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## Implications of habitat fragmentation on the diet of bearded saki monkeys in central Amazonian forest

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Forest fragmentation demonstrably alters plant species composition, distribution, and diversity, and, in turn, may affect the availability of food resources for primary consumers. We investigated to what extent fragmentation affected the diets of 6 groups of bearded saki monkeys (*Chiropotes chiropotes*) living in two 10-ha fragments, two 100-ha “fragments” that were no longer fully isolated, and 2 areas of continuous forest in central Amazonia. When changes occurred we tested whether differences in diet were due to plant species availability by comparing the prevalence of consumed items against their relative abundance at the 6 sites. In total, the monkeys consumed fruits, seeds, flowers, and leaves of 244 plant species, of which less than 2% were shared among all 6 groups. Although there was a positive correlation between relative abundance of diet species and consumption frequency, monkeys did not eat all available potential resources, and groups inhabiting the 10-ha fragments consumed items that were ignored in larger forested areas. Our findings suggest that bearded sakis living in small forest fragments are limited in their dietary choices as a consequence of the reduced number of plant species present, and therefore consume species that monkeys inhabiting continuous forests typically can ignore. We conclude that the ability to consume a diverse diet that includes seeds and unripe fruit helps this species survive in forest fragments, but it appears that these conditions are unviable unless connectivity increases among the forest fragments and continuous forest in the landscape.

Key words: Brazil, *Chiropotes*, forest fragment, frugivore, primate, seed predator

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Deforestation remains a widespread phenomenon throughout the Brazilian Amazon (Broadbent et al. 2008; Fearnside and Graça 2006). As these forests are removed, the remaining forest fragments are subject to abiotic (Achard et al. 2002; Broadbent et al. 2008; Kapos et al. 1997) and biotic (Bierregaard et al. 1992; Laurance et al. 1997) factors that subsequently may alter habitat suitability for the remaining fauna (Gascon et al. 2001; Laurance et al. 2000b). The extent of these ecological changes varies in time and space depending on characteristics of the remaining forest, the surrounding matrix, and local meteorological events (Laurance et al. 2011).

Central Amazonian forests harbor exceptionally high tree diversity, with approximately 280 tree species per hectare (de Oliveira and Daly 1999; de Oliveira and Mori 1999). Long-

term research projects on the impact of forest fragmentation on plant communities indicated that tree and liana species composition and richness in small 1-ha and 10-ha fragments were substantially altered from those typical of contiguous terra firme forests (Laurance et al. 1998, 2001). These changes in plant composition are primarily the result of increased tree mortality rates (Laurance et al. 2000a) and decreased species richness in the seedling community (Benítez-Malvido and Martínez-Ramos 2003), as well as the invasion of successional, pioneer tree species near the edge of small (1-ha and 10-ha)



fragments (Gascon et al. 2000; Laurance et al. 2006b). Changes in plant species richness, diversity, and composition also can impact the diet of animals living in forest fragments (Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Onderdonk and Chapman 2000), and may ultimately lead to the consumption of less-nutritious items (González-Zamora et al. 2009; Irwin 2008).

Primates vary in their overall diet composition and their dietary flexibility (Chapman and Chapman 1990; Estrada and Coates-Estrada 1988). Leaves, for example, can comprise as little as 25% to as much as 79% of a howler monkey's (*Alouatta* spp.) diet (Gaulin and Gaulin 1982; Julliot and Sabatier 1993; Palacios and Rodríguez 2001). Such flexibility in an individual species' diet has been linked to its ability to subsist in small areas (Bicca-Marques 2003; Estrada and Coates-Estrada 1996; Ferrari et al. 2003). In contrast to howler monkeys, frugivorous primates typically require large home ranges (Clutton-Brock and Harvey 1977; Milton and May 1976; Onderdonk and Chapman 2000); yet some species with large home ranges (e.g., *Ateles* spp. and *Chiropotes* spp.) sometimes reside in forest fragments that are drastically smaller than the species' characteristic home-range size (Boyle and Smith 2010a; Port-Carvalho and Ferrari 2004; Ramos-Fernández et al. 2004; Silva and Ferrari 2009).

Fruits and seeds are spatiotemporally variable resources (Foster 1982; Wheelwright 1986). Animals that rely on these resources for sustenance must find ways to obtain adequate resources during periods of low food availability through changes in diet and foraging behavior (van Schaik et al. 1993). Primates in some locales exhibit seasonal differences in fruit, flower, and insect consumption (e.g., *Ateles geoffroyi* [González-Zamora et al. 2009]; and *Ateles belzebuth*, *Lagothrix lagotricha*, *Cebus apella*, and *Alouatta seniculus* [Stevenson et al. 2000]), whereas some primates are influenced by the availability of a few key species (e.g., *Ateles chamek*—Felton et al. 2008), and some in other locales do not exhibit changes in diet related to resource availability (e.g., *A. geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*—Chapman 1988).

Feeding ecology studies of primates living in forest fragments or on islands also have shown variability in the primates' dietary responses (e.g., *A. palliata* [Cristóbal-Azkarate and Arroyo-Rodríguez 2007]; and *Pithecia pithecia* and *Chiropotes chiropotes* [Norconk 1996; Peetz 2001]). Although diademed sifakas (*Propithecus diadema*) in continuous forest had greater diet diversity than diademed sifakas living in forest fragments (Irwin 2008), black howler monkeys (*Alouatta pigra*) had greater diet diversity in forest fragments than in continuous forest, possibly due to the absence of a preferred food (*Ficus* spp.) in the forest fragments (Rivera and Calmé 2006). Tutin (1999) compared the diets of 5 African primates and found that all but 1 consumed more insects and leaves (and less fruit, seeds, and flowers) in forest fragments.

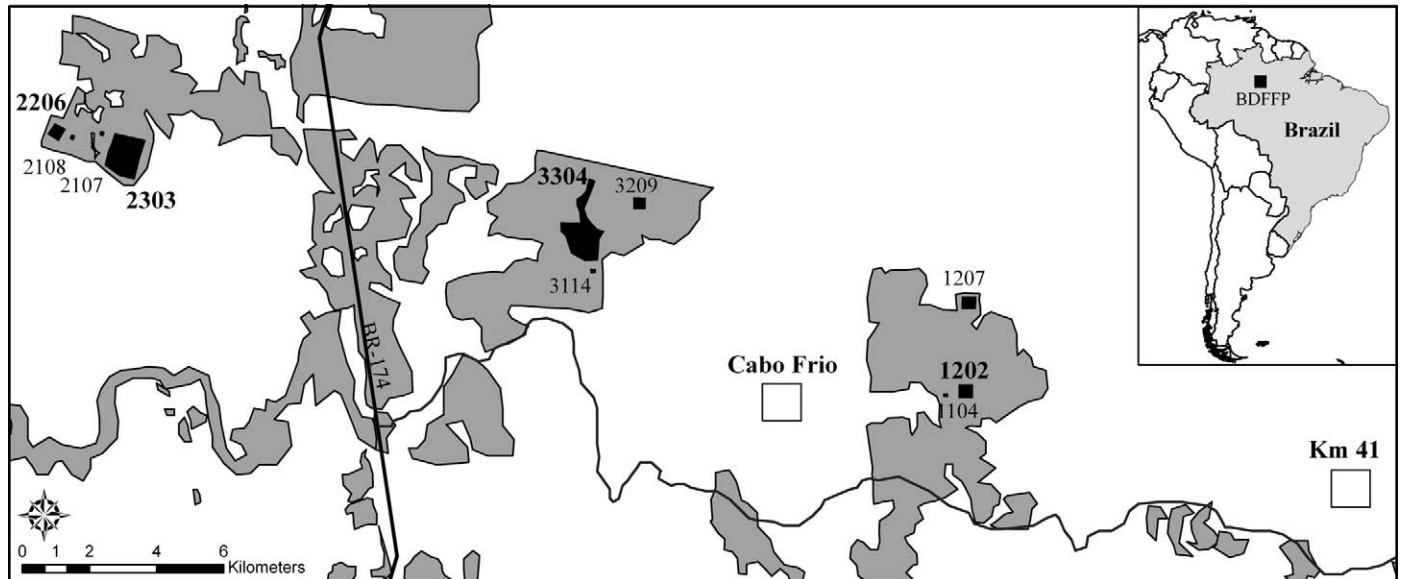
The purpose of our study was to determine if the diet of the bearded saki monkey (*C. chiropotes*) was impacted by forest fragmentation. The bearded saki monkey is a medium-bodied

(2.8-kg) monkey (Ford and Davis 1992). Bearded saki monkeys obtain approximately 88% of their diet from fruits and seeds (Ayres 1981; Frazão 1992; Kinzey and Norconk 1990; van Roosmalen et al. 1981). They also consume flowers, leaves, and arthropods, in smaller quantities (Frazão 1991; Norconk 1996; Peetz 2001; Veiga and Ferrari 2006). Although bearded sakis living in continuous forest have large home ranges of 200–559 ha (Ayres 1981; Boyle et al. 2009; van Roosmalen et al. 1981), other studies have found bearded sakis living in forest fragments as small as 8 ha (Port-Carvalho and Ferrari 2004) and on lake islands (17–365 ha) created by hydroelectric dams (Norconk 1996; Peetz 2001; Veiga and Ferrari 2006). It is possible that the high proportion of seeds in their diet helps bearded sakis during periods of low food availability (Norconk 1996, 2007), and seed-eating can minimize competition with other frugivores for resources (van Roosmalen et al. 1988). Our specific goal was to evaluate the feeding ecology of this monkey by determining to what extent dietary differences among groups of monkeys were attributable to the specific plant composition of the forest fragments.

Marked differences in plant species composition and diversity exist among the various forest fragments and continuous forest at the study site (Benítez-Malvido and Martínez-Ramos 2003; Laurance et al. 2006a, 2006b). Therefore we predicted that bearded saki monkeys living in the 10-ha fragments would consume different plant species, consume fewer plant species, and have greater seasonal differences in diet composition than animals living in continuous forest. Because large trees suffer greater mortality rates in proximity to (<300 m) fragment edges (Laurance et al. 2000a), we predicted that bearded saki monkeys in the 10-ha fragments would feed from trees with smaller diameter at breast height than monkeys in the continuous forest. Furthermore, we also expected that differences in dietary composition would be related to the plant composition of the forest in which the animals were living, and that monkeys living in small fragments would be forced to consume items not regularly a part of the typical bearded saki diet in continuous-forest habitats.

## MATERIALS AND METHODS

*Study site and species.*—We conducted this study at the Biological Dynamics of Forest Fragments Project (BDFFP), a long-term project on fragmentation approximately 80 km north of Manaus, Brazil (Fig. 1). The BDFFP forest fragments range in size from 1 ha to 100 ha, and they were initially isolated from the continuous forest by distances of 70–1,000 m 30 years ago (Laurance et al. 2006b). During our study in 2005–2006 bearded sakis were present in two 10-ha fragments (fragments 1,202 and 2,206) and two 100-ha “fragments” (“fragments” 2,303 and 3,304). The two 100-ha “fragments” were no longer fully isolated, but the 10-ha fragments remained isolated and bearded saki monkeys did not leave these two 10-ha fragments



**FIG. 1.**—Biological Dynamics of Forest Fragments Project (BDFFP) study site. The 6 study areas are indicated on the map in bold and larger font. Black polygons indicate BDFFP forest fragments, whereas gray polygons indicate the matrix and white polygons represent continuous forest. Figure adapted from Boyle (2008).

(Boyle and Smith 2010b). Because of the lack of movement in and out of the 10-ha fragments by the bearded saki monkeys, but frequent movements in and out of the 100-ha “fragments,” we define the two 10-ha fragments as fully isolated forest fragments, whereas the two 100-ha “fragments” are forested areas used by the bearded saki monkeys in a larger landscape.

We studied the diet of 6 groups of bearded sakis of which the average group size was 3.6 and 4 individuals in the 10-ha fragments (fragments 1,202 and 2,206, respectively), 10.3 and 13.5 individuals in the 100-ha “fragments” (“fragments” 2,303 and 3,304, respectively), and 21.7 and 25.3 individuals in the continuous-forest sites (Km41 and Cabo Frio, respectively—Boyle and Smith 2010a). A subadult male was in 1 of the 1-ha fragments (fragment 2,107) in 2003; however, none of the 1-ha fragments were occupied by bearded sakis in 2005–2006 and no bearded sakis were present in 10-ha fragment 3,209 (Boyle and Smith 2010a). There was never more than 1 bearded saki group in a fragment, but monkeys in the small fragments lived at greater densities than did monkeys in the continuous forest (Boyle and Smith 2010a). Study groups from the continuous forest did not overlap with other groups of bearded saki monkeys. Single-offspring births occurred in both 100-ha groups and both continuous-forest groups in October–November 2005; however, neither of the two 10-ha groups had infants or young juveniles throughout the study period (Boyle and Smith 2010a). Mean ( $\pm$  SE) day ranges were smaller in the 10-ha fragments ( $4.87 \pm 0.02$  ha) than in the 100-ha “fragments” ( $23.40 \pm 0.46$  ha) and continuous forest ( $32.92 \pm 4.27$  ha). Monkeys in the small fragments used the entire area of the fragment during the study; home ranges for the bearded sakis in the continuous forest were 559 ha (Km41) and 300 ha (Cabo Frio); home range was unknown for the bearded saki monkeys

using the two 100-ha “fragments” because these animals were not permanent residents of the “fragments” (Boyle et al. 2009).

The taxonomy of the genus *Chiropotes* is debated (Bonvicino et al. 2003; Hershkovitz 1985; Silva and Figueiredo 2002). Bonvicino et al. (2003) recognized bearded sakis west of the Branco River as *C. israelita* and bearded sakis east of the river as *C. chiropotes*, but Silva and Figueiredo (2002) referred to populations west of the river as *C. chiropotes* and those animals east of the river as *C. sagulatus*. Due to the disagreement, the International Union for the Conservation of Nature and Natural Resources (Veiga et al. 2008) used *C. chiropotes* for bearded saki monkeys north of the Amazon River, but on either side of the Branco River. In this study we follow the International Union for the Conservation of Nature and Natural Resources (2011) and use *C. chiropotes*, because the individuals we studied were located north of the Amazon River and east of the Branco River. The International Union for the Conservation of Nature and Natural Resources categorized the conservation status of *C. chiropotes* as Least Concern (Veiga et al. 2008). However, in recent years there has been an increase in human activities (e.g., deforestation, fires, and hunting) in the immediate study area (Laurance and Luizão 2007), which may greatly impact the conservation of the BDFFP primate populations (Boyle 2008). The other *Chiropotes* species, which are experiencing habitat loss and hunting pressures as well throughout their ranges in South America, are listed as Endangered or Critically Endangered (International Union for the Conservation of Nature and Natural Resources 2011).

**Data collection.**—From January 2005 to April 2006 we collected dietary data on the 6 groups of bearded saki monkeys. Because the 2 groups in the 100-ha “fragments” repeatedly left and reentered the forest fragments, this study focused on how

the 2 groups in the isolated 10-ha fragments differed from those animals not living in small, isolated forest fragments. Data collection consisted of a cycle through each of the forest fragments and 2 continuous-forest sites. We spent 4 days in each of the 6 study sites per data collection cycle. On day 1 we collected phenological data (see detailed methods below). On days 2–4 we tracked the bearded sakis and collected diet data. After 1 cycle through the 6 sites, we returned to the 1st site and repeated the cycle again, totaling 5 data cycles for all bearded saki groups except for the group in 1 of the 10-ha fragments (fragment 1,202), which had a 6th data cycle due to additional time available for data collection. Only the results from 5 data cycles were used in statistical comparisons. The dates of the cycles were: cycle 1: 17 January–4 April 2005; cycle 2: 13 April–22 June 2005; cycle 3: 5 August–10 October 2005; cycle 4: 19 October–12 December 2005; and cycle 5: 18 January–27 March 2006 (Boyle et al. 2009).

*Phenological data collection.*—We collected phenological data at each site for all 5 data cycles to quantify food resource availability (number of individuals with fruits or flowers per 100 m) in the 6 sites. We walked linear transects in each of the study areas, following methods similar to those of Barlow and Peres (2006) and Jorge (2007). Each 10-ha fragment had 2 parallel 330-m transects that went from one edge of the fragment to the other. Each 100-ha “fragment” had 1 linear 1,000-m transect that went from one edge of the fragment to the other. In the continuous forest, 10-ha and 100-ha study plots were demarcated in both continuous-forest study areas. Within each plot, we walked linear transects that were equivalent in width and length to those of their forest fragment counterparts.

We walked slowly along the transects, scanning the canopy for fruits using binoculars ( $8 \times 42$  magnification). All trees, lianas, and hemiepiphytes with fruits or flowers were counted and identified to genus, and their geographic positioning system location was recorded. We classified the fruit state (unripe or ripe) and flower state (bud or mature). The numbers of individuals with fruits or flowers were separately tallied per 100 m in each of the 6 sites for each cycle. We obtained monthly rainfall data from the BDFFP Web site (<http://pdfff.inpa.gov.br>) for the duration of the study period.

*Bearded saki data collection.*—We located the sleeping trees for each group and tracked each bearded saki group from the time the monkeys awoke in the morning until the time they settled down for the night. On 5-min intervals we scanned all sighted individuals of the group (Altmann 1974), and recorded the activity of each group member, and the group’s geographic location using a handheld global positioning system (GPS) receiver. All groups were habituated to our presence prior to the start of the study. If individuals were eating fruits, seeds, flowers, or leaves, the behavior was recorded and the tree, liana, or hemiepiphyte location was marked with plastic flagging and assigned a unique number. The number identification system allowed for the subsequent species identification. At each feeding site we recorded its GPS coordinates, the diameter at breast height of feeding trees, as

well as the condition of the fruits (ripe or unripe), seeds (ripe or unripe), flowers (mature or buds), or leaves (mature or immature) that were consumed. Feeding sites were relocated using the maps we produced from the GPS data. For species identification, we collected leaf and stem samples, which were verified for identification with voucher specimens at the Instituto Nacional de Pesquisas da Amazônia herbarium in Manaus, Brazil.

We confirmed that the general group was the same throughout each cycle based on the appearance of particular infants, juveniles, or adults for all study sites. Data collection was noninvasive and our research followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011), and was approved by the Conselho Nacional de Desenvolvimento Científico e Tecnológico in Brazil.

*Diet comparisons among study sites.*—To determine whether differences in diet among the groups were a result of plant species availability in the forest fragments, we used the BDFFP tree database to compare the dietary tree species with their relative abundance in each study site. This database was established for a long-term monitoring project (Laurance et al. 2006a), and provided the scientific names for a sample of trees in each of the 6 study sites where bearded saki monkeys were present in 2005–2006. The database contained data for 6,256 trees in fragment 1,202, 2,296 trees in fragment 2,206, 6,251 trees in “fragment” 2,303, 6,032 trees in “fragment” 3,304, 1,892 trees at Km41, and 5,337 trees at Cabo Frio.

*Data analysis.*—To determine if there were fluctuations in resources with seasonal rainfall patterns, we compared monthly precipitation with the number of flowering and fruiting trees, lianas, and hemiepiphytes per 100 m along the phenology transects using Spearman’s rank correlation (Zar 1999). To determine if resource abundance (number of individuals with fruit or flowers per 100 m) varied across forest size classes and data cycles, we used repeated-measures analysis of variance (ANOVA).

We determined the proportion of fruit, seeds, flowers, insects, and leaves in the bearded saki monkeys’ diets for each study group, as well as the proportion of the diet that came from trees, lianas, and hemiepiphytes. We calculated the proportion of time spent feeding on each plant species using the number of feeding records per species and the total feeding records, and determined the number of plant families, genera, and species consumed per hour. Comparisons among groups’ number of feeding sites, proportion of seeds and unripe fruits in the diet, and the diameter at breast height of the feeding trees in 10-ha fragments, 100-ha “fragments,” and continuous forest were made using 1-way ANOVA. All proportional data were arcsine square-root transformed to fit a normal distribution.

We used a *G*-test to determine whether the distribution of the unique dietary species varied among the 6 study sites. We tested whether the relative abundance of diet items was correlated with the relative abundance of the species and genera in the tree database using Spearman’s rank correlation. We calculated Cooks’ *D*-values for each genera, and considered values  $> 1.0$  to indicate that a genus was an outlier.

## RESULTS

**Phenology.**—Overall monthly fruit abundance (number of fruiting trees, lianas or hemiepiphytes per 100 m) was positively correlated to monthly precipitation ( $r_s = 0.58$ ,  $P = 0.024$ ), with lowest abundance from June to October 2005. Fruit abundance differed among the 5 data cycles ( $F_{4,4} = 8.08$ ,  $P = 0.034$ ), but neither forest size class nor the interaction of forest size class and cycle affected the number of fruiting individuals per 100 m ( $P > 0.10$  for both). Flower abundance was negatively correlated with precipitation ( $r_s = -0.53$ ,  $P = 0.043$ ), with values peaking in November. Although flower abundance fluctuated, the differences among the 5 cycles were not significant ( $F_{4,4} = 5.83$ ,  $P = 0.058$ ), and there were no differences among forest size classes or the interaction between forest size and cycle ( $P > 0.10$  for both).

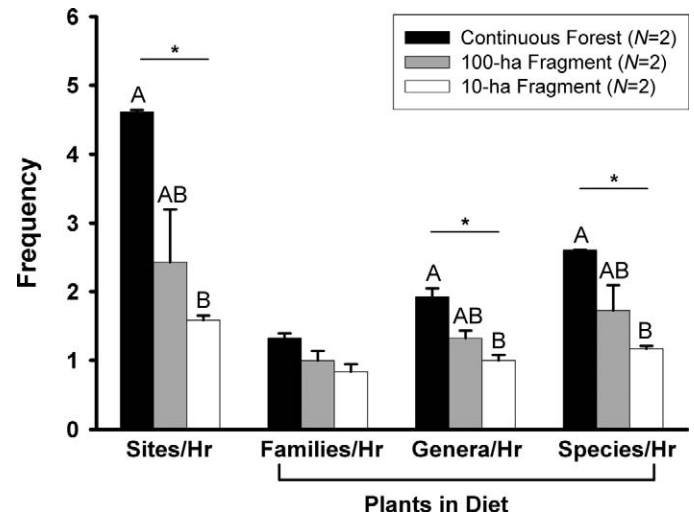
**Diet.**—We spent 535 contact hours with the monkeys. Contact hours were not evenly distributed among the 6 groups (range: 33.25–161.84 h) because the two 100-ha groups were not permanent residents of the 100-ha “fragments,” and we encountered difficulties tracking the monkeys at continuous-forest site Cabo Frio.

During the behavioral scan samples, we observed the 6 groups of bearded saki monkeys consuming items from 993 trees, lianas, and hemiepiphytes. These items included 47 families, 115 genera, and 244 species. The families Sapotaceae, Lecythidaceae, Chrysobalanaceae, and Euphorbiaceae were most prevalent overall in the bearded sakis’ diet. We could not identify 19 of the 993 specimens.

Diet patterns differed among forest size classes, because monkeys in the 10-ha fragments used fewer feeding sites per hour ( $F_{2,3} = 12.4$ ,  $P = 0.04$ ) and consumed fewer plant genera ( $F_{2,3} = 19.5$ ,  $P = 0.02$ ) and species ( $F_{2,3} = 11.4$ ,  $P = 0.04$ ) per hour than monkeys in the continuous forest (Fig. 2). Monkeys in the 100-ha “fragments” did not statistically differ in feeding patterns from those monkeys in the continuous forest and 10-ha fragments. There was no difference among forest size classes in the number of plant families consumed per hour ( $F_{2,3} = 4.94$ ,  $P = 0.11$ ).

Overall, based on 7,064 feeding records of the 6 groups, bearded sakis consumed seeds (76.6%), fruit (15.9%), flowers and buds (4.3%), insects (2.5%), and leaves (0.7%). The seeds and fruit were from unripe (54.6%) and ripe (45.4%) fruits. Diets for each of the 6 groups varied, but only the proportion of unripe seeds ( $F_{2,3} = 10.9$ ,  $P = 0.04$ ) and unripe fruit ( $F_{2,3} = 13.7$ ,  $P = 0.03$ ) differed among the forest size classes, with bearded sakis in the 10-ha fragments consuming the smallest proportion of unripe seeds and the greatest proportion of unripe fruit. Across all of the data cycles, bearded saki monkeys in each of the 6 sites consumed seeds and fruits more than any other dietary item, with the exception of 1 cycle of data collection (November 2005) in a 10-ha fragment when bearded saki monkeys consumed flowers of *Eschweilera coriacea* (50.4%) more often than seeds and fruit (47.4%).

Feeding tree diameter at breast height for all sites ranged from 9 to 134 cm ( $\bar{X}$  37.9 cm  $\pm$  0.6 SE). Diameter at breast height for all behavioral feeding scans differed across forest



**FIG. 2.**—Mean ( $\pm$  1 SE) number of feeding sites visited and mean number of plant families, plant genera, and plant species consumed per hour by 6 groups of bearded saki monkeys (*Chiropotes chiropotes*) living in 4 forest fragments and 2 areas of continuous forest at Biological Dynamics of Forest Fragments Project. An asterisk (\*) represents significance at  $P < 0.05$ , and letters (A, AB, and B) above the SE bars signify differences between forest sizes based on post hoc Tukey’s honestly significant difference pairwise comparisons, where A and B are statistically different but neither differ from AB.

size classes ( $F_{2,3} = 13.70$ ,  $P = 0.03$ ), with monkeys in the 10-ha fragments surprisingly eating more often from larger trees than monkeys in the 100-ha “fragments” and continuous forest, but when the diameters at breast height of the feeding sites were compared there was no difference among the forest size classes ( $F_{2,3} = 0.013$ ,  $P = 0.99$ ). Lianas and hemiepiphytes represented 10.6% of all feeding scans, and 17.0% of total feeding sites, and there were no differences among forest size classes for either feeding scans ( $F_{2,3} = 0.71$ ,  $P = 0.71$ ) or feeding sites ( $F_{2,3} = 0.62$ ,  $P = 0.60$ ).

**Diet overlap.**—There was little dietary overlap among the bearded saki groups (Appendix I). Only 4 species (1.6%) were consumed by each of the 6 groups of monkeys: *Ecclinusa guianensis*, *Eschweilera truncata*, *Hevea guianensis*, and *Micropholis guyanensis*.

A majority of all plant species consumed (65%,  $n = 158$ ) were designated as “unique” because they were consumed by a single group. Of the unique species, 18 (11.4%) were in fruit at another study site but were not consumed by the monkeys that resided in that study site; monkeys in the continuous forest ignored these fruits more often than did the monkeys in the 10-ha fragments ( $F_{2,3} = 9.83$ ,  $P = 0.048$ ). Eleven (7.0%) of the 158 unique species were tree species that were not present in any other forest fragment, according to the BDFFP database. Of these 11 species, 10 (90.9%) were found solely in the continuous forest. This distribution was not random ( $G_5 = 26.64$ ,  $P < 0.001$ ). Lianas and hemiepiphytes comprised 28% of the unique species. It was not possible to determine whether these liana and hemiepiphyte species were present in all study

sites because the BDFFP database only represented trees with a diameter at breast height of 10 cm or greater.

*Relative abundance of plant species.*—In our examination of 28,064 tree records in the database, the genera *Eschweilera*, *Pouteria*, and *Protium* were the 3 most prevalent genera in each of the 6 study sites. When each study site was examined separately, there was a positive correlation between the relative abundance of each genus in the database and the relative abundance of that genus in the diet for each of the 6 study sites (Fig. 3). In the 10-ha fragments, the genera *Protium* and *Eschweilera* were outliers with Cook's *D*-values > 1.0 (Figs. 3a and 3b), whereas in the continuous forest *Protium*, *Eschweilera*, and *Pouteria* were outliers in at least 1 site (Figs. 3e and 3f).

*Dietary preferences.*—The genera *Pouteria*, *Eschweilera*, *Micrandropsis*, and *Licania* were common in the diets of the 2 bearded saki groups living in continuous forest, and when these genera were present in the 10-ha fragments the monkeys consumed them (Fig. 4). On the contrary, the genera *Protium*, *Pourouma*, *Inga*, and *Miconia* were present in all 6 study sites, but these genera were not consumed by some of the bearded saki groups, even though we verified that there were fruiting trees of these genera present in the study areas (Fig. 5). For example, *Protium*, which produced fruit in 80% of the phenological data cycles in the continuous forest and 100-ha "fragments," was not important as a food source for bearded saki monkeys in these 4 sites; however, it was the most commonly consumed genus in both of the 10-ha fragments. There was no significant correlation between the relative abundance of *Protium* at the study sites and the relative abundance of *Protium* in the diet ( $n = 6$ , Spearman's  $\rho = -0.36$ ,  $P = 0.49$ ). The remaining 3 genera (*Pourouma*, *Inga*, and *Miconia*) were entirely ignored by monkeys in both continuous-forest sites and there were no correlations between the relative abundance of the genera in the diet and the relative abundance at the study site (*Pourouma*:  $n = 6$ , Spearman's  $\rho = -0.20$ ,  $P = 0.69$ ; *Inga*:  $n = 6$ , Spearman's  $\rho = -0.24$ ,  $P = 0.65$ ; *Miconia*:  $n = 6$ , Spearman's  $\rho = 0.57$ ,  $P = 0.23$ ).

Overall, bearded saki monkeys did not consume all species of available fruit in the forest. Of the 141 plant species in fruit during the phenological surveys of the 6 study sites, 51 (36.2%) of the plant species were never part of the monkeys' diet in any of the study sites. Bearded saki monkeys were never noted eating the fruit from 24 genera of trees, hemiepiphytes, and lianas that were in fruit during the censuses (Table 1). The mean ( $\pm$  SE) percent of fruit that was present during the phenological surveys but not consumed by the monkeys at that site was 48.5% ( $\pm$  1.5%) in the 10-ha fragments, 64.0% ( $\pm$  8.7%) in the 100-ha "fragments," and 67.5% ( $\pm$  13.2%) in the continuous forest, but there was no difference among the 3 forest size classes ( $F_{2,3} = 1.15$ ,  $P = 0.42$ ).

## DISCUSSION

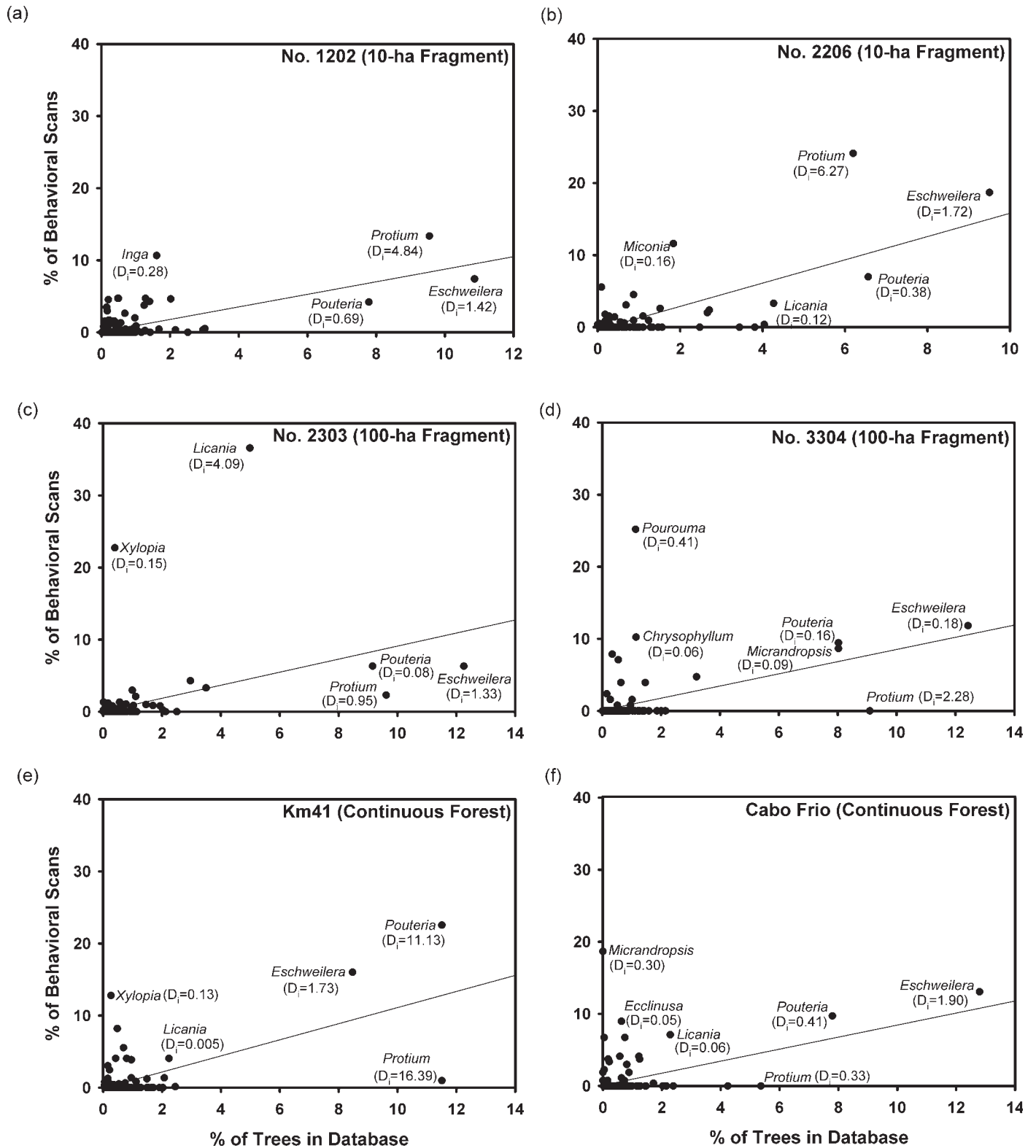
Our findings suggest that a relatively flexible and diverse diet helps the frugivorous bearded saki monkey reside in forest

fragments that are much smaller than the species' typical home-range size. However, the minimal dietary overlap among the 6 groups of bearded saki monkeys, the fewer plant genera and species consumed per hour by the monkeys in the isolated 10-ha fragments, and the positive relationship between the relative abundance of plant species and diet at the sites suggests that bearded saki diets are strongly influenced by the plant species composition of the study area. Over time there have been changes in plant species composition in the BDFFP forest fragments (Benítez-Malvido and Martínez-Ramos 2003; Laurance et al. 2006a, 2006b). If these patterns continue, the monkeys isolated in small forest fragments could be negatively impacted by such changes if the plant species present represent nondietary items for the monkeys, thereby further decreasing the amount of available resources. Overall, our findings on the animals' diet, combined with previous findings that the monkeys living in the small, isolated forest fragments have smaller group sizes, live at increased densities, spend less time traveling and more time resting, and revisit feeding trees more often throughout the day than do monkeys living in larger areas (Boyle et al. 2009; Boyle and Smith 2010a), suggest that bearded saki monkeys are greatly impacted by habitat fragmentation.

*Diet diversity.*—The diets of primates are not static (Chapman and Chapman 1990). In our study, there was little dietary overlap, because only 36% of the total plant species consumed were eaten by 2 or more bearded saki groups. Overall, these dietary differences can be explained by the specific composition of the plants at each site: the relative abundance of the plant species correlated with the relative abundance of the species in the diet.

Dietary overlap between the BDFFP monkeys and bearded sakis in Suriname (van Roosmalen et al. 1988), measured by the percentage of the diet in the Suriname population compared with that in our study, showed an 80% overlap in families and a 40% overlap in genera, but only a 16% overlap in species. A comparison between BDFFP and Venezuelan (Petz 2001) bearded saki populations indicated a 51% overlap in families, 22% overlap in genera, and 2% overlap in species, possibly due to the high beta diversity limiting the number of conspecifics occurring in both of the study areas. Overall, bearded saki monkeys eat a wide range of species; however, we recorded more species consumed by the bearded sakis than did other studies (Frazão 1992; Petz 2001; van Roosmalen et al. 1988; Veiga 2006), suggesting either greater alpha diversity of plant species available for consumption, differences in methodology, differences in sampling effort, or a combination of several factors.

The proportion of fruits in the diet remained high, even during periods of low fruit abundance. The consumption of both unripe fruit and of species that fruit during the dry season, as well as the consumption of seeds, allowed the monkeys to access a variety of resources (244 species) during the study. Although some seeds are high in lipids, proteins, and sugars (Norconk et al. 1998), the concentration of nutritional material varies among plant species, and bearded saki monkeys



**FIG. 3.**—Relative abundance of tree genera in the database of study site versus relative abundance in the diet, with regression line. Spearman's rank correlation results are a) Spearman's  $\rho = 0.50$ ,  $P < 0.0001$ ; b) Spearman's  $\rho = 0.30$ ,  $P < 0.0001$ ; c) Spearman's  $\rho = 0.37$ ,  $P < 0.0001$ ; d) Spearman's  $\rho = 0.35$ ,  $P < 0.0001$ ; e) Spearman's  $\rho = 0.29$ ,  $P < 0.0001$ ; and f) Spearman's  $\rho = 0.14$ ,  $P = 0.040$ . Common genera from the database and the feeding records are labeled. The Cook's  $D$ -value ( $D_i$ ) indicates to what extent the genus was an outlier.



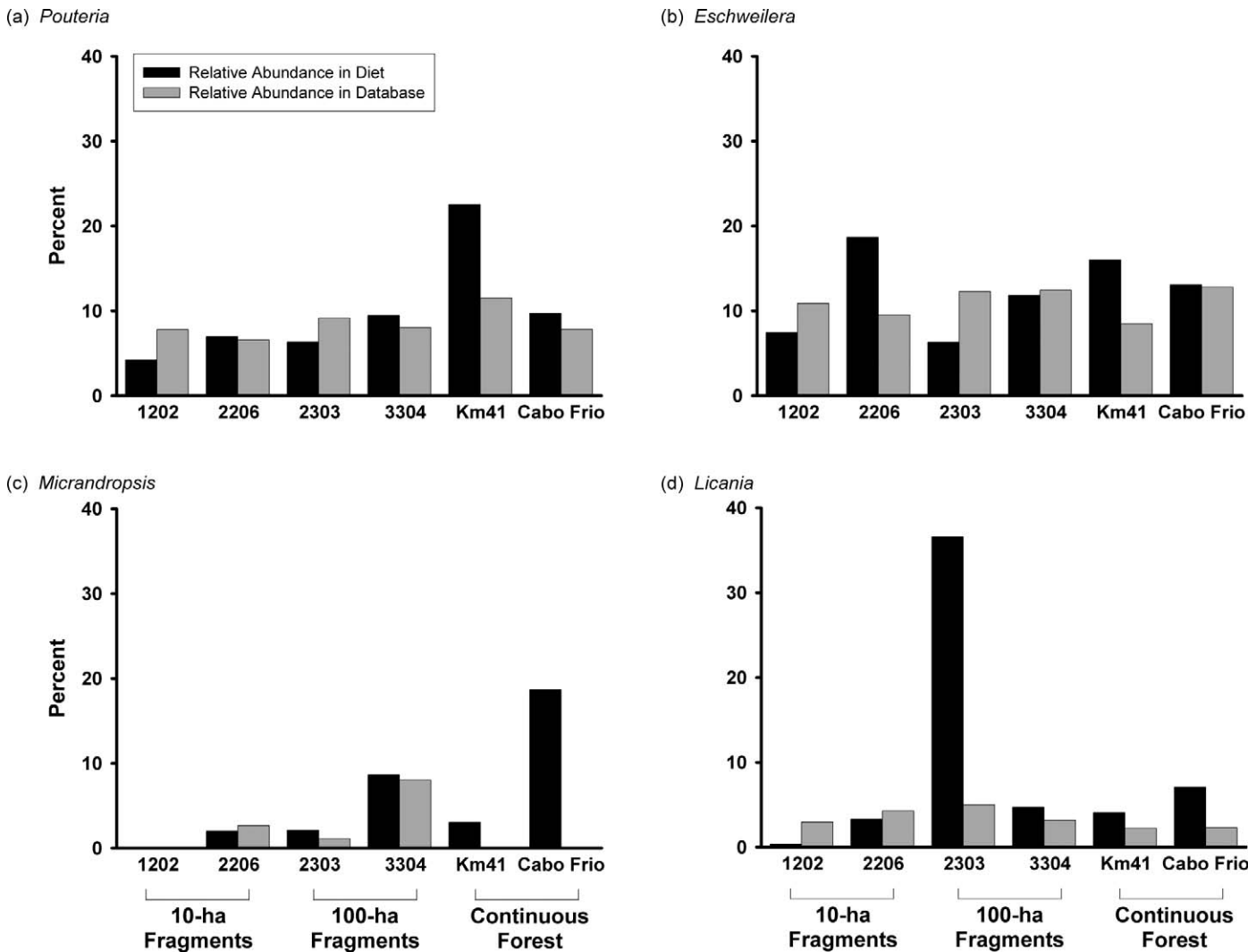


FIG. 4.—Tree genera prevalent in diets of the bearded saki monkey (*Chiropotes chiropotes*) in the continuous forest were also consumed by bearded saki monkeys in the fragments, except when those genera were not present.

consume seeds of varying quality (Kinzey and Norconk 1993; Norconk et al. 1998). Other species with high proportions of fruit in their diet that are not typically found in forest fragments primarily eat ripe fruit, for example, *Ateles* spp. (Estrada and Coates-Estrada 1996) and *Cebus* spp. (Spironello 2001), and neither genera are permanent residents of the BDFFP fragments (Boyle and Smith 2010b; Gilbert 2003). Indeed, animals such as bearded sakis that consume a combination of ripe and unripe fruit may be more resistant to resource shortages typical for many frugivores (Norconk 1996), which may explain their ability to persist in the isolated 10-ha fragments of the BDFFP.

Even though the bearded saki monkeys consumed a wide variety of plant species, and generally items that were most abundant were consumed most often, 17 genera that produced fruit during the study were not consumed by any of the bearded sakis. All but 2 of these genera also were ignored by bearded sakis in the continuous-forest site Km41 (Frazão 1992).

*Implications in forest fragments.*—Living in forest fragments can impact diet composition, and it also may impact diet quality, because animals are forced to eat items that they would regularly ignore in the continuous forest. For example, we found that the genera *Pourouma*, *Inga*, and *Miconia* were consumed in some of the forest fragments but ignored in both continuous-forest sites. Furthermore, the most frequently consumed species in both 10-ha fragments was *Protium hebetatum*, yet none of the bearded saki groups from the 100-ha “fragments” or continuous-forest sites ate this species or other species in this genus regularly, even though *Protium* was present, abundant, and producing fruit in all of the other study sites during 80% of the phenological surveys. On the contrary, the genera that were consumed the most in the continuous forests (i.e., *Pouteria*, *Eschweilera*, *Micrandropsis*, and *Licania*) also were consumed in the other study sites when these genera were present, suggesting that the monkeys in the 10-ha fragments were consuming genera that were not preferred by the monkeys living in continuous forests.

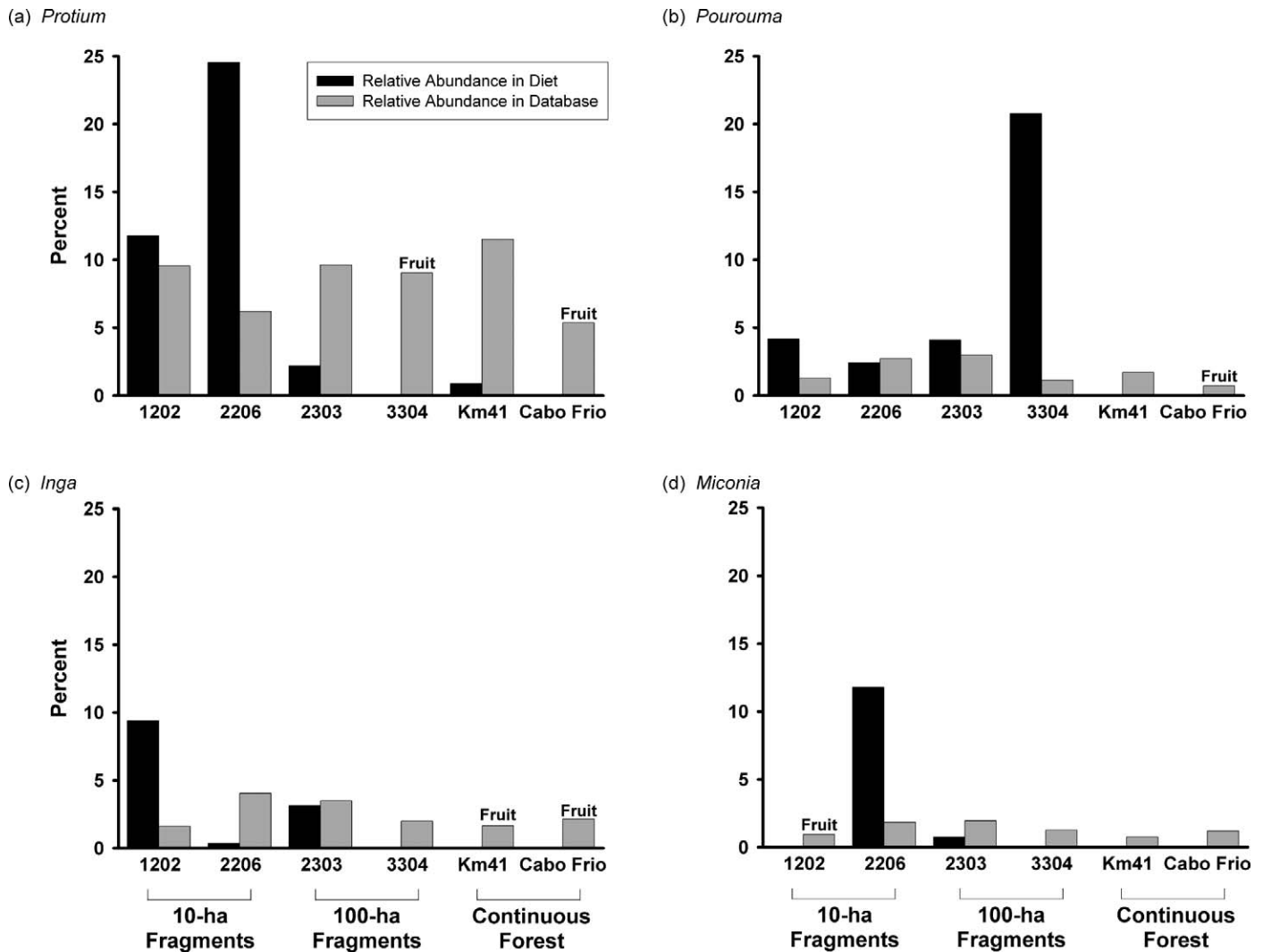


FIG. 5.—Tree genera prevalent in diets of some groups of bearded saki monkeys (*Chiropotes chiropotes*) were rarely consumed by bearded sakis in the continuous forest even though trees at some sites produced fruit during the phenological and bearded saki data collection (indicated by “Fruit” above the bar when there were no records of consumption of these genera).

Other studies of bearded sakis also have found little to no consumption of *Protium* in continuous forest (Frazão 1992), in a 1,300-ha forest fragment (Veiga 2006), and on a 365-ha island where only the ripe mesocarp of *Protium* was consumed (Norconk et al. 1997), whereas 4 *Protium* species were in the top 20 species consumed by a bearded saki group on a much smaller 19-ha island in Pará, Brazil (Veiga 2006). In Venezuela, *P. crassipetalum* had lower concentrations of nitrogen, phosphorous, potassium, calcium, and magnesium in its seed coat, and lower- to middle-range concentrations of these nutrients in the embryo or endosperm, in comparison with 11 other plant species (Grubb and Coomes 1997). However, we would need to conduct chemical analyses of all *Protium* species consumed by the bearded saki monkeys in order to draw conclusions regarding nutritional values and their potential toxicology. We also acknowledge that the monkeys likely consumed additional species when we were collecting data at other sites, but the stark difference in *Protium*

consumption among our different sites, combined with results from other studies, lead us to conclude that individuals in the 10-ha fragments were consuming less-preferred, and possibly lower-quality, food items.

*Conservation implications.*—Animals may face long-term consequences of living in small forest fragments. The BDFFP bearded sakis that resided in the 10-ha forest fragments lived in uncharacteristically small social groups and at a greater density than their counterparts living in continuous forest (Boyle and Smith 2010a); the increased density also may play a role in the diet limitations of the monkeys in the small fragments, thereby forcing them to consume unpreferred genera such as *Protium*. The animals also traveled uniformly throughout the 10-ha fragments, suggesting that the monkeys were maximizing all available forest (Boyle et al. 2009). Furthermore, the lack of young juveniles and infants in both 10-ha fragments also suggests that resources are limited in these fragments (Boyle and Smith 2010a). Chapman et al. (2003) documented declines

**TABLE 1.**—Plant genera that produced fruit during the phenology censuses, but were never consumed by bearded saki monkeys (*Chiropotes chiropotes*) in any of the 6 study sites.

Family	Genus
Annonaceae	<i>Ephedranthus</i> <i>Guatterioopsis</i>
Apocynaceae	<i>Aspidosperma</i> <i>Tabernaemontana</i>
Arecaceae	<i>Astrocaryum</i> <i>Euterpe</i> <i>Oenocarpus</i> <i>Socratea</i>
Bignoniaceae	<i>Cuspidara</i>
Cecropiaceae	<i>Cecropia</i>
Cyclantaceae <sup>a</sup>	<i>Asplundia</i>
Fabaceae	<i>Dinizia</i>
Lauraceae	<i>Licaria</i> <i>Mezilaurus</i>
Moraceae	<i>Sorocea</i>
Myristicaceae	<i>Virola</i>
Myrtaceae	<i>Calyptanthus</i> <i>Eugenia</i>
Passifloraceae	<i>Dilkea</i>
Rubiaceae	<i>Coussarea</i> <i>Isertia</i>
Sapindaceae <sup>a</sup>	<i>Talisia</i>
Sterculiaceae <sup>a</sup>	<i>Theobroma</i>
Violaceae	<i>Rinorea</i>

<sup>a</sup> Plant family never consumed during the study.

in fertility and population for some primate species but not other species over a 5-year period in forest fragments in Uganda. Continued monitoring of the bearded saki groups living in the forest fragments is critical, because the 10-ha fragments may not be providing adequate long-term resources.

We agree with Laurance et al. (2011) that conservation efforts should focus on protecting large tracts of land in Amazonia, and in the case of habitat that is already fragmented, it is important to understand how improved connectivity across the landscape would impact the movement, and subsequent population dynamics, of many species. The bearded sakis left and reentered both 100-ha “fragments” on several occasions during our study by traveling through corridors of tall, secondary growth forest (>5 years old), suggesting that the monkeys used these 100-ha “fragments” opportunistically. The 2 bearded saki groups that were restricted to 10-ha fragments appeared to face movement barriers due to the isolation of their forest remnants (>120 m to continuous forest and 30 m to another forest remnant > 0.5 ha [Boyle and Smith 2010b]). These barriers are not necessarily absolute, because the matrix surrounding these forest fragments could be managed so that adequate secondary growth is allowed to persist, which may facilitate future animal movement in the BDFFP through the presence of corridors (Boyle and Smith 2010b).

We conclude that the ability to consume a diverse diet that includes seeds and unripe fruits helps certain species survive in isolated forest fragments. Living in forest fragments can lead to the consumption of items that are ignored by individuals residing in continuous forests, and the items consumed may be of lower

nutritional value. Furthermore, severe changes in the fruiting phenology of the diet species in the small, isolated fragments could greatly impact the animals’ demographics. Overall, the ability to exploit different food resources appears to help bearded sakis that live in forest fragments that are a fraction of their home range in continuous forest; however, it does not appear that these conditions are viable for the isolated groups in the long term unless connectivity increases between their resident forest fragments and other areas of forest in the landscape.

## RESUMEN

Comprovadamente a fragmentação florestal altera a composição das espécies de plantas, sua distribuição e diversidade, afetando por sua vez a disponibilidade de recursos para consumidores primários. Neste contexto, investigamos se a fragmentação florestal afetou as dietas de 6 grupos de macaco-cuxiú (*Chiropotes chiropotes*) presentes em 2 fragmentos florestais de 10 ha isolados, 2 de 100 ha parcialmente isolados, e em 2 áreas de mata contínua na Amazônia Central. Quando mudanças foram detectadas, nós testamos se as diferenças nas dietas foram relacionadas à disponibilidade de recursos, comparando a prevalência de itens consumidos em relação à sua abundância relativa nos 6 sítios amostrados. No total, os macacos consumiram frutos, sementes e flores de 244 espécies vegetais, das quais menos de 2% foram consumidas por todos os 6 grupos. Embora houve uma correlação positiva entre abundância relativa de espécies utilizadas na dieta e frequência de consumo, os macacos não utilizaram todas as espécies de plantas disponíveis no ambiente, e grupos habitantes de fragmentos de 10 ha consumiram recursos que foram ignorados pelos demais em ambientes florestais de maior porte. Nossos resultados sugerem que cuxiús que habitam pequenos fragmentos florestais são limitados em suas escolhas alimentares em consequência do número reduzido de espécies vegetais presentes e, como consequência, consomem espécies de plantas que são ignoradas pelos que habitam floresta contínua. Nós concluímos que a capacidade de utilizar uma dieta diversa, como sementes e frutos imaturos, contribui para que este primata sobreviva em fragmentos florestais. No entanto, esta condição nos parece viável somente se houver maior conectividade entre os fragmentos e florestas contínuas dentro da paisagem.

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## APPENDIX I

Plant species ( $n = 244$ ) consumed by 6 groups of bearded saki monkeys (*Chiropotes chiropotes*) from 933 trees, lianas, and hemiepiphytes during behavioral scans in 2005–2006. Bearded sakis consumed seeds (S), fruits (F), flowers (W), and leaves (L). Nineteen plant specimens could not be successfully identified. If the fruits or seeds of the species were eaten, the condition of the fruit was indicated as unripe (U) or ripe (R). Site data represent percentage of feeding records for that site ( $n = 7,064$  records for all 6 sites) when species was consumed. Data are from 6 study sites: continuous-forest sites Km41 and Cabo Frio (CF), 100-ha “fragments” that were not fully isolated (“fragments” 3,304 and 2,303), and two 10-ha isolated fragments (fragments 2,206 and 1,202). Unique species (species that were consumed by only 1 of the 6 bearded saki groups) are indicated by an asterisk (\*).

Taxon	Item	Fruit	Continuous		100-ha		10-ha	
			Km41	CF	3,304	2,303	2,206	1,202
Anacardiaceae								
<i>Anacardium parvifolium</i> *	F	R	—	—	—	—	—	0.46
<i>Anacardium spruceanum</i> *	F	R	3.83	—	—	—	—	—
Anisophylleaceae								
<i>Anisophyllea manausensis</i> *	S	U	—	—	—	—	—	3.03
Annonaceae								
<i>Anaxogorea phaeocarpa</i> *	S	R	—	—	—	—	0.32	—
<i>Bocageopsis multiflora</i> *	S	U	—	—	—	—	—	0.08
<i>Duguetia chrysea</i>	S	R, U	—	—	—	1.42	0.63	—
<i>Duguetia pycnastera</i> *	S	R	—	—	—	1.16	—	—
<i>Duguetia stelechantha</i>	F, S	R	0.49	3.85	—	0.32	—	0.30
<i>Guatteria discolor</i> *	S	R	0.06	—	—	—	—	—
<i>Unonopsis duckei</i>	S, W	U	—	—	—	0.84	—	0.15
<i>Xylopia benthamii</i> *	S	U	0.49	—	—	—	—	—
<i>Xylopia calophylla</i>	F, S	R, U	11.54	—	—	10.34	—	—
<i>Xylopia cf. nitida</i> *	F, S	U	—	—	—	—	0.53	—
<i>Xylopia polyantha</i>	S	R, U	—	—	—	11.95	—	0.68
Apocynaceae								
<i>Couma guianensis</i> *	F, S	R	0.12	—	—	—	—	—
<i>Geissospermum argenteum</i> *	S	R, U	—	—	—	—	—	0.30
<i>Mandevilla</i> sp.*	S	R	—	—	1.32	—	—	—
<i>Odontadenia puncticulosa</i>	F, S	R, U	1.28	—	—	0.78	—	1.06
<i>Odontadenia</i> sp.	S	R, U	—	—	3.97	—	1.58	—
Araceae								
<i>Heteropsis flexuosa</i> *	S	U	—	—	—	—	—	0.23
<i>Philodendron goeldii</i> *	S	U	—	—	—	—	—	0.15

## APPENDIX I.—Continued.

Taxon	Item	Fruit	Continuous		100-ha		10-ha	
			Km41	CF	3,304	2,303	2,206	1,202
Arecaceae								
<i>Mauritia flexuosa</i> *	F	R	—	1.92	—	—	—	—
Bignoniaceae								
<i>Arrabidaea nigrescens</i> *	S	U	—	—	—	—	—	0.08
<i>Arrabidaea triplinervia</i> *	S	U	0.18	—	—	—	—	—
<i>Arrabidaea</i> sp.	S	U	—	0.77	0.66	—	—	—
<i>Lundia densiflora</i> *	W	—	—	—	—	—	—	0.68
<i>Mansoa alliacea</i> *	F, W	R	0.49	—	—	—	—	—
<i>Mansoa</i> sp.	W	—	—	—	—	0.13	—	—
<i>Memora longilinea</i> *	S, W	U	—	—	—	0.19	—	—
<i>Memora</i> sp.	W	—	0.97	—	—	—	—	—
<i>Tynnanthus panurensis</i> *	S	U	—	0.77	—	—	—	—
Bombacaceae								
<i>Castostemma albuquerquei</i> *	F, S	R	—	—	—	—	—	1.37
<i>Castostemma milanezii</i> *	S	U	—	—	1.99	—	—	—
<i>Scleronema micranthum</i> *	S, W	R	—	—	—	—	—	0.23
Bursaceae								
<i>Protium altsonii</i>	S	U	—	—	—	0.39	0.32	1.90
<i>Protium apiculatum</i>	S	U	0.24	—	—	0.32	—	0.15
<i>Protium decandrum</i> *	S	U	—	—	—	—	—	0.38
<i>Protium hebetatum</i>	S	R, U	0.43	—	—	1.29	20.86	7.97
<i>Protium nitidifolium</i> *	S	U	—	—	—	—	—	0.30
<i>Protium tenuifolium</i> *	S	R	—	—	—	—	—	0.91
Caryocaraceae								
<i>Caryocar glabrum</i>	S	R	—	0.77	—	—	0.42	—
<i>Caryocar pallidum</i> *	F	R	—	—	—	—	—	0.38
<i>Caryocar villosum</i> *	F	R	—	—	—	—	—	3.57
Cecropiaceae								
<i>Pourouma bicolor</i>	F, S	R, U	—	—	7.95	0.71	0.11	0.53
<i>Pourouma cecropiifolia</i> *	F	R	—	—	—	0.13	—	—
<i>Pourouma cucura</i> *	S	U	—	—	—	—	0.63	—
<i>Pourouma guianensis</i> *	F	R	—	—	—	—	—	0.61
<i>Pourouma ovata</i> *	S	U	—	—	—	0.58	—	—
<i>Pourouma tomentosa</i>	F, S	R, U	—	—	1.99	2.20	1.37	0.30
<i>Pourouma velutina</i>	S	U	—	—	—	0.45	—	—
<i>Pourouma villosa</i> *	F	R	—	—	5.96	—	—	2.28
Celastraceae								
<i>Goupia glabra</i> *	S	R, U	—	—	—	—	0.42	—
Chrysobalanaceae								
<i>Couepia longipendula</i>	S	R, U	0.97	6.92	—	0.52	—	—
<i>Couepia obovata</i> *	S	R	—	—	—	0.32	—	—
<i>Couepia</i> sp.	S	U	0.18	—	—	—	—	—
<i>Hirtella bicornis</i> *	S	U	—	—	—	0.26	—	—
<i>Hirtella rodriguseii</i> *	S	R	—	—	—	—	—	0.38
<i>Licania apetala</i> *	S	U	—	0.77	—	—	—	—
<i>Licania bracteata</i>	S	R, U	—	—	1.32	—	—	0.08
<i>Licania canescens</i> *	S	R	—	—	—	0.32	—	—
<i>Licania heteromorpha</i>	F, S	R, U	—	—	2.65	7.17	2.42	0.23
<i>Licania impressa</i>	S	R, U	0.97	—	—	—	0.32	—
<i>Licania lata</i> *	S	R, U	—	—	—	26.10	—	—
<i>Licania longistyla</i>	S	U	—	1.54	—	0.13	—	—
<i>Licania micrantha</i>	S	R, U	1.88	1.92	—	0.84	—	—
<i>Licania niloi</i> *	S	U	—	—	—	0.06	—	—
<i>Licania oblongifolia</i> *	S	R	—	—	—	—	0.21	—
<i>Licania sandwithii</i> *	S	U	0.06	—	—	—	—	—
<i>Licania sothersae</i>	S	R, U	0.18	—	—	0.06	—	—
<i>Licania unguiculata</i> *	W	—	0.24	—	—	—	—	—

## APPENDIX I.—Continued.

Taxon	Item	Fruit	Continuous		100-ha		10-ha	
			Km41	CF	3,304	2,303	2,206	1,202
Clusiaceae								
<i>Clusia grandiflora</i>	F, S	R	0.12	—	—	—	1.16	—
<i>Clusia insignis</i> *	S	U	—	—	—	—	1.69	—
<i>Clusia panapanari</i> *	F, S	R	—	—	2.65	—	—	—
<i>Clusiella axillaris</i> *	L	—	—	—	—	—	0.53	—
<i>Moronobea coccinea</i>	S	R	—	—	—	0.19	0.42	—
<i>Oedematopus cf. octandrus</i> *	W	—	—	—	—	—	0.84	—
<i>Tovomita cf. martiana</i> *	S	U	—	—	—	0.19	—	—
<i>Vismia sp.</i> *	S	U	0.12	—	—	—	—	—
Combretaceae								
<i>Buchenavia congesta</i> *	F	R	—	—	—	—	—	0.08
Convolvulaceae								
<i>Dicranostyles integra</i>	S	R	—	—	—	—	1.16	0.61
<i>Dicranostyles scandens</i> *	S	R	—	1.15	—	—	—	—
Cucurbitaceae								
<i>Gurania huebneri</i> *	S	U	—	—	0.66	—	—	—
Dilleniaceae								
<i>Davilla kunthii</i> *	S	R	—	—	—	0.26	—	—
<i>Pinzona coriacea</i> *	S	R	—	—	—	—	—	1.97
<i>Tetracera amazonica</i>	S	U	—	—	—	—	0.42	3.41
<i>Tetracera willdenowiana</i> *	S	R	—	—	—	—	—	0.08
Duckeodendraceae								
<i>Duckeodendron cestroides</i> *	F	U	—	—	—	0.13	—	—
Ebenaceae								
<i>Diospyros cavalcantei</i> *	S	U	—	—	—	—	—	0.15
<i>Diospyros pseudoxylopia</i> *	S	U	—	—	—	—	—	0.38
Elaeocarpaceae								
<i>Sloanea brachytepala</i> *	S	R, U	0.61	—	—	—	—	—
<i>Sloanea floribunda</i> *	S	R	—	—	—	—	—	0.61
<i>Sloanea sp.</i>	S	U	—	—	—	—	—	0.15
Euphorbiaceae								
<i>Croton lanjouwensis</i> *	S	R, U	—	—	—	—	—	4.10
<i>Hevea guianensis</i>	S, W	R, U	2.31	3.08	0.66	0.39	2.74	0.46
<i>Mabea caudata</i> *	S	U	—	—	—	—	—	0.08
<i>Mabea sp.</i> *	S	U	—	—	—	—	—	0.23
<i>Micrandropsis scleroxylon</i>	S	R, U	2.85	—	7.28	2.07	1.79	—
Fabaceae								
<i>Abarema cochleata</i>	S	R, U	0.79	—	—	0.78	—	—
<i>Bauhinia alata</i> *	S	U	—	—	—	—	0.21	—
<i>Derris amazonica</i> *	S	R	—	—	—	—	—	1.75
<i>Dipteryx magnifica</i> *	S	U	—	—	—	—	—	1.44
<i>Eperua glabrifolia</i>	S	R, U	0.36	1.15	—	—	—	—
<i>Hymenaea parvifolia</i> *	S	R	0.36	—	—	—	—	—
<i>Inga alba</i> *	S	U	—	—	—	0.39	—	—
<i>Inga bicoloriflora</i> *	S	U	—	—	—	0.45	—	—
<i>Inga huberi</i>	S	R, U	—	—	—	0.65	0.21	—
<i>Inga panurensis</i> *	S	R	—	—	—	—	—	1.29
<i>Inga paraensis</i> *	S	U	—	—	—	0.78	—	—
<i>Inga rubiginosa</i> *	S	R	—	—	—	—	—	0.15
<i>Inga splendens</i> *	S	R	—	—	—	—	—	7.81
<i>Machaerium aff. negrum</i> *	S	R	0.06	—	—	—	—	—
<i>Machaerium ferox</i> *	S	U	—	—	—	0.13	—	—
<i>Machaerium multifoliolatum</i> *	S	U	—	—	—	0.13	—	—
<i>Machaerium quinata</i> *	S	U	—	—	—	0.19	—	—
<i>Machaerium sp.</i>	S	U	0.12	—	—	—	—	—
<i>Macrobium limbatum</i> *	S	U	—	—	—	—	—	0.30
<i>Mimosa guilandinae</i> *	S	U	0.67	—	—	—	—	—



## APPENDIX I.—Continued.

Taxon	Item	Fruit	Continuous		100-ha		10-ha	
			Km41	CF	3,304	2,303	2,206	1,202
<i>Piptadenia minutiflora</i> *	S	U	—	—	—	—	0.32	—
<i>Pterocarpus officinalis</i> *	S	U	1.28	—	—	—	—	—
<i>Stryphnodendron</i> sp.*	S	U	—	—	—	0.32	—	—
<i>Swartzia cuspidata</i> *	S	U	0.12	—	—	—	—	—
<i>Swartzia recurva</i> *	S	U	—	—	—	—	—	4.02
Flacourtiaceae								
<i>Laetia procera</i> *	S	R	—	—	—	—	—	1.21
<i>Laetia</i> sp.	S	R	—	—	—	0.13	—	—
Hippocrateaceae								
<i>Cheiloclinium cognatum</i> *	S	U	0.97	—	—	—	—	—
<i>Cheiloclinium diffusiflorum</i> *	S	R	—	—	—	—	—	0.30
<i>Cheiloclinium hippocrateoides</i>	F, S	R, U	1.58	—	—	1.10	1.16	0.08
<i>Cheiloclinium</i> sp.	S	R, U	—	—	—	1.10	—	—
<i>Peritassa</i> sp.*	S	R	—	—	1.99	—	—	—
<i>Salacia impressifolia</i> *	S	U	0.30	—	—	—	—	—
<i>Salacia insignis</i>	S	R, U	0.60	—	0.66	0.52	—	0.30
<i>Tontelea fluminensis</i> *	S	U	—	—	—	—	—	0.15
<i>Tontelea</i> sp.	S	U	—	—	—	0.13	—	—
Humiriaceae								
<i>Endopleura uchi</i>	F, W	R	—	—	—	—	0.11	1.21
<i>Sacoglottis mattogrossensis</i>	F, S	R, U	0.24	—	—	0.06	—	1.14
<i>Vantanea macrocarpa</i>	S	R, U	—	—	—	—	0.11	2.28
Icacinaceae								
<i>Dendrobanhia boliviana</i> *	S	U	—	—	—	—	0.21	—
Lauraceae								
<i>Ocotea ceanothifolia</i> *	S	U	—	—	—	—	—	0.46
Lecythidaceae								
<i>Corythophora alta</i> *	S	R	—	—	—	—	—	0.30
<i>Corythophora rimosa</i>	S	R	—	—	—	—	1.16	0.08
<i>Couratari stellata</i>	S, W	R, U	—	—	6.62	0.06	0.21	—
<i>Eschweilera atropetiolata</i>	S, W	U	0.79	—	—	—	—	0.53
<i>Eschweilera coriacea</i>	S, W	U	0.97	—	—	—	7.06	—
<i>Eschweilera cyathiformis</i>	S, W	R, U	7.89	0.77	—	0.32	—	0.46
<i>Eschweilera grandiflora</i>	S, W	U	0.49	—	3.31	0.65	—	0.53
<i>Eschweilera micrantha</i>	S	U	0.18	—	—	0.13	—	—
<i>Eschweilera pseudodecolorans</i>	S, W	U	—	—	—	—	0.63	3.03
<i>Eschweilera romeu—cardosoi</i>	S	R, U	—	1.92	—	—	0.11	1.44
<i>Eschweilera truncata</i>	S	R, U	1.15	7.69	3.97	2.84	8.11	0.23
<i>Eschweilera wachenheimii</i>	S, W	R, U	3.22	—	2.65	0.78	0.63	0.23
<i>Lecythis gracieana</i> *	S	U	0.18	—	—	—	—	—
<i>Lecythis parvifructa</i> *	S, W	U	—	—	2.65	—	—	—
<i>Lecythis poiteaui</i> *	W	—	—	—	3.31	—	—	—
<i>Lecythis prancei</i> *	S	R, U	0.61	—	—	—	—	—
<i>Lecythis</i> sp.	W	—	—	0.38	—	—	—	—
Loganiaceae								
<i>Strychnos</i> aff. <i>asperula</i> *	S	R	—	—	—	0.65	—	—
<i>Strychnos cogens</i>	S	R	0.18	—	—	0.19	—	0.08
<i>Strychnos</i> sp.	S	U	—	—	—	0.39	—	—
Malpighiaceae								
<i>Byrsonima chrysophylla</i> *	F	R	—	—	—	—	—	1.29
<i>Byrsonima stipulacea</i>	F, S	R, U	—	—	—	—	1.26	0.08
Marcgraviaceae								
<i>Norantea guianensis</i> *	S	R	—	—	—	—	2.11	—
Melastomataceae								
<i>Bellucia dichotoma</i> *	F, S	R	—	—	—	—	1.37	—
<i>Miconia burchelli</i>	F, S	R, U	—	—	—	0.78	10.33	—

## APPENDIX I.—Continued.

Taxon	Item	Fruit	Continuous		100-ha		10-ha	
			Km41	CF	3,304	2,303	2,206	1,202
Memecylaceae								
<i>Mouriri collocarpa</i> *	F	R	0.36	—	—	—	—	—
Menispermaceae								
<i>Abuta imene</i> *	F	R	—	—	—	0.13	—	—
<i>Abuta rufescens</i> *	F, S	R	0.18	—	—	—	—	—
<i>Abuta sandwithiana</i> *	S	R	—	—	—	—	—	0.61
<i>Abuta</i> sp.	F, S	R, U	0.18	0.77	1.32	—	1.90	—
<i>Anomospermum solimoesanum</i> *	S	U	0.12	—	—	—	—	—
<i>Telitoxicum minutiflorum</i> *	S	R, U	—	—	—	0.13	—	—
<i>Telitoxicum rodriguesii</i> *	F, S	R	0.61	—	—	—	—	—
Moraceae								
<i>Brosimum acutifolium</i>	F, S	R, U	—	—	—	0.39	0.32	—
<i>Brosimum parinarioides</i>	F, S, W	R, U	1.34	—	1.32	0.19	—	—
<i>Brosimum potabile</i> *	S	U	—	—	—	—	3.58	—
<i>Brosimum rubescens</i>	S	U	2.49	0.77	—	0.26	0.11	—
<i>Clarisia racemosa</i>	F, S	R, U	0.24	—	—	—	—	1.06
<i>Ficus mathewsii</i> *	F, S	R	—	—	—	—	—	0.83
<i>Ficus</i> sp.*	F, S	U	—	—	—	—	—	0.61
<i>Helicostylis scabra</i>	F, S	R, U	0.79	3.85	—	—	0.63	—
<i>Helicostylis tomentosa</i>	F, S	R, U	—	—	1.32	—	—	1.06
<i>Helicostylis turbinata</i> *	S	U	—	—	—	—	—	0.38
<i>Naucleopsis caloneura</i> *	S	U	—	1.92	—	—	—	—
<i>Pseudolmedia laevis</i>	S	U	—	—	—	—	0.21	1.06
Myristicaceae								
<i>Iryanthera juruensis</i> *	S	U	—	—	0.66	—	—	—
<i>Iryanthera laevis</i> *	S	U	—	—	—	—	—	0.15
<i>Osteophloeum platyspermum</i>	S	R, U	—	0.77	—	0.26	4.95	2.58
Myrtaceae								
<i>Myrcia</i> sp.*	F, S	R	—	—	—	0.39	—	—
Olacaceae								
<i>Chaunochiton kappleri</i> *	S	U	—	—	—	—	—	0.08
<i>Dulacia guianensis</i> *	S	U	—	6.92	—	—	—	—
<i>Minquartia guianensis</i>	F, S	R, U	—	—	—	0.26	—	3.72
Passifloraceae								
<i>Passiflora edulis</i> *	S	U	—	—	—	0.06	—	0.23
Polygalaceae								
<i>Moutabea</i> aff. sp. 3*	S	U	—	—	—	0.97	—	—
<i>Moutabea guianensis</i>	S	U	2.61	—	7.95	—	—	—
<i>Moutabea</i> sp.	S	U	1.40	—	—	—	—	—
<i>Securidaca</i> cf. <i>volubilis</i> *	W	—	—	—	—	—	—	0.38
Quiinaceae								
<i>Touroulia guianensis</i> *	S	U	—	—	—	—	0.21	—
Rubiaceae								
<i>Malanea</i> sp.*	F	R	—	—	—	—	—	0.15
Sapotaceae								
<i>Chrysophyllum</i> aff. <i>argenteum</i> *	S	U	0.12	—	—	—	—	—
<i>Chrysophyllum amazonicum</i>	S	U	0.97	—	0.66	0.13	—	—
<i>Chrysophyllum manaosense</i>	S	R, U	1.58	1.54	—	0.32	—	—
<i>Chrysophyllum pomiferum</i>	S, L	U	0.30	—	—	—	—	0.23
<i>Chrysophyllum prieurii</i>	S	R, U	0.49	—	—	—	0.21	—
<i>Chrysophyllum sanguinolentum</i>	S	R, U	—	2.69	6.62	—	0.21	—
<i>Chrysophyllum sparsiflorum</i> *	S	U	—	—	—	—	0.42	—
<i>Chrysophyllum wilsonii</i>	S	R, U	0.18	—	1.32	0.32	—	—
<i>Ecclinusa guianensis</i>	S	R, U	5.22	9.23	3.31	1.03	1.37	3.11
<i>Ecclinusa lanceolata</i> *	S	U	—	—	—	—	—	0.15
<i>Manilkara bidentata</i>	F, S	R, U	6.68	—	—	0.65	0.42	—
<i>Manilkara cavalcantei</i>	F, S	R, U	0.36	—	—	0.19	—	—

## APPENDIX I.—Continued.

Taxon	Item	Fruit	Continuous		100-ha		10-ha		
			Km41	CF	3,304	2,303	2,206	1,202	
<i>Manilkara huberi</i>	S	U	0.67	—	—	0.45	0.42	1.75	
<i>Micropholis cylindropcarpa</i> *	S	U	—	—	1.32	—	—	—	
<i>Micropholis guyanensis</i>	S, W	R, U	1.03	3.46	1.99	0.19	2.32	0.15	
<i>Micropholis mensalis</i> *	S	U	—	0.77	—	—	—	—	
<i>Micropholis splendens</i> *	S	U	0.24	—	—	—	—	—	
<i>Pouteria</i> aff. <i>ambelaniifolia</i> *	S	R, U	—	—	—	0.78	—	—	
<i>Pouteria</i> aff. <i>gardneri</i> *	F, S	R	0.61	—	—	—	—	—	
<i>Pouteria anomala</i>	S	R, U	1.15	—	3.97	0.78	0.53	—	
<i>Pouteria campanulata</i> *	F, S	R	0.36	—	—	—	—	—	
<i>Pouteria cladantha</i>	S	U	1.58	—	—	—	—	0.30	
<i>Pouteria cuspidata</i> *	F, S	R	—	—	—	0.19	—	—	
<i>Pouteria erythrochrysa</i>	F, S	R	0.36	—	1.32	—	—	—	
<i>Pouteria eugenifolia</i> *	S	U	—	1.54	—	—	—	—	
<i>Pouteria filipes</i>	S	R, U	0.55	2.69	—	0.52	—	—	
<i>Pouteria fimbriata</i> *	S	U	0.43	—	—	—	—	—	
<i>Pouteria flavilata</i> *	S	U	0.43	—	—	—	—	—	
<i>Pouteria freitasii</i>	F, S	R, U	1.88	—	—	—	0.95	—	
<i>Pouteria fulva</i> *	S	U	—	—	—	0.06	—	—	
<i>Pouteria guianensis</i>	F, S	R, U	3.10	—	—	0.26	3.90	0.53	
<i>Pouteria hispida</i>	S	U	0.79	—	1.32	—	—	—	
<i>Pouteria laevigata</i> *	S	U	—	—	—	—	0.32	—	
<i>Pouteria maxima</i> *	S	R	0.18	—	—	—	—	—	
<i>Pouteria minima</i>	S	U	0.06	—	—	0.13	—	—	
<i>Pouteria pallens</i>	S	R, U	0.43	—	—	0.26	0.32	—	
<i>Pouteria peruviansis</i> *	S	U	0.36	—	—	—	—	—	
<i>Pouteria reticulata</i>	F, S	R, U	1.76	—	1.32	0.19	—	0.23	
<i>Pouteria</i> sp. 10*	S	U	—	—	—	—	—	2.35	
<i>Pouteria stipulifera</i> *	S	R, U	—	—	—	1.61	—	—	
<i>Pouteria torta</i> *	S	U	—	0.38	—	—	—	—	
<i>Pouteria venosa</i> *	W		0.91	—	—	—	—	—	
<i>Pouteria vernicosa</i>	F, S	R, U	0.55	—	—	0.39	—	—	
<i>Pouteria virescens</i> *	S	R	—	3.46	—	—	—	—	
<i>Pradosia cochlearia</i> *	S	U	—	0.77	—	—	—	—	
<i>Pradosia decipiens</i> *	S	U	—	—	—	0.19	—	—	
<i>Sarcaulus brasiliensis</i>	S	U	0.73	—	—	1.29	—	0.68	
Simaroubaceae									
<i>Simaba polyphylla</i> *	S	U	—	—	—	1.16	—	—	
<i>Simarouba amara</i> *	S	U	—	2.31	—	—	—	—	
Violaceae									
<i>Amphirrhox</i> sp.*	S	U	—	—	—	—	—	0.30	
Vochysiaceae									
<i>Erisma bicolor</i> *	S	R	0.55	—	—	—	—	—	
<i>Erisma bracteosum</i> *	S	R	—	—	—	—	0.53	—	
<i>Qualea labouriauana</i> *	S	U	—	—	—	—	—	4.10	
<i>Ruizterania albiflora</i> *	F, S	R	1.21	—	—	—	—	—	