

Ecological Responses of Frugivorous Bats to Seasonal Fluctuation in Fruit Availability in Amazonian Forests

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ABSTRACT

Lowland Amazon is climatically one of the least seasonal regions on the planet, but little is known about how this is reflected in ecological seasonality. The central objective of this study was to determine whether seasonal fluctuations in the availability of fruit resources in Neotropical forests are sufficiently marked to affect the ecology and physiology of frugivorous bats. Seasonal variations in the overall bat abundance and in the captures, body condition, and reproductive activity of the two most abundant species, *Carollia perspicillata* and *Artibeus planirostris*, were studied within a region of central Brazilian Amazonia dominated by a mosaic of nonflooded (*terra firme*) and seasonally flooded forests (*várzea* and *igapó*). Concurrent seasonal changes in fruit availability were measured. The abundance of fruits was markedly seasonal, with far fewer resources available during the low-water season. There was a positive correlation between fruit and bat abundance. Overall, bats did not increase the consumption of arthropods during the period of fruit shortage. In *A. planirostris*, the body condition declined when fruits were scarcer. In both *C. perspicillata* and *A. planirostris*, foraging and reproductive activity were positively correlated with fruit availability. Consequently, the results suggest that resource seasonality is sufficiently marked to affect frugivorous bats and force them to make important eco-physiological adjustments.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Amazonia; Chiroptera; flooding; frugivory; *igapó*; nutrient load; *terra firme*; *várzea*.

MOST PHENOLOGICAL OBSERVATIONS IN NEOTROPICAL FOREST AREAS show that fruiting is episodic (Foster 1982, Terborgh 1983, Haugaasen & Peres 2005). Indeed, ripe fleshy fruits are ephemeral in nature, patchily distributed, fluctuate seasonally in abundance, and are scarce relative to other dietary constituents, like foliage or insects (Leigh & Windsor 1982, Howe 1984). Seasonal shifts in fruit abundance may result in periods of food scarcity, which potentially drive a variety of eco-physiological responses in frugivorous bats, such as changes in body condition (Fleming 1988), activity rates (Aguiar & Marinho-Filho 2004), diet (Fleming *et al.* 1972, Kunz & Ingalls 1994, Kunz & Diaz 1995), and timing of reproduction (Fleming *et al.* 1972, Bonaccorso 1979, Racey & Entwistle 2000).

Lowland Amazonia is characterized by a mosaic of flooded and unflooded forests. This mosaic is dominated by *terra firme*, upland forests that never flood and that tend to be nutrient-poor (Haugaasen & Peres 2006). Within this large matrix of *terra firme* are forest areas that are flooded seasonally. The most extensive type among these floodplain forests is *várzea*, which suffers seasonal inundation by nutrient-rich 'whitewaters' that originate partly in the Andes ice-melt. Another important floodplain forest type is *igapó*, seasonally inundated by oligotrophic 'blackwaters' that originate mostly in the tertiary Amazonian lowlands. These contrasting inundation regimes and nutrient contents of floodwaters result in distinct tree phenological responses (Haugaasen & Peres 2005).

Little is known about how seasonal changes in fruit availability affect aspects of the population dynamics and life history of bats, particularly in lowland Amazonian areas comprised of this mosaic of forests under distinct flooding regimes. Because of plant diversity

and fruiting asynchrony, it is possible that fruit resources are plentiful throughout the yearly cycle, and may never reach levels of scarcity that affect frugivorous bats. The central objective of this project was to determine whether, in humid equatorial Amazonian forests comprised of a mosaic of flooded and unflooded habitats, fruit availability is ever sufficiently low to affect frugivorous bats. We explored the following possible responses of bats to such periods of fruit scarcity: (1) bats may lower their level of activity to save energy, as some tropical bats appear to have the capacity to adjust their activity levels in response to food availability (Aguiar & Marinho-Filho 2004); (2) if fruit production is not synchronous across the different forest types, then bats may respond to fruit shortages by shifting between them; (3) predominantly frugivorous species may increase the consumption of arthropods during times of lower fruit availability; (4) pregnant and lactating females have considerable energy requirements (Speakman & Racey 1987, Kurta *et al.* 1989), and thus frugivorous bats could avoid reproducing during times of fruit scarcity; and finally (5) if fruit scarcity is severe, bats may be unable to maintain their optimal body condition, in which case we would expect measurable declines in their body condition that are coincident with low fruit abundance. To achieve our objectives, we studied seasonal variations in the overall bat captures and their diet. Additionally, we looked for seasonal changes in the reproductive activity and body mass of the most abundant species, *Carollia perspicillata* Linnaeus and *Artibeus planirostris* Spix. This was carried out within a region in central Brazilian Amazonia dominated by a mosaic of *terra firme*, *várzea*, and *igapó* forest, where we also measured the concurrent seasonal changes in fruit availability in these three habitats. We focused on the dry and rainy seasons, which are known to correspond to periods of low and high fruit abundance, respectively (Ayres 1993, Haugaasen & Peres 2005).

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METHODS

STUDY AREA.—Fieldwork took place around Lake Amanã, within the Amanã Sustainable Development Reserve (1°35′–3°16′ S, 62°44′–65°23′ W; Amazonas, Brazil), which encompasses large extensions of flooded forests, in a matrix of *terra firme* forests (Fig. 1). Inundation is a consequence of both the ice-melt in the Andes, brought in by the Japurá River, and of rainfall over the region. Lake Amanã is a mostly blackwater lake fed primarily by streams draining catchments dominated by *terra firme* forests. However, during seasonal floods, the south of the lake also receives some inflow of whitewater. The daily variation in temperature (*ca* 10°C) is greater than the annual average variation (Ayres 1993). In the middle of June, the temperature may decline to *ca* 18°C due to cold fronts coming from the Antarctic, but average monthly temperatures are about 29.5°C. The area receives *ca* 2500 mm of annual precipitation, two-thirds of which comes during the rainy season, which usually lasts from January to June. The dry season typically spans between July and December. Seasonal water-level variation may reach up to 10 m. Flowering and fruiting peaks generally occur in the dry and the rainy season, respectively (Rankin-De-Merona *et al.* 1992, Ayres 1993, Haugaasen & Peres 2005).

PLANT PHENOLOGY AND FOOD AVAILABILITY.—We established a total of ten sampling stations, of which four were in *terra firme*, three in *várzea*, and three in *igapó*. At each of these stations, we set up a 2-km line transect (divided into 100 sectors of 20 m) along which we made an inventory of trees and shrubs. With the help of a local field assistant with previous extensive experience in the collection of plant phenology data, we located all fruiting trees with canopies intersecting the transect line. We visually estimated the number of

ripe and unripe fruits in each of these trees, often using binoculars. In some situations, we estimated the number of fruits in a section of the canopy and then used this as a reference to make an estimate for the full canopy. All fruiting shrubs within 2 m from the transect line were also located, and the number of ripe and unripe fruits on them was estimated. The ripeness of fruits was determined with the help of the field assistant, using his extensive knowledge of the morphology and color of the fruits of each species. The results of these methods are approximate, and should not be interpreted as unbiased estimates of fruit abundance. As we used the same methodology in both seasons and in the three habitats, however, they are suitable for the types of comparisons made in this study. The estimates of fruit availability were performed once in the high-water season and repeated in the low-water season, during the same periods used for bat sampling. At all sampling stations, a part of the plant phenology transect coincided with the location of mist-nets that were used to capture bats.

We estimated the approximate availability of fruiting resources to bats by pooling all detected fruits, mostly to increase the stability of the estimates. This is possible because the phenology of the fruits consumed by bats tends to be coincident with that of the generality of Neotropical rain forest fruits. This coincidence is evident when comparing the phenology of ‘bat-fruits’ (*e.g.*, Parolin *et al.* 2002, Mello *et al.* 2004, Thies & Kalko 2004) with that of the generality of fruits (Kubitzki & Ziburski 1994, Wallace & Painter 2002, Haugaasen & Peres 2005, Ferreira & Parolin 2007). In both wet and dry Neotropical forests, maximum fruit production tends to occur early in the wet season, probably because germination conditions are best then (Garwood 1983). The general fruiting pattern may also be a good representation of the full range of fruits consumed by bats. In fact, although phyllostomid frugivores focus their diet on

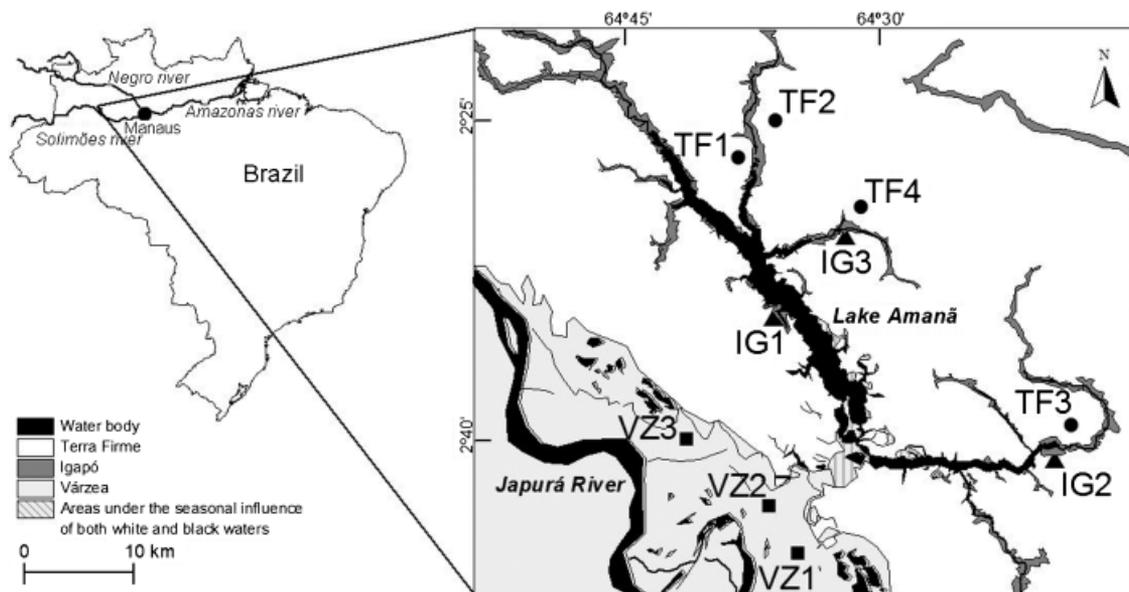


FIGURE 1. Main habitats in the study area, the Amanã Sustainable Development Reserve (Amazonas, Brazil), and at sampling stations (TF, *terra firme*; VZ, *várzea*; IG, *igapó*). The southern part of Lake Amanã usually has blackwater, but can receive whitewater temporarily. The distribution of habitats is based on cartography of the Mamirauá Sustainable Development Institute, and on satellite imagery.

some core plant species, they supplement this core with a large variety of other plant resources (Fleming 1988, Lobova *et al.* 2009).

BAT SAMPLING.—We sampled the bat community between April and June 2007, when *várzea* and *igapó* forests are fully inundated, and again between October and December, in the low-water season, when all the forests are dry. Bats were captured at the ten above-noted sampling stations. The type of forest sampled in consecutive sessions was changed, and so there was a temporarily balanced sampling of the three types of forest. Each station was sampled over four consecutive nights. Bats were caught using ten 12 × 3 m mist-nets, for a total trapping effort of 4800 net hours (one net hour corresponds to one 12-m net opened for 1 h). During the high-water season, mist-nets were set immediately above water in both *várzea* and *igapó*. The nets remained open during 1800–2400 h, during which time they were checked every 20 min. Bat sampling during full moon was generally avoided. Each captured bat was identified and weighed using a 20, 50, or 100 g Pesola® spring balance. Bats were classified as adults or juveniles according to the degree of ossification of the carpal joints and the development of nipples or testes (Baagøe 1977). All individuals were marked temporarily in the patagium using a pen marker, to allow for recognition of recaptures over the same sampling period, but there were only four recaptures and these were not included in the analyses. We collected fecal pellets of the mist-netted bats to analyze their diet. Each animal was kept in a separate cotton bag for about 30 min to collect its individual pellets. Fecal contents, usually seeds, fruit pulp, or arthropod parts, were identified using a stereo-microscope. The presence of these items in the feces was quantified using the frequency of occurrence in the droppings of individual bats.

DATA ANALYSIS.—To test for differences in the number of frugivore bats captured between seasons and between habitats within each season, we applied one-way analysis of variance (ANOVA), using each site as a sample. The same approach was used to compare the number of ripe fruits available within different habitat types and seasons. Tukey's HSD *post-hoc* tests were used to detect significant differences between pairs of habitats. To test for seasonal differences within each habitat, we used Pearson χ^2 analysis.

The significance of differences in the structure of frugivore assemblages between habitats and seasons was assessed by means of analysis of similarity (ANOSIM), a nonparametric permutation test that is analogous to an ANOVA for similarity matrices (Clarke & Gorley 2006). Data were normalized per site to account for differences in total abundance, and then square-root-transformed to reduce the influence of the most abundant species and to overcome the unity-sum constraint. Seasonal change differences in captures, body mass, and in the proportion of pregnant and lactating females were studied in the most abundant species: *C. perspicillata* and *A. planirostris*. To avoid biases due to incompletely grown individuals or pregnant females, comparisons of body mass excluded juveniles and females. Differences were detected using *t*-tests and Fisher exact tests. Changes in the frequency of occurrence of fruit and arthropods in the diet of bats between seasons were analyzed using

generalized binomial linear regression models; because of small sample sizes, diet data were pooled across all captured species.

RESULTS

VARIATION IN FRUIT AVAILABILITY.—Overall, we identified plants belonging to 46 families. The most abundant taxa were Sapotaceae, Caesalpinioideae, Mimosoideae, and Lecythidaceae. In *igapó*, we identified 26 tree families, the lowest number among the three sampled habitats: Sapotaceae were the most abundant family, although subfamilies Mimosoideae and Caesalpinioideae were also common. In *várzea*, we identified 33 plant families, with families Euphorbiaceae and Sapotaceae and subfamilies Caesalpinioideae and Lecythidaceae the most represented. *Terra firme* was the most diverse of the studied habitats; we recorded 40 plant families, usually represented by a few individuals per family. Here, Lecythidaceae, Myristicaceae, Caesalpinioideae, and Sapotaceae were the most represented taxa.

Ripe fruits were more abundant during the high-water season than during the low-water season (Table 1) and this happened in the two sampled strata, understory, and canopy (Fig. 2). There were significant differences in the abundance of ripe fruits between habitats in each of the seasons. In the high-water season, the abundance of ripe fruits was greater in *várzea* than in either *terra firme* or *igapó*. Ripe fruits were scarce during the low-water season in all habitats, but *igapó* had slightly more ripe fruits than *várzea*.

VARIATION IN BAT CAPTURES.—During the 80 nights of mist-netting, we captured 650 bats representing 27 frugivore or partial-frugivore species (Table S1). These included species of nectarivores also known to consume fruits, in particular those of the genera *Glossophaga*. The most frequently captured species were *C. perspicillata*, *A. planirostris*, *Artibeus obscurus*, and *Glossophaga soricina*. *Carollia perspicillata* and *A. planirostris* represented 55 percent of the frugivores captured. Total captures of frugivorous bats were higher during the high-water season (Table 1; Fig. 3). Captures were higher in *várzea* and *terra firme* than in *igapó* during the high-water season. During the low-water season, there were no significant differences between the three habitats.

The number of frugivorous bats captured was positively correlated with the abundance of ripe fruits ($r = 0.47$, $P = 0.03$). The patterns found suggest that bats are more abundant, or at least more active, when ripe fruits are more available (Fig. 4). There was no evidence of seasonal movements across habitats. In fact, there were no significant changes in the assemblage structure across seasons within each forest type (average seasonal dissimilarity according to ANOSIM: *terra firme* $r = -0.24$, $P = 0.95$; *várzea* $r = 0.11$, $P = 0.30$; *igapó* $r = -0.33$, $P = 0.99$).

Although seasonal habitat shifts were not sufficiently general to result in significant seasonal changes in the composition of bat assemblages in the three habitats, we did find evidence that the two most abundant species may partly shift habitats between seasons. Inspecting the patterns of abundance in *C. perspicillata* and *A. planirostris*, there was evidence of variation in their abundance within and between habitats (Table 1; Fig. 3). There were differences in

TABLE 1. Test statistics for comparisons of number of fruit-eating bats and ripe fruits between seasons and habitats (analysis of variance F), between pairs of habitats (Tukey's HSD), and for seasonal differences within each habitat (pearson χ^2). P-values are given in parentheses.

Between seasons	Bats		<i>Carollia perspicillata</i>		<i>Artibeus planirostris</i>		Ripe fruits	
	High water	Low water	High water	Low water	High water	Low water	High water	Low water
All habitats (F)	4.45 (0.02)	0.51 (0.49)	5.59 (0.04)	5.75 (0.04)	5.35 (0.04)	5.11 (0.06)	9.20 (0.01)	5.34 (0.04)
<i>Terra firme</i> (χ^2)	15.1 (0.04)	—	(0.40)	(0.04)	(0.95)	—	(0.34)	(0.68)
<i>Igapó</i> (χ^2)	4.35 (0.53)	—	(0.04)	(0.98)	(0.23)	—	(0.01)	(0.29)
<i>Várzea</i> (χ^2)	12.71 (0.02)	—	0.03	(0.04)	(0.02)	—	(0.04)	(0.07)
Between forests	High water	Low water	High water	Low water	High water	Low water	High water	Low water
All forests (F)	6.01 (0.03)	0.51 (0.49)	5.59 (0.04)	5.75 (0.04)	5.35 (0.04)	5.11 (0.06)	9.20 (0.01)	5.34 (0.04)
<i>Terra firme</i> and <i>igapó</i> (HSD)	(0.03)	—	(0.40)	(0.04)	(0.95)	—	(0.34)	(0.68)
<i>Terra firme</i> and <i>várzea</i> (HSD)	(0.63)	—	(0.04)	(0.98)	(0.23)	—	(0.01)	(0.29)
<i>Igapó</i> and <i>várzea</i> (HSD)	(0.04)	—	0.03	(0.04)	(0.02)	—	(0.04)	(0.07)

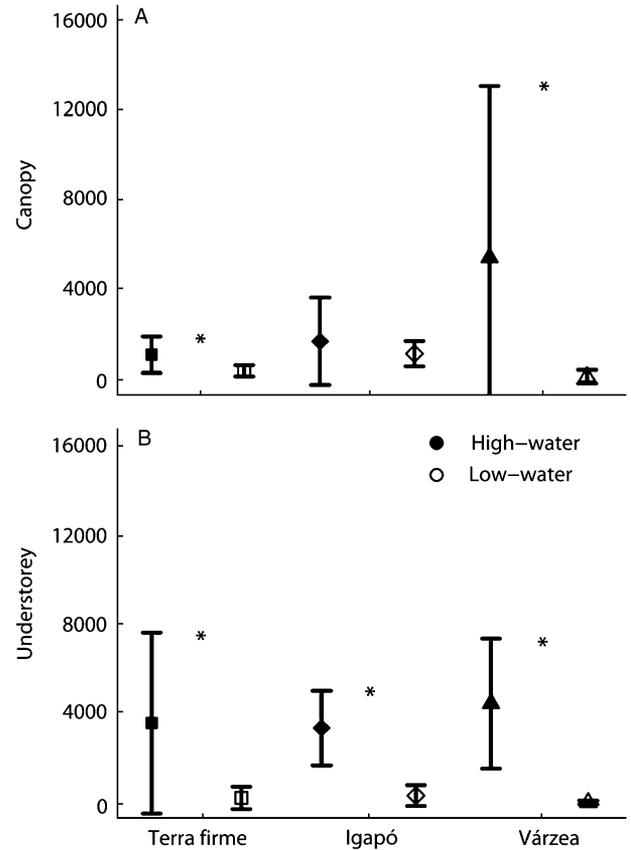


FIGURE 2. Mean fruit availability in the understory (A) and canopy (B) in each habitat during the low- and high-water seasons. Error bars represent 95% CI. Asterisks represent statistically significant differences between seasons (* $P < 0.05$).

the number of captures of *C. perspicillata* between habitats during each season. During the high-water season, this species was captured in higher numbers in *várzea* than in either *terra firme* or *igapó*. This pattern changed during the low-water season, with *igapó* presenting significantly more captures than either *terra firme* or *várzea*. There were no significant changes, however, in the number of captures of *C. perspicillata* between seasons, probably because the higher number of captured bats in *várzea* during the high-water season was offset by the inverse pattern detected in *igapó*. Similarly, there were some variations in the number of captures of *A. planirostris* between seasons, with a slight decrease in *várzea* and a simultaneous increase in *igapó* toward the low-water season, but these differences were not statistically significant. During the high-water season, there were differences in the number of captures of *A. planirostris* between habitats, and these were higher in *várzea* than in either *terra firme* or *igapó*.

CHANGES IN DIET, BODY CONDITION, AND REPRODUCTIVE ACTIVITY.— We examined whether bats, overall, increased the consumption of arthropods during the period of fruit shortage, the low-water season, but there were no significant differences between the two

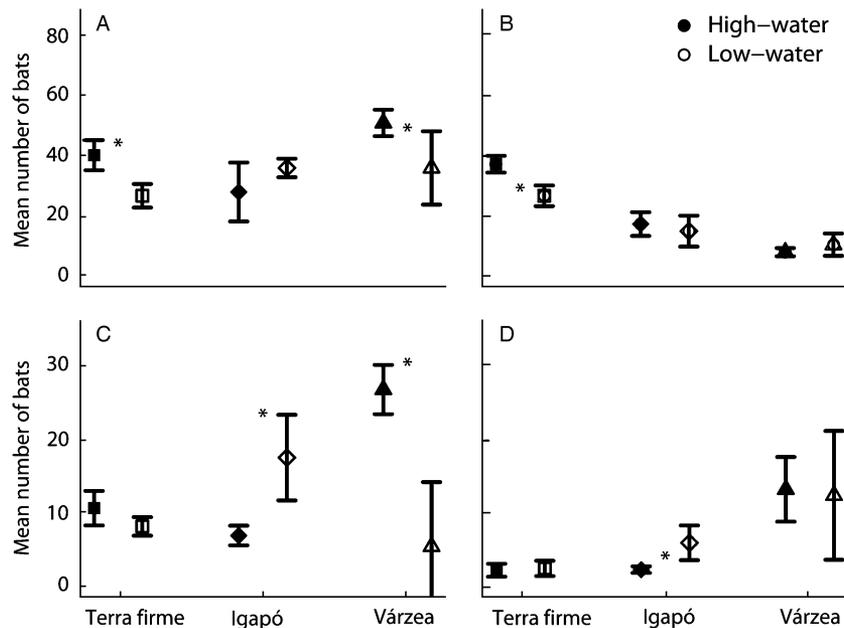


FIGURE 3. (A) Frugivorous bats captured in each habitat; (B) captures excluding *Carollia perspicillata* and *Artibeus planirostris*; (C) and (D) captures of *C. perspicillata* and *A. Planirostris*, respectively. Error bars represent 95% CI. Asterisks represent statistically significant differences between seasons (* $P < 0.05$).

seasons ($F = 0.15$, $P = 0.89$). The frequency of occurrence of fruits in the pellets (seeds or pulp) also showed no differences between the high-water season and the low-water season ($F = 0.31$, $P = 0.75$).

The mean weight in *A. planirostris* was higher during the high-water season (*i.e.*, the peak of fruit abundance), but there were no detectable differences in *C. perspicillata* (Fig. 5).

Each species exhibited significantly more pregnant and lactating females during the high-water season (Fig. 5).

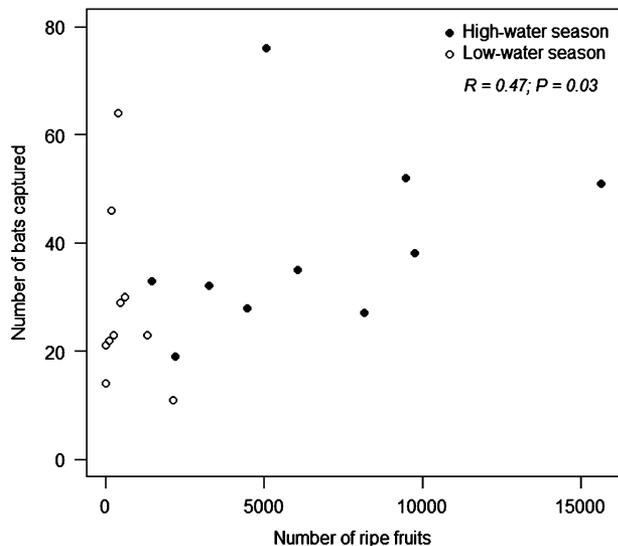


FIGURE 4. Relationship between ripe fruit abundance and the number of frugivorous bat captures in the two seasons.

DISCUSSION

SPATIO-TEMPORAL DIFFERENCES IN FRUIT AVAILABILITY.—Fruiting was a highly seasonal event in all three forest types. There were far more fruits during the high-water season in all habitats, but they were particularly abundant in *várzea*. During the low-water season, ripe fruits were much less abundant in all forests, but slightly more abundant in *igapó*. These results should be interpreted with care, as we sampled fruit abundance at a relatively small number of sites and do not have replicates across years. Nevertheless, this pattern of greater fruit availability during the high-water season has been observed in other Amazonian floodplain forests (Parolin *et al.* 2002, Haugaasen & Peres 2005). In addition, fruiting peaks during the onset of the high-water season in *terra firme* have been reported (Janzen 1967, Foster 1982, ter Steege & Persaud 1991, Haugaasen & Peres 2005), but our data did not have the temporal resolution to test for that pattern in the study area.

A seasonal variation in the availability of fruits does not necessarily imply that food is limiting for frugivorous bats during part of the year. Food may be plentiful throughout the year, and during the peak of fruiting, there may be a surplus of food that is not consumed.

CHANGES IN ACTIVITY LEVELS.—We captured 20 percent fewer frugivorous bats during the low-water season. The fact that the decline in captures was observed across all the major habitats in the region suggests that it was not mostly due to switches between habitats within the region in search for food. The decline in the

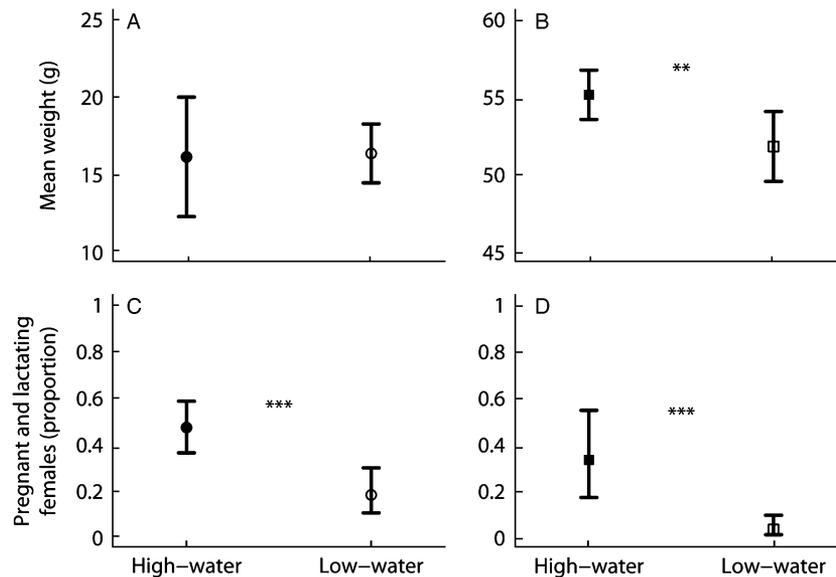


FIGURE 5. Weight and proportion of pregnant and lactating females among *Carollia perspicillata* (A and C) and *Artibeus planirostris* (B and D). Error bars represent 95% CI. Asterisks represent statistically significant differences between seasons (** $P < 0.01$, *** $P < 0.001$).

captures is more parsimoniously explained by an overall decrease in flying activity.

Flight is an energy-demanding activity for bats (Speakman & Thomas 2003), and the greatest energy demand bats have is collecting enough food to provide the energy they need to get through the next night (Altringham 1996), and so a reduction in foraging activity may allow tropical bats to preserve energy during times of food shortage. Seasonal variations in the capture rates of tropical bats associated with food availability have been reported (Aguilar & Marinho-Filho 2004, Hodgkison *et al.* 2004) and greater temporal differences in activity are expected in frugivorous species that depend on plants that experience peak fruit production during particular seasons (Presley *et al.* 2009). It is important to note, however, that our bat sampling was limited in time and not replicated across years; hence, further work is desirable to confirm the existence of temporal changes in activity due to changes in food availability.

MOVEMENT BETWEEN HABITATS.—The study area is a mosaic of different types of forest; thus, shifting habitats or commuting daily to foraging areas in habitats where resources are more abundant is a potential strategy by which to respond to periods of fruit shortage.

Only radio tracking of animals or a high number of inter-habitat captures of marked animals could determine with confidence whether there are movements between habitats. The pattern of abundance of *C. perspicillata* may be partly explained by such seasonal inter-habitat movements. Its peak abundance was recorded in *várzea* during the high-water season, when this habitat provided more abundant fruit resources than the other two types of forest. The situation changed in the low-water season, as the greatest

abundances of both ripe fruit and *C. perspicillata* shifted to *igapó*. Still, the decline in the number of captures of these bats in both *terra firme* and *várzea* was not totally compensated for by the observed increase in *igapó*. It is also possible that inter-habitat movements driven by the abundance of fruit resources are more common in some age guilds such as juveniles and/or nondominant adults (Cosson 1994). Interestingly, the data for *A. planirostris* suggest a pattern similar to that of *C. perspicillata*, but changes were insufficient to demonstrate statistical significance.

Some phyllostomids have the capacity to commute long distances (Morrison 1978). *Artibeus jamaicensis*, a sibling species to *A. planirostris*, is known to commute up to 10 km between roosts and feeding areas (Morrison 1978). The much smaller *C. perspicillata* usually forages within 1–3 km of its daily roosts (Fleming & Heithaus 1986, Bernard & Fenton 2003), but Fleming and Heithaus (1986) mention that site fidelity depends on the existence of enough food supply in the foraging areas. Therefore, why are inter-habitat seasonal shifts in abundance not more pronounced in our study area? Presumably, this is because there is a partial synchrony in the periods of fruit abundance and scarcity within the three habitats, and so there is little advantage in seasonally shifting one's foraging habitat. However, our *terra firme* and *igapó* sampling stations are quite far from *várzea* forest, and habitat shifts could be more common in areas closer to *várzea*.

DIETARY SHIFTS.—Many phyllostomid bats, most of which are predominantly frugivorous, are known to consume arthropods, and so one possible strategy they might use to cope with periods of fruit scarcity would be to increase their consumption of arthropods. We failed to detect any significant increase in the frequency of arthropods in the pellets during the period of fruit scarcity. This suggests

that, in general, it is more efficient for the studied bats to search for the few ripe fruits available, using their acute sense of smell (Laska 1990a, b; Korine & Kalko 2005), than to shift toward the capture of arthropods.

SEASONAL CHANGES IN REPRODUCTIVE ACTIVITY.—Seasonal bimodal polyoestry is a common reproductive pattern among frugivorous phyllostomids (Gardner 1977, Fleming 1988), including *C. perspicillata* and *A. planirostris*. We found seasonal changes in the reproductive activity in both *C. perspicillata* and *A. planirostris*, however, with far more pregnant and lactating females captured during the high-water season, coinciding with the period of greater fruit abundance.

Reproduction is energetically expensive, because its costs include not only growth of the fetus and milk production but also the increased costs of flight during pregnancy, and maternal care (Racey & Entwistle 2000). Consequently, if resources are strongly seasonal, bats adjust their reproductive cycles so that births and lactation occur during periods of food abundance (Bonaccorso 1979, Fleming 1988, Ramirez Pulido *et al.* 1993).

SEASONAL CHANGES IN BODY CONDITION.—In bats, the optimal body condition should be a balance between the bat's requirement to satisfy its short- and long-term energy needs and the added energy costs and mortality risks of flying with energy reserves (Hamilton & Barclay 1998). A low condition indicates that bats are unable to consume enough food to maintain such an optimal body mass, and fruit shortages may lead to decreased body mass in frugivorous bats (Smythe 1986, Charles-Dominique 1991). Body mass may also be affected by reproductive activities, such as lactation, courtship, or territorial defense.

Our results revealed seasonal changes in body condition in *A. planirostris*, but not in *C. perspicillata*, and this difference may be related to their distinct diets and foraging strategies. Large *Artibeus* are generally fig-eaters, while *C. perspicillata* feeds largely on *Piper* and *Vismia* fruits in rain forest areas, but it has generalist feeding habits (Palmeirim *et al.* 1989, Geiselman *et al.* 2002, Giannini & Kalko 2004). In general, in Amazonia, fig fruits are available throughout the year, and may even represent a keystone species during resource bottlenecks (Terborgh 1986, Kalko *et al.* 1996). Still, our data suggest that figs are less abundant during the low-water season. When figs are scarcer, *A. planirostris* may have to use complementary food resources, which may be sub-optimal for this large-bodied species, and this could explain the decline in body condition during the low-water season. The diverse diet of *C. perspicillata* may minimize the impact of the decline in fruit availability in the low-water season, allowing it to maintain a relatively stable body condition.

In conclusion, although the climatic conditions of lowland Amazonia are relatively stable throughout the year, the availability of fruit resources varies seasonally. Overall, our results suggest that this variation is sufficiently marked to influence the ecology and physiology of frugivorous bats, forcing them to make adjustments in their yearly cycle to cope with periods of relative food shortage.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *List of fruit-eating bats and number of captures of each species captured in the three habitats and in both seasons.*

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LITERATURE CITED

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