Seed dispersal by frugivorous bats in Central Guyana and a description of previously unknown plant-animal interactions.

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Bat Seed dispersal in Central Guyana.

ABSTRACT:

Species of bats in the subfamilies Stenodermatinae and Carolliinae are primarily frugivores, and through the ingestion of fruit and defecation of seeds, they play a crucial role in their environment through the dispersal of early successional and pioneer plants contributing to reforestation. These ecosystem services provided by frugivorous bats are becoming more critical with time, as anthropogenic habitat destruction continues to rise. The objective of this study was to survey the plant species dispersed by frugivorous bats in a tropical rainforest in Guyana. Fecal samples were taken from captured frugivorous bats and stomach contents were taken from a representative collection. The four most common bats were *Artibeus planirostris, A. obscurus, A. lituratus,* and *Carollia perspicillata*, which accounted for 67% of total captures in mist nets set in the forest understory. Twenty plant species were identified in fecal and stomach content samples with the most abundant (*Ficus nymphaeifolia, Piper bartlingianum, Cecropia latiloba,* and *C. sciadophylla*) accounting for 60% of the total. *Cecropia latiloba*, which is an early colonizer of floodplains throughout the Guiana Shield and Amazon River Basin was previously unknown to be bat dispersed. Seven plant species were documented as being dispersed by nine bat species for the first time. These results enhance our understanding of seed dispersal by Neotropical bats, specifically by revealing previously unknown bat/plant relationships.

INTRODUCTION

Bats are ecologically important as mediators of seed dispersal in tropical forests (Heithaus et al. 1975). This provision of ecosystem services is fundamental to forest dynamics and regeneration. Over 80% of plant species in the Neotropics rely on frugivorous vertebrates for the dispersal of their diaspores (the effective dispersal unit) (Howe and Smallwood 1982). Geiselman et al. (2002 onward) reported a total of 549 species in 191 genera forming 62 plant families that are dispersed by bats. In many cases, bats are the sole or primary dispersal agents for numerous tropical plants (Fleming and Heithaus 1981, Fleming 1988, Galindo-González et al. 2000). Lopez and Vaughan (2007) found that five of the six most commonly caught sympatric frugivorous bats in Costa Rica had a diet that was composed of predominately one or two species of plant, however, the frequency and extent to which bats change among food items depends on food resource abundance and competitors (Humphrey and Bonaccorso 1979).

Many neotropical phyllostomid bats rely on one or more of the five plant genera *Cecropia*, *Ficus*, *Piper*, *Solanum*, and *Vismia* (Fleming 1986). These bats are critical to the dispersal of these genera (Bonaccorso and Gush 1987); their fruits are nutritionally poor, requiring the consumption of large quantities to meet the bats dietary needs (Fleming 1986). Between foraging bouts, bats carry fruit to feeding roosts where they drop the indigestible material (Nowak 1994), and defecate seeds along the way. This process results in a single bat dispersing up to thousands of diaspores each night.

In Guyana, the phyllostomid genera *Artibeus* and *Carollia* are found in disproportionately high abundances compared with other species (Lim and Engstrom 2001a, 2005), and are therefore likely important seed dispersers that contribute disproportionately to the local forest dynamics in these relatively undisturbed forests. The objective of this study was to survey the plant species dispersed by frugivorous bats within the Iwokrama Forest in Guyana, with an emphasis on the genera *Artibeus* and *Carollia*. This is the first study of frugivorous bat diet conducted in Guyana.

METHODS

Study site

The Iwokrama Forest is composed of 371,000 ha of largely pristine rainforest located in central Guyana in the Potaro-Siparuni Region (Figure 1). Iwokrama was set aside by the government of Guyana in 1990 under the auspices of the Commonwealth Secretariat (Hawkes and Wall 1993). It is divided into two approximately equal parts: half is strictly a wilderness reserve set aside for the study of biodiversity, whereas the other area is for research in harvest of rainforest resources. A 70 km road passes through the center of the reserve. The Surama Forest is located just outside Iwokrama, bordering the southwest corner. The reserve is characterized by low-lying terra firme tropical rainforest dominated by emergent trees such as *Chlorocardium rodiei*, *Eperua falcata*, *Dicorynia guianensis*, *Mora excelsa* and *Swartzia leiocalycina*. Average annual rainfall for the region is approximately 3000 mm yr, 400-500 mm during rainy season months (April to July) and 200 mm during most other months. Temperatures range from an average low of 22°C at night during the July wet season to an average high of 36°C in the daytime during the October dry season (Bicknell et al. 2011).

In this study, four sites in this region were surveyed for bats. Turtle Mountain (4.731° -58.717°), Kabocalli (4.287° -58.508°), and Sandstone (4.383° -58.921°) are located within Iwokrama; and Rock Landing (4.179° -59.082°) is within the Surama Forest (Figure 1). The Turtle Mountain site is located within a large area of flooded forest adjacent to the Essequibo River. The other sites are subject to flooding from the Essequibo or Burro-Burro Rivers. However, the flooded forest at Turtle Mountain is the most substantial of the surveyed sites.

Kabocalli is the only site located within the wilderness preserve of Iwokrama and is the least developed of any site.

Sampling strategy

Bat surveys were conducted in the Iwokrama and Surama Forests during the wet-season in July and August 2013. Turtle Mountain was surveyed for 4 nights (July 20-23), Kabocalli for 5 nights (July 25-29), Rock Landing for 4 nights (August 1-4), and Sandstone for 4 nights (August 6-9). Sites were surveyed using 18 understory mist nets arranged in a 100 m grid comprised of three transects through the forest. Pairs of 12 m nets were positioned perpendicular to each other and separated by 50 m along each of the three transects. Nets were opened at 18:00 h and closed at 00:00 h. In the event of ongoing heavy rain, nets were closed. Species were identified using keys developed by Lim and Engstrom (2001b).

Fecal samples were collected from captured frugivores. Bats were held in cloth capture bags for no longer than two hours to allow time for individuals to defecate in order to maximize sample yield (Lopez and Vaughan 2004). Bags were cleaned of remnant feces between captures to prevent cross contamination of fecal samples. Bats were released after collection of data and fecal samples, if provided. Voucher specimens were collected of one individual per species per night of surveying to represent the species diversity of bats at each of the four sampling localities, and stomach contents were taken from collected frugivorous individuals for dietary analysis. Stomach content samples were not collected from individuals that had provided an earlier fecal sample. All procedures followed animal research guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and the Institutional

Animal Care and Use Committee at Angelo State University (IACUC Approval Number 1312). Specimens were deposited at the Centre for the Study of Biological Diversity in Georgetown, Guyana, Angelo State Natural History Collection in San Angelo, Texas, and the Royal Ontario Museum in Toronto, Ontario. Fecal samples were stored in 2 ml screw-cap microcentrifuge tubes filled with 70% ethanol.

Fallen fruit and any fruit available on plants surrounding the bat nets at each site, in addition to available accompanying plant parts, were collected and stored in Whirl-pak™ bags containing 70% ethanol for use as a comparative reference source for identification of seeds defecated by bats. Furthermore, any fruit carried into the nets by bats were documented and collected, and the species of bat carrying the fruit was recorded. All collected fruit and fecal samples were identified, and the contained diaspores were dried in order to build a reference collection. Diaspores from collected fecal samples and stomach contents were sorted into morphotypes and identified using a reference collection at Old Dominion University in Norfolk, Virginia. The number of types, number of diaspores of each type, and morphometric data of each type were recorded for each collected sample. Additionally, all diaspore types were photographed for digital documentation. Bat and plant genus associations were tested using a permutation test for independence (Chihara and Hesterberg 2011) using a chi-square test function in the coin package in R (Hothorn et al. 2006, 2008).

RESULTS

We accumulated 1,656 net hours of survey effort among the four sites, capturing 241 individuals from 26 species of bats. Capture rates ranged from a high of 0.262 captures/nh at Rock Landing to a low of 0.060 captures/nh at Kabocalli. The five most commonly captured species were *Artibeus planirostris* (70), *A. obscurus* (31), *Carollia perspicillata* (31), *A. lituratus* (30), and *Rhinophylla pumilio* (15). Overall, 75 fecal samples and 39 stomach content samples were collected from 14 bat species. Collectively, 63 of the combined 114 samples contained diaspores. The remaining 51 samples contained a combination of fruit pulp, plant material, and some insect material. Additionally, four fruits were collected from bats carrying them into nets: two *Chrysobalanaceae* species, one dispersed by *A. obscurus* and the other dispersed by *A. lituratus*, *Ficus maxima* dispersed by *A. planirostris*, and *Piper bartlingianum* dispersed by *Carollia perspicillata*. Of the 63 samples containing diaspores, *Artibeus lituratus*, *A. planirostris*, and *A. obscurus* accounted for 27 samples; *Carollia perspicillata* accounted for 25 samples; and other bat species (*Artibeus gnomus*, *Phyllostomus hastatus*, *Platyrrhinus helleri*, *Rhinophylla pumilio, Sturnira lilium, S. tildae,* and *Vampyressa bidens*) represented 11 samples.

Overall, 20 plant species were identified in collected samples, including *Cecropia latiloba*, a species previously unknown to be bat dispersed (Figure 2, Table 1) (Lobova et al. 2009). *Cecropia latiloba* was dispersed most commonly by *Artibeus planirostris* (three samples) and *A. obscurus* (two samples). However, a single dispersal record also was observed for *A. lituratus*, *C. perspicillata, P. helleri,* and *V. bidens.* Seven bat-dispersed plant species were found to be dispersed by bat species that have not previously been recorded as dispersers of those plant species, and thus are newly recorded bat/plant relationships (Lobova et al. 2009) (Table 1). When considering bat/plant genus associations, there was a significant association between *Artibeus* and *Ficus/Cecropia* and *Carollia* and *Piper/Solanum* (χ^2= 42.1, df= 3, p<0.001) (Figure 3). *Artibeus* accounted for 83% of *Ficus* records and 74% of

Cecropia records, and *Carollia* species accounted for 75% of *Piper* records and 100% of *Solanum* records.

Discussion

Overall, *A. lituratus, A. planirostris, and A. obscurus* fed on three plant genera *Ficus, Cecropia*, and *Philodendron*. *Carollia perspicillata* fed on nine genera: *Piper, Solanum, Rollinia, Senna, Anthurium, Paullinia, Philodendron, Vismia*, and *Cecropia*. Delaval et al. (2005) attained similar results in their analysis of niche breadth among frugivorous phyllostomid guilds in French Guiana. They found large *Artibeus* species exhibited low niche breadth, foraging on predominantly *Cecropia* and *Ficus* species, and conversely *Carollia* species foraged on a variety of fruits (predominantly *Solanum* and *Piper* species) with a much higher niche breadth. In the current study, minimal dietary overlap occurred between *Artibeus* and *Carollia*, with only two overlapping plant genera, *Philodendron* and *Cecropia.* Furthermore, each of these plant genera was represented by only a single sample in each group of bats: one *Artibeus* sample contained *Philodendron sp.* and a single *Carollia* sample contained *Cecropia latiloba*.

Cecropia latiloba is one of the most efficient colonizers of flood plains throughout its distribution within the Amazon Basin and the Guiana Shield (Parolin 2002, Lobova et al. 2003, Zalamea et al. 2011). The peak flowering and fruiting period of this species is during the wet season, contrary to most other fruit-producing plant species over its range (Milton 1991). Fruits of *C. latiloba* mature only at the end of the high water phase, occurring in July and August, and are adapted for aquatic dispersal by fish (Parolin 2002, Parolin et al. 2010). *Artibeus lituratus, A. planirostris,* and *A. obscurus* were responsible for six of the nine dispersal records of *Cecropia latiloba* in our study. It is unknown whether foraging on *C. latiloba* by bats was opportunistic or preferential. Futhermore, as many bird species are known to consume and disperse *Cecropia* species (Eisenmann 1961) and many *Cecropia* species are known to have multiple animal dispersers (Eisenmann 1961, Fleming and Williams 1990, Lobova et al. 2003, Anderson et al. 2009), future studies are necessary to determine if *C. latiloba* is dispersed by birds in the Iwokrama Forest, and compare the roles and germination rates as a result of fish, bat, and bird dispersal.

In the present study, 37% of the fecal/stomach content samples from 9 species of frugivorous bats represented new dispersal records for 7 species of plants, including the first report of *Cecropia latiloba* being bat dispersed (Lobova et al. 2009). Continued dietary research on the bat community within Iwokrama would undoubtedly add to our current understanding of bat/plant interactions in wet and seasonally inundated habitat as well as the ecological contribution of bats during forest regeneration.

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TABLE 1. *Inventory of Bat Dispersed Plant Species*-- The 20 dispersed plant species identified in fecal and stomach content samples of bats collected in 2013 from study sites within the Iwokrama Forest, Guyana. Along with plant species, the number of samples in which each plant species occurred and bat species whose samples contained each plant species are displayed. An asterisk (*) denotes a new record of plant species documented in fecal samples of bat species acting as a dispersal agent, or in the case of *C. latiloba,* a plant species that has been newly discovered to be bat dispersed.

Plant Species	**Total Number of Samples**	**Bat Species (Number of Samples)**
Ficus nymphaeifolia	12	*A. lituratus* (2), *A. obscurus*, *A. planirostris* (7), *V. bidens** (2)
Piper bartlingianum	12	*C. perspicillata* (8), *R. pumilio*, *S. tildae* (3)
*Cecropia latiloba**	9	*A. lituratus, A. obscurus* (2), *A. planirostris* (3), *C. perspicillata*, *P. helleri*, *V. bidens*
Cecropia sciadophylla	8	*A. lituratus* (4), *A. obscurus, A. planirostris, P. hastatus, S. lilium**
Solanum rugosum	5	*C. perspicillata* (5)
Ficus panurensis	4	*A. gnomus*, A. planirostris** (3)
Rollinia exsucca	4	*C. perspicillata* (4)
Piper trichoneuron	2	*C. perspicillata* (2)
Senna quinquangulata	2	*C. perspicillata* (2)
Anthurium trinerve	1	*C. perspicillata*
Cecropia obtusa	1	*A. obscurus*
Cecropia sp.	1	*A. lituratus*
Ficus insipida	1	*A. planirostris*
Ficus maxima	1	*A. obscurus**
Paullinia sp.	1	*C. perspicillata**
Philodendron guianense	1	*C. perspicillata**
Philodendron sp.	1	*A. lituratus*
Piper anonifolium	1	*C. perspicillata*
Piper hostmannianum	1	*C. perspicillata*
Vismia cayennensis	1	*C. perspicillata*

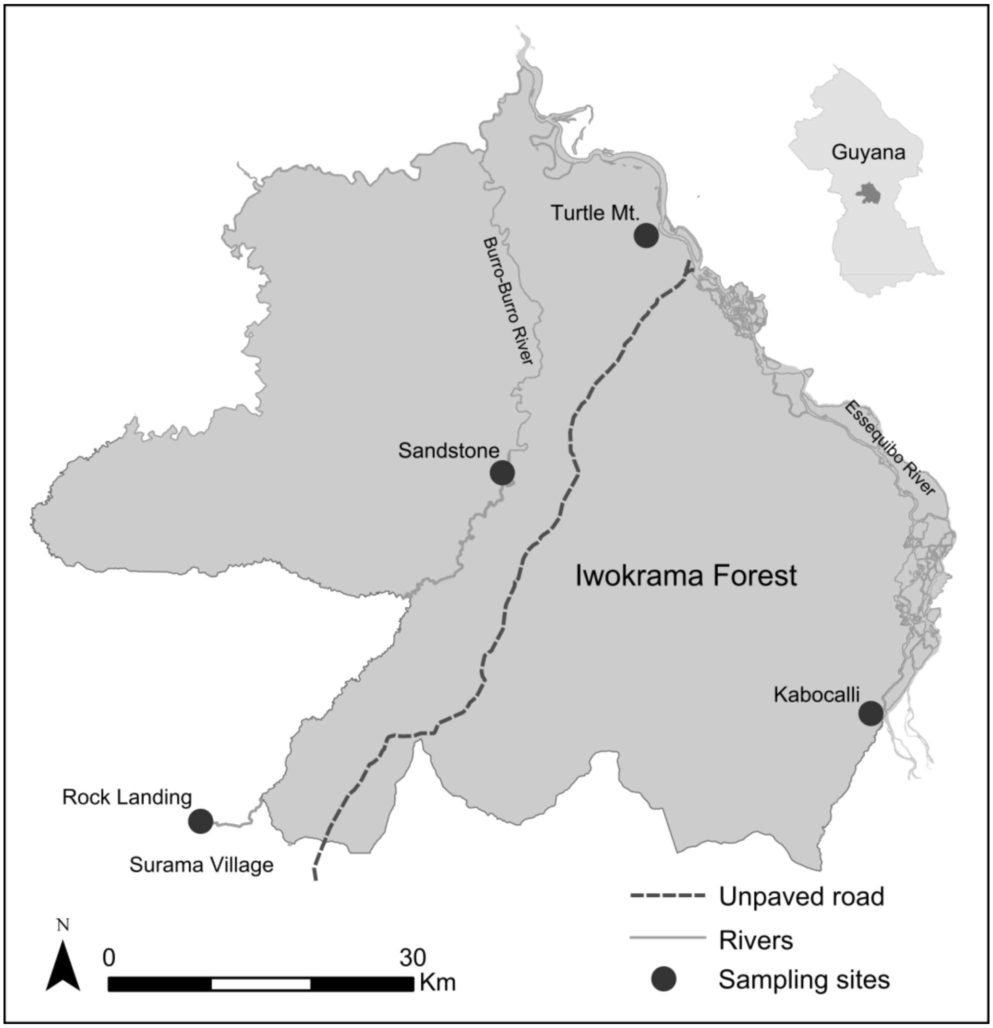

FIGURE 1. Map of the Iwokrama Forest in central Guyana with the study sites labeled.

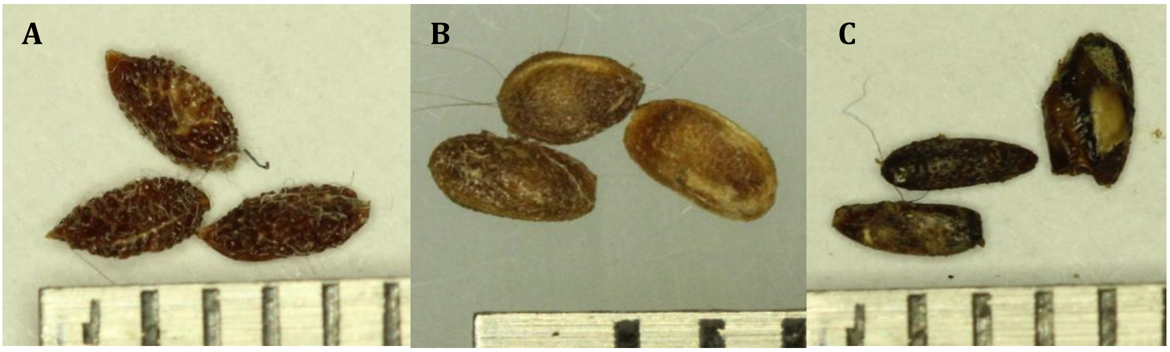

FIGURE 2. Images showing diaspores of *Cecropia sciadophylla* (A), *Cecropia latiloba* (B), and *Cecropia obtusa* (C). Diaspores were isolated from the following collected fecal samples: *C. sciadophylla – Artibeus lituratus*; *C. latiloba – Artibeus obscurus*; and *C. obtusa – Artibeus obscurus*. Samples collected July-August 2013 from the Iwokrama Forest, Guyana. Scales in images in millimeters.

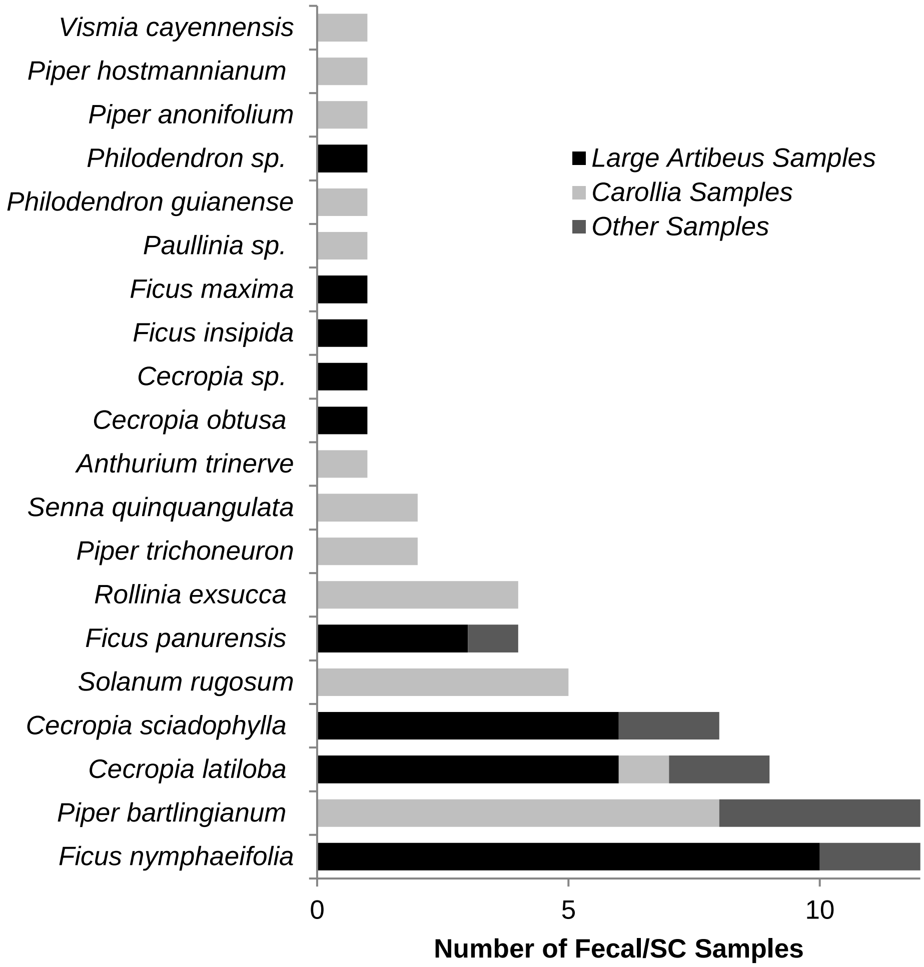

FIGURE 3. Plant species identified in collected fecal and stomach content (SC) samples, and the number of samples in which each plant species occurred from *Artibeus* (black), *Carollia* (light grey), or other bat genera (*Rhinophylla*, *Phyllostomus*, *Platyrrhinus*, *Sturnira, Vampyressa,* and non-focal *Artibeus*; dark grey). Non-focal *Artibeus* species are represented by a single sample collected from *Artibeus gnomus*, a smaller *Artibeus* species within the subgenus *Dermanura* (Simmons 2005). Samples collected July-August 2013 from the Iwokrama Forest, Guyana.