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Availability of food for frugivorous bats in lowland Amazonia: the influence of flooding and of river banks

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In Neotropical forests fruits are key resources for a great diversity of vertebrates, including many frugivorous bats, but little is known about the factors that determine their availability. We studied forest inundation and river banks as determinants of the spatial variation in the availability of fruits for bats in lowland Amazonia. We sampled the bat assemblage composition, fruit availability, and bat diet in terra firme upland forest and in two types of flooded forest — várzea and igapó. Two distinct frugivore bat guilds were found in both terra firme and flooded forests: (1) canopy frugivores, feeding mainly on *Ficus* and *Cecropia*, and (2) understorey frugivores that feed mainly on *Vismia* and *Piper*. Fruits consumed by the canopy guild were more abundant in the flooded forests — particularly in the nutrient-rich várzea, but those dominating the understory guild diet were most abundant in terra firme. Availability of both fruit genera most consumed by the canopy guild was greater along river banks than in the forest matrix. For the understory guild, the greater abundance of *Vismia* along river banks was compensated for by a higher availability of *Piper* in the matrix. In conclusion, both factors influence the availability of fruits, although differently for the canopy and understory guilds. The resulting differences in fruit abundance may explain variations in bat assemblages of the different forest types. River banks play a particularly important role in providing food for bats of both guilds, but are under particularly heavy human pressure.

Key words: Amazonia, Chiroptera, frugivory, guild, igapó, terra firme, várzea, Brazil

INTRODUCTION

Most trees and shrubs of tropical rainforests produce fleshy fruits (Jordano, 2000), which are important and abundant food resources consumed by a diverse array of vertebrates; in some Neotropical forests the bulk of the bird and mammal biomass is supported by fleshy fruits (Fleming *et al.*, 1987).

Bats constitute up to 60% of the Amazonian mammalian fauna, dominating the community in diversity and biomass (Simmons and Voss, 1998), and playing essential ecological functions. Frugivorous bats are particularly abundant in these Neotropical forests, where they are key seed dispersers of many plants that produce fleshy fruits (Giannini and Kalko, 2004; Lopez and Vaughan, 2004) and have an important role in forest regeneration and succession (Muscarella and Fleming, 2007; Willig *et al.*, 2007).

Bats have high energetic requirements because flight is very costly (Kurta *et al.*, 1989) and they have high metabolism, particularly in the case of frugivorous species (McNab, 1986). As the nutritional value of fruits tends to be low (Wendeln *et al.*, 2000), bats need to eat large amounts of food to satisfy these high requirements (Morrison, 1978). Flight facilitates the fulfilment of these requirements, as it allows the selection of high quality feeding areas (Law, 1995) and, in fact, foraging frugivorous bats tend to be most active in the most productive habitats and sites (Willig *et al.*, 2007; Ramos Pereira *et al.*, 2009; Vargas-Contreras *et al.*, 2009). Consequently, like for nectarivorous (Lemke, 1984) and insectivorous bats (Wang *et al.*, 2010), the quality of foraging patches may be one of the main factors driving foraging decisions of frugivorous bats.

In the lowlands of Central Amazon, frugivorous bats seem to make a distinct use of different existing forest types (Ramos Pereira *et al.*, 2009). Most of this vast region is covered by terra firme forests that never flood, which are nutrient-poor because they have long been deprived of alluvial sediments (Irion *et al.*, 1997). However, approximately 10% of the region is dominated by two forest types that are flooded for much of the year: the nutrient-rich várzea, seasonally flooded by 'white-waters' loaded with sediments from the ice-melt and steep slopes of the Andes, and the oligotrophic igapó, seasonally flooded by nutrient-poor 'black-water', stained by organic compounds and originating in the forest plains (Prance, 1979; Ayres, 1993).

Amazonian forests have a mostly continuous and dense canopy layer, but along water courses this layer is interrupted, allowing abundant light to reach the ground (Bongers *et al.*, 2001). This availability of light along the river banks and the proximity of water are likely to influence both the floristic composition of the forest and the fruiting phenology and productivity of its trees and shrubs (van Schaik *et al.*, 1993). Along river margins these plants face less competition for solar radiation than inside the forest (Bongers *et al.*, 2001), allowing them to allocate more energy to flower and fruit production (van Schaik *et al.*, 1993). Consequently, it is likely that plants in river banks provide resource-rich patches to frugivores, including bats. Moreover, the distinct floristic composition of river bank forest (e.g., Salo *et al.*, 1986) may diversify foraging opportunities for a variety of bat foraging guilds.

In lowland Amazonia, another factor potentially increasing fruit availability along river banks is their frequent natural disturbance due to lateral river erosion, and the subsequent formation of sediment beaches (Salo *et al.*, 1986; Peixoto *et al.*, 2009). These newly exposed soil and beaches are areas of primary succession (Parolin *et al.*, 2002; Myster, 2009), and many frugivorous bats may exploit the abundant fruit resources provided by some pioneer and early-successional plants that become established in them, such as *Cecropia*, *Piper*, and *Solanum* (Fleming, 1988; Palmeirim *et al.*, 1989; Bernard, 2002; Aguiar and Marinho-Filho, 2007).

This evidence suggests that in Neotropical rainforests vegetation along river banks may play a disproportionally important role in the provision of food resources for its rich fauna of frugivorous vertebrates, but to our knowledge this possibility has never been evaluated. There is also very little information about the relative availability of fruit in the different types of flooded and unflooded forests present in the central Amazonian floodplain, as only one paper presents data on this topic (Haugaasen and Peres, 2007).

In this study we assessed the potential value of river bank vegetation as foraging habitat for the diverse guild of Amazonian frugivorous bats, in lowland landscapes with flooded and unflooded forests. Our specific objectives were: (1) to study the feeding guild structure of an assemblage of frugivorous bats in a region dominated by a mosaic of terra firme, várzea, and igapó forests; (2) to identify differences in food availability in the three types of forest; and (3) to determine the potential importance of the vegetation along river banks to provide food for frugivorous bats.

MATERIALS AND METHODS

Study Area

Field work took place in the Amanã Sustainable Development Reserve (ASDR, Amazonas, Brazil), a reserve covering 2,350,000 ha that contains nutrient-rich várzea forests and nutrient-poor igapó forests, within a matrix of terra firme forests (Fig. 1). Lake Amanã (2º37'S, 64º37'W) is a mostly black-water lake fed predominantly by streams draining catchments dominated by terra firme. Igapó occurs mainly along the streams and margins of Lake Amanã, while most várzea is located in the floodplain of River Japurá. Human population density is very low and only ca 4000 people live inside the reserve. The area receives about 2500 mm of annual precipitation, mostly during the high-water season, from January to June. The low-water season usually extends from July to December. Water levels vary up to 10 meters between the two seasons. Flowering and fruiting peaks usually occur in the low and high-water seasons, respectively (Ayres, 1993). The dominant trees belong to the families Sapotaceae, Lecythidaceae, Euphorbiaceae, Myristicaceae, and Leguminosae (Ayres, 1993; Ramos Pereira *et al.*, 2010*a*). Canopy height is usually between 15 and 35 m, with emergent trees reaching at least 50 m (Ayres, 1993).

Bat and Diet Sampling

Bats were captured between April and June 2007, when várzea and igapó forests are flooded, and between October and December 2007, when all forests are dry. We sampled ten stations, of which four were in terra firme, three in várzea, and three in igapó. Each station was sampled during four consecutive nights using three 3 × 12 m mist nets set at canopy level (17–35 m high) and ten 12 × 3 m nets at ground level. During the high-water season ground mist nets were set above water in both várzea and igapó, but canopy nets were not used in these habitats because of logistical difficulties. The nets remained open between 18:00 and 24:00 h, because most bats tend to be captured in the early evening, and were checked every 20 minutes. Each captured bat was sexed, weighed, and identified using identification keys (Lim and Engstrom, 2001; E. M. Sampaio, E. K. V. Kalko and D. E. Wilson, personal communication). We made temporary marks on the patagium of bats using a pen marker, to allow recognition of recaptures over the same four day sampling period. However, there were only four recaptures and these were not included in the analyses.

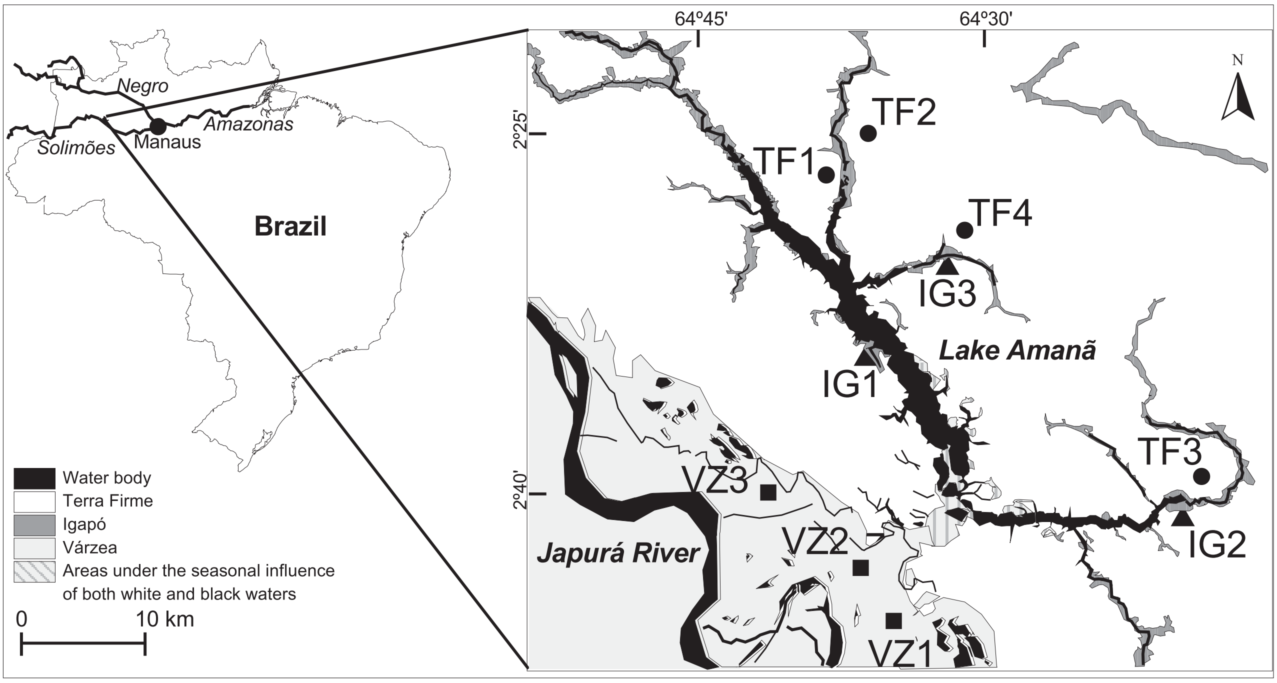

Fig. 1. Location of sampling sites (TF — terra firme, VZ — várzea, IG — igapó). The southern part of the lake usually has black water but can temporarily receive white waters. Distribution of habitats based on cartography by the Mamirauá Sustainable Development Institute and satellite imagery

The diet of the captured bats was studied by analyzing items found in feces. We kept each bat in a separate cotton bag for about 30 minutes to collect feces. These were then air dried and, using a stereo microscope, their contents were separated in five categories: seeds, fruit pulp, arthropods, pollen and flower parts, and undetermined. Seeds were identified using a reference collection from the site. It is worth noting that the medium- and large-sized frugivorous bats included in our analysis may consume forest fruits that were not recorded because the seeds are not ingested (e.g., Sapotaceae, Humiriaceae, Chrysobalanaceae, and Araceae — see Lobova *et al.*, 2009).

Fruit Availability

In each of the ten sampling stations we used two 1 km long fruit availability transects. One of the transects was located in the forest interior, partly coinciding with the location of the mist-nets, while the other was located along the nearest river bank. We identified all trees with canopies intersecting the transect line. Using binoculars and with the help of a local field assistant with extensive experience in the collection of plant phenology data, we determined which of those trees had ripe fruits. We also identified all fruiting shrubs within two meters of the transect line. The results of this method are approximate but since we used the same methodology and observer at all sites, we consider them suitable for the comparisons that we made. We estimated fruiting tree abundance in both high-water and low-water seasons, coinciding with the periods of bat captures. We present results on the availability of the main fruit genera consumed by the different bat foraging guilds. We also estimated the numbers of ripe fruits on trees and shrubs. However, the huge variability in numbers of fruits, especially because of figs, rendered these data unsuitable for the comparisons.

Data Analysis

The importance of each fruit type in the bats' diet was quantified using the frequency of occurrence, i.e., the percentage of samples containing seeds of that fruit. Diet data were pooled by plant genus because we were often unable to identify the fruit remains to the species level. Only bat species with a minimum of eight diet samples containing seeds were included in the diet data matrix. This matrix was explored for the presence of feeding guilds by visually searching for clusters of species and fruits in the plot of the first two axes of a Correspondence Analysis implemented with PAST version 1.90 (Hammer *et al.*, 2001).

Differences in fruit production between the three forest types and between the forest matrix and river bank vegetation were evaluated using the numbers of fruiting plants. Prior to statistical analyses the variables were log-transformed to approximate normality and reduce the influence of extreme values (Zuur *et al.*, 2007). We used two-way repeated measures ANOVA to assess differences between the three forest types and transect location (forest matrix versus river bank). This method accounts for the lack of independence (i.e. pseudoreplication — Hurlbert, 1984) caused by estimating fruit availability on the same transects during both seasons. ANOVA tests and Tukey HSD were done in R (version 2.10.1). The threshold for statistical significance was $P \leq 0.05$, although we also report and discuss near significant probability values, i.e. $P < 0.1$.

Results

During the 80 nights of mist-netting we captured 1242 bats of 60 species, and collected a total of 599 diet samples from 32 bat species (305 in the high-water season and 294 in the low-water). Frugivore species represented 69.5% of the total of diet samples, and the best represented species were the frugivorous *Carollia perspicillata* and the omnivorous *Phyllostomus elongatus* (Table 1).

Diet and Feeding Guild Identification

Ten frugivorous bat species were included in the diet matrix, using a total of 199 diet samples for the high-water season and 171 samples for the low-water (Table 1). The correspondence analysis of the diet matrix revealed a clear structure relating frugivorous bats and the plant genera they consume. Bats that fed on fruits in the canopy were clearly separated from those that usually forage in the forest understorey along the first axis (Fig. 2), which had an eigenvalue of 0.68, indicating a good separation of the species along that axis. The 'canopy guild', included bats that consumed almost exclusively *Ficus* and *Cecropia* fruits — *Platyrrhinus helleri*, *Vampyriscus brocki*, *Uroderma bilobatum*, *Artibeus planirostris*, *A. lituratus*, and *A. obscurus*. The 'understorey guild', included *Rhinophylla pumilio*, *Carollia castanea*, *Sturnira tildae*, and *C. perspicillata*, which fed mostly on understorey plants, in particular of the genera *Vismia*, *Piper*, and *Philodendron.* Of the 745 captured frugivorous bats, 703 belonged to the ten species that we were able to assign to one of the two feeding guilds (359 of the canopy guild and 344 of the understory guild).

To assess the contribution of each fruit genus to the diet of the two feeding guilds in our study region, we graphed the combined data for all bat species included in each guild. We identified at least six species (or morphotypes) of *Piper* (*P. alatabacum*, *P. arboreum*, *P. dilatatum*, *Piper* sp. 1, *Piper* sp. 2, and *Piper* sp. 3), three of *Cecropia* (*C. sciadophylla*, *C. membranacea*, and *Cecropia* sp. 1), six species of figs (*Ficus maxima*, *F. nymphaeolia*, *Ficus* sp. 1, *Ficus* sp. 2, *Ficus* sp. 3, and *Ficus* sp. 4), three species of *Vismia* (*V. cayennensis*, *Vismia* sp. 1 and *Vismia* sp. 2) and four morphotypes of *Philodendron*. The diet of the canopy guild was mainly composed of *Ficus* and *Cecropia* fruits (Fig. 3), whereas that of the understorey guild was dominated by fruits of *Vismia* trees and *Piper* shrubs (Fig. 3).

Bats of each guild consumed mainly fruits of their corresponding height stratum, irrespectively of the forest type (Fig. 4); canopy bats consumed mainly fruits available in the forest canopy in terra firme, igapó and várzea forests, and understorey bats consumed mainly fruits only available in the understorey, even in the flooded forests.

Fruit Availability — Differences between Forest Types

We assessed the availability of food resources for the canopy bat guild using the fruiting trees of *Ficus* and *Cecropia*, which dominated the diet of this guild. Fig trees bearing fruits were more abundant in várzea than in igapó and terra firme

TABLE 1. Numbers of bat captures and diet samples, and frequency of food items on fecal samples of bat species captured more than 15 times

Species	Captures	Diet samples				Food items				
		High -water	Low -water	Ground level	Canopy level	Seeds	Insects	Fruit pulp	Nectar, pollen	Und.[b]
Carollia perspicillata[a]	253	114	69	161	22	132	31	29	–	9
Artibeus planirostris[a]	193	26	49	59	16	59	2	14	–	2
Phyllostomus elongatus	135	44	60	–	–	4	98	14	–	–
Glossophaga soricina	65	6	12	–	–	1	6	7	7	–
Rhinophylla pumilio[a]	46	14	9	13	6	11	2	6	–	8
Sturnira tildae[a]	26	11	4	12	2	13	2	3	–	3
Artibeus lituratus[a]	19	6	4	6	4	8	1	3	–	–
A. obscurus[a]	70	9	6	12	3	9	1	6	–	1
Carollia castanea[a]	19	10	6	14	2	14	2	3	–	2
Lophostoma sylvicolum	24	8	9	–	–	–	15	2	–	–
Mesophylla macconelli	42	6	3	–	–	4	–	5	–	2
Phyllostomus hastatus	16	10	4	–	–	5	9	4	–	1
Plathyrrhinus helleri[a]	41	4	9	6	7	12	2	–	–	–
Uroderma bilobatum[a]	20	4	8	5	7	11	1	1	–	–
Vampyriscus brocki[a]	16	1	7	1	7	8	–	–	–	1
Tonatia saurophila	25	7	6	–	–	5	9	3	–	–

[a] — Bat species with eight or more fecal samples with seeds that were selected for further analysis (see Materials and Methods); [b] — undetermined

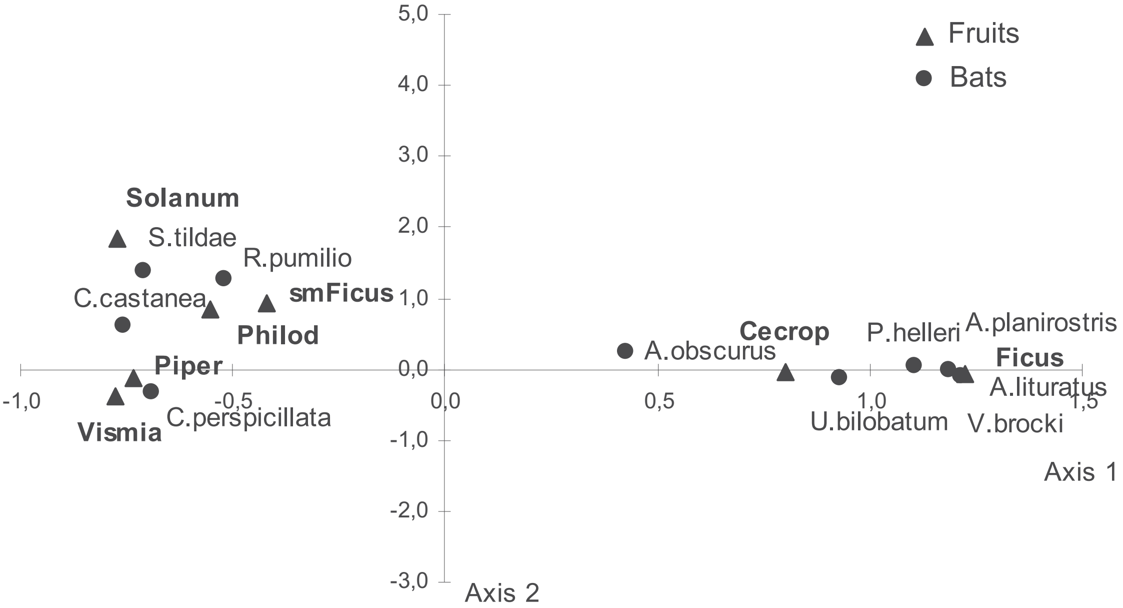

FIG. 2. Correspondence analysis of the diet matrix with bat species and fruits consumed (eigenvalues: axis 1 = 0.687 and axis 2 = 0.201). Fruit labels in bold: Solanum — *Solanum* spp.; smFicus — small seeded *Ficus* species; Philod — *Philodendron* spp.; Piper — *Piper* spp. fruits; Vismia — *Vismia* spp. fruits; Cecrop — *Cecropia* spp.; Ficus — *Ficus* spp.

($F_{2,\ 14} = 6.35$, $P = 0.01$). *Cecropia* fruiting trees appeared to be more abundant in várzea, although differences from the other two types of forests were only nearly significant ($F_{2,\ 14} = 2.97$, $P = 0.08$).

Core fruits consumed by the understorey foraging guild, including the highly consumed *Vismia*. and *Piper* genera, were in general very scarce; in the fruit availability transects we only recorded fruiting *Vismia* and *Piper* plants in terra firme, and always in relatively low numbers (Fig. 5).

Fruit Availability — Differences between Riverbank and Matrix Vegetation

We found similar numbers of *Ficus* trees in transects of river bank vegetation and forest interior, but individuals bearing fruits were more numerous in river banks than in the forest matrix ($F_{1,\ 14} = 5.29$, $P = 0.04$ — Fig. 5). *Cecropia* trees were also more numerous in river bank vegetation than in the forest matrix, but differences were only nearly significant ($F_{1,\ 14} = 3.65$, $P = 0.06$). The number of fruiting *Cecropia* was several times higher in river bank vegetation than in the forest interior of igapó and várzea (Fig. 5), but presumably due to high variability in the data the differences were not statistically significant ($F_{1,\ 14} = 0.74$, $P = 0.40$).

Understorey fruit availability also varied between river bank vegetation and the forest matrix (Fig. 5). *Vismia* fruiting shrubs were only recorded in river banks of terra firme, and even there at very low densities. In contrast, *Piper* fruiting plants were only recorded in the forest matrix, so the overall river bank/matrix contrast in understory fruit

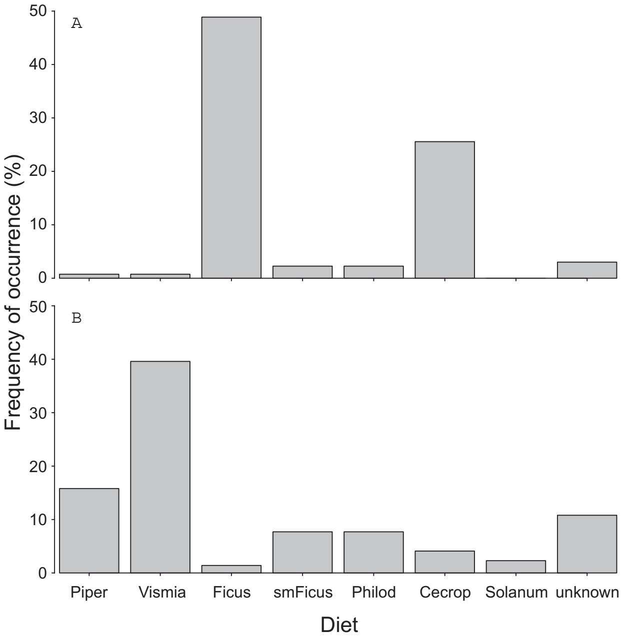

FIG. 3. Diets of canopy (A) and understory (B) guild bats, expressed as frequency of occurrence of seeds in samples. Data of low and high-water seasons are pooled. Fruit labels as in Fig. 2

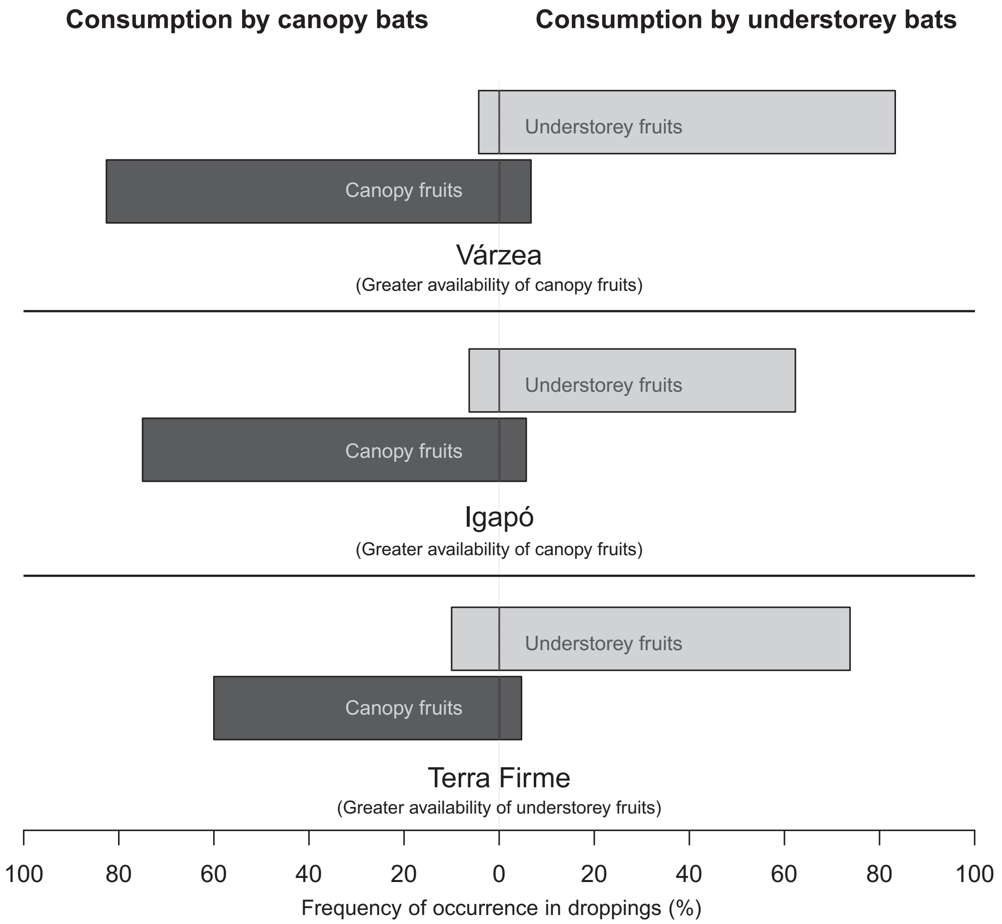

FIG. 4. Strength of the association of bats to their feeding guild. Bats continue selecting fruits typical of their guild even in habitats where they are scarce, instead of switching to the types of fruit that exist in greater abundance in each habitat, demonstrating a strong association with their feeding guild

availability was not as marked as that observed for the canopy guild.

DISCUSSION

Feeding Guild Structure

Several studies conducted in terra firme forests have identified two guilds of frugivorous bats, the canopy and understory guilds (Bonaccorso, 1979; Palmeirim *et al.*, 1989; Bernard, 2001; Delaval *et al.*, 2005; Rex *et al.*, 2008). We were able to confirm for the first time the presence of both guilds in two seasonally flooded forest types, várzea and igapó, in spite of the structural differences between these forests and terra firme. Flooded forests usually have lower canopy cover and sparser understorey than terra firme (Borges and Carvalhães, 2000; Haugaasen and Peres, 2006).

Our results confirm that *Ficus* and *Cecropia* fruits are key resources for the majority of canopy frugivores. The group that dominates this guild, the Stenodermatini, are considered *Ficus* specialists (e.g., Bonaccorso, 1979; Giannini and Kalko, 2004), although as we observed, they can also consume large numbers of *Cecropia* fruits (Lobova *et al.*, 2009; Teixeira *et al.*, 2009). In the study region, the high abundance of *Cecropia* and its long fruiting period (Myster, 2009; JTM and MJRP, personal observation), suggests that these plants provide a reliable food supply throughout most of the year.

One of the bat species included in this guild, *V. brocki*, is a poorly known Amazonian endemic (Marinho-Filho and Sazima, 1998). Our results indicate that this rare species feeds mainly on *Ficus* and should therefore be included in the canopy frugivore guild, as suggested by Bernard (2002). In fact, most of the few known captures of this species took place in the canopy (Bernard, 2001; Barnett *et al.*, 2006; Ramos Pereira *et al.*, 2010*b*).

Vismia fruits were most consumed by understorey frugivores, particularly by *C. perspicillata*.

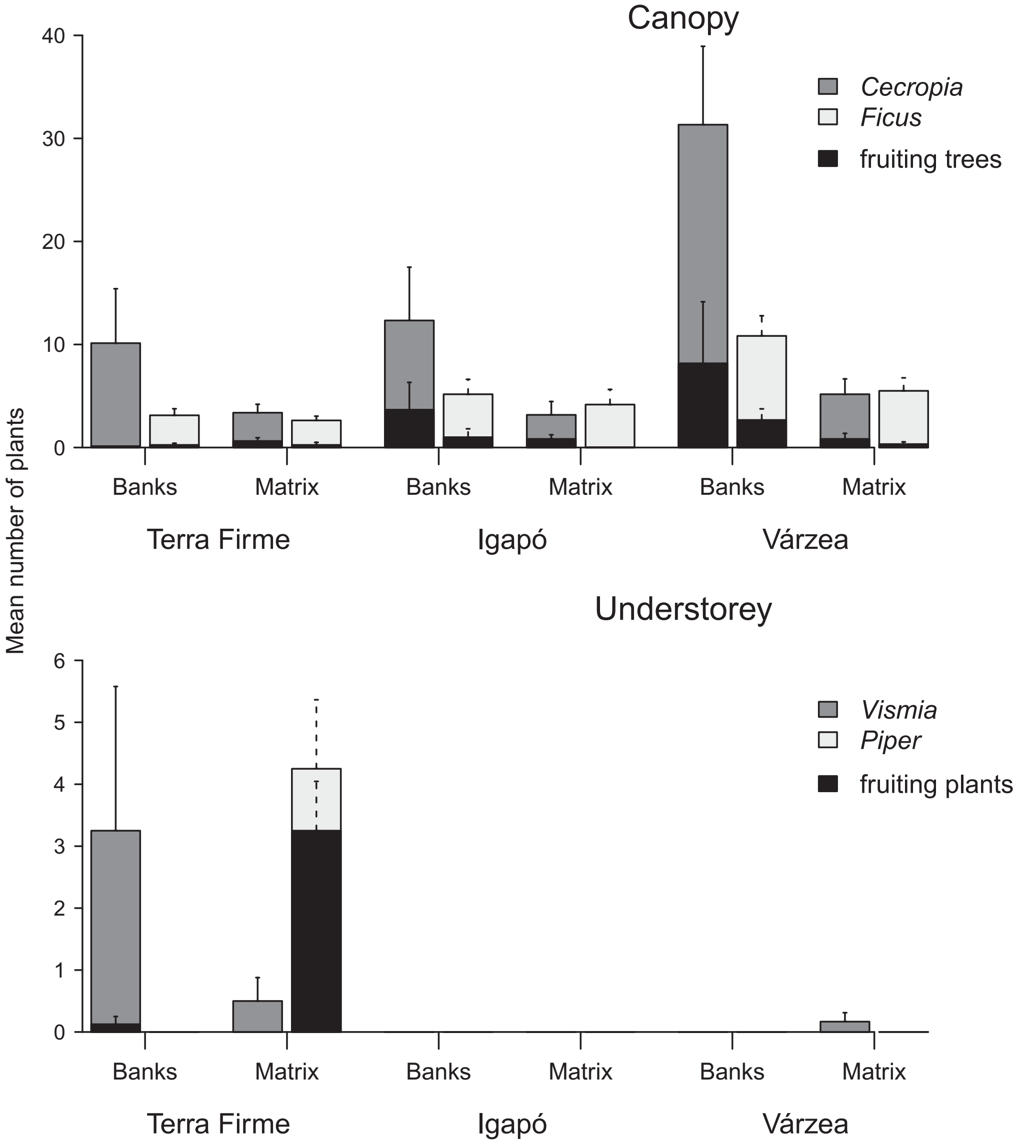

FIG. 5. Number of plants and of plants with fruits of the genera most consumed by the two bat guilds in the three types of forest, contrasting river banks with forest matrix. Lines represent standard error of the mean

Several other studies have also found *Vismia* dominating the diet of understorey bats (Gorchov *et al.*, 1995; Bernard, 2002; Sampaio *et al.*, 2003; Lobova *et al.*, 2009), but in many regions *Piper* is their main food resource (Fleming, 1988; Palmeirim *et al.*, 1989; Thies and Kalko, 2004; Aguiar and Marinho-Filho, 2007). Presumably, understorey bats switch between *Vismia* and *Piper* in response to the local availability of these plants. This may explain the dominance of *Vismia* in our data; *Piper* is quite scarce in the study area, possibly because its forests are nearly pristine, and mature forests tend to have a low abundance of *Piper* (Fleming, 2004).

In spite of the prevalence of *Vismia*, none of the understory frugivores is entirely dependent on fruits of this genus. *Rhinophylla pumilio*, *C. castanea*, and *S. tildae* frequently also consumed *Philodendron*, *Piper*, and *Solanum*, respectively. *Philodendron* fruits actually constituted the main dietary item of *R. pumilio*, corroborating their reported preference for epiphyte infructescences (Henry *et al.*, 2007). *Carollia castanea* seems to be more dependent on *Piper* fruits than *C. perspicillata*, as reported for other regions (Palmeirim *et al.*, 1989; Thies and Kalko, 2004). *Sturnira tildae* consumed mostly fruits of *Solanum* spp., in spite of the apparent scarcity of these plants in the study region. Henry *et al.* (2007) also noted their paucity in undisturbed forests in French Guyana and suggest that they are usually scarce in this habitat.

Strength of Association of Frugivorous Bats to their Feeding Guild

The consistent structuring of Neotropical frugivorous bat assemblages in two major feeding guilds, canopy and understory, suggests that species have adaptations that make them specialists in the exploitation of either forest strata. But how strong is the association of these bats to their feeding guild? Where the foods typical of their guild are scarce will they switch to those of the other guild? Our study area is particularly suited to answer this question, because it encompasses forest types in which the availability of the typical foods of the two guilds are very different. If the level of specialization of canopy bats to fruits of that stratum is low then we predict that in terra firme, where *Ficus* and *Cecropia* are scarce, they would switch to understorey fruits; conversely, if their level of specialization is high, we predict that their diet would remain the same, and their abundance would decline when canopy fruits are scarce. Likewise, if understorey bats are highly specialized, then we can assume that they will not switch to canopy fruits in flooded habitats, where their preferred understorey fruits are less abundant.

Our diet data and the results of the correspondence analysis corroborate the predictions made under the scenario of specialization and strong association with one of the guilds — bats did not switch to fruits of the other guild, even where the typical foods of their own guild were scarce. In terra firme, where canopy fruits were least abundant, understory fruits were present in less than 10% of diet samples of canopy guild bats, indicating a strong attachment to their typical fruits. Likewise, in the flooded forest types, where understory fruits were very scarce, the proportion of canopy fruits in the samples of understory guild species was very low (5.7% in igapó and 6.7% in várzea). We conclude that there must be important constraints that limit bats to exploit the fruits of a specific vertical stratum (e.g., flight or trophic morphology and/or sensory adaptations). This specialization may have resulted from an evolutionary process of niche partitioning to reduce competition among Neotropical frugivorous bats (DeLaval *et al.*, 2005). It is worth noting, however, that some canopy bats did eat a few understory fruits, and that several understory bats ate canopy fruits. In fact, the most abundant bat of the understorey guild, *C. perspicillata*, is known to have a particularly diverse diet that can include fruits of both *Cecropia* and *Ficus* (Bonaccorso, 1979; Lobova *et al.*, 2009), fruits that are typical of the canopy guild.

Influence of Forest Type on the Availability of Fruits for the Canopy and Understorey Guilds

The main sources of food for the canopy guild, fruits of *Ficus* and *Cecropia*, were more abundant in várzea, a nutrient-rich habitat, than in igapó and terra firme, both nutrient-poor forests. In fact, *Ficus* trees tend to be more abundant in rich soils (Gentry, 1990), and *Cecropia* is known to form large monospecific stands in várzea areas (Parolin *et al.*, 2002). Consequently, the greater availability of canopy fruits recorded in várzea probably results from the high nutrient content of the water that inundates and fertilizes these forests (Furch, 1997). Data in Haugaasen and Peres (2007) also suggest a higher productivity of fruits in várzea than in igapó and terra firme forests. The greater availability of *Ficus* and *Cecropia* fruits in várzea may explain why its bat biomass, dominated by canopy guild species, was twice that of the other two nutrient-poor types of forest (Ramos Pereira *et al.*, 2009). Sampaio *et al.* (2003) also explained the low abundance of canopy bats in terra firme forests near Manaus as resulting from the low availability of *Ficus* trees, possibly a consequence of nutrient poor soils (Gentry, 1990).

Contrasting with most canopy guild species, the fig-eater *V. brocki* was more abundant in terra firme forests (Ramos Pereira *et al.*, 2009). This may be explained by its roosting preferences; presumably it roosts under leaves in the forest understorey, as described for related species (Kunz *et al.*, 1994), and such roosts are likely to be rarer in the comparatively sparse understory of flooded forests.

Although the diet of the understory bat guild was more diverse overall than that of the canopy guild, these bats were also heavily dependent on just two plant genera, *Piper* and *Vismia*. It is thus somewhat surprising that fruiting plants of both genera seem to be rare in terra firme, and nearly absent in flooded forests. The absence of *Piper* shrubs in flooded forests is probably a consequence of an inability to resist the annual flooding; most species of this genus are generally found on well-drained soils (Marquis 2004). In the case of terra firme the low observed abundance may be due to the fact that the sampled sites are virtually dominated by closed undisturbed forest. In similar forests Bonaccorso *et al.* (2007) also found very few *Piper* plants that were small in stature and bearing almost no fruit, and Fleming (2004) reports that *Piper* tends to become scarcer with increasing maturity of the forest. Moreover, *Piper*s may have non-uniform distributions (Bernard and Fenton, 2003), because many are pioneer species, occurring mostly in gaps and along edges (Lobova *et al.*, 2009). The scarcity of fruiting *Vismia* may also be explained by their marked pioneer character (Lobova *et al.*, 2009). In most of the study region habitats disturbed by human activities are quite rare and localized, so pioneer plants are probably only present in naturally disturbed areas. As in some species of *Piper*, this dependency on habitat disturbances may also result in a patchy distribution, which makes their abundance difficult to estimate. This limitation should be considered when interpreting our estimates of understory fruit abundance.

In spite of the apparent scarcity and patchiness of *Vismia* and *Piper* fruits, they remain important in the diet of some species of the understory guild, implying that foraging bats travel to patches with particular characteristics to feed. In the case of flooded forests, understory bats presumably travel to elevated areas, islands or adjacent terra firme, which should have more fruit-producing shrubs than the surrounding inundated areas. A similar foraging strategy is followed by several terrestrial mammal species inhabiting Amazonian flooded forests (Bodmer, 1990).

In conclusion, we found that the availability of food for frugivorous bats varies among the three types of forest, a situation already described for other vertebrates in similar Amazonian forest mosaics (Haugaasen and Peres, 2007). The main fruits consumed by canopy bats are more abundant in várzea than in both igapó and terra firme, and the abundance of canopy bats reflects this difference. The situation is different for understory bats, as their key fruits were scarce in the three habitats, although less so in terra firme.

The Importance of River Banks

Our results suggest that river bank vegetation is very important for bats foraging in lowland Amazonian forests because these areas have more fruits available for bats to eat. However, the differences in occurrence and abundance of fruits between river banks and forest interior do not have the same implications for understorey and canopy bats.

Canopy bats had far more food available, particularly fruits of *Ficus* and *Cecropia*, along river banks in the two types of flooded forests. Such pioneer and early successional trees are usually abundant in the new soils that result from the accumulation of sediments along the inner banks of river meanders (Parolin *et al.*, 2002; Muscarella and Fleming, 2007; Schöngart *et al.*, 2007). This occurs in igapó and várzea but is more accentuated in the latter because white water has higher sediment loads (Furch, 1997).

In our study area terra firme was an exception to this trend for greater abundance of *Ficus* and *Cecropia* along the river banks. This is due to the fact that this type of forest only occurred on the high outer curve of the meanders. The remaining river bank area was occupied by igapó. These high banks, which are retreating due to river erosion, are steep and occupied by mature forest to the edge, so there is very little space for the establishment of pioneer and early successional trees. The situation may be different in Amazonian regions where igapó does not dominate the river bank areas; the beaches that build up in the inner banks are then occupied by the very early stages of the terra firme forest, which usually have a great availability of pioneer *Cecropia* spp. trees (Kalliola *et al.*, 1991).

Of the two fruits most consumed by understorey bats, *Vismia* and *Piper*, the first was only found along river banks but the second was mostly present, albeit in low numbers, in the forest matrix. Different resistance to flooding probably explains the distinct spatial distribution of the two genera. In fact, *Vismia* shrubs and trees are mainly found near creeks and rivers (van Roosmalen, 1985; Ferreira, 2000), while *Piper* species prefer well-drained soils (Marquis, 2004). Consequently, in terra firme the higher abundance of *Vismia* on the edges is balanced by a greater abundance of *Piper* in the forest interior. This makes the contrast in food availability between bank and forest matrix less marked for the understory guild than for the canopy guild.

The main reason why bat fruits are so abundant in river banks is because they are often pioneer and early successional plants. In pristine Amazon habitats such plants occur mostly in the areas that are disturbed by river dynamics or light gaps due to tree falls, with the former covering much greater areas. Salo *et al.* (1986) estimated that 12% of the Peruvian lowland Amazon is in successional stages along rivers, whereas the proportion of forest in early regeneration due to tree falls is typically 3–7% (e.g., Hartshorn, 1978). Moreover, river bank vegetation is predictable in space because it occurs in continuous strips (Salo *et al.*, 1986), so presumably bats find food along them more efficiently than in the dispersed tree fall gaps. In fact, it has been demonstrated that bats more readily find fruits along their flyways (Palmeirim and Etheridge, 1985) and they use tropical river systems as flyways (Fleming *et al.*, 1972; Delaval *et al.*, 2005; Medina *et al.*, 2007), taking advantage of the less cluttered air space (Meyer *et al.*, 2005).

Because frugivorous bats often fly along rivers and defecate in flight (Whittaker and Jones, 1994), seed dispersal may also reinforce the abundance of bat fruits in riverine vegetation; river banks may receive more seed rain of bat-consumed plants than matrix habitats. Fishes, which are known to be important dispersers of *Cecropia* (Kubitzki and Ziburski, 1994) and *Ficus* fruits (Banack *et al.*, 2002), may also contribute to the greater abundance of these plants on river banks. Other frugivores, including birds and mammals, may disperse seeds mostly along rivers, but to our knowledge this has not been studied.

The greater abundance of bat-consumed fruits in river bank vegetation makes this a potential keystone habitat within lowland Amazonia. Of particular importance is the greater abundance of *Ficus* spp., which are known to be a key resource not just for bats but also for other vertebrate groups (Shanahan *et al.*, 2001), such as primates (e.g., Peres, 1994) and birds (e.g., Shanahan and Compton, 2001). It would now be interesting to study if the nutritional content of fruits in river bank vegetation differs from those of the different types of forest matrix, as this may be relevant for the choice of foraging habitats by frugivores.

Our conclusion that bat fruits are more abundant along Amazonian river banks explains why some frugivorous bats occur in greater numbers in this habitat (Fleming *et al.*, 1972; Delaval *et al.*, 2005). Bat species that exploit these river bank resources tend to become more numerous, which has consequences for the structuring of bat communities. Delaval and Charles-Dominique (2006) demonstrated that edge effects on frugivorous bats are evident at least 3 kilometres away from the disturbed edges, presumably because bats can commute long distances to feed. It is thus likely that the abundant fruit resources of river banks influence the structure of frugivorous bat communities far into the forest matrix.

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