DIET AND TROPHIC STRUCTURE IN A COMMUNITY OF FRUIT-EATING BATS IN LACANDON FOREST, MÉXICO

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Assemblages of neotropical frugivorous bats display a trophic structure composed of groups of species reflecting diet preferences. The structure is hypothesized to be an ancestral trait, suggesting that very similar diets would be observed throughout a species’ range. We examined the frequency of occurrence of seeds in feces of a community of frugivorous bats in Lacandon Forest, México. Using metric multidimensional scaling, we found 3 groups of species, similar to those found in other regions and congruent with phylogenetic groupings, lending support to a historical origin of this structure. However, the diets of some species differed from those observed in other regions, in particular Barro Colorado Island (BCI), Panama. Here, we found species of the tribe Ectophyllini to be specialized on plants of the genus *Cecropia,* rather than *Ficus*-specialists as on BCI. This discrepancy can be related to differences in plant composition or in disturbance regimes, and we suggest that Ectophyllini (including *Artibeus*) are facultative specialists of the genera *Ficus* and *Cecropia* rather than strict *Ficus*-specialists.

Key words: bats, frugivory, Lacandon Forest, Phyllostomidae, tropical rain forest, trophic structure

Phyllostomidae is one the most trophically diverse families of mammals (Freeman 2000; Giannini and Kalko 2004; Wetterer et al. 2000), with discrete guilds separated by size, morphology, diet, bite force, and feeding behavior (Bonaccorso 1979; Bonaccorso and Gush 1987; Dumont 1999; Findley and Black 1979). Within Phyllostomidae, phytophagous phyllostomids are an abundant and diverse group (Giannini and Kalko 2004; Medellín 1994; Stevens 2004), forming an essential component of neotropical frugivore communities. Functionally, these bats play a fundamental role in pollination, seed dispersal, and forest regeneration (Fleming 1988; Kalko 1997; Medellín and Gaona 1999; Proctor et al. 1996; Thies and Kalko 2004). Trophic structure for phytophagous phyllostomids has been described several times, either by comparing lists of food items using parametric statistics (e.g., Giannini 1999; Medellín and Gaona 1999) or by inferring structure through ordination procedures (e.g., Giannini and Kalko 2004; Humphrey et al. 1983). In general, it has been found that phytophagous phyllostomids show a trophic structure defined by specialization on certain plant species (Fleming 1986; Giannini and Kalko 2004). The most recent study postulated a general trophic structure with 3 main groups, 1 composed of *Piper*-specialists, a 2nd of 2*Ficus*-specialists, and a 3rd of generalist species (Giannini and Kalko 2004). Within this structure, species of the genus *Carollia* are classified as *Piper*-specialists, species of the tribe Ectophyllini (sensu Giannini and Kalko 2004; e.g., *Artibeus jamaicensis* and *A. lituratus*) are classified as *Ficus*-specialists, and species of the tribes Glossophagini and Phyllostomini are classified as general plant eaters.

The origin of this trophic structure is hypothesized to have a significant historical component. Giannini and Kalko (2004) show a strong correlation between phylogenetic structure and trophic structure in phytophagous phyllostomids on Barro Colorado Island (BCI), Panama. This result led the authors to propose a unique origin for diet dominance within each clade. For instance, the species within the tribe Ectophyllini inherited fig-eating specialization from their common ancestor. The hypothesized selective pressure proposed to have driven diet specialization in this group is past competition among plant species for dispersal agents, through a process of diversification.
of types of fruits, phenology, and other fruiting attributes, which in turn led to dietary specialization of dispersal agents (Fleming 1986).

The hypothesis of a unique origin for diet dominance leads to the prediction that these species will tend to have similar diets throughout their range, with consistently high proportions of the specific food item on which each species is specialized (Giannini and Kalko 2004). The purpose of our paper was to examine a phytophagous phyllostomid community in the Lacandon Forest of Chiapas, México, to identify the diet dominance for each species and describe the trophic structure of the community. In particular, we were interested in comparing diet composition and dominance and trophic structure of the phytophagous phyllostomid community at Lacandon Forest with the diet dominance and trophic structure hypothesized for the group.

**MATERIAL AND METHODS**

Our study was carried out near the Chajul Tropical Biology Station (16°06′N, 90°56′W; 120 m elevation) situated in the Lacandon Forest of Chiapas, México. The area comprises 1.5 million ha of lowland tropical rain forest (Medellín 1992), home to at least 61 species of bats (Medellín 1994). The climate is seasonal, with drought conditions from February to May, and rain during the remainder of the year (Medellín 1994).

We sampled phytophagous phyllostomid bats by mistnetting in mature rain forest and secondary forest understory from September to December 1993 and from April to August 1994. All captured animals were treated in a manner compatible with guidelines of the American Society of Mammalogists (Gannon et al. 2007). Bats were identified using a field identification key (Medellín et al. 1997). We report species names following nomenclature in Simmons (2005), which suggests that *Carollia brevicauda* found in and north of Panama is in fact *C. sowelli*. Captured bats were placed in individual clean canvas bags for 30 min before release. Bags were then searched for fecal pellets containing seeds. Those fecal pellets containing only pulp were recorded, but not included in this study. Collected seeds were dried and identified to genera, and whenever possible to the species level, using a reference collection deposited at UNAM. The final dataset consisted of a table of frequency of occurrence of plant species (columns) for each bat species (rows). In the final tally, zero was recorded whenever a plant species was not sampled for a bat species.

To describe the trophic structure we used a multidimensional scaling approach, namely principal coordinate analysis (Gower 1966), a method of analysis that makes minimal assumptions, yet can uncover hidden structure in the data. Principal coordinate analysis is an ordination procedure that takes as input a (dis)similarity matrix of any kind (i.e., pairwise Jaccard similarities, or Euclidean distances), and finds the best representation in a q-dimensional Cartesian space of the distances, or similarities, found in the original n-dimensional space (q < n) of the data (Kruskal and Wish 1978). Here, each point is a bat species, positioned in the graph in accordance to its diet dominance in relation to the diet dominance of other species.

Principal coordinate analysis was conducted using the labdsv package (Roberts and Oksanen 2005) within R (R Development Core Team 2005). Species with <20 fecal samples were excluded from the final analysis because these produced biologically uninformative results in preliminary explorations. For the species with >20 samples, we rarefied the sample size to 20 occurrences to assure a uniform comparison with the species with only 20 occurrences (the smallest sample size with informative results). Rarefaction was carried out through a routine written and implemented by AGS in Mathematica (Wolfram Research, Inc. 2004). For each bat species, we averaged 10,000 random samples with replacement of 20 seed species from the original seed species count to obtain the most likely sample of 20 seed occurrences for each species. Each sample of 20 was drawn only from the original seed count for a species; therefore, if a plant species was not observed originally it was not included in the resampling scheme. As suggested in Kruskal and Wish (1978), both Euclidean and Bray–Curtis distances were calculated. The observed configurations under both distances were evaluated for their interpretative value, and the degree of variance explained by the first 2 dimensions.

**RESULTS**

A total of 13 bat species was represented in our sample (Table 1), and the seeds of 17 species of plants were identified in 632 seed occurrences (Table 2). Of these, 42 occurrences (~6.6% of the total) could not be identified beyond the genus level (Table 2; *Ficus*, *Phoradendron*, and *Cestrum*). *Cecropia peltata* (170), *Piper hispidum* (162), and *P. auritum* (139) accounted for roughly 75% of the total occurrences (total 471; Table 2). Of the 13 bat species, 5 were removed from the principal coordinate analysis because they had <20 samples (Table 1). Of the remaining 8 species, only 7 had >20 seed occurrences, which were therefore rarefied to 20. The 8th species had a seed count of exactly 20 (Table 1).
As to diets, *C. peltata* comprised approximately 77% (38/49) and 81% (39/48) of the food items consumed by *A. jamaicensis* and *A. lituratus*, respectively. *P. hispidum* accounted for almost 39% (72/185) and *P. auritum* for 35% (66/185) of the seed occurrences for *C. sowelli*. For *Carollia perspicillata*, both *P. hispidum* and *P. auritum* had the same number of occurrences, and were each responsible for 30% (28/91) of the diet items. In addition, *C. perspicillata* was responsible for almost 80% (23/29) of the occurrences of *C. peltata*. *Stenodermus lilium* had roughly the same number of occurrences of *C. peltata* (25/123), *P. auritum* (24/123), and *P. hispidum* (34/123), with a slight dominance of *P. hispidum*. *Glossophaga soricina* also displayed a mixed diet, but showed a higher proportion of *C. peltata* (31/81) and *P. hispidum* (26/81), whereas *P. auritum* (7/81) and *C. obtusifolia* (7/81) were not as highly represented. *Glossophaga commissarisi* displayed a similar pattern, with *C. peltata* (8/22) and *P. hispidum* (8/22) having a greater representation in the diet than *P. auritum* (2/22) and *C. obtusifolia* (2/22). Finally, *Platyrrhinus helleri* showed a high representation of *C. peltata* (12/20), and *P. hispidum* and *P. auritum* were found once each.

As to trophic structure, Euclidian and Bray-Curtis distances produced very similar final configurations, but because Euclidian distances explained more of the observed variance all results are presented for Euclidian distance only (Fig. 1). Only the first 2 dimensions of the principal coordinate analysis, together explaining nearly 94% of the variance, are displayed. The structure uncovered with principal coordinate analysis confirmed the structure shown in Table 1, constructed on the diet composition discussed above. Principal coordinate 1 described a gradient of bat species that had an increasingly greater dominance of their diets by *Cecropia* (mainly *C. peltata*) to species that had a greater dominance by *Piper* (mainly *P. auritum* and *P. hispidum*; Fig. 1). There were 2 clearly defined groups along principal coordinate 2, separating diet specialists and generalists (Fig. 1). Species specializing on core plant species are represented lower along this axis, whereas generalist species are represented higher along this axis. *C. perspicillata* and *C. sowelli* were the 2 species with the largest percentage of *Piper* in their diets (84% and 69%, respectively; Table 1). At the other extreme, *A. jamaicensis* and *A. lituratus* were the 2 species with the largest percentage of *Cecropia* in their diets (88% and 85%, respectively; Table 1). *S. lilium* and *P. helleri* had slightly mixed diets (as seen above), but still showed a high level of dominance by *Piper* and *Cecropia*, respectively. Finally, *G. commissarisi* and *G. soricina* exhibited no dominance by either plant genus, with equal representation in their diets (Table 1), and accordingly appear roughly midway between the 2 specialized diet groups in our principal coordinate analysis (Fig. 1).

**Table 2.**—Total seed count for each of the 17 plant species found during our study at Lacandon Forest, Chiapas, México, from September to December 1993 and April to August 1994.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>No. occurrences</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td><em>Spondias radilofera</em></td>
<td>5</td>
</tr>
<tr>
<td>Moraceae</td>
<td><em>Cecropia obtusifolia</em></td>
<td>26</td>
</tr>
<tr>
<td></td>
<td><em>Cecropia peltata</em></td>
<td>170</td>
</tr>
<tr>
<td></td>
<td><em>C. petiolaris</em></td>
<td>4</td>
</tr>
<tr>
<td></td>
<td><em>Ficus</em></td>
<td>3</td>
</tr>
<tr>
<td></td>
<td><em>Ficus atrensis</em></td>
<td>7</td>
</tr>
<tr>
<td></td>
<td><em>Ficus pertusa</em></td>
<td>9</td>
</tr>
<tr>
<td>Piperaceae</td>
<td><em>Piper auritum</em></td>
<td>139</td>
</tr>
<tr>
<td></td>
<td><em>Piper campanulata</em></td>
<td>5</td>
</tr>
<tr>
<td></td>
<td><em>Piper hispidum</em></td>
<td>162</td>
</tr>
<tr>
<td></td>
<td><em>P. lapathifolium</em></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Piper nitidum</em></td>
<td>30</td>
</tr>
<tr>
<td>Santalaceae</td>
<td><em>Phoradendron</em></td>
<td>7</td>
</tr>
<tr>
<td>Solanaceae</td>
<td><em>Cestrum</em></td>
<td>32</td>
</tr>
<tr>
<td></td>
<td><em>Lycianthes nitida</em></td>
<td>8</td>
</tr>
<tr>
<td></td>
<td><em>Solanum atrensis</em></td>
<td>13</td>
</tr>
<tr>
<td></td>
<td><em>Witheringia nelsoni</em></td>
<td>10</td>
</tr>
</tbody>
</table>

**Fig. 1.**—Inferred trophic structure for the phytophagous phyllostomid bats in Lacandon Forest, Chiapas, México. First dimension separates *C. peltata*, generalists, and *Piper* trophic groups. Second dimension separates specialist and generalist species. Axis labels include in parentheses the percentage of the variation explained by each dimension.

**Discussion**

Given that the species included in the principal coordinate analysis represent about 94% of all bats captured in the understory of the Lacandon Forest (Medellín et al. 2000), and that our sample included representatives of all clades of phytophagous phyllostomid bats (Giannini and Kalko 2004), our study realistically reflected the community structure of the frugivorous species of bats in the area. Similarly, our sample of more than 600 fecal samples spread over 9 months of the year (skipping the period January–March for causes beyond our control—see Medellín et al. 2000) represented accurately the diets of the bat species studied. The high prevalence of *P. hispidum* and *P. auritum* in the diets of *C. sowelli*, *C. perspicillata*, and *S. lilium* is correlated with high prevalence of these species of plants in the surrounding habitat (Gaona 1997). The same can be said for the high prevalence of *C. peltata* in the diets of *A. jamaicensis*, *A. lituratus*, and *P. helleri*. Both these plant species are characteristic of secondary areas in neotropical rain forests that have undergone some level of disturbance (Fleming and Raymond Heithaus 1981; Thies and Kalko 2004), and are abundant, even locally dominant in the
sampled region of this study (Benitez-Malvido 2006; Medellín et al. 2000). In addition, these species tend to produce fruits across seasons, with ripe fruits being found in Lacandon in almost every month of the year (R. A. Medellín and O. Gaona, in litt.). Species of the genus Ficus, on the other hand, use a different strategy, with each individual tree clustering its fruit production in time and space, thus promoting seed dispersal by a large number of frugivorous species, not only bats (Shanahan et al. 2001). However, fruiting is irregular, and, although it may be an important source of food items for the local phyllostomid bat community, Ficus does not dominate their diet.

When compared to observed diets on BCI, as described in Giannini and Kalko (2004), there are some marked differences. The genus Carollia is often described as having a diet primarily dominated by plants of the genus Piper (e.g., Fleming 1991; Giannini and Kalko 2004; Thies and Kalko 2004). Our study included 2 species in this genus, C. sowelli and C. perspicillata. As expected, both displayed a diet markedly dominated by Piper plants. Nevertheless, the 2 species of Piper most frequently observed in Lacandon Forest (P. auritum and P. hispidum) were rare or not detected at all as dietary items on BCI (Giannini and Kalko 2004). S. lilium was another species observed here to have a diet dominated by Piper plants. However, S. lilium was rarely observed on BCI (Giannini and Kalko 2004). In regions where the species is more abundant, S. lilium is often associated with Solanum and Piper (e.g., Giannini 1999). Our study found the diet of this species to be dominated by Piper rather than Solanum, with roughly 50% (61/123) of the seed count consisting of plants from the genus Piper, and only 19% (24/123) consisting of plants from the family Solanaceae. Nevertheless, S. lilium was responsible for almost 40% (24/61) of all seed occurrences within the Solanaceae. Of the 3 main food items found for S. lilium in our study, none seem abundant on BCI (Giannini and Kalko 2004). This suggests that the rarity of S. lilium from BCI might be caused, among other things, by limited availability of favored food items, possibly linked to the limited level of disturbance on BCI.

Species of the genus Glossophaga are primarily described as nectar-feeders (e.g., Lemke 1984; Sazima and Sazima 1978). However, some species, such as G. commissarisi, can include fruits seasonally in their diets when nectar is scarce (Tschapka 2004, 2005). Our sampling method did not allow us to assess whether nectar was important for Glossophaga in Lacandon Forest; however, our results showed that fruits were consumed in the area, with both species including an equally high proportion of both Piper and Cecropia in their diets (Table 1). At BCI, Giannini and Kalko (2004) found in 23 dietary records for G. soricina that 70% of the diet consisted of fruits (mainly Cecropia and Ficus species) and 30% consisted of pollen. In the 2 dietary records for G. commissarisi, those authors only found pollen. Even though their analysis excluded the latter species because of the small sample size, the authors classified both Glossophaga species as generalist species with respect to their diets. At any rate, there are no records from BCI of these species eating fruits from plants of the genus Piper, in marked contrast with what we found in Lacandon Forest, and Tschapka (2005) reported for La Selva, Costa Rica.

Finally, the larger species of Artibeus were initially hypothesized to be Ficus-specialists (i.e., A. jamaicensis and A. lituratus—Fleming 1986); this hypothesis was later extended to the whole Ectophyllini tribe, which includes P. helleri (Giannini and Kalko 2004). However, we found that all 3 species of Ectophyllini analyzed here (A. jamaicensis, A. lituratus, and P. helleri) ate mostly fruits from plants of the genus Cecropia (mostly C. peltata). Nevertheless, of the 19 seeds we found of the genus Ficus, 42% (8/19) were found in fecal pellets of these species. Although this is contrary to what has been hypothesized previously and to what has been reported for BCI, it is not uncommon. For instance, A. lituratus in the Brazilian Atlantic Forest has a Cecropia-biased diet, with 96.3% of the 2,210 seeds found in 26 fecal pellets being of Cecropia (Passos and Passamani 2003). Additionally, in a sample of 173 seeds found in fecal pellets of A. jamaicensis in Costa Rica, 50.3% were of Cecropia (Fleming and Williams 1990).

The difference in diets observed could be caused by differences in vegetation and disturbance regimes between Lacandon Forest and BCI (Hopper et al. 2004; Medellín 1994; Medellín and Gaona 1999). With respect to Piper species, Chiapas is considered to be in the same biogeographical region as BCI (Quijano-Abril et al. 2006). However, the Lacandon Forest region has lower species richness than the BCI region (10 versus 52 species—Quijano-Abril et al. 2006). This difference can help explain the differences seen among the Piper-specialists in terms of the Piper species consumed in both locations. With respect to Ficus species, the 3 most common species in the diets of phyllostomids on BCI are found in Chiapas (Serrato et al. 2004). In particular, Ficus insipida, the species with the most seed records at BCI (Giannini and Kalko 2004), is relatively widespread in México, and has numerous records within Chiapas, and Lacandon Forest specifically (Martínez et al. 1994). But, as mentioned before, in Lacandon trees of the genus Ficus have irregular fruiting cycles, suggesting they may not be as reliable a food source as Cecropia for bats in this area. Finally, we could not locate any information pertaining to the relative abundance of Cecropia species on BCI. However, Cecropia is a common genus throughout the Neotropics associated with early successional stages (Guariguata and Ostertag 2001). Given the small area of BCI and the fact that hardly any disturbance other than treefall gaps occurs on the island (Hubbell et al. 1999), Cecropia is likely to sustain much lower relative abundances on BCI than in Lacandon Forest. On the other hand, we know that in Lacandon secondary forests are often dominated by Cecropia (Benitez-Malvido 2006). This suggests that food items available to bats in Lacandon Forest and BCI differ significantly, with Cecropia being much more abundant in Lacandon Forest than on BCI.

In relation to trophic structure, the principal coordinate analysis indicated a community structured around 2 main groups, 1 that was specialized primarily on single core plants and a 2nd, more generalist group that consumed both core plant.
species. The specialized group was further divided into 2 subgroups, centered on 2 different core plant species: a group specialized on species of the genus *Piper*, and another specialized on species of the genus *Cecropia* (Fig. 1). The general structure, and the species within each group, conform to what has been hypothesized by the group for Fleming (1986) and extended by Giannini and Kalko (2004; Table 3). The major difference, as outlined in Table 3, is that *Ficus*-specialists were found here to be *Cecropia*-specialists, and we found no *Ficus*-specialists. Nevertheless, the fact that the general structure is the same across these 2 different areas is of major significance. This, we believe, corroborates the hypothesis of a significant historical component to the current trophic structure. However, the actual selective pressures that acted on the ancestral communities might not be exactly as put forth by Fleming (1986).

The question then becomes, how significant is this departure from the core diets hypothesized by Fleming (1986) and Giannini and Kalko (2004)? Giannini and Kalko (2004) argued that in areas where the core plant species are not available in abundance, the bat species that are specialized on them should occur in smaller numbers. Although this may apply to some *Piper*-dominated, disturbed areas of our study site, others, precisely the least disturbed, are dominated by *Artibeus* (Medellin et al. 2000). In addition, the fact that *Cecropia* is an important food item in other areas of the distribution of *Artibeus* raises the question of whether or not *Artibeus* and Ectophyllini, in general, are really specialized fig-eaters, even in areas where *Artibeus* are numerically dominant. It is possible that *Artibeus* are really *Ficus*-specialists, but switch to *Cecropia* (a genus from the same family) in disturbed areas, and as disturbance increases they decrease in abundance (Medellin et al. 2000).

In conclusion, there is a well-defined trophic structure in assemblages of phytophagous phyllostomids with some species displaying diet specialization and others displaying more generalist diets. Moreover, this trophic structure is consistent over different regions of the species distribution. The same species that are found to be specialists in one site seem to be specialists in others, and the same is seen for the generalist species. However, there is some variation in the core plant species upon which specialization occurs in different areas. Of particular note here is the difference for *Artibeus* in Lacandon Forest versus BCI. This suggests that *Artibeus* is more of a *Ficus-*and-*Cecropia* facultative specialist that can use either genus depending on whether the area is slightly or moderately disturbed, and declining in abundance where disturbance is greater. The trophic groupings we observed conform to phylogenetic groups (Giannini and Kalko 2004), indicating that this structure might have originated in the past. However, the current hypothesized selective pressures seem incompatible with the observed patterns, and deserve further attention.

**RESUMEN**

Los murciélagos frugívoros neotropicales usualmente forman grupos tróficos especializados por grupos de especies de plantas y otro grupo de especies generalistas. Una hipótesis reciente sugiere que existe un componente histórico significativo en el origen de esta estructura. En particular, esta hipótesis sugiere que la especialización en la dieta es un carácter heredado, que lleva a la predicción de que las especies tendrán dietas muy similares a lo largo de su área de distribución. Examinamos la frecuencia de ocurrencia de semillas en especies de murciélagos frugívoros capturados en el sureste de México y describimos la estructura trófica subyacente. Usando escalamiento multidimensional métrico (un procedimiento de ordenación), encontramos que la comunidad está dividida en 3 grupos de especies cada uno centrado en un grupo de especies de plantas. Estos grupos fueron similares a grupos encontrados en otras localidades geográficas y se ajustan a los grupos filogenéticos, lo que apoya la idea de un origen histórico de esta estructura. Sin embargo, aún existen discrepancias cruciales, en particular con lo reportado de la Isla Barro Colorado en Panamá. Nuestros resultados muestran que la tribu Ectophyllini se especializa en frutos de *Cecropia*, mientras que en BCI han sido caracterizadas como especialistas en *Ficus*. Esta discrepancia puede estar relacionada con diferencias en la composición de la vegetación o en regímenes de perturbación entre las áreas, y sugerimos que los Ectophyllini (incluyendo *Artibeus*) son especialistas facultativos en los géneros *Ficus* y *Cecropia*, más que especialistas estrictos en *Ficus*.

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