

## Phyllostomid Bat Community Structure and Abundance in Two Contrasting Tropical Dry Forests<sup>1</sup>

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### ABSTRACT

Although tropical wet forests are generally more diverse than dry forests for many faunal groups, few studies have compared bat diversity among dry forests. I compared ground level phyllostomid bat community structure between two tropical dry forests with different precipitation regimes. Parque Nacional Palo Verde in northwestern Costa Rica represents one of the wettest tropical dry forests (rainfall 1.5 m/yr), whereas the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of central Mexico represents one of the driest (750 mm/yr). Mist net sampling was conducted at the two study sites to compare changes in ground level phyllostomid bat community structure between regions and seasons. Palo Verde was more diverse than Chamela and phyllostomid species showed low similarity between sites (Classic Jaccard = 0.263). The distinct phyllostomid communities observed at these two dry forest sites demonstrates that variants of tropical dry forest can be sufficiently different in structure and composition to affect phyllostomid communities. At both dry forest sites, abundance of the two most common foraging guilds (frugivores and nectarivores) differed between seasons, with greatest numbers of individuals captured coinciding with highest chiropterophilic resource abundance.

### RESUMEN

A pesar de que los bosques tropicales húmedos, en general, son más diversos que los bosques tropicales secos para muchos grupos de fauna, pocos estudios han comparado la diversidad de murciélogos en los bosques tropicales secos. El presente estudio compara la estructura de la comunidad de los murciélagos filostómidos a nivel del suelo entre dos tipos de bosque tropical seco con diferentes regímenes de precipitación. El parque Nacional Palo Verde está localizado en el Noroeste de Costa Rica y representa uno de los bosques tropicales secos más húmedos (con una precipitación de 1.5 m/año), mientras que la Reserva de la Biosfera Chamela-Cuixmala está localizada en la costa oeste del pacífico de México y representa uno de los bosques más secos (750 mm/año). Se realizó un muestreo con redes de niebla en los dos sitios para comparar los cambios en la estructura de la comunidad de murciélagos filostómidos a nivel de suelo. Palo Verde fue más diverso que Chamela y se encontró la simultaneidad de las especies filostómidos entre los dos sitios fue bajo (Classic Jaccard = 0.263). Las comunidades distintas de filostómidos observado en estos dos sitios de bosque seco demuestra que las variantes en el bosque tropical seco pueden ser suficientemente diferentes en estructura y composición para poder afectar la comunidad de filostómidos. En ambos bosques secos la abundancia de los dos gremios tróficos más comunes (frugívoros y nectarívoros) fue diferente en las estaciones, con un mayor número de individuos capturados coincidiendo con una mayor abundancia de recursos quiropterofílicos.

*Key words:* bat community structure; Chamela-Cuixmala Biosphere Reserve; Costa Rica; México; Palo Verde; Phyllostomidae; tropical dry forest.

BATS CONSTITUTE THE MOST DIVERSE GROUP OF MAMMALS in tropical regions, with only rodents approaching them in number of species (Handley 1966, Eisenberg 1989, Nowak 1994, Emmons 1997). These small, volant mammals, especially those in the family Phyllostomidae, are critical components of tropical ecosystems for their roles in seed dispersal and pollination (Dobart & Peikert-Holle 1985, Charles-Dominique 1986, Foster *et al.* 1986, Fleming 1991). Some studies have attempted to explain bat community structure in tropical forests in terms of foraging guilds based on food partitioning (McNab 1971, Heithaus *et al.* 1975, Aguirre 2002, Aguirre *et al.* 2003) or space use (Bernard *et al.* 2001, Lim & Engstrom 2001, Henry *et al.* 2004, Korine & Pinshow 2004); nevertheless, one recent study suggested that competitively induced community structure of tropical bats may exist only under very narrow environmental conditions (Stevens & Willig 2000).

Several studies have documented that tropical wet forests, in general, are more diverse than tropical dry forests for many faunal groups including birds (Stiles 1983), herpetofauna (Duellman 1958,

1990; García-Aguayo & Ceballos 1994), and mammals (Mares *et al.* 1981, Glanz 1990, Janson & Emmons 1990; but see Mares 1992 for opposing view). Recently, however, Stoner & Timm (2004) documented how similar the number of mammal species are between the tropical wet forest site of La Selva ( $N = 123$ ) and the dry forest site of Palo Verde ( $N = 114$ ), Costa Rica. It is not clear whether bats follow the general pattern of greater species diversity in tropical wet forests, as there is considerable variation reported for bat species diversity in Neotropical forests (Table 1). For example, essentially no difference exists in the number of species of bats found at La Selva (68) compared to Palo Verde (67), Costa Rica (Stoner & Timm 2004). Nevertheless, if only the most diverse family of phyllostomids is considered, La Selva contains more species (42) than Palo Verde (32).

Despite the multitude of studies documenting bat faunas at different tropical sites (Table 1), we are still far from understanding the factors that structure bat communities in tropical forests. In particular, few studies compare bat community structure between the extremes within a forest type. These types of comparisons are important for identifying characteristics intrinsic to an environment that may influence community structure.

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TABLE 1. Summary of some studies on bat diversity in the Neotropics that represent different forest types.

No. of species	Site	Forest type	Annual rainfall	Sampling method	Sampling effort <sup>a</sup>	Reference
20	Veracruz, México	Tropical dry	1500	Ground mist nets	2 yr 120 nights	Moreno and Halffter 2001
21	Chamela, Jalisco, Mexico	Tropical dry	750	Ground mist nets	1 yr 117 nights	Stoner 2002
44	Lacandona, Chiapas, México	Tropical wet	3000	Ground mist nets	6 mo 43 nights	Medellín 1993
39	Los Tuxtlas, Mexico	Tropical wet	4900	Ground mist nets	3 yr 292 nights	Estrada and Coates-Estrada 2002
20	Tikal National Park, Guatemala	Tropical moist	1350	Ground mist nets	5 mo	Schulze <i>et al.</i> 2000
36	Lamanai, Belize	Tropical dry	1010	Ground mist nets, Acoustic monitoring, Tuttle traps	4 mo 24 nights	Fenton <i>et al.</i> 2001
67	Palo Verde, Costa Rica	Tropical dry	1500	Ground mist nets, Acoustic monitoring	3 yr 56 nights	Stoner and Timm 2004
31	Cabo Blanco, Costa Rica	Tropical wet	3100	Ground mist nets	26 nights 5 yr	Timm and McClearn in press
67	La Selva, Costa Rica	Tropical wet	3000	Various	Review	Timm 1994
66	Barro Colorado Island, Panama	Tropical moist	2600	Ground mist nets, Acoustic monitoring, Roost surveys	10 yr	Kalko <i>et al.</i> 1996
72	BDFFP <sup>b</sup> , Amazon basin, Brazil	Tropical wet	2200	Ground and canopy mist nets	3.5 yr 314 nights	Sampio <i>et al.</i> 2003
73	Iwokrama, Guyana	Tropical wet	2500	Ground and canopy mist nets, Harp traps	1 yr 79 nights	Lim and Engstrom 2001
17	Saint-Eugene Station, French Guyana	Tropical wet	3000	Ground mist nets	3 yr	Cosson <i>et al.</i> 1999
38	Espíritu, Bolivia	Savanna	2000	Ground mist nets	7 mo 51 nights	Aguirre 2002
20	Mbaracayu Reserva Natural, Paraguay	Tropical dry	1650	Ground mist nets	4 yr	Gorresen and Willig 2004

<sup>a</sup>Since no studies present sampling effort in the same way, I present the time frame in which the sampling was conducted and the number of nights sampled when given.

<sup>b</sup>Biological Dynamics of Forest Fragments Project.

One of the problems in comparing bat diversity between sites is the great variability in sampling effort and methods. Furthermore, recent studies have shown that the only way to systematically sample the entire bat community at one site is with a combination of sampling techniques that include ground level mist nets, canopy mist nets, and acoustic sampling (Bernard *et al.* 2001, Sampaio *et al.* 2003). Due to study-to-study heterogeneity in sampling techniques, it is difficult to come to conclusions about bat diversity between different habitats.

The current study attempts to identify and explain patterns in phyllostomid bat community structure using similar sampling efforts between study sites. Phyllostomids are used for two reasons. First, this is the most diverse bat family in the Neotropics which includes a variety of guilds within one family. Second, this is one of the few Neotropical bat families that is well sampled by mist nets. The objectives of the study were to compare ground level phyllostomid bat community structure between two extremes of tropical dry forest, and to determine if the number of phyllostomid species, foraging guilds, or number of individuals represented by each guild changes in a predictable way over seasons within these forests.

If phyllostomid bat community structure is determined by habitat type, I expect to find different community structures within the two extremes of tropical dry forest. Previous studies have demonstrated that tropical forest composition and structure vary over different precipitation regimes (Gentry 1982, Trejo & Dirzo 2002). Specifically, I expected to find more phyllostomid bat species and foraging guilds represented in *wetter* than *drier* dry forest, because of the greater structural complexity and diversity of plant species characteristic of the former. Furthermore, since seasonality strongly affects phenological patterns (Opler *et al.* 1976) and thus resource availability (especially for frugivores and nectarivores) in tropical regions, I predict that patterns of changes in phyllostomid species abundance over seasons will coincide with periods of change in resource availability in both extremes of tropical dry forest.

## METHODS

STUDY SITES.—The first study site is located in Parque Nacional Palo Verde, Guanacaste Province, in northwestern Costa Rica (ca 10°19' to 10°24'N, 85°18' to 85°25'W). Palo Verde covers

about 20,000 ha and encompasses a variety of habitats including lowland deciduous forest, upland deciduous forest, riparian forest, seasonal wetland, mangrove habitat, desert habitats associated with limestone cliffs, pastures, and regenerating forests (Hartshorn 1983). The canopy is *ca* 20 m high and dominant tree species include *Astronium graveolens*, *Spondias* spp., and *Brosimum alicastrum* (Hartshorn 1983, Janzen 1983). Average annual temperature is 26°C and average annual rainfall is 1440 mm (Maldonado *et al.* 1995). Rains usually begin in mid April and continue until mid December; the months of January through March are usually completely dry. Based on rainfall (Maldonado *et al.* 1995) and fruit and flower availability (Frankie *et al.* 1974, Fleming 1988), four seasons were recognized: (1) dry season: no rain, peak in flowering of Bombacaceae, small fruiting peak, January to March; (2) early rainy season: beginning of rains, few species in fruit and flower, April to June; (3) mid-rainy season: heavier rains, largest peak in fruiting, second flowering peak of chiropterophilic species, July to September; and (4) late rainy season: last rains of the year, lowest availability of fruits and flowers, October to December.

The second study site is located on the central Pacific coast of Mexico within the Chamela-Cuixmala Biosphere Reserve (*ca* 19°22'–19°35'N, 104°56'–105°03'W). Chamela is located approximately between Puerto Vallarta, Jalisco, and Manzanillo, Colima, and has an extension of 13,200 ha. The predominant vegetation type in this region is lowland deciduous forest, but other habitats include riparian forest, coastal vegetation, mangroves, palm forests, and spiny-thorn forest (Lott 1993). The canopy is approximately 15 m high and dominant tree species include *Astronium graveolens*, *Cordia* spp., and *Tabebuia* spp. (Lott *et al.* 1987). Average annual temperature is 25°C and average annual precipitation is 750 mm with a marked dry season from November until June (Bullock 1995). Based on rainfall, fruit (Bullock & Solís-Magallanes 1990), and flower availability (Stoner *et al.* 2003), four seasons are recognized: (1) early dry season: smallest amount of rain, second highest peak in chiropterophilic flowers in January, second highest peak of canopy trees in fruit, January to March; (2) late dry season: first rains often begin at end, few chiropterophilic species in flower and few canopy trees in fruit, April to June; (3) beginning of rainy season: highest peak in chiropterophilic flowers in July, few species in fruit, July to September; and (4) end rainy season: last rains of the year, intermediate chiropterophilic species in flower, highest number of canopy trees with fruit, October to December.

**DATA COLLECTION.**—At both study sites, bats were captured in Japanese-style mist nets (50/2 denier, 38 mm mesh, 2.6 m wide; Avinet Inc., Dryden, NY). Three mist nets, 6, 9, and 12 m long, were opened each sampling night at dusk for 5 h, during the peak foraging times of most phyllostomid bats (LaVal 1970, Davis & Dixon 1976, Fenton & Kunz 1977). Fifty-six nights were sampled at Palo Verde from January 1994 through January 1997, with an average of 4–5 nights sampled per season each year or  $14.7 \pm 2.1$  nights sampled each season through the entire study period (range 12–16) (Stoner & Timm 2004). Seventy-two nights were sampled at Chamela from March 1999 to August 2000 with an average of  $15.6 \pm 3.2$  nights per season (range 13–17).

Mist net sampling was conducted at Palo Verde near the Guayacán waterhole (10°20'N, 85°20'W), *ca* 3 km W of the Hacienda Park Ranger Station. This natural, freshwater spring is oval-shaped and varies from 4 m in diameter during the rainy season to 1 m (or less) in diameter during the driest months. It generally retains some water throughout the dry season but does dry out completely about once every 10 yr (R. Timm, pers. comm.). The water runs out of the basin and down a 15 m cement canal and empties into a watering trough. As it is one of the few remaining natural sources of fresh water within Parque Nacional Palo Verde, the waterhole attracts numerous mammals from the surrounding area and therefore was the best sample location within the study area to maximize the number of species captured. Two large rivers, the Río Tempisque and Río Bebedero, border Parque Nacional Palo Verde, however, contain brackish water. The Guayacán waterhole is one of the main sources of fresh water in Palo Verde, not only in the dry season, but also in the rainy season, since rainwater is principally absorbed into the limestone soils. Nets were placed in the same general area but never in the exact same position each time to avoid bats learning where the nets were (LaVal & Fitch 1977). The 9 m net was placed parallel to the length of the water hole and the other two nets were placed in the forest approximately 50 m on either side of the 9 m net.

To make the sampling as similar as possible to Palo Verde, mist net sampling was conducted at Chamela along *arroyos*, which function as temporary rivers during the rainy season. After the rainy season ends, standing water is still found within low-lying areas of the arroyos for up to several months. These arroyos are used as an important water source for many mammals in the region, and even when they are dry, they provide an area with less vegetation and are used as flyways by bats.

Each individual bat captured was identified to species using dichotomous keys (Medellín *et al.* 1997, Timm & LaVal 1998). Adults were marked with permanent plastic numbered collars (modified from Gannon 1993) and released.

**COMMUNITY AND SEASONAL COMPARISONS.**—Even when sampling effort is equal between different sites, the use of diversity indexes has been questioned. In particular, the presence or absence of rare species, which often occurs just by chance (Colwell & Coddington 1994), may affect the outcome of diversity indexes, while having no true biological meaning (Feinsinger 2001). Rank-abundance graphs have been suggested as an alternative to using diversity indexes to compare communities in different habitats (Feinsinger 2001). These simple graphs are useful because they allow the comparison of all biologically important aspects of species diversity among samples including: (1) the number of species is reflected by the number of points each graph contains; (2) the relative abundance of species is observed by the position it falls upon the line; (3) the number of rare species is reflected by the length of the tail, indicating the number of species that contain only one individual; and (4) community structure can easily be compared between sites by simply evaluating the shape of the curve. Rank-abundance graphs are constructed by plotting the rank of each species on the *x*-axis from most to least abundant and  $\log_{10} p_i$  for each species on the *y*-axis. Each point

on the graph is labeled with the species identity. This qualitative comparison is first used to make initial comparisons between the phyllostomid bat community of Palo Verde and Chamela.

To further compare phyllostomid species richness between sites, the program EstimateS (Version 7.5.0, Copyright R. K. Colwell: <http://viceroy.eeb.uconn.edu/estimates>) was used to calculate species accumulation curves (sample-based rarefaction) and 95 percent confidence intervals. The Shannon index of diversity and evenness were also calculated for each site and the Classic Jaccard index is used to evaluate similarity between the Palo Verde and Chamela phyllostomid community (Version 7.5.0, Copyright R. K. Colwell: <http://viceroy.eeb.uconn.edu/estimates>).

Generalized linear models (GENMOD, SAS 2000) were used to determine if site or season affected the number of species or the number of foraging guilds captured each night. The model used site, season, and the interaction term as categorical independent variables, and number of species and the number of foraging guilds captured each night as the dependent variables for each analysis, respectively. To determine if the number of individuals captured within each foraging guild depended upon site or season, generalized linear models also were used to evaluate the number of individuals captured during each season for the two most common foraging guilds, nectarivores and frugivores. Because the number of species, number of foraging guilds, and individuals from the nectarivorous and frugivorous guilds captured each night did not follow a normal distribution, a poisson distribution was used for these analyses.

**RESULTS**

At Palo Verde, 56 nights were sampled for a total of 280 h, 840 net hours, and 3931 m<sup>2</sup> of net. A total of 1245 individuals were captured representing 47 species and 7 families of bats. Of this total, 1088 individuals were from the family Phyllostomidae (33 species), including 14 species of frugivores, 5 species of nectarivores, 7 species of gleaning insectivores, 3 species of carnivores, 2 species of sanguivores, and 1 omnivore (Table 2). The remaining 157 individuals included aerial insectivores of the families Emballonuridae, Molossidae, Mormoopidae, Natalidae, and Vespertilionidae, and fish-eating bats of the family Noctilionidae (Stoner & Timm 2004).

TABLE 2. *Relative importance of phyllostomid foraging guilds from tropical dry forest in Chamela, Mexico and Palo Verde, Costa Rica.*

	Chamela		Palo Verde	
	Species/ Guild	Individuals/ Guild	Species/ Guild	Individuals/ Guild
Foraging guild				
Frugivore	9	617	15	948
Nectarivore	4	230	5	48
Gleaning insectivore	1	1	8	62
Sanguivore	1	42	2	17
Carnivore	0	0	3	12
Omnivore	0	0	1	1

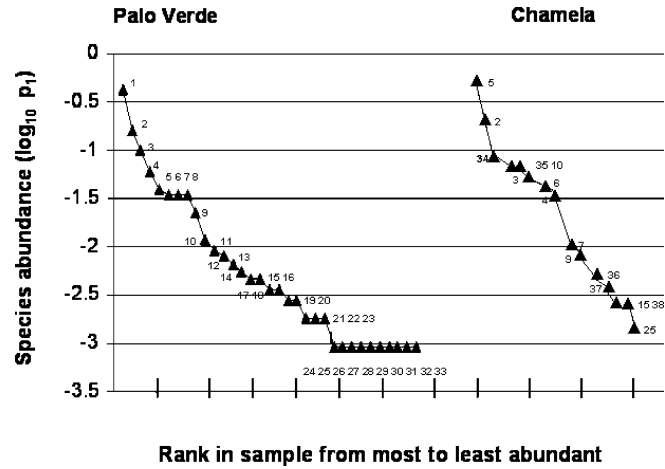


FIGURE 1. Rank-abundance (dominance-diversity) graph of species captured at Palo Verde and Chamela. Numbers represent species captured and parentheses represent foraging guild (C: Carnivore, F: Frugivore, GI: Gleaning Insectivore, N: Nectarivore, O: Omnivore, S: Sanguivore). 1: *Carollia perspicillata* (F), 2: *Artibeus jamaicensis* (F), 3: *Sturnira lilium* (F), 4: *Artibeus lituratus* (F), 5: *Glossophaga soricina* (N), 6: *Artibeus phaeotis* (F), 7: *Centurio senex* (F), 8: *Miconycteris brachyotis* (GI), 9: *Artibeus watsoni* (F), 10: *Desmodus rotundus* (S), 11: *Trachops cirrhosus*, 12: *Miconycteris minuta* (GI), 13: *Uroderma bilobatum* (F), 14: *Carollia brevicauda* (F), 15: *Miconycteris megalotis* (GI), 16: *Platyrrhinus helleri* (F), 17: *Carollia castanea* (F), 18: *Vampyressa nymphaea* (F), 19: *Miconycteris nicefori* (GI), 20: *Miconycteris schmidtorum* (GI), 21: *Chrotopterus auritus* (C), 22: *Diphylla ecaudata* (S), 23: *Tonatia brasiliensis* (GI), 24: *Carollia subrufa* (F), 25: *Chiroderma villosum* (F), 26: *Glossophaga commissarisi* (N), 27: *Glossophaga leachii* (N), 28: *Hylonycteris underwoodi* (N), 29: *Lichonycteris obscura* (N), 30: *Macrophyllum macrophyllum* (GI), 31: *Phyllostomus discolor* (O), 32: *Vampyrum spectrum* (C), 33: *Miconycteris hirsuta* (GI), 34: *Artibeus intermedius* (F), 35: *Leptonycteris curasoae* (N), 36: *Choeroniscus godmani* (N), 37: *Artibeus toltecus* (F), and 38: *Musonycteris harrisoni* (N).

At Chamela, 70 nights were sampled for a total of 342 h, 1050 net hours, and 4914 m<sup>2</sup> of net. A total of 971 individuals were captured representing 22 species and 5 families. Of this total, 890 individuals were from the family Phyllostomidae (15 species), including 9 species of frugivores, 4 species of nectarivores, 1 gleaning insectivore, and 1 sanguivore (Table 2). The remaining 81 individuals come from the families of aerial insectivores Emballonuridae, Mormoopidae, Natalidae, and Vespertilionidae.

The rank abundance graph (Fig. 1) for phyllostomid species showed a broader span across for Palo Verde, indicating more species at this site; however, this was largely due to the longer tail, indicating that many of the species were captured only once. The similar curves observed for Palo Verde and Chamela indicate that equitability was similar between the two sites; however, only one of the ten shared species showed a similar abundance between sites, the second most important species, *Artibeus jamaicensis*. Five species were found only in Chamela, while 15 species were found only in Palo Verde, with 9 of these being captured only once. One endemic species, *Musonycteris harrisoni*, was found at

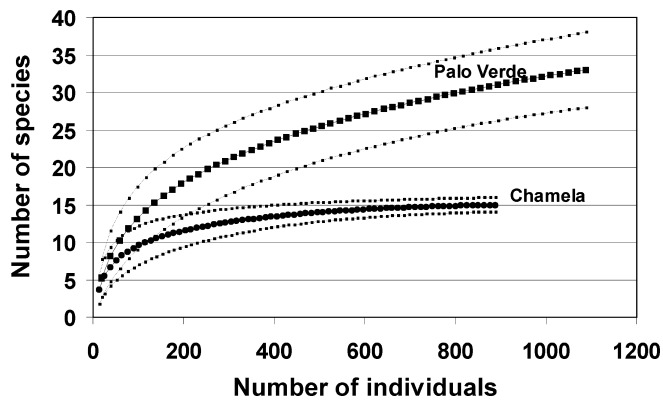


FIGURE 2. Rarefaction (sample-based) curves for phyllostomid bats from Palo Verde and Chamela with 95 percent confidence intervals for expected species richness.

Chamela; Palo Verde has no endemic species (Stoner & Timm 2004).

The rarefaction curve (Fig. 2) clearly shows that Palo Verde was more diverse than Chamela when as few as 280 individuals were sampled from each site. Similarly, Shannon diversity was greater at Palo Verde ( $1.956 \pm 0.157$ ) than Chamela ( $1.642 \pm 0.088$ ). In spite of the greater diversity observed at Palo Verde, evenness was similar between the two sites (0.559 for Chamela vs. 0.606 for Palo Verde). The Classic Jaccard index was 0.263, showing low similarity in the species composition of phyllostomids between these two dry forest sites.

Significantly more species were captured each night at Palo Verde ( $5.47 \pm 0.33$ ) than Chamela ( $3.67 \pm 0.43$ ;  $\chi^2 = 23.02$ ,  $P = 0.0001$ ,  $df = 1$ ). Furthermore, significant differences were found over seasons within each site ( $\chi^2 = 8.27$ ,  $P = 0.04$ ,  $df = 3$ ). The greatest number of species was captured at Chamela in the early wet season and at Palo Verde in the early wet and early dry seasons (Fig. 2).

Six foraging guilds were observed at Palo Verde, whereas only four were observed at Chamela (Table 1). The two most highly

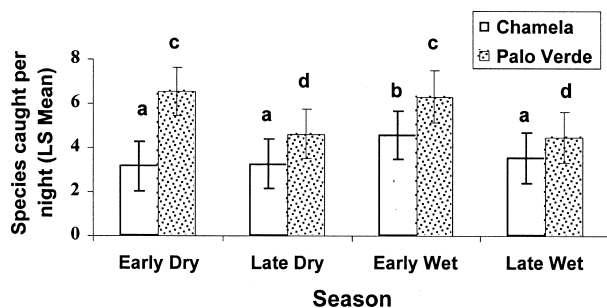


FIGURE 3. Average number of phyllostomid species captured each night over seasons at Chamela and Palo Verde. Within each site, different letters indicate significant differences over seasons ( $P < 0.05$ ).

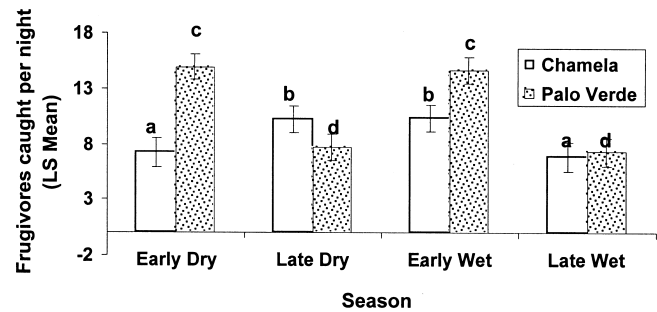


FIGURE 4. Average number of individuals from the frugivorous guild captured each night over seasons at Chamela and Palo Verde. Within each site, different letters indicate significant differences over seasons ( $P < 0.05$ ).

represented foraging guilds at both sites were frugivores and nectarivores; nevertheless, the relative composition of these foraging guilds differed between sites. At Chamela, nine species of frugivores made up 69 percent of total captures and four species of nectarivores made up 26 percent of total captures. At Palo Verde, 14 species of frugivores comprised 87 percent of total captures and 5 species of nectarivores comprised 4.4 percent of total captures. No significant differences were found between the numbers of foraging guilds captured each night over seasons ( $\chi^2 = 2.41$ ,  $P = 0.49$ ,  $df = 1$ ) or between sites ( $\chi^2 = 0.99$ ,  $P = 0.32$ ,  $df = 1$ ). However, significantly more individuals in the frugivorous guild were captured each night at Palo Verde ( $17.8 \pm 2.69$  vs.  $8.8 \pm 0.94$ , respectively, for Palo Verde and Chamela;  $\chi^2 = 5.86$ ,  $P = 0.01$ ,  $df = 3$ ). For nectarivores, significantly more individuals were captured each night at Chamela ( $3.27 \pm 0.66$  vs.  $0.83 \pm 0.20$ , respectively for Chamela and Palo Verde;  $\chi^2 = 9.96$ ,  $P = 0.0016$ ,  $df = 3$ ). Furthermore, the number of individuals within foraging guilds was significantly different over seasons (frugivores:  $\chi^2 = 15.58$ ,  $P = 0.001$ ,  $df = 3$ ; nectarivores:  $\chi^2 = 8.47$ ,  $P = 0.037$ ,  $df = 3$ ). More frugivores were found at Chamela in the late dry and early wet season and at Palo Verde in the early dry and early wet season (Fig. 4). Nectarivores were more abundant at both Chamela and Palo Verde in the early wet season (Fig. 5).

## DISCUSSION

PHYLLOSTOMID BAT COMMUNITY STRUCTURE IN TROPICAL DRY FORESTS.—As predicted, phyllostomid bat community structure differed between the two dry forest sites sampled both in terms of number of species represented, as well as the composition of species. Palo Verde was more diverse than Chamela as shown by the Shannon diversity index and the rarefaction curve. Furthermore, the Classic Jaccard index (0.263) and detailed analysis of the species abundance curve show that species composition also differed between Palo Verde and Chamela. Therefore, variants of tropical dry forest can be different enough in structure and composition that they may contain unique phyllostomid communities. Significantly more ground level phyllostomid species were observed

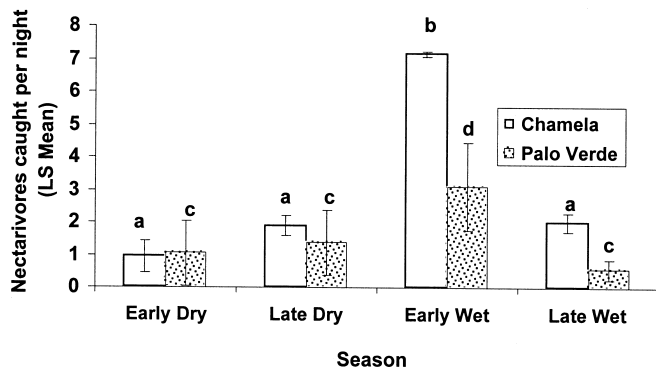


FIGURE 5. Average number of individuals from the nectarivorous guild captured each night over seasons at Chamela and Palo Verde. Within each site, different letters indicate significant differences over seasons ( $P < 0.05$ ).

at Palo Verde. It appears that the phyllostomid bat community from the *wetter* dry forest site of Palo Verde may have more in common with bat communities from tropical humid or wet forests, whereas the *drier* dry forest site of Chamela has greater affinity with savanna habitats. For example, all six foraging guilds observed at Palo Verde are found in tropical wet and humid forests with similar number of species within them (Timm 1994, Kalko *et al.* 1996). In addition, the structure of the phyllostomid community at Chamela was similar to that observed in the tropical savanna habitat in Bolivia which contains 14 species including 7 frugivores, 1 nectarivore, 3 gleaning insectivores, 1 sanguivore, and 1 carnivore (similar to the community structure observed at Chamela: 9 species of frugivores, 4 species of nectarivores, 1 gleaning insectivore, and 1 sanguivore).

Community structure, in terms of guilds represented also varied between the two sites (Table 1). The guild of carnivores, represented by *Vampyrum spectrum*, *Chrotopterus auritus*, and *Trachops cirrhosus* was completely absent from Chamela. This is likely a consequence of the geographic range of these three species, which all arrive at their northern most distribution in southern Mexico (Nowak 1994). The relatively greater abundance of individuals in the nectar guild at Chamela is likely due to the greater abundance of chiropterophilic flowers at this site (23 species, Stoner *et al.* 2003) compared to the Palo Verde region (14 species, Heithaus *et al.* 1975, Fleming 1988). Similarly, a greater abundance of fruit resources at the *wetter* dry forest of Palo Verde is likely one of the main factors that influence the greater abundance of species and individuals observed in the frugivore guild at this site. At least 28 plant species are known to be utilized by frugivorous bats in the Palo Verde region (Fleming 1988), whereas this information is not yet available for Chamela.

It is possible that the differences in phyllostomid bat community structure between these two dry forest sites may be a consequence of the distinct precipitation regimes that characterize them. Nevertheless, more studies are needed in different tropical dry forests that vary in precipitation regimes in order to recognize patterns in phyllostomid bat community structure that occur with similar precipitation. A review of bat diversity at several sites in the Neotrop-

ics shows no clear trend related to average annual precipitation (Table 1); however, there is so much variation in sampling among studies that this is not a valid comparison. A review of different studies in the Atlantic forest of southeastern Brazil showed that the number of bat species varied from 5 to 27 in any one site (Godoy Bergallo *et al.* 2003) and that most of this variation was attributed to differences in sampling protocol and effort between sites. Similar comparisons, using the same sampling protocol and effort, should be conducted in different forest types to determine if phyllostomid bat community structure and the number of species within foraging guilds are affected in a predictable way by precipitation, habitat structure, and composition, or are largely a consequence of geographic distribution.

SEASONAL CHANGES IN SPECIES DIVERSITY AND ABUNDANCE OF FRUGIVORES AND NECTARIVORES.—Significant changes in the number of species caught each night over seasons were observed in the two dry forests sampled; however, these changes were not the same in both forests. The number of species captured per night depended on the season, with more species being captured during the seasons with greater chiropterophilic resources at each site. For example, at Chamela, significantly more species were captured per night during the early wet season (July to September), July being the month with greatest chiropterophilic resources available (Stoner *et al.* 2003). Similarly, at Palo Verde more species were captured in the early wet season, the period of peak fruit production (Frankie *et al.* 1974), and the early dry season, the period of peak flowering of Bombacaceae (Fleming 1988).

The number of individuals in the two most common foraging guilds, frugivores and nectarivores, differed significantly between sites and over seasons. Again, these changes appear to be largely related to changes in the abundance of chiropterophilic resources. At Chamela, the number of frugivores was significantly greater at the beginning of the wet season, which corresponds to one of the two observed peaks in fruit production at this site (Bullock & Solís-Magallanes 1990) and at the end of the dry season. Although the end of the dry season at Chamela does not experience a peak in fruit production at the community level, several chiropterophilic species have fruits at this time including *Spondias purpurea*, *Ficus* spp., and several species of cactus. Nectarivores were most abundant at Chamela in the early dry and early wet seasons, both coinciding with peaks in abundance of chiropterophilic flowers (Stoner *et al.* 2003). At Palo Verde, the number of frugivores captured was greatest in the early wet season, corresponding to a peak in fruit availability (Frankie *et al.* 1974) and the early dry season. Although no peak in fruit occurs in the early dry season at this site, this represents a peak in chiropterophilic flowers and many frugivores rely heavily on nectar during this period in this region (Heithaus *et al.* 1975).

The changes in the number of frugivores and nectarivores observed over seasons at these dry forest sites suggest that some species in these habitats may be moving in and out of the area depending on the availability of resources. This agrees with several other studies that have noted seasonal changes in abundance of some phyllostomid bats and suggested that many species are migrating in search of food (Álvarez & González-Quintero 1970,

Herrera-Montalvo 1997, Iñiguez 1997, Soriano *et al.* 2000, Timm & LaVal 2000, Stoner 2001, LaVal 2004, Stoner & Timm 2004, Timm & McClearn 2005). For example, Stoner (2001) showed significant differences in abundance over seasons for two frugivores, *Carollia perspicillata* and *Artibeus jamaicensis* at Palo Verde, with peaks in the early wet season and early dry season.

In conclusion, phyllostomid bat community structure varied substantially among these two variants of tropical dry forest. Therefore, it is important to specify the type of dry forest that is being examined, considering not only precipitation, but also vegetation features such as structure and composition. By conducting standardized sampling protocols in a variety of habitats, we will be able to compare phyllostomid bat community structure across a gradient of complexity of dry forests exposed to different precipitation regimes. If this information is obtained for several different variants of tropical dry forest, we will be able to predict bat community structure and dominating guilds within each dry forest variant.

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