

Trophic structure in a large assemblage of phyllostomid bats in Panama

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Bats of the family Phyllostomidae are fundamental components of Neotropical mammalian diversity and display the greatest dietary diversity seen in any mammalian family. We studied trophic structure in a species-rich local assemblage of phyllostomids for which dietary data were collected during 10 years on Barro Colorado Island, Panama. Correspondence analysis of > 3800 dietary records from 30 syntopic species showed a structure supporting traditional divisions of animalivorous and phytophagous phyllostomids. Putatively omnivorous species actually grouped among the latter. Phytophagous phyllostomids separated into *Piper*-specialists, *Ficus*-specialists, and eclectic plant eaters which in turn were the main consumers of flower products. Discrete dietary groups were compatible with several clades of the two current phylogenetic hypotheses of phyllostomids. We show that the trophic structure of the local contemporary assemblage is largely conservative with respect to traceable ancestral habits, strongly suggesting that overall trophic structure was likely determined historically.

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Assemblages of Neotropical rainforest bats show general patterns of species composition and rank abundance. Local assemblages studied so far are dominated by phyllostomids – leaf-nosed bats of the New World family Phyllostomidae (Brosset and Charles-Dominique 1990, dos Reis and Muller 1995, Ascorra et al. 1996, Kalko et al. 1996a, Bernard 1997, 2001, Kalko 1997, Simmons and Voss 1998, Kalko and Handley 2003, Bernard and Fenton 2002). The community importance of phyllostomids goes far beyond that compositional contribution, as phyllostomids play crucial functional roles as arthropod and vertebrate predators (Humphrey et al. 1983, Medellín 1988) and dispersers of seeds and pollen (van der Pijl 1941, 1956, 1957, 1972, Dobat and Peikert-Holle 1985, Fleming 1988, 1991, Handley et al.

1991, von Helversen 1993, Kalko 1997, Proctor et al. 1996).

Phyllostomids represent the most diverse family not only of bats but also of mammals as a whole with respect to feeding habits (Gardner 1977, Findley 1993, Ferrarezi and Gimenez 1996, Kalko et al. 1996a, Freeman 2000, Wetterer et al. 2000). In recent classifications of trophic groups based on studies carried out on Barro Colorado Island, Republic of Panama (hereafter BCI), phyllostomids were the exclusive members of six out of 10 bat guilds (Kalko et al. 1996a, Schnitzler and Kalko 1998). Guild definition was based on three categories: foraging habitats, foraging mode, and predominant diet. The first category refers to the acoustic environment of the echolocating bat (uncluttered, background cluttered,

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and highly cluttered space); the second to the style of acquiring food (aerial vs gleaning behavior); and the third to the actual items consumed (e.g. arthropods, fruits). Phyllostomids are an ecologically distinct group of highly-cluttered space gleaners that feed upon a variety of food items: arthropods, small vertebrates, blood, fruit pulp, nectar, pollen, and tree leaves (Gardner 1977, Bonaccorso 1979, Handley et al. 1991, Findley 1993, Willig et al. 1993, Zortea and Mendes 1993, Zortea 1994, Kunz and Diaz 1995, Bernard 1997).

A number of studies have investigated the coexistence of syntopic phyllostomids, many of them emphasizing trophic structure (Bonaccorso 1979, Humphrey et al. 1983, Fleming 1986, 1991, Marinho-Filho 1991, Gorchov et al. 1995, Hernández-Conrique et al. 1997, Giannini 1999). Most of these studies focused on a small, selected sub-set of species for which substantial dietary data were available. Bonaccorso (1979) thoroughly analyzed five species on BCI and seven species in Costa Rica (Bonaccorso and Gush 1987), whereas Heithaus et al. (1975) studied seven species in Costa Rica. Dietary structure of local assemblages was then extrapolated from those few well-known, common species, as pointed out by Willig et al. (1993). However, local phyllostomid assemblages contain many more species; Simmons and Voss (1998) report 31–49 syntopic species in 14 well-sampled Neotropical rainforest localities. Forty two species are known to occur on BCI of which 21 are listed at least as common (Kalko et al. 1996a, E. Kalko, unpubl.). So far, trophic structure of local assemblages is still poorly understood, essentially because dietary records for the majority of the syntopic species are mostly anecdotal and often from different localities with quantitative and qualitative differences in resources and (micro)climates.

In this paper, we examine trophic structure of the large local assemblage of phyllostomids that inhabits the lowland tropical forest of BCI. Using multivariate techniques, we analyzed dietary data gathered from a long-term demographic study on BCI (Kalko et al. 1996a). Over 3,800 dietary records were obtained from 30 out of 39 species that accounted for 99% of phyllostomids captured in the BCI long-term project (Kalko et al. 1996a). Given the high species richness and representativity of phyllostomids occurring on the island, and the unprecedented volume of dietary information, this data-set provides a unique opportunity for exploring total trophic structure of this highly diverse mammalian assemblage. In addition to the description of trophic structure per se, we specifically evaluate a hypothesis founded on a handful of well-known species of frugivores. Fleming (1986) proposed that the evolution of feeding habits in frugivorous phyllostomids involved principally the specialization on core plant taxa; large *Artibeus* specialized on *Ficus*, *Carollia* on *Piper*, and *Sturnira* on *Solanum* and *Piper*. It was

particularly important to put Fleming's hypothesis under test because his is, in our view, the most clear statement of expected trophic patterns, with a high predictive power. Thus, one of our aims in this study is to assess whether the predictions of group-wise dietary specialization still hold when most of the syntopic species are studied simultaneously.

Because perceived trophic organization in phyllostomids was articulated on the basis of presumed monophyletic groups (Humphrey et al. 1983, Fleming 1986, 1991), it is also important to evaluate the bearing of historical correlations on the observed assemblage structure. Ferrarezi and Gimenez (1996) proposed a hypothesis of dietary evolution in which all predominantly phytophagous bats were monophyletic; in turn, animalivory was a plesiomorphic trait, with insectivory being the primitive food habit of the family. However, this hypothesis was based upon a composite tree (i.e. a branching scheme that was not directly derived from a character-based analysis). Presently, two comprehensive phylogenetic analyses are available for the family Phyllostomidae, one morphological (Wetterer et al. 2000) and one molecular (Baker et al. 2000). Their results provided us with a comparative framework to understand trophic structure and its relationship with phylogeny. This allowed us to postulate a largely historical determinant of trophic structure of local, contemporary assemblages of phyllostomids—a mammalian group of prime interest from the perspective of evolutionary trophic ecology as well as from the perspective of conservation because of both high syntopic richness and high dietary diversity.

Methods

Study site

Barro Colorado Island (15.6 km², 9°09'N, 79°51'W) is located in Gatún Lake, Panama Canal, Republic of Panama, where a field station of the Smithsonian Tropical Research Institute operates. The island is covered with moist lowland semi-deciduous forest in different successional stages ranging from younger (about 80–100 years) to patches of older forest (400–600 years; Leigh 1999). Climate is seasonal (tropical monsoon), with an annual rainfall of 2600 mm. The dry season extends from the middle of December until the middle of April; 90% of all rain falls between the end of April and the beginning of December. Daily temperature variation (range 21–32 °C) is greater than the mean monthly variation (2.2 °C). For more details on the physical and biological environment of BCI, see Croat (1978), Kalko et al. (1996a), and Leigh (1999).

Study animals

The family Phyllostomidae comprises 158 species placed in 55 genera (Simmons, in press). Voss and Emmons (1996) estimated that up to 40 species of phyllostomids in five sub-families are widespread and possibly ubiquitous in Neotropical rainforests. Phyllostomids occurring on BCI, as well as at other species-rich localities, are a highly representative sample of the family's diversity (Kalko et al. 1996a, Simmons and Voss 1998). As defined by Simmons (in press), 26 of the 50 continental genera of the family occur on BCI. The remaining genera are limited to the Antilles. Continental nectar-feeding bats (Glossophaginae) are poorly represented, with only 3 uncommon species belonging to 2 out of the 13 extant genera. The opposite is true for the remaining phyllostomids (Kalko et al. 1996a). Twelve of 16 genera of Phyllostominae occur on BCI as well as 11 of 14 continental genera of Stenoderminae. All 'missing' genera are closely related to those present on BCI (i.e. those genera belong to the immediate suprageneric clades that include the forms represented on BCI Fig. 1, 2).

Our dietary sampling included 30 species that comprise 99.8% of total captures of phyllostomids during a 10-year long-term study, the Bat Project (Handley et al. 1991, Kalko et al. 1996a). The nine remaining species were extremely rare and thus did not contribute quantitatively to the general pattern of the dietary data. Because of its species richness and abundance pattern, we consider the assemblage we sampled on BCI as typical of rainforest phyllostomids (Simmons and Voss 1998), except for: 1) the under-representation of nectarivores; and 2) the rarity of the frugivorous *Sturnira* species that are common elsewhere (Fleming 1986, Marinho-Filho 1991, Barquez et al. 1999). It is worthwhile to note that these absences are not an island-effect because those species absent from BCI do not occur in nearby mainland forests (D. von Staden, pers. com.).

Data-set

Dietary data were obtained from bats mist-netted during the Bat Project from 1975–1985 (Handley et al. 1991, Kalko et al. 1996a). The standard setting consisted of 10 mist nets (12 m long) set at ground level. A total of 105 netting stations was used on BCI and 15 more on nearby mainland areas; the sampling was somewhat concentrated during the dry season, but all months were (variably) covered (Kalko et al. 1996a). In part, netting stations were set in areas with ripe fruit trees preferred by bats, in particular *Ficus* spp., *Quararibea asterolepis*, *Dipteryx panamensis*, *Spondias* sp. and other species (Handley et al. 1991). This protocol likely introduced a bias in the estimation of the diet of some species. However, if this bias was severe, only a very limited and probably predictable subset of bats would have been

captured. On the contrary, the captures from nets near fruiting trees and elsewhere on BCI were highly diverse, including bats with very different feeding habits as well as high numbers of frugivorous bats that rarely eat the fruits of canopy trees (e.g. understory frugivores in the genus *Carollia*, Kalko et al. 1996a). These observations suggest that our sample permits a meaningful exploratory analysis of trophic structure.

The dietary data-set consisted of samples collected from captured bats, including feces recovered from clean capture bags as well as fruits transported by bats into mist nets. Dietary samples were dried and subsequently analyzed. Color and consistency of the fresh fruit pulp was noted. Seeds were identified by comparing them with a local reference collection. Presence of pollen on fur or feces was recorded. Whenever plant remains were present, the identified material was considered one dietary record. If a particular sample contained remains of two or more plant species, it was counted as two or more dietary records (Gorchov et al. 1995, Giannini 1999). Part of the data on *Piper* are based on Thies (1998) and Thies and Kalko (2004). Remains of animal material found in samples was classified either as 'arthropods' (remains of chitinous structures) or 'vertebrates' (principally remains of bones).

Ordination

We used correspondence analysis (CA; ter Braak 1986) to describe the structure of dietary patterns among BCI phyllostomids. This multivariate technique is appropriate when unimodal (bell-shaped) responses of species to underlying gradients are expected, and/or data are counts containing many zeroes that should be treated as proportions (ter Braak and Verdonschot 1995). CA produces a simultaneous ordination and graphical representation of row and column elements of a matrix, in our case bat species and plant species, allowing the joint interpretation of their co-occurrences (Greenacre and Vrba 1984). We used CA diagrams (joint plots) to identify dietary gradients as well as groups among bats, by taking advantage of its ability for detecting matrix blocks (i.e. sub-matrices within the data matrix; ter Braak 1995). From the joint plots of bat + dietary items, we drew conclusions regarding structural patterns among bats (i.e. the presence and composition of either groups or gradients of bat species) and the items that were correspondent with such structures.

We began our analyses by including all phyllostomid species for which at least one dietary record existed. We then checked the preliminary ordination results to evaluate the influence of species or dietary items with the smallest sample sizes. Poorly sampled species or dietary items were removed if they appeared as outliers in ordination diagrams, and retained if no such effect

was present. Outlying species show up as isolated objects in ordination diagrams, collapsing most of the variation that relates to the other species. Thus, outliers of this kind (i.e. poorly sampled species, not truly distinct ones) unduly influence ordination results without adding any interpretable information (ter Braak 1995). We calculated the fit of bat species and food items as the fraction of variation of bats and items accounted for by the axes examined (ter Braak and Šmilauer 1998). Our interpretation of gradients and groups are based on the bat species and food items that showed the highest fit in ordination space. The program CANOCO 4.0 (ter Braak and Šmilauer 1998) was used in all CA applications, with down weighting of rare species and symmetric bi-plot scaling of untransformed data.

Historical effects

For depicting the possibly hierarchical structure of trophic relations among bats, we applied cluster analysis. We used Horn's modification of Morisita's index of overlap as applied by Palmeirim et al. (1989) as the input distance matrix. To construct the dendrogram, we applied the unweighted pair-group method using arithmetic averages (UPGMA) algorithm. Here, the between-group (dis)similarity is the average (dis)similarity between all possible pairs formed by one member from each group (van Tongeren 1995).

We estimated the impact of historical patterns on dietary structure by using an overall correlational approach. We used two comprehensive hypotheses of phylogenetic relationships among phyllostomid bats. Wetterer et al. (2000) presented a parsimony analysis of 62 phyllostomid species based on 150 characters from diverse morphological systems. This study encompassed all the species treated in this study except *Micronycteris schmidtorum*. The parsimony analysis of Baker et al. (2000) comprised 57 phyllostomid species for which a segment of ca 1.4 kbp from the nuclear Recombination-Activation Gene 2 was sequenced. In this case, several BCI species were lacking in the analysis, although others currently recognized as closely related were present. We added the missing species to the consensus tree of each phylogenetic hypothesis at the point where the most likely sister species was located – species of the same genus (demarcated with a double line in Fig. 1, 2). We then pruned each tree so that it included only the species present on BCI while fully preserving the grouping patterns (Fig. 1, 2). The two pruned topologies – one derived from the morphological analysis (Fig. 1) and the other from the molecular analysis (Fig. 2) – were the basis for subsequent analyses. From each topology, we derived a matrix of patristic pairwise distances among taxa; i.e. a set of distances between pairs of taxa that are determined by the tree structure (Rohlf 1990). A similar

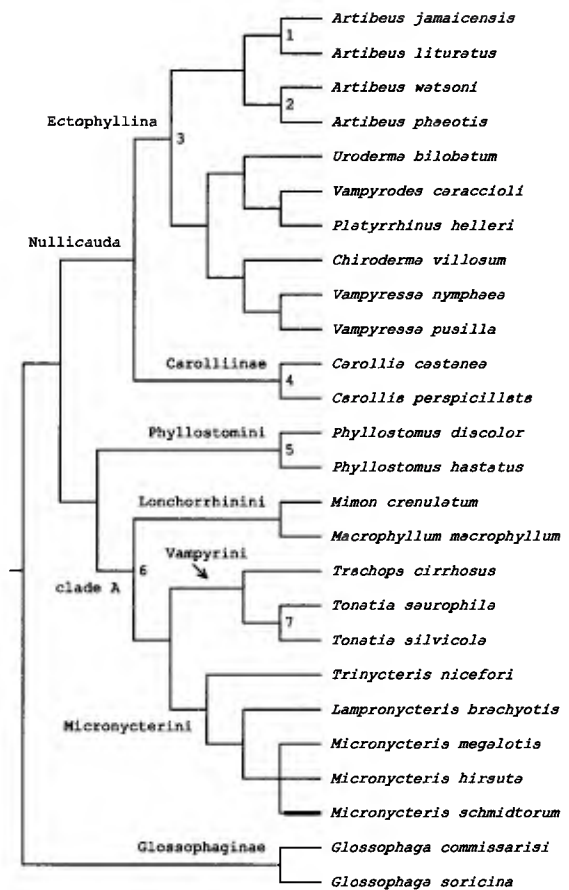


Fig. 1. Pruned consensus tree showing phylogenetic relationships among BCI phyllostomids on the basis of the morphological parsimony analysis of Wetterer et al. (2000). The names of groups were assigned by the authors. Double lines denote species that were not included in the original study and were added here as sister taxa of species of the same genus. Numbers on branches indicate the groups of the dietary dendrogram (Fig. 3) that are mutually congruent with groups recovered in the cladogram.

matrix of distances was obtained from the consensus topology of the dendrograms based on dietary overlap (Fig. 3).

We used a Mantel test to compare the distances derived from the consensus topology of the dendrogram with each of the matrices of patristic distances (Mantel 1967, Rohlf 1990, Manly 1997). Significance was evaluated via 999 permutations of normalized Mantel Z, calculated with the program NTSYS-pc 1.6 (Rohlf 1990). We report Pearson's r-value as the test statistic, which varies monotonically with Z (Rohlf 1990).

Results

Dietary data consisted of 3876 samples from 30 species of phyllostomids. Food items included vertebrates, arthropods, pollen, and remains of fleshy fruits from

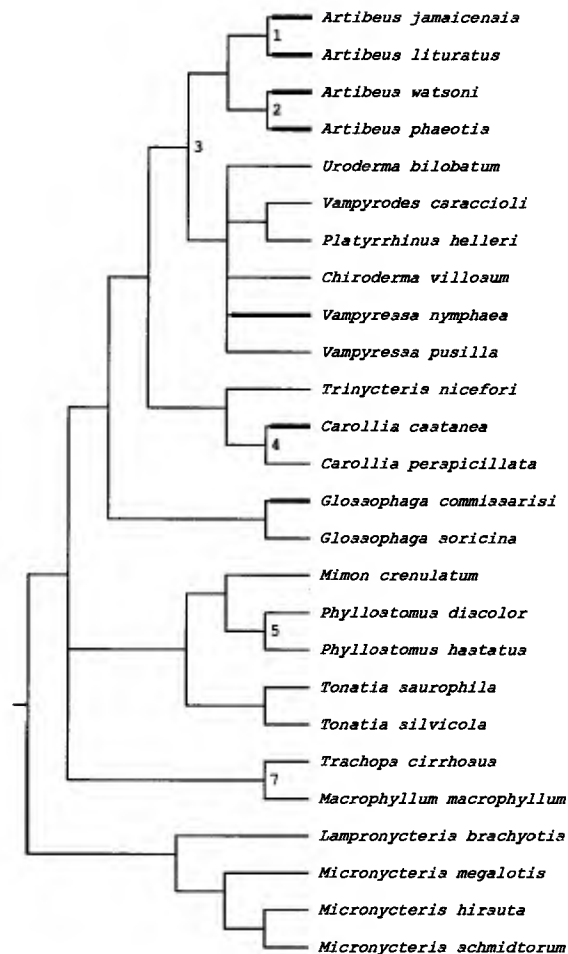


Fig. 2. Pruned consensus tree showing phylogenetic relationships among phyllostomids according to the molecular parsimony analysis of Baker et al. (2000). The authors did not propose names to the groups recovered. Double lines denote species that were not included in the original study and were added here as sister taxa of species of the same genus. Numbers on branches indicate the groups of the dietary dendrogram (Fig. 3) that are mutually congruent with groups recovered in the cladogram.

53 plant species, eight of which remained unidentified. Plants consumed by the bats are detailed in Table 1. Sample sizes varied widely among bat species. For 23% of the species <10 dietary records were available, whereas a similar proportion of species yielded >100 dietary records (Table 2).

Ordination

We excluded two species with very low sample sizes from the analysis, namely *Centurio senex* (N = 4) and *Phyllostoma stenops* (N = 3), together with their exclusive food items (*Guettarda foliacea* and an unidentified cucurbit, respectively), given that they behaved as outliers (see

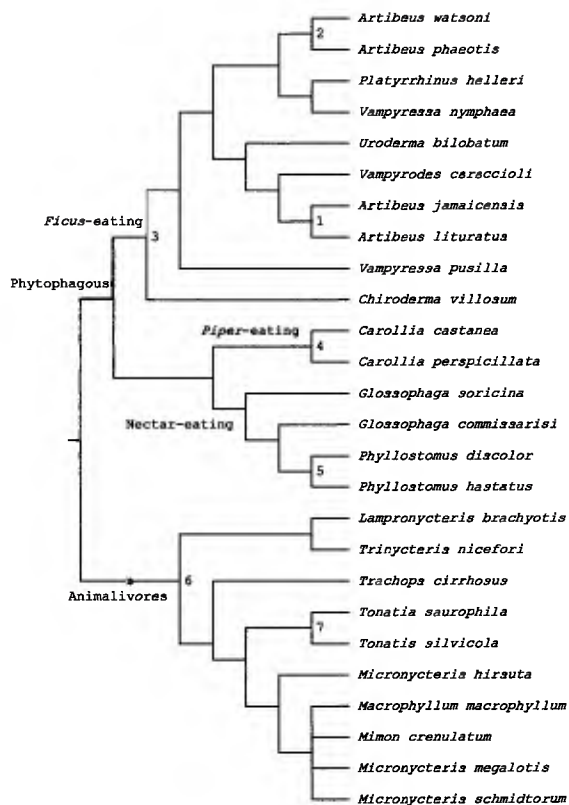


Fig. 3. Consensus topology of 15 tied dendrograms based on dietary data (UPGMA tree based upon a Horn's modification of Morisita's index of dietary overlap). The symbol inserted (>) denotes the longest branch (i.e. the greatest dissimilarity) in all the original dendrograms. Numbers on branches indicate the groups of the dendrogram that are mutually congruent with groups recovered in the cladogram (Fig. 1, 2).

Methods). For these two species, down-weighting was not enough. However, other species with very small sample sizes in which the dietary composition was not as unique (e.g. *Carollia brevicauda*, N = 2) were retained in the analysis.

The first four CA axes explained ca 70% of total variation in diet. Axis 1 represented a clear-cut separation of mainly phytophagous versus mainly animalivorous (consumers of arthropods and small vertebrates) phyllostomids (Fig. 4). The latter group corresponded to the members of the sub-family Phyllostominae except *Phyllostomus* — 'clade A' phyllostomines in the tree of Fig. 1. The diet of 'clade A' phyllostomines consisted mainly of animal prey (95% vertebrates + arthropods), whereas *Phyllostomus* ate >85% plant products. Highly frugivorous species were members of *Nullicauda* (Fig. 1), as well as *Glossophaga soricina* (Glossophaginae), which also incorporated substantial amounts of flower products (ca 30%).

Although phytophagous bats seemingly displayed a gradient-like structure along axis 2, the fit of the species

Table 1. List of plant species identified in the dietary samples of Panamanian bats. Remotion records represent the number of times seeds of a given plants were present in the dietary samples of bats. Systematics follows Croat (1978).

Family	Species	Remotion records	
Piperaceae	<i>Piper aequale</i>	37	
	<i>Piper arboreum</i>	17	
	<i>Piper carrilloanum</i>	2	
	<i>Piper cordulatum</i>	3	
	<i>Piper dilatatum</i>	11	
	<i>Piper grande</i>	24	
	<i>Piper hispidum</i>	1	
	<i>Piper marginatum</i>	5	
	<i>Piper reticulatum</i>	46	
	<i>Piper calebratum</i>	1	
	<i>Philodendron</i> sp.	6	
Araceae	<i>Calophyllum longifolium</i>	10	
	<i>Havetiopsis flexilis</i>	2	
Clusiaceae	<i>Vismia</i> sp. 1	1	
	<i>Vismia</i> sp. 2	2	
Passifloraceae	<i>Passiflora punctata</i>	1	
Fabaceae ^a	<i>Dipteryx panamensis</i>	38	
Moraceae	<i>Brosimum alicastrum</i>	3	
	<i>Ficus bullenei</i>	76	
	<i>Ficus citrifolia</i>	30	
	<i>Ficus colubrina</i>	1	
	<i>Ficus costaricana</i>	17	
	<i>Ficus dugandii</i>	12	
	<i>Ficus insipida</i>	1076	
	<i>Ficus maxima</i>	8	
	<i>Ficus nymphifolia</i>	8	
	<i>Ficus obtusifolia</i>	237	
	<i>Ficus parensis</i>	2	
	<i>Ficus pertusa</i>	8	
	<i>Ficus popenoi</i>	17	
	<i>Ficus tonduzii</i>	5	
	<i>Ficus trigonata</i>	161	
	<i>Ficus yoponensis</i>	361	
	<i>Poulsenia armata</i>	27	
	Cecropiaceae	<i>Cecropia</i> spp.	53
	Cucurbitaceae	Unidentified ^b	2
Myrtaceae	<i>Eugenia</i> sp.	1	
Malvaceae ^c	<i>Quararibea</i> sp. ^d	77	
Meliaceae	<i>Trichilia</i> sp.	24	
Anacardiaceae	<i>Anacardium excelsum</i>	36	
	<i>Spondias mombin</i>	92	
	<i>Spondias radlkoferi</i>	118	
Lecythidaceae	<i>Gustavia superba</i>	1	
Solanaceae	<i>Solanum</i> sp.	7	
Rubiaceae	<i>Guettarda foliacea</i>	2	

^a Papilionoidea.

^b Most likely *Gurania*.

^c Includes Bombacaceae, the group to which *Quararibea* belongs.

^d Most likely *Quararibea asterolepis*.

indicated that the axis variation is dominated by two separate groups, mainly *Piper*- and *Ficus*-eating bats (Fig. 4). In the former group, *Carollia castanea* held a more extreme position, in accordance with its high specialization on *Piper* (82% of diet, Table 2). *Carollia perspicillata*, a less specialized bat (ca 40% of *Piper* in its diet), was located closer to the other frugivores. Some plants appeared associated with the group of ten species of *Piper* because they were consumed principally by *Carollia*. Those species belong to the genera *Vismia*, *Havetiopsis*, *Gustavia*, *Eugenia*, *Solanum* and *Trichilia* (Fig. 4).

Fig-eating bats were tightly clumped in the plane of axes 1 and 2 (Fig. 4). The plane of axes 3 and 4 showed that *Vampyressa pusilla*, *Uroderma bilobatum* and *Chiroderma villosum* were clearly distinct from other fig-eating bats (Fig. 4, inset). We will analyze the dietary variability within Ectophyllina bats in greater detail elsewhere. Axis 4 isolated the bats for which pollen was an important dietary component: *Glossophaga* and *Phyllostomus* (Fig. 4, inset). These bats also preferred *Cecropia* fruits (Table 2).

Results from the cluster analysis closely resembled those obtained by CA. Fifteen tied trees differed only in minor details (strict consensus shown in Fig. 3). The main dichotomy consisted of animalivores versus phytophagous bats. Within the former, *Lamproncyteris brachyotis* and *Trinycteris nicefori* formed a cluster likely on the basis of the modest proportion of fruits in their diets (12–14%, Table 2). In turn, phytophagous bats were divided into two main clusters: 1) all Ectophyllina, which ate > 50% figs (Table 2); and 2) a group formed by *Carollia*, *Glossophaga*, and *Phyllostomus*. *Carollia* species segregated from the other two genera that incorporated significant proportions of flower products. Within fig-eating bats, the analysis successively separated *Chiroderma villosum*, *Vampyressa pusilla*, and the remaining bats. The largest bats (*Artibeus jamaicensis*, *A. lituratus* and *Vampyrodes caraccioli*, Table 2) formed a cluster together with *Uroderma bilobatum*.

Historical correlation

The dietary pattern (Fig. 3) and the phylogenetic structure derived from the morphological phylogeny (Fig. 1) were significantly correlated ($r = 0.71$, $P = 0.001$). Seven nodes in the dietary analysis corresponded with phylogenetic groups (Fig. 1, 3). The taxonomic level of such groups, as traditionally understood, ranged from sub-family (e.g. Carollinae, node 4) to sub-genera (e.g. *Dermanura* within genus *Artibeus*, node 2, Fig. 1).

To a lesser extent, the dietary pattern also correlated with the phylogenetic structure derived from the molecular phylogeny ($r = 0.43$, $P = 0.001$). Six nodes corresponded with dietary groups (Fig. 2, 3). These nodes are the same as in the previous comparison; the missing group is 'clade A' phyllostomines (number 6 of Fig. 1).

Discussion

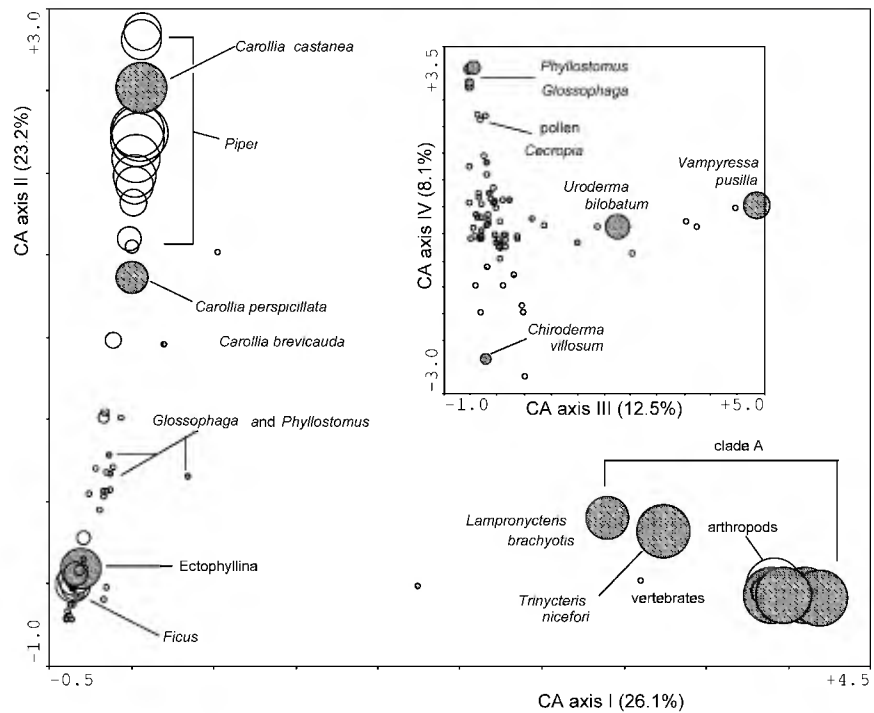
Trophic structure

The main trophic structure was a clear-cut separation between animalivorous and phytophagous bats. For animalivores, we could not evaluate fine-grained within-group patterns because our data consisted of only three types of dietary items: arthropods, verte-

Table 2. Body size and dietary data of the 30 species of phyllostomids on BCI. Data on mean body weight are from Kalko et al. (1996a). Data are percentages across columns. Abbreviations: N – number of dietary records; Arth – arthropods; Vert – vertebrates. All data are percentages of total diet.

Bat species	Weight (g) $\bar{X} \pm 1SD$	N	Arth.	Vert.	Pollen	Fruits					
							Total	<i>Ficus</i>	<i>Cecropia</i>	<i>Piper</i>	Others
<i>Macrophyllum macrophyllum</i>	8.4 ± 1.3	5	100	–	–	–	–	–	–	–	
<i>Mimon crenulatum</i>	15.0 ± 1.3	19	100	–	–	–	–	–	–	–	
<i>Lamproncyteris brachyotis</i>	14.3 ± 1.9	16	78.6	–	7.1	14.3	0.1	–	–	14.2	
<i>Micronycteris hirsuta</i>	15.5 ± 0.8	41	97.6	–	–	2.4	–	–	–	2.4	
<i>Micronycteris megalotis</i>	7.2 ± 0.9	18	100	–	–	–	–	–	–	–	
<i>Micronycteris schmidtorum</i>	7.1 ± 0.5	12	100	–	–	–	–	–	–	–	
<i>Trinycteris nicefori</i>	11.1 ± 1.2	9	87.5	–	–	12.5	–	–	12.5	–	
<i>Phyllostoma stenops</i>	61.4 ± 2.7	3	–	–	–	100	–	–	–	100	
<i>Phyllostoma discolor</i>	42.1 ± 3.1	33	–	–	70.4	29.6	3.7	3.7	–	22.2	
<i>Phyllostomus hastatus</i>	125.6 ± 5.9	37	9.4	3.1	46.9	40.6	6.3	28.1	–	6.2	
<i>Tonatia saurophila</i>	36.8 ± 2.0	45	95.5	–	–	4.5	4.5	–	–	–	
<i>Tonatia silvicola</i>	34.3 ± 2.2	100	97.9	–	–	2.1	1.0	–	–	1.1	
<i>Trachops cirrhosus</i>	34.9 ± 2.0	23	81.8	18.2	–	–	–	–	–	–	
<i>Chrotopterus auritus</i>	84.4 ± 5.2	4	25.0	25.0	–	50.0	50.0	–	–	–	
<i>Carollia brevicauda</i>	14.7 ± 1.3	2	–	–	–	100	–	–	–	100	
<i>Carollia castanea</i>	13.3 ± 2.0	335	0.3	–	–	99.7	0.3	–	81.7	17.7	
<i>Carollia perspicillata</i>	19.7 ± 1.6	434	0.3	–	2.1	97.6	1.6	5.6	41.1	49.3	
<i>Glossophaga commissarisi</i>	7.2 ± 0.8	2	–	–	100	–	–	–	–	–	
<i>Glossophaga soricina</i>	11.3 ± 0.8	23	–	–	29.4	70.6	41.2	29.4	–	–	
<i>Centurio senex</i>	20.5 ± 3.9	4	–	–	–	100	0.0	–	–	100	
<i>Artibeus jamaicensis</i>	49.3 ± 3.7	1732	0.2	–	1.1	98.7	82.3	0.7	0.1	15.6	
<i>Artibeus lituratus</i>	68.5 ± 5.2	441	–	–	6.3	93.7	83.0	–	0.7	10.0	
<i>Artibeus phaeotis</i>	13.0 ± 1.4	34	–	–	3.2	96.8	61.8	–	–	35.0	
<i>Artibeus watsoni</i>	12.5 ± 1.2	19	–	–	–	100	52.6	–	–	47.4	
<i>Chiroderma villosum</i>	22.1 ± 1.4	112	0.9	–	–	99.1	97.3	–	–	1.8	
<i>Platyrrhinus helleri</i>	15.8 ± 2.0	23	–	–	–	100	82.6	17.4	–	–	
<i>Uroderma bilobatum</i>	17.8 ± 2.1	189	–	–	2.1	97.9	95.8	–	2.1	–	
<i>Vampyressa nymphaea</i>	13.7 ± 0.9	25	–	–	–	100	96.0	4.0	–	–	
<i>Vampyressa pusilla</i>	8.6 ± 0.9	45	–	–	–	100	100	–	–	–	
<i>Vampyrodes caraccioli</i>	55.3 ± 1.1	91	–	–	–	100	85.3	–	1.3	13.4	

Fig. 4. Ordination diagram showing the results of correspondence analysis. This is a joint plot in which the position of both bat species and dietary items are represented together in the ordination space. We show the plane of axes I and II, and the plane of axes III and IV (inset). Variation explained by each axis is given in parenthesis. Gray circles stand for bat species, empty circles stand for dietary items. Fit of each bat species and dietary item to the corresponding plane (variation of species and dietary items explained by the plain) is proportional to size of circle. Although all bat and dietary items are actually plotted, only selected ones are indicated. Note that *Phyllostomus* and *Glossophaga* species are very poorly fitted in the plane of axes I and II but fit better to the planes III and IV. The plant species in the genera *Vismia*, *Havetiopsis*, *Gustavia*, *Eugenia*, *Solanum* and *Trichilia* are placed among *Piper* species.



brates, and species of plants. A modestly distinct pattern was the separation of *Lamproncycteris brachyotis* and *Trinycteris nicefori* as a result of minor proportions of fruit found in their diets (Fig. 1, 4, Table 2).

Among the highly phytophagous phyllostomids, we recognize three discrete groups: *Ficus*-eating bats (Ectophyllina), *Piper*-eating bats (*Carollia*), and eclectic plant-eaters. The later group consumed a high proportion of fruit and flower products as well as traces of animal matter (*Phyllostomus* and *Glossophaga*). Among the plants, only *Dipteryx panamensis*, *Spondias mombin* and *Cecropia* spp. were commonly used by the three groups of phytophagous bats. This result supports previous observations that these fruits are important dietary items for many frugivores (Croat 1978, Fleming 1979, Estrada et al. 1984, Fleming and Williams 1990). In contrast, fruits of other plants were taken almost exclusively by a single sub-group of phytophagous bats.

Our results demonstrate an agreement between the trophic structure described in our study of many (30) syntopic species, and the structure expected from previous studies that considered only a few (≤ 7) species (Heithaus et al. 1975, Bonaccorso 1979, Humphrey et al. 1983, Fleming 1986). This structure was also expected on phylogenetic grounds (see next section). It is important to point out that some species of phyllostomids have been customarily considered omnivores on a qualitative basis. For instance, *Phyllostomus hastatus* consumes fruits, flower products, arthropods, and vertebrates (Gardner 1977, Kalko et al. 1996a). The expected position of such omnivores in ordinations might thus be intermediate between animal and plant eaters, producing a general gradient-like structure of the whole assemblage. This pattern did not occur in our results. Instead, both species of *Phyllostomus* appeared among the plant eaters and close to *Glossophaga* as a result of their high consumption of flower products and *Cecropia* fruits (Fig. 4, Table 2). It is widely known that glossophagines are primarily nectar-feeding bats and important pollinators of many plant species (Carvalho 1960, 1961, Heithaus et al. 1974, Lemke 1984, Dobat and Peikert-Holle 1985, Fischer 1992, Helversen 1993, Silva and Peracchi 1999, Tschapka and Helversen 1999) but also that they include fruits and arthropods in their diets on a seasonal basis (Howell and Burch 1974, Heithaus et al. 1975, Gardner 1977, Herrera et al. 2001). Their ecological similarity to *Phyllostomus* as consumers of flower products is not surprising because high levels of palinivory and nectarivory have been documented for both *P. discolor* and *P. hastatus* in many studies (reviewed by Dobat and Peikert-Holle 1985).

Two potentially problematic aspects of our data analysis must be addressed. First, our interpretation of trophic structure is based principally upon CA ordination, but CA is not free of problems, as it may distort

ordination diagrams with analytical artifacts like the so-called arch effect. If the arch effect is present, the pattern displayed by the second CA axis is just a quadratic function of the first axis – not a pattern on its own. Detrending techniques (Hill and Gauch 1980, ter Braak 1987) are specifically devised to correct these problems. However, it is not always the case that the second axis is artifactual, even if it shows some curvilinear pattern, because the variation displayed by the second axis may be ecologically meaningful. Then, detrending can flatten out that variation in a misleading way (Minchin 1987, ter Braak and Šmilauer 1998). In our case, the second axis separates *Piper*-eating bats from all other bats, which reflects real ecological information that is not the by-product of a lack of variation. Therefore, the adoption of CA seems justified for the analysis of our dietary information.

Finally, the quality of our dietary data, as measured by sample size, varied greatly across species and is certainly not free of the general problems of dietary analysis such as differing detectability of dietary items in the feces, possible misidentifications, and seasonal variability. However, in spite of those caveats, our analysis provided solid hypotheses of trophic relationships – i.e., position in trophic space – for many of the species in which dietary data were rare. One example is *Carollia brevicauda*, a species whose diet is known from only 2 samples in our study. Despite this small sample, *C. brevicauda* fitted readily among its *Piper*-eating congeners. Other species, such as *Phyllostoma stenops* (likely a phytophagous bat), will require a much better documentation of their diet and feeding habits to allow further conclusions.

The general picture of trophic relationships must be completed with the two species of vampire bats that inhabit BCI (*Desmodus rotundus* and *Diaemus youngii*; Kalko et al. 1996a, E. Kalko pers.obs.). These species were not included in the multivariate analyses because no actual dietary samples were available. Although some records of non-blood food items exist for *D. rotundus* (Gardner 1977), overall evidence indicates that vampires are highly specialized sanguivores (reviewed by Greenhall et al. 1983).

Phylogenetic patterns

We found an overall correlation between trophic structure and phylogenetic structure as recovered by the morphological study of Wetterer et al. (2000). Additionally, 6–7 nodes were congruent between the phylogenetic trees of Baker et al. (2000) and Wetterer et al. (2000) and the dietary phenogram. These nodes represented groups from sub-family to sub-genera, suggesting that the diet-phylogeny relationship is based on a heterogeneous array of clades. That is, to the extent that the patterns observed

are attributable to history, persistent old trends of large groups coexist with new trends in recently diverged sister species. This implies that main feeding habits have been acquired in the past by the ancestors of the 6–7 congruent groups at various times, and that these habits were subsequently retained with little if any change in the descendant species that comprise contemporary assemblages.

Besides the general agreement between diet and phylogeny, a finer examination of the historical patterns is necessary because the two available phylogenetic hypotheses differ in aspects important to the interpretation of trophic structure. The most fundamental discrepancy between the two phylogenies is the status of Phyllostominae bats. This sub-family was recovered, even though with low support, only in the morphological study (Wetterer et al. 2000). In the molecular phylogeny (Baker et al. 2000), the paraphyly of Phyllostominae is so extensive (i.e. not as a consequence of the exclusion of a few particular taxa) that its traditional members barely bear any relationship to each other. The net effect of this discrepancy is at a single node: 'clade A' phyllostomine as recovered in the morphological phylogeny, is missing in our comparison between dietary structure and the molecular phylogeny. This result raises the question of the nature of the ecological clustering of animalivores: these bats are either a derived group in which predominant animalivory is apomorphic (as explicitly suggested by Wetterer et al. 2000), or a paraphyletic array that retained a plesiomorphic feeding habit (as suggested by the examination of the molecular phylogenetic hypothesis). The latter statement is an oversimplification, because not all the species fit exactly this pattern; for instance, the predominant insectivory in one phyllostomine genus (*Glyphonycteris* – not included in the current study) is interpreted as an independent derivation in the molecular phylogeny (Fig. 4 in Baker et al. 2000). Also Ferrarezi and Gimenez (1996) proposed high insectivory to be the primitive feeding habit of phyllostomids given that this is the feeding habit of the natural outgroups of phyllostomids – Noctilionoidea bats (Simmons and Geisler 1998, Van Den Bussche and Hooper 2000).

Phytophagy also poses some problems related to the incongruence between the phylogenetic hypothesis. For instance, the partially phytophagous habit of *Phyllostomus* has evolved either from predominant insectivory (Ferrarezi and Gimenez 1996, Baker et al. 2000), or it was a conservative feature inherited from partially phytophagous, ancestral phyllostomids (Wetterer et al. 2000).

The available phylogenies must be interpreted with caution, because low support values for many groups, including those of direct interest for the present study, were common. Resolution of these problems rests on developing a robust 'total evidence' phylogeny. This highlights the need for continuous improvement of

phylogenetic hypotheses in order to increase our understanding of historical effects over ecological patterns.

Integrated trophic ecology

The trophic-phylogenetic pattern shown in this study can be directly related with Fleming's (1986) view of the mechanisms of coexistence of syntopic frugivorous phyllostomids via dietary specialization. We found strong support to Fleming's hypothesis of dietary specialization on core plant taxa, both in our study and in others. For example, the predicted preference of *Solanum* and *Piper* by *Sturnira* was confirmed in a large number of studies (Marinho-Filho 1991, Willig et al. 1993, Gorchoy et al. 1995, Hernández-Conrique et al. 1997, Iudica and Bonaccorso 1997, Giannini 1999). The same support holds for *Carollia* as a *Piper* specialist (Palmeirim et al. 1989, Fleming 1991, Marinho-Filho 1991, Gorchoy et al. 1995, Thies 1998, Thies et al. 1998, Thies and Kalko, 2004, this study). Regarding fig-eating bats, our data permit us to extend Fleming's hypothesis from the large *Artibeus* to the entire tribe Ectophyllina, which also includes the smallest frugivores (e.g. *Vampyrissa pussilla*, Handley et al. 1991, Kalko et al. 1996b, Wendeln et al. 2000). It is most parsimonious to attribute a unique origin of fig specialization to the last common ancestor of this tribe. Our working hypothesis is that members of Ectophyllina (44 extant species in 9 genera, Simmons in press) had an ancestral specialization on *Ficus* as core dietary item sensu Fleming (1986), that was inherited by the descendant contemporary species. This hypothesis does not imply exclusive feeding on *Ficus*, rather it proposes that the diet is dominated by figs. Fleming's hypothesis also contemplated the bat's ability to use some other chiropterocorous fruits if seasonally available. This prediction is confirmed from anecdotal observations, for instance in *A. jamaicensis*, which seasonally takes other fruits such as *Spondias* and *Dipteryx* on BCI (Handley et al. 1991, this study). Furthermore, large *Artibeus* also occur in areas in which figs are missing or rare – but at such sites, the abundance of *Artibeus* is much lower (Barquez et al. 1991, Sampaio et al. 2003). Data from other independent localities will provide support or limitations to our extension (from few to all species of Ectophyllina) of Fleming's hypothesis. Particularly important sites for future research will be those located in regions with marked spatial variation in the distribution of different *Ficus* species, and subtropical areas in which *Ficus* species are not dominant.

We demonstrated a historical basis for some important patterns of the observed dietary variation in phyllostomid bats in a local, contemporary community. Trophic relationships among phylogenetically deeply-rooted groups (sensu Vitt et al. 1999) were discrete –

i.e., they conformed to a group structure rather than to a gradient-like structure. This pattern suggests a possible operating mechanism: dietary diversification may have proceeded by dietary shifts at certain nodes (e.g. at the node where all fig-eating bats originated), followed by a relative stasis within derived clades. This has the net effect that, whenever members of a clade occur together in a community, they tend to be similar in resource use, lying close to each other in resource space. Thus, the phylogenetic structure undoubtedly plays a significant role in the coexistence of the rich syntopic assemblages of phyllostomids that we observe today.

Conclusions

Despite potential sampling biases, our analyses revealed a strong dietary structure in the assemblage of BCI phyllostomids. In the contemporary BCI assemblage, dietary patterns are scaled at all taxonomic levels. The main trophic pattern consisted of discrete groups of specialized diet, which are congruent with several clades. Specialization on core plant taxa (sensu Fleming 1986) is probably characteristic of large monophyletic groups of phyllostomid frugivores. In light of the overall correlation of phylogenetic and dietary patterns, we postulate that historical factors largely determined contemporary trophic structure. Vitt et al. (1999) found a similar pattern in lizards, suggesting that strong historical effects in dietary structure may be widespread in present-day communities. Whether the trophic pattern we observed, which can be in great part explained by similarity due to common descent, determines other aspects of the internal structuring of ensembles (sensu Fauth et al. 1996), like degree of species packing (Stevens and Willig 1999) or density compensation (Stevens and Willig 2000), should be matter of a renovated debate (Patterson et al. 2003).

Bats are one of the principal components of Neotropical mammalian diversity (Fleming et al. 1972, Emmons 1990, Willig et al. 1993, Timm 1994a, b, Voss and Emmons 1996). Phyllostomids in particular contribute more than any other group to bat diversity at several localities (e.g. BCI; Kalko et al. 1996a, Simmons and Voss 1998). Given that phyllostomids are monophyletic (Simmons and Geisler 1998), and species-rich local assemblages are widespread (Voss and Emmons 1996), this group continues to be an ideal model for studying the ecological diversification of a lineage, as well as the contemporary and historical factors that affect the establishment and maintenance of diversity.

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