the white-footed tamarin (*Saguinus leucopus*) in a fragmented landscape of Colombia: small bodied primates and seed dispersal in Neotropical forests. *Tropical Conservation Science* Vol. 9 (2): 788-808. Available online: www.tropicalconservationscience.org

Disclosure: Neither Tropical Conservation Science (TCS) or the reviewers participating in the peer review process have an editorial influence or control over the content that is produced by the authors that publish in TCS.

Introduction

Most tropical ecosystems are experiencing a pervasive trend of anthropogenically-driven habitat loss and a rapid decline of wild vertebrate populations [1, 2]. Habitat fragmentation can influence primates' feeding ecology, especially in scenarios where habitat disturbance affects the presence, abundance, distribution, or phenology of their main food items [3-8]. Primates play a key role in the complex processes associated with tropical forest maintenance and recovery [3, 9, 10]. They represent a significant proportion of frugivorous vertebrate biomass in tropical communities [11, 12]. Approximately 90% of neotropical rainforest plants rely on animals to disperse their seeds [13]. In natural scenarios where medium and large-sized mammals have become rare or locally extinct, the role of small primates in community-wide seed dispersal may become even more crucial [14].

The tamarin (genus *Saguinus sensu lato*) is a small-bodied primate (360g - 575g) that lives in a wide variety of habitats in Panama, northern Colombia, and throughout the Amazon basin [15, 16]. All tamarins are considered frugivore-insectivores as they feed mainly on ripe fruit and invertebrates, supplementing their diet to varying degrees with plant exudates, nectar, and vertebrate prey [15, 17]. In comparison to marmosets, the tamarin only feeds on exudates opportunistically, although, for some populations, gums can represent an important food item during parts of the year [18]. While the plant diet of the tamarin can be quite diverse [17, 19, 20], most studies have shown that most of its diet comprises only a small number of plant species [17,20]. The tamarins is able to swallow small to medium-sized seeds of a wide diversity of canopy and subcanopy plants, which are subsequently defecated intact [20-22]. Given its ability to move across anthropogenically disturbed areas and to cross large distances between forest fragments [22], the tamarin can play a key role in forest regeneration processes because of its seed dispersal services, especially in forests where larger frugivores have been extirpated or have low population densities due to habitat loss and hunting [23].

The white-footed tamarin (*Saguinus leucopus*) is endemic to the lowland forests within the Magdalena-Cauca interfluvium between the Central and Eastern cordilleras of the Andes in Colombia [24]. Its geographic distribution is one of the most limited for the genus [24] and constitutes a part of the

Tumbes-Chocó-Magdalena biodiversity hotspot [25]. Currently, the Inter-Andean forests, where *S. leucopus* ranges, are being rapidly deforested and transformed into large agro-industrial plantations or cleared for large-scale cattle ranches or gold mines [26-28]. Understanding how the white-footed tamarin copes with habitat fragmentation is of critical importance for the conservation of its remaining natural population.

Our study focussed on the behavior and ecology of the white-footed tamarin in this increasingly fragmented landscape. In this paper we describe its diet and address the following question: Does habitat-wide resource availability influence the activity patterns, feeding ecology, and ranging behavior of the white-footed tamarin? We also compare the results of our study with earlier reports on the dietary habits of other species of *Saguinus*. Finally, we provide preliminary evidence about the role that this small-bodied primate may play in forest regeneration through its seed dispersal services, especially in sites where large and medium-sized mammals have been extirpated.

Methods

The study was conducted at Hacienda “La Brillantina”, a private cattle ranch located between the Ité and Pescado Rivers in the lowland tropical forests of Remedios, Antioquia, in northern Colombia (06°02'48" N, 74°16'00" W). This region has a bimodal rainfall pattern with two dry periods from January to February and August to September [29]. The study site consists of a mosaic of forest fragments scattered within a matrix of cattle ranching pasture. During the past decade, extensive areas of forests have been transformed into pasture, and selective logging has also taken place in most forest remnants. The study area is also intersected by an oil pipeline, which divided the former 120 ha forest fragment into two smaller fragments of 35 ha and 85 ha, separated by a 20 m wide gap (Fig. 1). Although the tamarin is found throughout both fragments, our study groups lived in the smaller fragment and only occasionally crossed into the larger fragment and adjacent areas (Fig. 1).

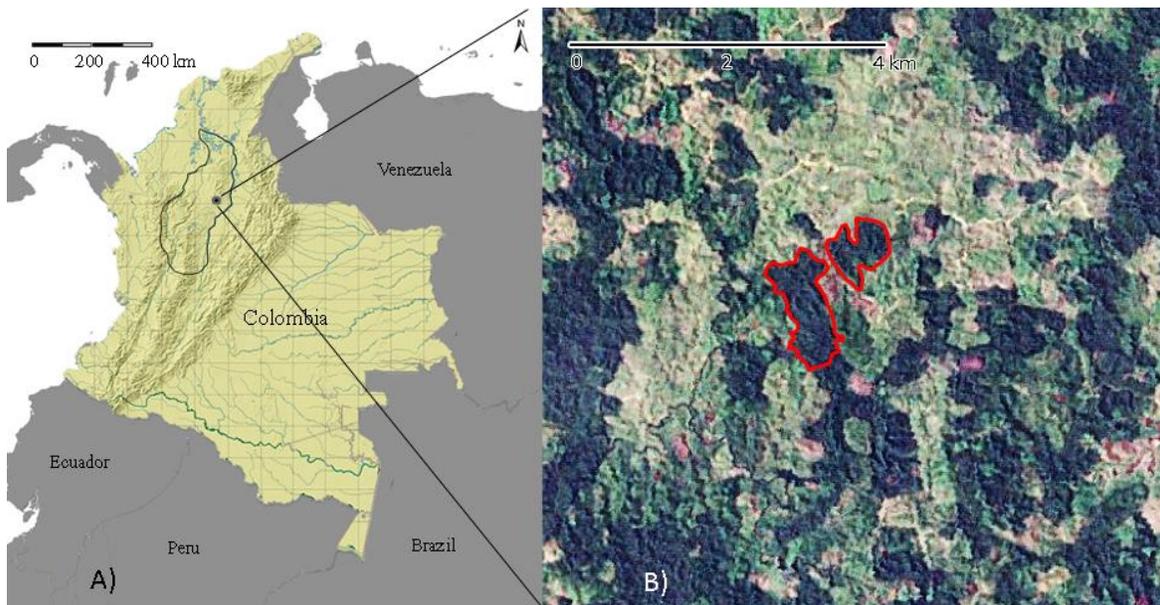


Fig. 1. A) Location of the study site within in Colombia and B) map of vegetation cover at Hacienda La Brillantina, in Remedios, Antioquia. The red contour shows the study area comprising two contiguous forest fragments within a matrix of cattle ranching pastures.

Although we attempted to follow four neighboring groups of white-footed tamarins (A, B, C, D), we only collected ecological and behavioral data on groups A and C. At the time of the study group A comprised nine individuals (3 adult males, 2 adult females, 4 subadults/juveniles), and group C comprised seven individuals (2 adult males, 2 adult females, 1 subadult/juvenile, and 2 infants). Subadults and juveniles were independently locomoting individuals and it was difficult to determine their sex in the field. During 2010, we spent three months habituating each study group and, from January 2011 until December 2011, two researchers conducted behavioral follows. Overall, monthly sampling effort averaged 38 hours (range 10-70) between the two groups. Although we had visual contact with our study groups on 204 days during the 12 month study period, we only conducted behavioral follows on 148 days, and these lasted an average of 3 hours (range 1-11 hours). Long behavioral daily follows were difficult to achieve during this study due to the difficult terrain in Remedios. Overall, we collected 209 hours of behavioral data on group A and 250 hours on group C.

We used scan sampling [30] to record quantitative behavioral data and 1 minute scans collected at 5 minute intervals. During a scan, we recorded the behavioral state of each visible group member as either feeding (including actively foraging for invertebrates), resting, moving, or engaging in social behavior. Other behavioral data (for example documenting aggressive interactions or grooming) were recorded as *ad libitum* events. Data recorded through *ad libitum* methods were not used in the analyses and estimation of rates of occurrence of different types of behavior. In order to describe habitat use and the ranging patterns of our two study groups, we recorded each group's location every 15 minutes using a handheld GPS unit (Garmin model GPSMap 76CSx) and noted the forest strata being used in the following categories: Canopy, subcanopy and understory, or ground.

We collected data on feeding behavior by recording each plant or animal item on which an individual fed. We recorded 1000 feeding bouts that accounted for approximately 63 hours of feeding behavior. For each feeding bout we recorded its duration, marked the feeding tree with a unique number, measured its diameter at breast height (DBH), and recorded its spatial location. In addition, we recorded the plant item eaten (fruit, flowers, exudates, for example) and collected botanical vouchers in order to identify each plant to species or morphospecies level. We calculated the relative contribution of each food item and plant species to the tamarin's diet as the length of time an individual fed on a particular item, divided by the total time spent feeding. We classified habitat types where animals ranged, foraged, or defecated as [i] forest interior (> 10 meters from the border between forest and surrounding pasture), [ii] forest edge (between 0 and 10 meters from pasture), and [iii] pasture. These categories were based on the structure of the forest. Pastures were defined as areas intensively used for cattle ranching with isolated mature trees within them. The forest edge had been subjected to more anthropogenic disturbance and had smaller trees and more light than inner forest areas.

We estimated habitat-wide fruit productivity through phenological transects along trails every two weeks, following the methods developed by Stevenson [31]. Briefly, on each survey we walked 4 km of transects within the forest fragments and recorded all trees bearing ripe, fleshy fruit whose crowns overhung the transect. For each tree bearing ripe fruit, we identified it as to species or morphospecies, recorded its location, and measured its DBH (in order to estimate its basal area). We used both the number of trees bearing ripe fruit per area surveyed and the total basal area of fruiting trees as measures of habitat-wide fruit availability during each phenological period, following the protocol of previous studies conducted in other tropical forests [31, 32, 33, 34].

Estimates of habitat-wide productivity were calculated on a monthly basis drawing on two monitoring sessions per month. If a tree had ripe fruit for more than one sampling period, but fewer than six, we calculated the proportion of its DBH by using Pascal's triangle coefficients, which assumes a peak of production around the middle of the fruiting season [31]. For example, if the DBH of a particular tree was 80 cm and fruited for four periods we assigned 10 cm, 30 cm, 30 cm, and 10 cm to each of the four fruiting periods respectively. If the production of a single tree was recorded for more than six periods (three months), we divided its DBH into the number of periods assuming a constant production pattern for those trees (see [31] for details). We then added up all the contributions of individual trees (in number of trees and basal area) during each month and assigned this value to the habitat-wide productivity of the forest on that particular biweekly period. In order to better understand the influence of fruit availability on the behavioral ecology of tamarins, we estimated habitat-wide productivity based only on those species that appeared in our phenological sample and were also recorded in the *Saguinus leucopus*' diet.

In order to describe the potential role of the white-footed tamarin as seed disperser, we collected fecal samples opportunistically and counted, identified, and measured the seeds contained in each fecal sample. We also recorded the location and habitat type where each fecal sample was retrieved. We then classified seeds based on their size, as pioneers which included species with a small seed size of <5 mm or non-pioneers which included species with seeds > 5 mm [22]. On the days that we followed our focal groups for long periods (> 6 hours, N=16 days), we collected preliminary data about retention times and seed dispersal distances. We only made these estimations on occasions when we were confident that one or all group members had fed on a single individual of a particular plant species during the early part of a behavioral follow and we subsequently recovered seeds from that species in fecal samples collected later during the same follow.

All statistical analyses were conducted using SPSS Statistics (version 20) with $\alpha = 0.05$. We used non-parametric tests if variables did not conform to conditions of normality and homoscedasticity after transformation. A Mann-Whitney Test was used to assess differences between groups' behavior and monthly diet variability. We used Spearman's rank correlation test to evaluate the relationship between habitat-wide productivity and the tamarins' activity patterns. Simple linear regression was used to determine if productivity affected feeding behavior and habitat use. We used an ANOVA to test if pioneer and non-pioneer seeds were dispersed more frequently in high productivity or low productivity months. The diversity of dietary items (such as fruit, invertebrates and exudates) in the *S. leucopus*' diet was calculated using a Shannon's Index (H') and the diversity of plants consumed by white-footed tamarins during each month of the study was calculated using a richness index (S). We estimated the home ranges and core areas used by the two study groups as 95%, with 50% kernel density estimates, respectively, based on the total set of location records for each group. Maps and spatial analyses were drawn using QGIS with default settings for estimating bandwidth and cell size [35].

Results

Movement was the most common activity of the white-footed tamarin, accounting for 56% of the behavioral records, followed by resting (24%) and feeding (19%). Social behavior accounted only for 1% of the records. Several social events described in previous studies on tamarins [21] were recorded as *ad libitum* events, including social play, grooming, aggression, scent marking, food sharing, and food stealing. We found no difference in the proportion of time that individuals from the two study groups spent on different activities (Mann-Whitney U Test: Feeding: $U=133$, $p=0.70$; Resting: $U=123.5$, $p=0.48$; Moving: $U=127.5$, $p=0.59$; Social: $U=142$, $p=0.94$) (Table 1). In relation to diet, we

found no differences in the food items the two groups fed on, even after applying a Bonferoni correction (Insects: $U=128$, $p=0.07$; Fruits: $U=236.5$, $p=0.897$; Exudates: $U=198$, $p=0.261$). Finally, when analyzing the feeding data describing the duration of feeding bouts, we found no difference in the time each group spent feeding on different items (Fruits: $U=126$, $p=0.94$; Insects: $U=31.5$, $p=0.41$; Exudates: $U=1.5$, $p=0.12$; Others: $U=34$, $p=0.55$) (Table 1). Overall, the activity patterns of the tamarins did not change in relation to changes in forest productivity (Table 2, Fig 2). Resting showed an inverse relationship with productivity, and productivity explained only about one-fifth of the variation in resting time (Table 2).

Table 1. Percentage of time spent by two groups of white footed tamarins on each behavioral category and on feeding on different items. Data on activity patterns and frequency of points for eating each food item were derived from records obtained through scan sampling, while the time spent feeding on each food item was derived from the duration of feeding bouts.

| | Total | | Group A | | Group C | |
|-------------------------|-----------------|------------------|-----------------|------------------|-----------------|------------------|
| Activity Pattern | | | | | | |
| Feeding | 19% | | 19% | | 20% | |
| Moving | 56% | | 56% | | 56% | |
| Resting | 24% | | 24% | | 23% | |
| Socializing | 1% | | 1% | | 1% | |
| Feeding Pattern | | | | | | |
| | Duration | Frequency | Duration | Frequency | Duration | Frequency |
| Fruits | 89% | 66% | 94% | 77% | 84% | 59% |
| Insects | 5% | 16% | 2% | 10% | 7% | 20% |
| Exudates | 1% | 4% | 1% | 3% | 2% | 4% |
| Other | 1% | 2% | 1% | 3% | 1% | 2% |
| Unidentified | 4% | 12% | 2% | 7% | 6% | 15% |

In Remedios, we found that the white-footed tamarin had a diverse diet and fed from at least 95 species of plants belonging to 34 families (Appendix 1). Its diet comprised mainly ripe fleshy fruit, supplemented by insects, plant exudates and a very small proportion of leaves, flowers, and vertebrate prey (Table 2). It did not gouge the trees that it exploited for exudates, and fed on them by superficially licking the tree bark. The white-footed tamarin actively searched for prey in the middle layer of the canopy, exploring holes, bark, old leaves and epiphytes. Individuals caught prey, even in flight, holding onto branches with their hind legs. Infants continuously attempted to steal prey caught by adults. Most feeding trees were subcanopy trees (75.3% $N=437$), although tamarins also fed from canopy trees (22.5%) and understory vegetation (2.2%). The size of trees they fed on varied as well, with DBHs as small as 2.9 cm and as large as 180 cm (mean DBH = $27.5 \pm SD 23.3$ cm).

Table 2. Simple linear regression between habitat-wide productivity (of plant species consumed by *Saguinus*) and behavioral categories (N=22 biweekly periods).

| | F | p-value | r ² | |
|--------------------|------|---------|----------------|--|
| Feeding | 2.36 | 0.140 | 0.11 | |
| Moving | 2.6 | 0.123 | 0.11 | |
| Resting | 5.08 | 0.036 | 0.20 | |
| Socializing | 1.92 | 0.180 | 0.09 | |

The most important plant families in the white-footed tamarin’s diet were Cecropiaceae (17.9%), Fabaceae (13.1%), and Melastomataceae (10.2%) (Appendix 1). Lianas and epiphytes accounted for 25% of food consumption. Of these the most important was *Mendoncia antioquiensis* (Acanthaceae) accounting for 4% of the total diet (Appendix 1). Seven morphospecies included in the diet were not identified to species level and we categorized them as “unidentified”. The tamarins in our study fed on flowers from only three species of plants: *Byrsonima* sp. (Malpighiaceae), *Piper* sp. (Piperaceae), and *Bellucia pentamera* (Melastomataceae). They also fed on leaves from *Leonia glycyarpa* (Violaceae) and on exudates from nine species that they visited only rarely; of these, the most frequently visited were *Simarouba amara* (Simaroubaceae), *Vochysia ferruginea* (Vochysiaceae), and *Macrolobium acaciifolium* (Fabaceae) (Appendix 1). Although species of insect they preyed upon in insect feeding bouts were not identified, at least 18% of those bouts were on grasshoppers (Orthoptera). Finally, we recorded a single feeding bout that included the capture and consumption of an arboreal lizard.

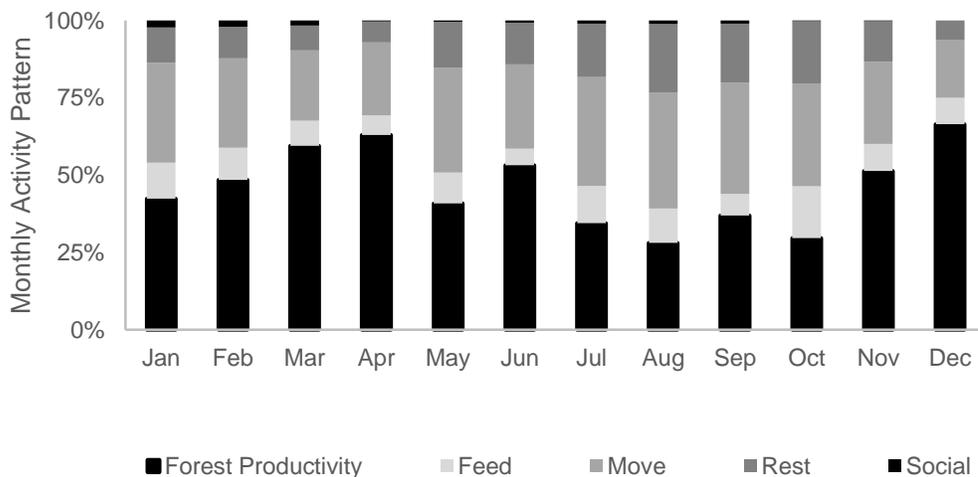


Fig. 2. Activity patterns of white-footed tamarins and fruit productivity at Remedios, Colombia

Forest productivity and feeding behavior.

Although palms were the plant guild that had the highest overall productivity in the forest fragments in Remedios, tamarins fed on palm fruits only 0.6% of the time. Based on our monthly measures of habitat-wide productivity obtained only from those plant species included in white-footed tamarins' diet, we grouped months into two seasons: high productivity months (January, February, March, April, June, November and December) and low productivity months (May, July, August, September and October) (Fig. 3). The three species fed upon most by tamarins during the low season were *Pouroma bicolor* (fruits, 222 minutes), *Leonia glyxicarpa* (leaves and fruits combined, 312 minutes) and *Bellucia pentamera* (fruits, 138 minutes).

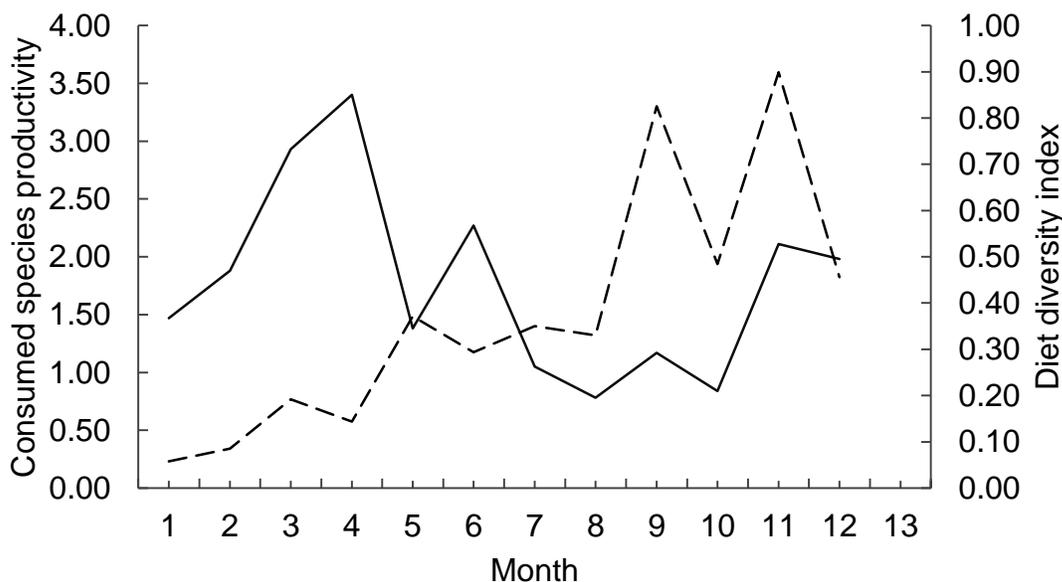


Fig. 3. Forest productivity (solid line) and monthly dietary diversity index (H') (dashed line) for *Saguinus leucopus*.

Habitat-wide productivity influenced the diversity of the tamarins' diet and their feeding behavior. We found that the diversity of food items, measured as the number of species of fruits, insects, and exudates, was inversely related to fruit productivity (simple linear regression: $F(1,20)=10.55$, $p=0.004$, $R^2=0.345$; Fig. 4a) and plant species richness was positively related to fruit productivity (simple linear regression: $F(1,20)=18.75$, $p=0.0003$, $R^2=0.480$; Fig. 4b). We found no relation between the proportion of fruit and productivity in their diet (simple linear regression: $F(1,20)=2.38$, $p=0.142$, $R^2=0.10$), but insect and exudate consumption were inversely related to productivity (insects: $F(1,18)=25.73$, $p=0.0001$, $R^2=0.59$; exudates: $F(1,20)=4.92$, $p=0.038$, $R^2=0.20$). Regardless, fruit was the most common item eaten every month, accounting for at least 50% of the tamarins' diet in every month (Fig. 5).

Seasonality and habitat use

The 3812 location records we generated showed that the white-footed tamarin uses the forest interior most intensively (90%), followed by forest edges (8%). Pastures were mainly used to reach adjacent forest fragments or isolated trees (2%), although the tamarin visited pastures more frequently during months of lower habitat-wide fruit productivity ($H= 4.337, P<0.05, N=12$). The tamarin also used forest edges more often during periods of low fruit productivity, and spent more time in the forest interior during periods of high productivity, but there were not any differences in the pattern of visits and use of any of these habitats between seasons (forest interior: $H= 0.32, P=0.57, N=12$; forest edge: $H=0.54, P=0.46, N=12$). During periods of lower fruit availability, the tamarin also ate the exudates of *Carludovica palmata*, *Cordia bicolor*, and *Macrolobium acaciifolium*. The *Bellucia pentamera* fruit, which was the third most consumed species overall, was mainly eaten during periods of low productivity and tended to be located at the edges of the forest fragments.

Overall, group A had a home range of 31.2 ha and a core area of 9.2 ha, while group C had a home range of 15.0 ha and a core area of 4.5 ha. The home range overlap of these two adjacent groups was 3.0 ha. The two study groups used larger areas during periods of low fruit productivity (group A: 36.8 ha; group C: 16.8 ha) compared to periods of high productivity (group A: 25.8 ha, group C: 15.9 ha). Also, the core areas were larger during periods of low productivity (group A: 10.8 ha; group C: 5.1 ha) compared to periods of high productivity (group A: 7.1 ha, group C: 4.5 ha). Home range overlap was also greater during periods of fruit scarcity (4.2 ha) than during periods of high fruit availability (1.7 ha) (Fig. 6).

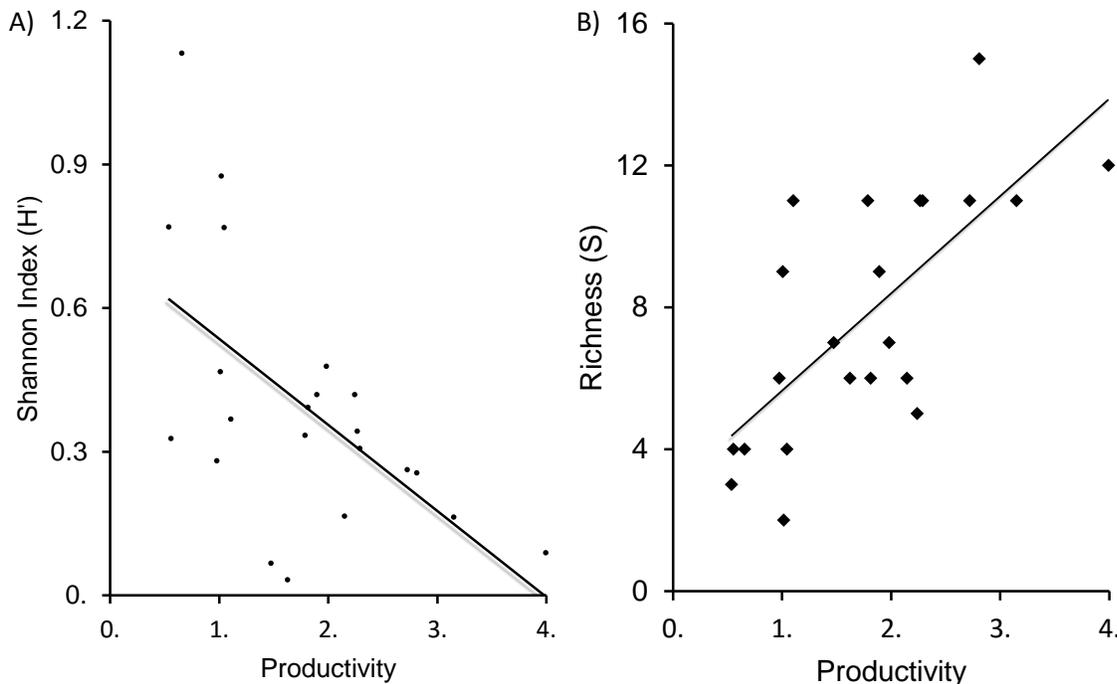


Fig. 4. Simple linear regression between habitat-wide productivity and A) feeding item diversity (H') and B) species richness in the tamarin's diet.

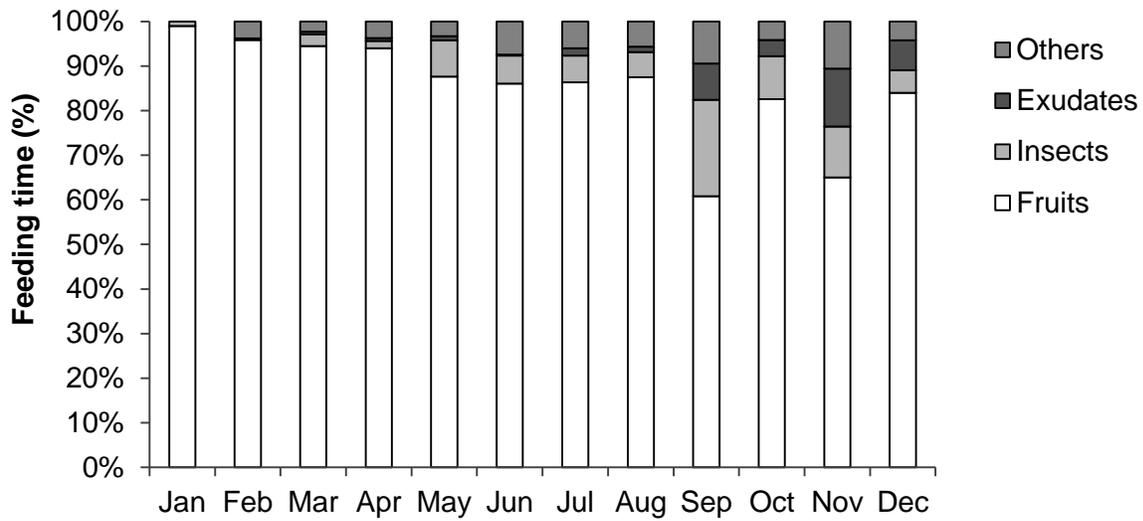


Fig. 5. Monthly variation in the composition of the diet of *Saguinus leucopus*. The category “others” includes flowers, leaves, bark, water, and vertebrate prey.

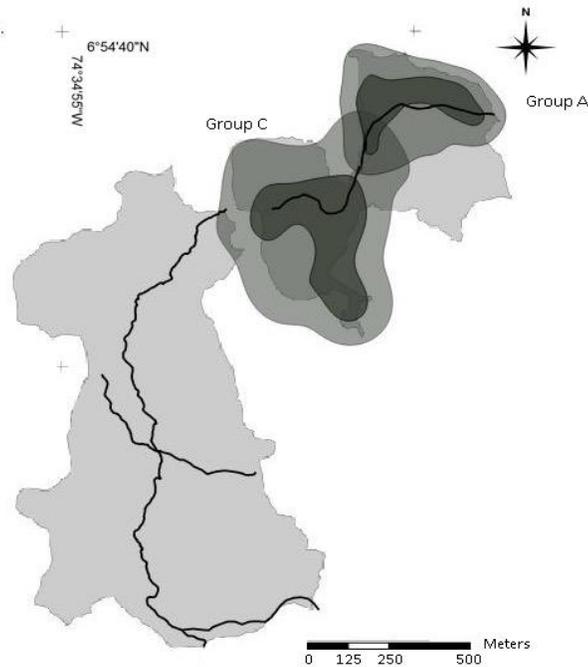


Fig. 6. Study fragments (light grey), home ranges (intermediate grey) and core areas (darker grey) of two groups of *Saguinus leucopus*. Home ranges were defined as 95% kernel density estimates, and core areas as 50% kernel density estimates. The black lines illustrate the trails used for the phenological monitoring of the study site.

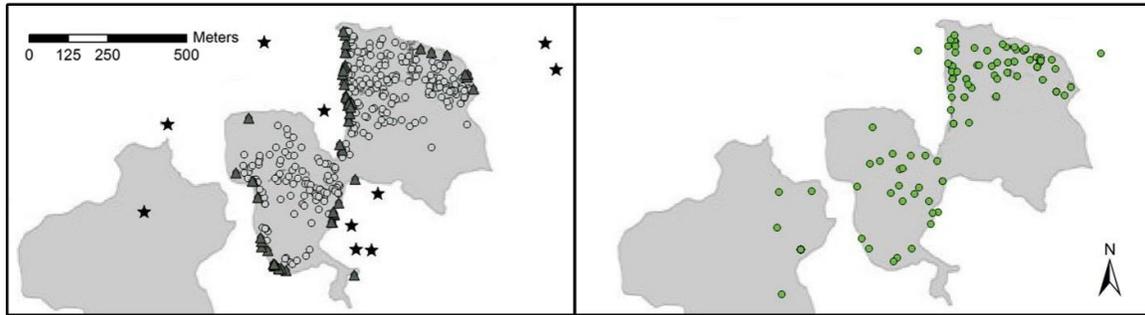


Fig. 7. A) Distribution of feeding trees (Circles = Forest, Triangle = Border, Stars = Pasture) and B) Defecation/seed dispersal sites.

Seed dispersal

Overall, we collected 134 fecal samples in the forest, forest borders, pastures and adjacent forest fragments (Fig. 7). From these samples, we recovered 4246 dispersed seeds from at least 44 species of trees and lianas. Most fecal samples contained between one and five seeds, and 22% of samples contained more than 10 seeds, with a maximum of 504 seeds found in a single sample. Dispersed seeds ranged in size <1 - 26 mm, with an average size of 11 mm. Non-pioneer plants represented 58% of dispersed seeds, while the remaining 42% were from pioneer plants.

Seeds of pioneer species were found in fecal samples more frequently during periods of high productivity than during the low productivity months ($F=8.861$ $P=0.004$). The same trend was seen for non-pioneer seeds ($F=3.440$, $P=0.07$). The four species most represented in fecal samples based on the number of seeds per sample were *Carludovica palmata* (Cyclanthaceae), *Piper sp.* (Piperaceae), *Cecropia obtusifolia* (Cecropiaceae), and *Ficus sp.* (Moraceae). All of these species had small seeds ranging between 0.9 and 2.1 mm. *Carludovica palmata* was also one of the species found in the greatest proportion of fecal samples, along with *Inga sp.* (Fabaceae), *Leonia sp.* (Violaceae), and *Pouroma sp.* (Cecropiaceae). As expected, the tamarin dispersed seeds to all three types of habitats. Based on a limited data set ($N = 16$ days), we estimated an average gut passage time for seeds of 201 min \pm SD 107 min ($N = 52$ samples) and an average dispersal distance of 206 m \pm SD 95 m ($N=51$ samples), with a maximum dispersal distance of 529 m.

Discussion

Seasonality, behavioral patterns, and diet

The white-footed tamarin in Remedios has a diverse diet, similar to that described for other tamarin species. They feed mainly on ripe fruit and supplement their diet with insects, exudates, nectar, leaves, and vertebrate prey [19, 36-39]. The tamarins can access different plant forms vertically distributed from the understory to the forest canopy [22]. During our study, white-footed tamarins fed from trees and lianas from different forest strata and in a variety of substrates, but seldom, if ever, were seen foraging on the forest floor. Although habitats that have been disturbed by anthropogenic activities may have a lower diversity and availability of feeding resources, in Remedios fruit was the main dietary component, suggesting that these forests are still a suitable habitat for *Saguinus*. In fact, in the relatively large forest fragments in Remedios, the tamarin has a more diverse diet compared to those reported in earlier studies of *S. leucopus* in sites such as Mariquita, where

there has been a more intensive human impact on the environment, and where the tamarins have been reported to feed only from 13 plant species over a six month period [39]. Thus, the diet diversity of the white-footed tamarin may decrease when it is restricted to small and more heavily impacted fragments [40].

The white-footed tamarin mainly supplements its frugivorous diet by feeding on insects. However, the contribution of insects to its diet found during this study may be underestimated, given that most feeding bouts on insects took place during short periods that could have been missed by researchers. In Remedios, Orthopterans are presumably a key dietary item for the white-footed tamarin as they accounted for at least 18% of the observed preying bouts. Grasshoppers are reported to be one of the main food items of *S. geoffroyi*, whose diet is composed of 60% to 70% of Tettigonids [17, 41]. Insects are an important food item for small-bodied primates, such as the tamarin, as they may represent a staple food resource during periods of fruit scarcity [17]. Similar to other tamarins, the *S. leucopus* opportunistically feeds on plant exudates, although in Remedios they only represented a small proportion of overall diet [21-23, 42]. We found that the tamarins fed on exudates during those months when habitat-wide productivity was lower, suggesting exudates are a fallback item. Feeding on exudates may be particularly important during periods of scarcity as they can provide carbohydrates, water, proteins and minerals such as calcium, phosphorous, zinc and iron [18, 43, 44].

Similar to what has been found in wild populations of *S. fuscicollis* and *S. mystax* [44], habitat-wide productivity did not explain the proportion of fruit included in the tamarin's diet. Fruit was the main feeding item throughout the year, and variations in fruit consumption between months was relatively small. However, dietary diversity changed substantially throughout the study. The tamarin had a more diverse diet during periods of lower productivity, which included a larger proportion of insects and exudates. Insects may provide key minerals as well as proteins, oligoelements and lipids [43] and may thus become key items in the tamarin's diet, especially during scarcity periods.

Seasonality and habitat use

Our study of the white-footed tamarin showed that the tamarin species is ecological flexible, using different habitats ranging from mature forest to secondary forest, forest borders and pastures [39, 45-47]. During our study, tamarins ventured across pastures almost exclusively during periods of low fruit productivity. They used fences and the ground to cross from one forest fragment to another, or to reach isolated trees within cattle ranching pastures. This behavioral flexibility may well explain how the tamarin copes with landscapes that have undergone intensive anthropogenic activity and where other sympatric species, such as the brown spider monkey (*Ateles hybridus*), are not present [47]. Moreover, the *S. leucopus* may be playing a key role in maintaining the forest dynamics and ecosystem services of the degraded forests of the Magdalena River Valley in Colombia.

Earlier studies of *Saguinus* have suggested that the tamarin frequently uses antipredatory strategies to avoid areas with sparse vegetation for long periods of time, in order to reduce the chances of being detected by aerial predators [48]. Some species of tamarin opportunistically use the forest floor and actively forage for invertebrates even if this might increase their exposure to terrestrial predators (e.g. *Saguinus tripartitus*, Link personal observation). Even though we did not observe tamarins on the forest ground during our study, they did use it to cross to isolated feeding trees or to reach adjacent isolated forest patches. The fact that the white-footed tamarin uses exposed feeding trees within a matrix of pastures during periods of low fruit availability suggests that it might be

willing (or forced) to incur higher predation risks in order to fulfill its nutritional requirements during periods of scarcity.

The white-footed tamarin uses larger home ranges and core areas during periods of fruit scarcity, likely as a strategy to cover greater distances and to use larger areas in order to obtain the resources needed for all group members. In addition, overlap areas between the two study groups were larger (although they represented a small fraction of their territories) during the period of fruit scarcity. These results support the hypothesis that, as groups increase in size, or as fewer resources are available, social groups will need to cover larger areas in order to fulfill each individual group member's energetic and nutritional requirements [49].

Seed dispersal

The white-footed tamarins in our study dispersed seeds from at least 44 plant species, including pioneer and non-pioneer plants throughout the year. Given their small body size, they dispersed relatively large seeds (up to 26 mm) [50], as has previously been described for *S. mystax* and *S. fuscicollis* [22]. Retention times and dispersal distances estimated in this study fall within the range reported for other tamarins [20, 21] and demonstrate the ability of tamarins to move seeds away from parental trees. Their dispersal shadow reached different habitats, including degraded habitats such as edge forests or pastures.



Fig. 8. (A) Juvenile of white footed tamarin (B) Fragmented landscape at study site (C Fruit of the species with the largest average seed size dispersed by white footed tamarins (*Diospyros vestita*) (D) Adult feeding on fleshy fruit (*Protium sp.*) (E) Adult tamarin using a fence to access trees in the pastures (Photos taken by: (a,c) Daniela Ramirez, (b) Ivan Gonzalez, (d) Yesenia García-Morera, (e) John Aristizabal)

Implications for Conservation

Early stages of forest regeneration in fragmented landscapes require abiotic factors, bats and birds [51, 52] as primary seed dispersal agents. It has been proposed that neotropical primates influence later stages of forest regeneration through their seed dispersal services as they are assumed to be unable to use highly degraded areas such as pastures. We found, however, that the white-footed tamarins in our study dispersed seeds across fragments in the earlier stages of forest succession (Fig. 8). They also dispersed both small and large seeds into habitats such as pastures and second growth forests. We can thus conclude that the tamarin increases dispersal services for many plant species, especially subcanopy and canopy trees and lianas. Finally, in areas where large mammals have been extirpated the role of the *S. leucopus* might become crucial for large-seeded trees and lianas, as they may partially compensate seed dispersal services [53].

Acknowledgments

We thank all field assistants and collaborators involved in this research project, and special thanks to Angela Sanchez for her contribution to data collection during part of this study. We also thank Natalia Alvis, Ciro Velez, Eliana Yepes, Daniela Ramirez, Nelson Galvis and Jacobo Campuzano for all their help in the field. This study was possible thanks to the support of Gustavo Campuzano and his family who are preserving the forest fragments where these primates live and who provided logistical support for all team members. We thank Paul Garber, Anthony Di Fiore, Siobhan Cooke and an anonymous reviewer whose comments significantly improved the quality of the manuscript. This study was funded by the Conservation Leadership Programme (CLP) and the Mohamed Bin Zayed Species Conservation Fund. This research complies with all legal and ethical requirements in Colombia.

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Appendix 1. Plant species fed upon by *Saguinus leucopus*

| Family | Species | Feeding time | | Item ^a | Habitus |
|--------------|--|--------------|------|-------------------|---------|
| | | M i n | % | | |
| Acanthaceae | <i>Mendoncia antioquiensis</i> | 144 | 4.09 | Fr | Liana |
| | <i>Mendoncia lindavii</i> | 41 | 1.16 | Fr | Liana |
| Annonaceae | <i>Duguetia antioquiensis</i> | 1 | 0.03 | Fr | Tree |
| | <i>Guatteria recurvisepala</i> | 6 | 0.17 | Fl | Tree |
| | <i>Guatteria</i> sp. | 91 | 2.58 | Fr | Tree |
| | <i>Rollinia pittieri</i> | 1 | 0.03 | Fr | Tree |
| Apocynaceae | <i>Lacmellea panamensis</i> | 50 | 1.42 | Fr | Tree |
| | <i>Tabernaemontana amplifolia</i> | 1 | 0.03 | Fr | Tree |
| Araceae | Araceae sp. | 1 | 0.03 | Fr | Liana |
| | <i>Monstera pinnatipartita</i> | 11 | 0.31 | Fr | Liana |
| | <i>Monstera</i> sp. | 2 | 0.06 | Fr | Liana |
| | <i>Philodendron</i> cf. <i>heleniae</i> | 3 | 0.09 | Fr | Liana |
| | <i>Syngonium</i> cf. <i>macrophyllum</i> | 5 | 0.14 | Fr | Liana |
| | <i>Syngonium crassifolium</i> | 2 | 0.06 | Fr | Liana |
| Arecaceae | Arecaceae sp. | 1 | 0.03 | xx | Tree |
| | <i>Oenocarpus bataua</i> | 5 | 0.14 | Fr | Tree |
| | <i>Oenocarpus mapora</i> | 5 | 0.14 | Fr | Tree |
| | <i>Wettinia hirsuta</i> | 24 | 0.68 | Fr | Tree |
| Bombacaceae | <i>Quararibeacaldasiana</i> | 35 | 0.99 | Fr | Tree |
| Boraginaceae | <i>Cordia bicolor</i> | 1 | 0.03 | Fr | Tree |
| | <i>Cordia</i> sp. | 12 | 0.34 | Fr | Tree |
| Burseracea | <i>Crepidospermum rhoifolium</i> | 51 | 1.45 | Fr | Tree |

| | | | | | |
|-----------------|--------------------------------------|-----|-------|----------|-------|
| | <i>Protium calanense</i> | 2 | 0.06 | Fr | Tree |
| | <i>Protium sp.</i> | 48 | 1.36 | Fr | Tree |
| | <i>Tetragastris panamensis</i> | 4 | 0.11 | Fr | Tree |
| Caesalpinaceae | <i>Dialium guianense</i> | 7 | 0.20 | Fr | Tree |
| | <i>Macrolobium cf. acaciifolium</i> | 7 | 0.20 | Ex | Tree |
| Caryocariaceae | <i>Caryocar glabrum</i> | 2 | 0.06 | Fr | Tree |
| Cecropiaceae | <i>Cecropia obtusifolia</i> | 33 | 0.94 | Fr | Tree |
| | <i>Pouroma bicolor</i> | 530 | 15.04 | Fr | Tree |
| | <i>Pouroma cecropiifolia</i> | 101 | 2.87 | Fr | Tree |
| Convolvulaceae | <i>Maripa cf. nicaraguensis</i> | 9 | 0.26 | Fr | Liana |
| Costaceae | <i>Dimerocostus strobilaceus</i> | 3 | 0.09 | Fr | Shrub |
| Cyclanthaceae | <i>Carludovica palmata</i> | 1 | 0.03 | Fr | Shrub |
| | <i>Evodianthus funifer</i> | 4 | 0.11 | Fr | Liana |
| Dilleniaceae | <i>Doliocarpus brevipedicellatus</i> | 36 | 1.02 | Fr | Liana |
| Ebenaceae | <i>Diospyros vestita</i> | 312 | 8.86 | Fr/Ex | Tree |
| Fabaceae | <i>Inga edulis</i> | 3 | 0.09 | Fr | Tree |
| | <i>Inga pezizifera</i> | 430 | 12.21 | Fr/Ex | Tree |
| | Fabaceae sp. | 13 | 0.37 | Fr/Ot/Ex | Tree |
| Flacourtiaceae | <i>Banara cf. guianensis</i> | 5 | 0.14 | Fr | Tree |
| Hypericaceae | <i>Vismia baccifera</i> | 6 | 0.17 | Fr | Tree |
| | <i>Vismia sp.</i> | 5 | 0.14 | Fr | Tree |
| Lauraceae | Lauraceae sp. | 2 | 0.06 | Fr | Tree |
| Lecythidaceae | <i>Lecythis mesophylla</i> | 2 | 0.06 | Fr | Tree |
| Malpighiaceae | <i>Byrsonima sp.</i> | 1 | 0.03 | Fl | Tree |
| Melastomataceae | <i>Bellucia grossularioides</i> | 26 | 0.74 | Fr | Tree |
| | <i>Bellucia pentamera</i> | 161 | 4.57 | Fr/Fl | Tree |
| | <i>Bellucia sp.</i> | 115 | 3.26 | Fr | Tree |

| | | | | | |
|----------------|---|-----|------|-------|-------|
| | <i>Miconia minutiflora</i> | 53 | 1.50 | Fr | Tree |
| | <i>Tessmannianthus</i> sp. | 5 | 0.14 | Fr | Tree |
| Menispermaceae | <i>Odontocary atripetala</i> | 44 | 1.25 | Fr | Liana |
| | <i>Orthomene schomburgkii</i> | 48 | 1.36 | Fr | Liana |
| | Menispermaceae sp. | 1 | 0.03 | Fr | Liana |
| Mimosaceae | <i>Mimosa</i> sp. | 4 | 0.11 | Fr | Tree |
| Moraceae | <i>Brosimum guianense</i> | 42 | 1.19 | Fr | Tree |
| | <i>Cestrum</i> sp. | 32 | 0.91 | Fr | Tree |
| | <i>Helicostylis tomentosa</i> | 1 | 0.03 | Fr | Tree |
| | <i>Pseudolmedia laevigata</i> | 25 | 0.71 | Fr | Tree |
| Myristicaceae | <i>Virola</i> sp. | 1 | 0.03 | Fr | Tree |
| Myrtaceae | <i>Calyptranthes killipii</i> | 1 | 0.03 | Fr | Tree |
| | <i>Eugenia florida</i> | 4 | 0.11 | Fr | Tree |
| | Myrtaceae sp. | 28 | 0.79 | Fr | Tree |
| Passifloraceae | Passifloraceae sp. | 5 | 0.14 | Fr | Liana |
| Piperaceae | <i>Piper</i> sp. | 4 | 0.11 | Fr/Fl | Shrub |
| Rubiaceae | <i>Faramea occidentalis</i> | 55 | 1.56 | Fr | Tree |
| | <i>Psychotria monsalvae</i> | 2 | 0.06 | Ex | Tree |
| | <i>Psychotria</i> sp. | 2 | 0.06 | Fr | Tree |
| Sapotaceae | <i>Chrysophyllum argenteum</i> | 5 | 0.14 | Fr | Tree |
| | <i>Chrysophyllum</i> cf. <i>argenteum</i> | 1 | 0.03 | Fr | Tree |
| | <i>Pouteria</i> sp.1 | 221 | 6.27 | Fr/Ex | Tree |
| | <i>Pouteria</i> sp.2 | 28 | 0.79 | Fr | Tree |
| Simaroubaceae | <i>Simarouba amara</i> | 138 | 3.92 | Fr/Ex | Tree |
| Violaceae | <i>Leonia glydicarpa</i> | 321 | 9.11 | Fr/L | Tree |
| | <i>Leonia triandra</i> | 10 | 0.28 | Fr | Tree |
| Vochysiaceae | <i>Vochysia ferruginea</i> | 8 | 0.23 | Fr/Ex | Tree |

| | | | | | |
|---------------|-----------|-------------|-------------|----|--------------|
| Unidentified | Sp. 1 | 5 | 0.14 | Fr | Unidentified |
| Unidentified | Sp. 2 | 19 | 0.54 | Fr | Unidentified |
| Unidentified | Sp. 3 | 11 | 0.31 | Fr | Liana |
| Unidentified | Sp. 4 | 1 | 0.03 | Fr | Tree |
| Unidentified | Sp. 5 | 13 | 0.37 | Fr | Tree |
| Unidentified | Sp. 6 | 11 | 0.31 | Fr | Tree |
| Unidentified | Sp. 7 | 13 | 0.37 | Fr | Liana |
| Total: | 84 | 3523 | 100% | | |

^aThe items eaten are abbreviated as follows: Fr = Fruits; L = Leaves; Fl = Flowers;
Ex = Exudates; Ot = Other.
