15. NEW WORLD NECTAR-FEEDING VERTEBRATES: COMMUNITY PATTERNS AND PROCESSES

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Abstract

New World nectar-feeding vertebrates occur primarily in the mammalian family Phyllostomidae (subfamilies Glossophaginae and Phyllonycterinae with a total of about 34 species) and the avian family Trochilidae (about 330 species). In this paper we compare and contrast patterns and processes in the community structure of these two groups to identify evolutionary commonalities and differences. Both groups show similar latitudinal trends in regional species diversity with peak diversities occurring in northwestern South America and southern Central America. Diversity at the community level shows parallel trends with species richness increasing as a power function of annual rainfall per site. Nectar-bat diversity ranges from 1-6 species per site; hummingbird diversity ranges from 3-28 species per site. Higher per site hummingbird diversity has arisen in part from the evolution of distinct sets of canopy- *vs.* understory-feeding species. The major factor controlling both regional and local diversity in these groups is the species richness of their flowers. Hummingbird flowers have evolved more frequently and in a wider range of plant habits and habitats than nectar-bat flowers. The two groups also show a parallel trend regarding body size and jaw/bill length distributions in different habitats: the largest species tend to occur in dry habitats. This trend reflects differences in mean flower sizes among habitats. The density and biomass of both nectar-feeding bats and birds tend to be low at most sites, reflecting the low energy density of nectar compared with other food resources (*e.g.*, fruit).

Resumen

Los vertebrados nectarívoros del Nuevo Mundo pertenecen principalmente a las familias Phyllostomidae (subfamilies Glossophaginae y Phyllonycterinae con un total de 34 especies) y Trochilidae (cerca de 330 especies). En este trabajo, comparamos y contrastamos las tendencias y procesos en la estructura de comunidades de estos dos grupos e identificamos las similitudes y diferencias evolutivas. Ambos grupos muestran tendencias latitudinales similares en riqueza regional de especies con picos de diversidad en el noroeste de Sudamérica y el sur de Centroamérica. La diversidad al nivel de comunidad muestra tendencias paralelas con la riqueza de especies incrementándose como la potencia de la precipitación anual por sitio. La diversidad de murciélagos nectarívoros va de 1-6 especies por sitio; la diversidad de colibríes va de 3-28 especies por sitio. La mayor diversidad de colibríes por sitio ha surgido debido, en parte, a la evolución de distintos grupos de especies que se alimentan en el dosel y en el sotobosque. El factor principal que controla la diversidad local y regional en estos grupos es la riqueza de especies de las flores. Las flores de que se alimentan los colibríes han evolucionado más frecuentemente en un espectro más amplio de hábitos y hábitat de plantas, que las flores de que se alimentan los murciélagos nectarívoros. Ambos grupos también muestran tendencias paralelas en relación al tamaño del cuerpo y la distribución de la longitud mandíbula/pico en diferentes hábitat: las especies más grandes tienden a ocurrir en hábitat secos. Esta tendencia refleja diferencias en el tamaño promedio de las

In both groups, seasonal migration is a prominent feature of community organization. Hummingbirds exhibit a more diverse array of foraging strategies than nectar bats. Whereas both groups contain species that forage via trap-lining, only in hummingbirds is resource defense a common foraging strategy. Island communities of these nectarivores usually contain only 2-4 species as a result of low floral diversity.

Key words: glossophagine bats, hummingbirds, community diversity, morphological diversity, migration

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flores entre los hábitat. La densidad y biomasa de las aves y murciélagos nectarívoros tienden a ser bajos en la mayoría de los sitios, reflejando la baja densidad de energía del néctar comparado con otros recursos alimenticios (*e.g.*, fruta). En ambos grupos, la migración estacional es una característica prominente en la organización de la comunidad. Los colibríes muestran una mayor diversidad de estrategias de alimentación que los murciélagos nectarívoros. En tanto ambos grupos muestran especies que se alimentan estableciendo rutas de forrajeo, sólo en los colibríes la defensa de recursos es una estrategia de alimentación común. Comunidades de islas de estos nectarívoros incluyen comúnmente de 2-4 especies como resultado de una baja diversidad floral.

Palabras clave: murciélagos glosofaginos, colibríes, diversidad de comunidades, diversidad morfológica, migración.

As is well known, Bernardo Villa-R's favorite mammals are bats, which were the subject of his doctoral thesis (Villa-R. 1966). In one of his early publications (Martinez and Villa-R. 1940), he described a new species of bat, *Leptonycteris yerbabuenae* (Phyllostomidae, Glossophaginae), which was collected near Yerbabuena in his home state of Guerrero. This bat, which has since been called *L. sanborni* and then *L. curasoae* (Arita and Humphrey 1988), has been the subject of intense study in Mexico and Arizona for several decades (Ceballos *et al.* 1997; Cockrum 1991; Fleming and Nassar 2002; Hayward and Cockrum 1971). A common member of one of two nectar-feeding subfamilies of the Phyllostomidae, it is responsible for pollinating the flowers of many species of columnar cacti and paniculate agaves, among other species of night-blooming "bat" flowers.

Don Bernardo's early interest in nectar-feeding bats has inspired us to review the community ecology of *Leptonycteris* and its relatives and to compare this ecology with that of hummingbirds (Apodiformes, Trochilidae), the other major group of nectar-feeding vertebrates in the New World. Both groups contain species of small, agile fliers with relatively large energy budgets (compared with insects) and large carrying capacities for pollen. Because they are highly mobile, cognitively advanced, and long-lived, these animals are effective pollinators of many kinds of widely dispersed tropical and subtropical plants. Of these two groups, hummingbirds are evolutionarily older, having split from swifts (Apodidae) in the Paleocene nearly 60 Mya (Bleiweiss 1998a). Hummingbirds occur in two subfamilies (Phaethornithinae, the hermits, containing six genera and 34 species and Trochilinae, the nonhermits containing 96 genera and 294 species;

Schuchmann 1999). The major adaptive radiation of extant lineages apparently began in the early Miocene (about 18 Mya) (Bleiweiss 1998a). This radiation produced seven major species groups (one hermit and six nonhermit groups) containing a total of about 330 extant species (Bleiweiss *et al.* 1997). Although their place of origin is currently unknown (Bleiweiss 1998a), it was likely in the Andean region of northern South America (Rahbek and Graves 2000). Early hummingbirds probably lived in tropical lowland habitats; at least two major radiations of nonhermits have occurred in the Andean uplands (Bleiweiss 1998b). Hermits are found primarily in lowland tropical habitats of tropical America. Nonhermits occur in a wide variety of habitats throughout North, Central, and South America and the West Indies.

The chiropteran family Phyllostomidae first appears in the fossil record in the Miocene when many of its extant lineages, including the Glossophaginae and Phyllonycterinae (*sensu* Wetterer *et al.* 2000), likely first evolved. Compared with hummingbirds, the adaptive radiation of nectar-feeding phyllostomids has been rather modest. Subfamily Glossophaginae contains 13 genera and about 31 species classified in two tribes (Glossophagini and Lonchophyllini); subfamily Phyllonycterinae contains two genera and three species (Wilson and Reeder 1993). Glossophagines are found throughout the lowlands and uplands of the neotropics, including the West Indies. Phyllonycterines are restricted to the Greater Antilles and the Bahamas.

Nectar-bats and hummingbirds are often considered to be each other's temporal ecological analogues. But is this really true? How many ecological similarities do these two groups share? Despite vastly different evolutionary histories and morphological backgrounds, have these two groups converged in their community attributes and ecological function? Here we compare and contrast the community ecology of nectar-bats and hummingbirds in a search for evolutionary commonalities and differences.

Sources of data and specific motivating questions

We gleaned data on local diversity, habitat distributions, diets, and morphology of nectar-bats and hummingbirds from the literature. Nomenclature for bats follows Wilson and Reeder (1993); hummingbird nomenclature follows Sibley and Monroe (1990) and AOU (1998). To quantify local species richness in mainland communities (including Trinidad), we recorded the number and identity of coexisting species of bats and hummingbirds from a total of 43 sites (29 sites for bats, 32 sites for birds); nine of the sites (21%) were the same for bats and birds. We classified each site into one of the following eight habitat classes based on elevation (*lowland* < 1500 m; *montane* > 1500 m but < 3000 m; *highland* ≥ 3000 m) and total annual rainfall (*very dry* < 500 mm; *dry* > 500 mm but < 2000 mm; *moist* ≥ 2000 mm but ≤ 3000 mm; *wet* > 3000 mm). Habitats include *desert* (very dry at any elevation), *lowland dry forest*, *lowland moist forest*, *lowland wet forest*, *montane dry forest*, *montane moist forest*, *montane wet forest*, and *highland*. To characterize the general morphology of bats and hummingbirds at these sites, we collected data on body mass for both bats and hummingbirds and forearm length and length of the maxillary (upper) toothrow (a correlate of jaw length) for bats and wing chord length and length of the exposed culmen (= bill length) for hummingbirds. Our morphological databases included 34 species of bats and 231 species of hummingbirds. Morphological data for bats came from Swanepoel and Genoways (1979) and Simmons and Wetterer (2002). Morphological data for hummingbirds came from many sources; contact JFO for these sources. In both databases, each species was assigned to a primary habitat, based on distributional data in the literature. We classified bats in one of two principal habitats: *dry* (annual rainfall < 1000 mm) and *non-dry* (annual rainfall ≥1000 mm). We classified hummingbirds in one of three principal habitats: *dry* (xeric environments, including tropical dry forest), *open forest* (temperate pine and oak woodlands, clearings, open habitats), or *wet forest* (tropical rain forest, cloud forest). To quantify the morphological diversity of bats and hummingbirds at the 29 and 32 sites, respectively, we calculated arithmetic means and coefficients of variation (= standard deviation/ mean) of (i) forearm or wing chord length and (ii) jaw (i.e., maxillary toothrow) or bill length based on each site's species list. Forearm and wing length were used to indicate a species' overall size, and jaw or bill length were used to indicate the size of a species' trophic (feeding) apparatus. Data and their sources for the 43 sites are found in Appendices 1 and 2.

Bats have been the subjects of many mist-netting studies, and we determined the relative abundances of phyllostomid nectar-feeders compared with fruit-eaters (subfamilies Carolliinae and Stenodermatinae) at 14 well-studied mainland sites. Comparable data are not generally available for frugivorous and nectarivorous birds at the same site. We also collected data on number of species of bat- or hummingbird-pollinated flowers and general habits of these species (i.e., herbs, epiphytes, vines or lianas, shrubs (including paniculate *Agaves*), and trees (including columnar cacti)) at 16 well-studied mainland sites (seven sites for bats, nine sites for hummingbirds). At five bat sites and eight hummingbird sites, we were able to compare average jaw or bill lengths with average flower lengths to see if these two variables are correlated.

We analyzed these data to answer the following specific questions:

1. What processes determine the species richness (S), relative abundances, and morphological diversity (MD) of vertebrate nectar-feeding guilds in the New World?
2. Are the same processes operating in both bats and hummingbirds? Are there parallel trends in these two groups?
3. To what extent does S change seasonally within these guilds? Based on residence status and relative abundance, can we identify "core" vs. "satellite" members of these guilds (*sensu* Hanski 1982)?

4. How do island guilds compare with mainland guilds regarding S and MD?

Statistical analyses were conducted using Statmost ver. 3.5 (Dataxiom Software, Inc., Los Angeles, CA) and Systat ver. 10 (SPSS Inc., Chicago, IL). Descriptive statistics are presented as mean ± 1 SE throughout this chapter.

Community patterns

Species diversity. Basic patterns of S are similar in both groups at the regional and local levels. At the regional level, S in nectar-bats and hummingbirds is highest in northwestern South America and southern Central America with the Andean region containing higher diversity than adjacent lowlands (Fleming 1995; Johnsgard 1997; Rahbek and Graves 2000). At the local or community level, S in nectar-bat communities averaged 3.1 ± 0.3 species (range: 1-6 species) (Table 1). Mean values of S did not differ among habitat types ($P > 0.20$ in a one-way ANOVA). Species richness in hummingbird communities was 3.7 times higher than that of nectar-bats and averaged 11.5 ± 1.2 species (range: 3-28 species) (Table 1). Mean values of S differed significantly among habitats; lowland wet forests and montane moist forests contained more species than other habitats ($F_{6,25} = 7.35$, $P < 0.001$).

In both groups, S increased asymptotically with annual rainfall, but the relationship was stronger in hummingbirds (Fig. 1). Equations describing these relationships are: nectar-bats, $Y = 0.35X^{0.27}$ ($r^2 = 0.10$; $P < 0.001$); hummingbirds, $Y = 0.35X^{0.46}$ ($r^2 = 0.44$; $P < 0.0001$). Stepwise multiple regression analyses indicated that neither elevation nor latitude significantly explained additional variation after the effect of rainfall was accounted for. Species richness per site reached an asymptote of about five nectar-bats and 22 hummingbirds at about 2500 mm of annual rainfall. Peak nectar-bat diversity is about one-quarter of peak hummingbird diversity.

Although variation in annual rainfall accounts statistically for most of the geographic variation in S, this community parameter also varies with elevation. S declines with increasing elevation in both groups, but the rate of decline is higher in nectar-bats than in hummingbirds (Fig. 2) (also see Graham (1990) and Patterson *et al.* (1996)). In many mainland areas, hummingbird diversity is actually

Table 1. Species richness of nectar-bats and hummingbirds by habitat on the New World mainland and West Indies. Data are means ± 1 SE (range).

Habitat[a]	A. Bats	
	n	Number of species
D	2	2.0 ± 1.0 (1-3)
LDF	8	2.6 ± 0.5 (1-5)
LMF	8	3.9 ± 0.4 (3-5)
LWF	6	3.5 ± 0.7 (1-6)
MMF	5	2.4 ± 0.7 (1-5)
All mainland sites	29	3.1 ± 0.3 (1-6)
West Indies[b]	9	1.9 ± 0.4 (0-3)
	B. Hummingbirds	
D	3	4.3 ± 1 .3 (3-7)
LDF	4	8.8 ± 1 .0 (6-10)
LMF	6	8.8 ± 0.8 (6-11)
LWF	5	19.0 ± 1.9 (13-22)
MDF	4	6.0 ± 1.8 (3-11)
MMF	9	15.9 ± 2.2 (8-28)
H	1	4
All mainland sites	32	11.5 ± 1.2 (3-28)
West Indies	9	2.8 ± 0.2 (2-4)

[a]Habitats include: D = desert, LDF = lowland dry forest, LMF = lowland moist forest, LWF = lowland wet forest, MDF = montane dry forest, MMF = montane moist forest, H = highlands
[b]Islands include: Greater Antilles, Bahamas, Antigua, Guadaloupe, Martinique, and St. Vincent. Sources of data come from Appendices 1 and 2 (mainland sites) and Lack (1973) and Rodriguez-Duran and Kunz (2001)(West Indies).
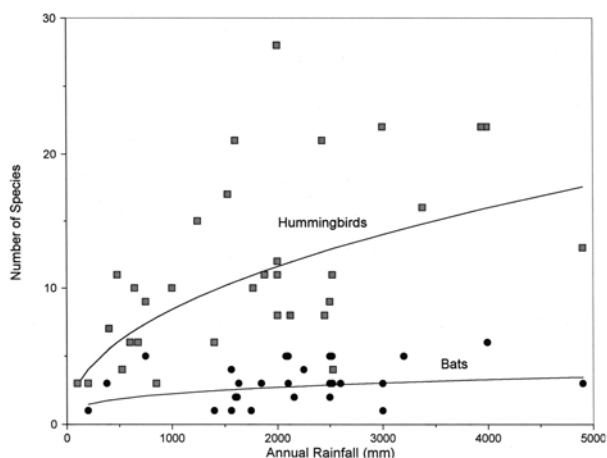

Fig. 1. Relationship between local species richness and annual rainfall at 29 nectar-bat sites and 32 hummingbird sites on the neotropical mainland. The curves were produced using nonlinear regression. Sources of data are indicated in Appendices 1 and 2.
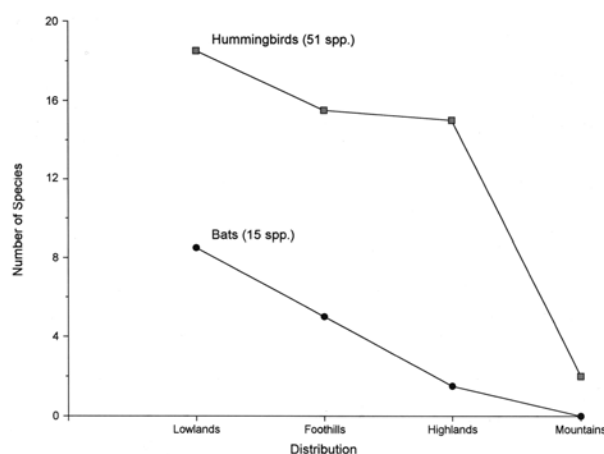
Fig. 2. Changes in the species richness of nectar-bats and hummingbirds with elevation in 15 species of Venezuelan glossophagine bats and 51 species of Panamanian hummingbirds. Elevational categories as defined in Ridgely (1981) from which the hummingbird data were taken. Bat data come from Handley (1976).

higher at mid- elevations (*e.g.*, 1000-1500 m in Costa Rica) than in the lowlands (Stiles 1981) as a result of the extensive diversification of trochilines in montane habitats. A similar radiation of mid-elevation nectar-bats has not occurred.

Species richness changes seasonally in most communities of nectar-bats and hummingbirds. In the extreme case, nectar-bats and hummingbirds are present only seasonally at the northern North American limits of both families. Tropical and subtropical bats (*e.g.*, *Leptonycteris curasoae*, *L. nivalis*, and *Choeronycteris mexicana*) and several species of hummingbirds undergo latitudinal migrations to seasonally occupy the Sonoran and Chihuahuan

Deserts or montane habitats in western North America, respectively (Brown and Kodric-Brown 1979; Cockrum 1991; Grant and Grant 1968; Moreno-Valdez 2000). Within tropical latitudes, seasonal changes in the composition of hummingbird communities occur as a result of both altitudinal and latitudinal migrations. At six well-studied sites in Costa Rica, for example, the proportion of migrant species ranged from 12 to 60 percent (Table 2). Altitudinal migrants generally outnumber latitudinal migrants at these sites. Hummingbird communities in the Amazonian lowlands also contain a few species of local migrants (Cotton 1998b).

The extent of altitudinal or latitudinal migrations in tropical nectar-bats is less well-known. In addition to the three species that migrate into northern Mexico and the southwestern United States, seasonal migrations have been reported in the cactus-visiting bat *Platalina genovensium* in the Andes of southern Peru (Sahley and Baraybar 1996) and in *Leptonycteris curasoae* in the dry inter-montane valleys of the Venezuelan Andes (Sosa and Soriano 1993). Tschapka (1998) reported that two of four glossophagine bats at La Selva, Costa Rica, were present only seasonally. In this case, the migrant species (*Lonchophylla robusta* and *Lichonycteris obscura*) probably are altitudinal migrants.

The occurrence of seasonal changes in the composition of nectar-bat and hummingbird communities indicates that their structure likely includes "core" (= common permanent residents) and "satellite" (= uncommon and/or migrant) species (*sensu* Hanski 1982). In lowland tropical bat communities, species of *Glossophaga* are core taxa whereas species of *Anoura* are core taxa in montane

Table 2. Number of species of permanent resident and migrant hummingbirds at six well-studied sites in Costa Rica, based on data in Stiles (1983).

Site	Habitat (location)[a]	Number of Species			
		Permanent residents	Altitudinal migrants	Latitudinal migrants	Total (percent migrants)
La Selva	LWF (N)	13	8	1	22(41%)
Osa Peninsula	LWF (S)	17	1	1	19 (12%)
Santa Rosa	LDF (N)	7	2	1	10 (30%)
Monteverde	MMF (N)	14	6	1	21 (33%)
Las Cruces	MWF (S)	18	4	0	22 (18%)
Villa Mills	H (S)	2	3	0	5 (60%)

[a] Habitat designations as in Table 1; location: N = northern part of country; S = southern part of country.

sites (see below). Both of these genera are geographically widespread, basal members of tribe Glossophagini (Koopman 1981; Simmons and Wetterer 2002). Based on studies in Costa Rica and Colombia, core taxa in lowland hummingbird communities include hermits of the genera *Phaethornis*, *Glaucis*, and *Threnetes* and nonhermits of the genera *Amazilia*, *Chlorostilbon*, and *Thalurania*. Core nonhermit taxa in montane communities include species of *Amazilia*, *Chlorostilbon*, *Coeligena*, *Colibri*, and *Lesbia* (Cotton 1998a; Snow and Snow 1980; Stiles 1983).

Population densities and relative abundances.- Compared with other mammalian and avian food sources (*e.g.*, leaves, fruits, seeds, insects, and other animals), nectar is a scarce food resource. For example, except in large light gaps, most flowers visited by nectar-bats and hummingbirds occur in low densities in many tropical forests (Buzato *et al.* 2000; Cotton 1998a; Feinsinger 1978, 1976; Tschapka 1998). In contrast, during peak blooming periods (April-May), nectar densities of columnar cacti can be as high as 1400 kJ per ha in the Sonoran Desert; this nectar supply is 3-4 times greater than the estimated energy demand of nectarivorous bats and birds (Fleming *et al.* 2001; Horner *et al.* 1998). Because of generally low nectar energy densities, the densities and biomasses of nectar-feeding bats and hummingbirds are likely to be low in most habitats. The relative abundances of nectar-feeders are likely to be unevenly distributed among species with a few common ("core") and many uncommon ("satellite") species per site. Available data support these expectations.

Many mist-net studies indicate that nectarivorous phyllostomid bats are much less common than frugivorous phyllostomids (Table 3). On average, fruit-bats outnumbered nectar-bats in abundance and in numbers of species by factors of 17.0 and 5.6, respectively, at 14 sites in Central and South America. Mean abundance ratios, but not species ratios, varied among habitats with lowland wet forests (mean $= 21.5 \pm 6.2$) differing strongly from montane moist forests (mean $= 5.4 \pm 1.6$) ($P = 0.022$ in a Kruskal-Wallis one-way ANOVA; the extremely high abundance ratio from LMF in Panama was excluded from this analysis). Similarly, community-wide bird surveys in lowland moist forests in Panama and Peru indicate that frugivores exceed nectarivores by factors of 50-207 (biomass) and 1.6-2.3 (number of species) (Robinson *et al.*, 2000; Terborgh *et al.* 1990). Biomass of avian frugivores and nectarivores in these forests is 35-36 kg/100 ha and 0.2-0.6 kg/100 ha, respectively.

Table 3. Relative abundances of glossophagine bats compared with frugivorous phyllostomid bats (subfamilies Carolliinae and Stenodermatinae) at various locations in tropical America.

Habitat[a]	Country	Number of captures (*n* species)		No. of frugivores/No. nectar-bats (No. frug. spp/No. nectar spp.)	Most common nectar-bat (proportion capts.)[b]
		Frugivores	Nectarivores		
LDF	Panama	875 (11)	103 (1)	8.5 (11.0)	GS (1.00)
LDF	Costa Rica	5231 (11)	739 (2)	7.1 (5.5)	GS (0.99)
LDF	Costa Rica (riparian)	718 (8)	99 (1)	7.3 (8.0)	GS (1.00)
LDF	Brazil	170 (7)	40 (3)	4.3 (2.3)	GS (0.55)
LMF	Panama	8439 (17)	37 (3)	228.1 (5.7)	GS (0.76)
LMF	Brazil	777 (18)	11 (3)	70.6 (6.0)	GS (0.46)
LWF	Panama	1127 (13)	50 (1)	22.5 (13.0)	GS (1.00)
LWF	Costa Rica	1231 (15)	137 (6)	9.0 (2.5)	GC (0.59)
LWF	Fr. Guiana	1046 (19)	57 (5)	18.4 (3.8)	LT (0.49)
LWF	Fr. Guiana	535 (14)	12 (3)	44.6 (4.7)	LT (0.58)
LWF	Colombia	154 (12)	12 (3)	12.8 (4.0)	GS (0.58)
MMF	Costa Rica	539 (8)	69 (6)	7.8 (1.3)	GC (0.49)
MMF	Colombia	698 (7)	119 (1)	5.9 (7.0)	
MMF	Ecuador	69 (8)	29 (2)	2.4 (4.0)	AC (0.83)

[a]Habitat designations as in Table 1.
[b]Species include: AC = *Anoura caudifer*, GC = *Glossophaga commissarisi*; GS = *G. soricina*; LT = *Lonchophylla thomasi*
Sources of data: Arango (1990), Bernard (2001), Cosson et al. (1999), Fleming (1988), Fleming *et al.* (1972), Handley *et al.* (1991), Heithaus *et al.* (1975), LaVal and Fitch (1977), Muchhala and Jarrín-V.(2002), Pedro and Taddei (1997), and Simmons and Voss (1998).

In terms of relative abundances, tropical nectar-bat communities are dominated numerically by 1-2 species whereas hummingbird communities typically contain 3-6 abundant species and many less common species (for hummingbird summaries, see Cotton (1998a), Feinsinger and Colwell (1978), and Stiles (1983)). Species of *Glossophaga* tend to dominate most lowland tropical sites where they account for 46-100% of nectar-bat captures (Table 3). At many montane sites, *Anoura* replaces *Glossophaga* as the numerically dominant taxon.

Between-site turnover in species. Whereas local species richness is commonly called *alpha diversity*, the between-habitat component of diversity within a region represents *beta diversity* (Whittaker, 1975). Do nectar-bats and hummingbirds exhibit similar levels of species turnover among habitats and hence similar beta diversities? We addressed this question by tallying the number of times each species of nectar-bat or hummingbird occurred in the 29 and 32 mainland bat and bird communities, respectively. High beta diversity will occur when species are each restricted to a low number of sites, causing the species composition of different sites to differ strongly; otherwise, low beta diversity will occur.

The distribution of species across sites differed significantly between nectar-bats and hummingbirds (Fig. 3). Hummingbirds were distributed across fewer sites per species than were nectar-bats ($X^2 = 13.6$, $df = 2$, $P = 0.001$; data were classified into three categories: 1-5 sites per species, 6-10 sites per species, and > 10 sites per species). Two bats, *Glossophaga soricina* and *Anoura caudifer*, occurred at more than 10 sites; no species of hummingbird occurred at > 10 sites. Two of the three humming-
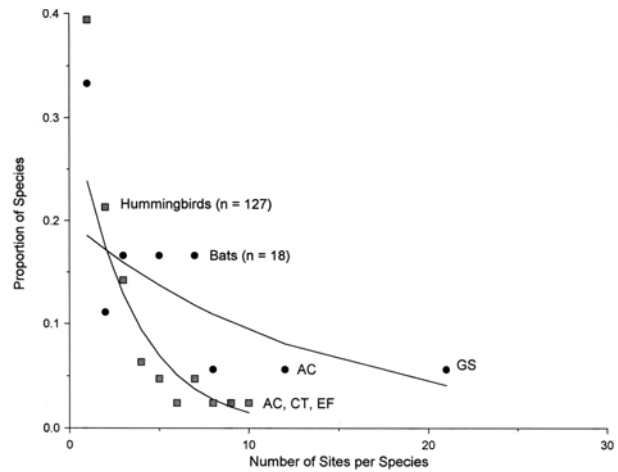

Fig. 3. The frequency distribution of 18 species of nectar-bats and 127 species of hummingbirds expressed as number of sites per species in the neotropical mainland. Maximum number of possible sites for bats and hummingbirds was 29 and 32, respectively (see Appendices 1 and 2 for sources of data). The curves were produced using nonlinear regression. Species abbreviations are: bats – *Anoura caudifer* (AC) and *Glossophaga soricina* (GS); hummingbirds – *Archilochus colibris* (AC), *Colibri thalassinus* (CT), and *Eugenes fulgens* (EF).

birds occurring at 10 sites (*Archilochus colubris*, *Eugenes fulgens*) are wide-ranging latitudinal migrants. We conclude that beta diversity is higher in hummingbirds than in bats.

Morphological diversity. Size and jaw/bill length diversity is substantial in nectar-bats and hummingbirds (Table 4). Overall, nectar-bats are less variable in forearm length and jaw length than hummingbirds. Based on coefficients of variation, wing lengths and bill lengths of hummingbirds are 1.5 and

Table 4. Summary of morphological data for nectar-feeding bats and hummingbirds. Data include mean ± 1 S.E. (range). Superscripts indicate means that differ significantly (P < 0.05) in t-tests (bats) or one-way ANOVAs (hummingbirds). See text for sources of data.

Taxon	Habitat	n	Forearm or Wing Chord Length (mm)	Maxillary Toothrow or Culmen Length (mm)	Mass (g)
Bats	Dry	7	45.9 ± 2.5[a] (38.4-56.3)	10.0 ± 0.6[a] (8.0-12.5)	17.7 ± 2.9[a] (9.3-30.0)
	Non-dry	27	38.2 ± 0.9[b] (32.0-47.0)	7.9 ± 0.2[b] (5.9-10.9)	12.1 ±0.8[b] (7.5-21.0)
	All species	34	39.8 ± 1.0 (0.15)*	8.3 ± 0.3 (0.18)	13.3 ± 0.9 (0.41)
Hummingbirds	Dry	69	57.4 ± 1.7[a] (35.0-132.0)	21.5 ± 1.3[a] (8.0-119.0)	5.2 ± 0.3[a] (2.0-20.0)(n=60)
	Open forest	50	54.0 ± 2.0[a] (31.6-75.2)	20.1 ± 1.5[a] (10.0-40.2)	4.6 ± 0.4[a] (1.8-9.5) (n=42)
	Wet Forest	110	57.3 ± 1.4[a] (29.0-81.0)	21.7 ± 1.1[a] (9.9-43.7)(n=88)	5.3 ± 0.3[a] (2.0-13.0)(n=88)
	All species	231	56.5 ± 0.8 (0.22)*	21.2 ± 0.6 (0.45)	5.1 ± 0.2 (0.46)(n=192)

*Coefficient of variation (=standard deviation/mean).

2.5 times more variable, respectively, than comparable measurements in bats. Bill length variation (and degree of curvature) is especially impressive in hummingbirds. Hummingbird bill lengths range from 8 to 119 mm whereas bat jaw lengths only range from 6 to 13 mm (Table 4). In both groups, jaw or bill length is significantly correlated with forearm or wing length, but the correlation is much tighter (*i.e.*, a higher r^2 value) in bats than in birds (Fig. 4). Several species of hummingbirds (*e.g.*, *Ensifera ensifera*) are extreme outliers in bill length. *Musonycteris harrisoni* has an extreme value for jaw length among nectar-bats, but it deviates far less from its regression line than does *Ensifera* (Fig. 4). In terms of mass, nectar-bats average 2.6 times heavier than hummingbirds.

Morphological variation is related to habitat in nectar-bats but not in hummingbirds (Table 4). Bats living in dry habitats (*e.g.*, deserts, thorn scrub, or very dry tropical 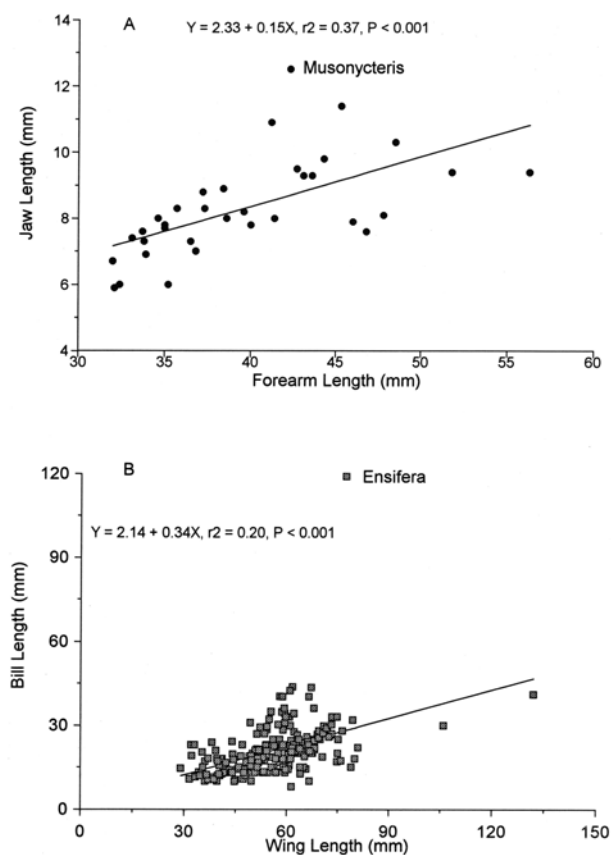forests) are significantly larger than bats living in more mesic habitats ($F_{5,28} = 15,650$, $P << 0.001$ in a multivariate ANOVA based on wing length, jaw length, and mass) Although mean values for hummingbirds do not differ among habitats ($F_{6,370} = 0.40$, $P = 0.88$ in a multivariate ANOVA based on wing length, bill length and mass), it is worth noting that, as in nectar-bats, extremely large values of wing length, bill length, and mass occur in species associated with dry habitats (Table 4). *Patagona gigas*, the world's largest hummingbird, occurs in arid Andean habitats where it visits the flowers of columnar cacti along with the long-snouted nectar-bat *Platalina genovensium* (Sahley 1996).

We further explored trends in morphological diversity (MD) by asking, Does MD vary in similar ways in nectar-bats and hummingbirds across the species diversity gradient associated with annual rainfall? To what extent does morphology and its variation within communities change with increased species richness? To answer these questions, we plotted average body size, as measured by forearm or wing length, and its variation, as indicated by coefficient of variation, against annual rainfall for 29 nectar-bat and 29 hummingbird communities (Figs. 4A, B and 5A, B). For hummingbirds, we eliminated the three mainland sites that lacked complete morphological datasets. We made similar plots for average jaw or bill length and its variation (Figs. 4C, D and 5C, D).

Trends in MD were different in nectar-bats and hummingbirds. In bats, average body size and jaw length *decreased* significantly with increasing rainfall (Fig. 5A, C). Although variation in size and jaw length also decreased with increasing rainfall, neither correlation was significant (Fig. 5B, D). Thus, communities of low bat S in drier habitats contain larger bats than do higher S communities in wetter habitats. In contrast, average body size and bill length of hummingbirds and its variation *increased* significantly with increasing rainfall (Fig. 6). Thus, hummingbird communities in drier habitats contain smaller, more morphologically uniform sets of species than those in wetter habitats. It is worth noting that small, morphologically uniform sets of hummingbirds only occur in very dry habitats receiving < 500 mm annually. Over most of the rainfall gradient, hummingbird sizes and range of variation do not differ among communities, as indicated by data summarized in Table 4.
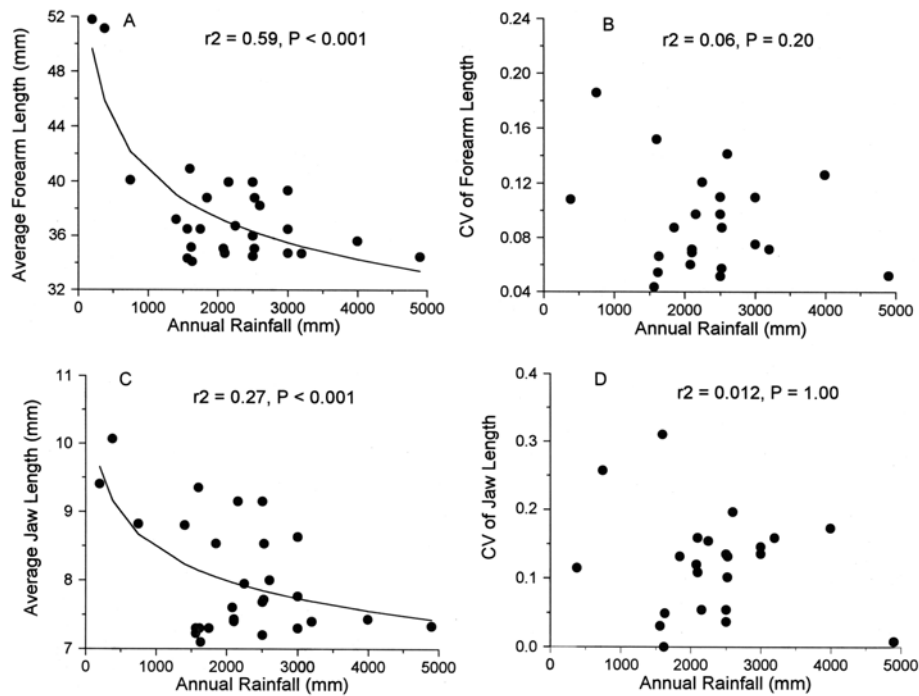

Fig. 4. Relationship between forearm or wing length and jaw or bill length in nectar-bats (A) and hummingbirds (B). See text for sources of data.

Fig. 5. Trends in the morphological diversity of nectar-bats across a rainfall gradient. Data represent average forearm and jaw length (A, C) and their coefficients of variation (B, D). Each point represents a single site (see Appendix 1). The curves were produced using nonlinear regression. See text for further explanation. Sources of data: Appendix 1 plus our morphological dataset.
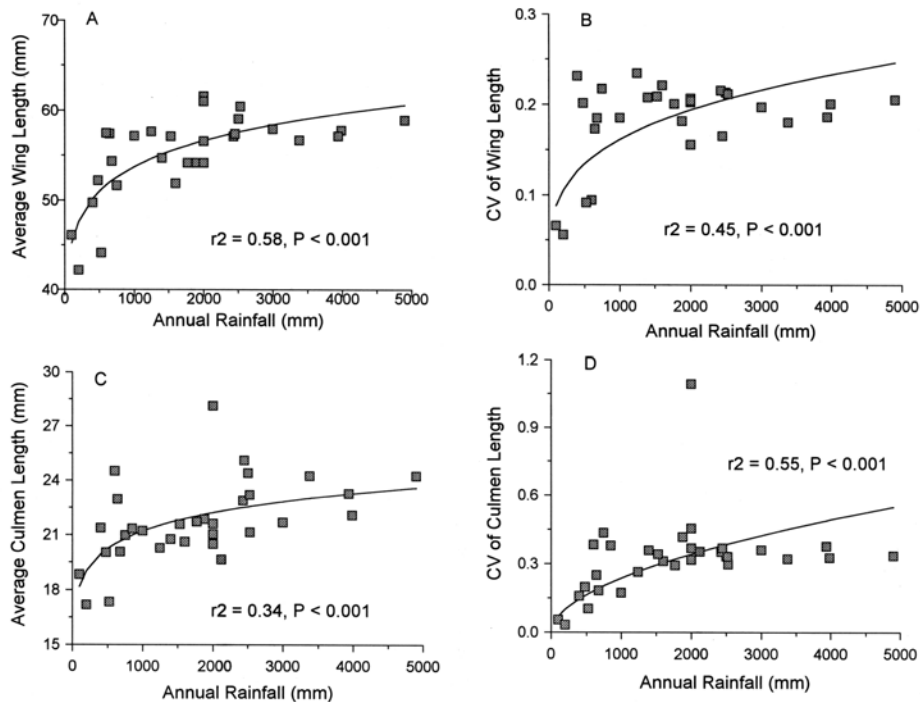

Fig. 6. Trends in the morphological diversity of hummingbirds across a rainfall gradient. Data represent average wing and bill length (A, C) and their coefficients of variation (B, D). Each point represents a single site (see Appendix 2). The curves were produced using nonlinear regression. See text for further explanation. Sources of data: Appendix 2 and our morphological dataset.

Patterns of flower species richness and plant habit distributions. How many different species of flowers do nectar-bats and hummingbirds visit in their habitats, and what are the distributions of these flowers among plant habits? Does the four-fold difference in peak S in bat and hummingbird communities reflect a four-fold difference in flower S? Data summarized in Table 5 indicate that flower S in seven nectar-bat communities ranged from four species in the Sonoran Desert to 19 species in a Costa Rican lowland wet forest. In nine hummingbird communities, flower S ranged from 14 species in a very dry lowland forest in Mexico to 51 species in a Costa Rican montane moist forest (Table 5). Within the same habitat type, hummingbird flower S averaged about 3.4 times higher than nectar-bat flower S, and the number of nectar-bat or hummingbird species was strongly correlated with the number of flowers at these sites ($r^2 = 0.80, P < 0.001$) (Fig. 7). The regression equation for this relationship is Y (number of bat or bird species per site) $= -0.96 + 0.37 X$ (number of flower species per site). The dis-

tributions of bat and hummingbird flowers among plant habits differed significantly ($X^2 = 64.8, df = 4, P < 0.001$). Bat flowers are produced mainly by trees and epiphytes whereas hummingbird flowers are produced mainly by epiphytes and herbs (Table 5).

To what extent does site-site variation in the size of nectar-bats and hummingbirds reflect differences in the size of the flowers these animals visit? Do nectar-bats have larger jaws in dry habitats than in more mesic habitats because they visit larger flowers? To answer this question, we regressed average jaw or bill length against average flower length in five bat communities and eight hummingbird communities. Results differed for the two taxa (Fig. 8). The regression was highly significant for bats, despite the small sample size ($r^2 = 0.94, P = 0.01$); it was non-significant for hummingbirds ($r^2 = 0.0004, P = 0.96$). Thus, average jaw length in nectar-bat communities appears to reflect average flower size; this is not the case in hummingbird communities. The average size of nectar-bat and hummingbird

Table 5. Plants providing flowers for nectar-bats and hummingbirds by habitat and plant habit.

Habitat[a]	Country	Number of species by plant habit					
		Herbs	Vines	Epiphytes	Shrubs	Trees*	Total Species
			A. Nectar-bats				
D	Mexico	0	0	0	1	3	4
LDF	Costa Rica	0	0	0	1	8	9
LDF	Venezuela	0	0	0	1	5	6
LMF	Brazil	0	4	4	0	2	10
LWF	Costa Rica	0	5	5	1	8	19
MMF	Brazil	1	0	3	0	2	6
MMF	Ecuador	0	2	6	0	2	10
Total (proportion)		1 (0.016)	11 (0.172)	18 (0.281)	4 (0.063)	30 (0.469)	64
			B. Hummingbirds				
LDF	Mexico	4	4	1	0	5	14
LDF	Costa Rica	3	2	0	3	8	16
LMF	Panama	13	8	12	6	3	42
LMF	Brazil	7	3	24	5	0	39
LWF	Costa Rica	20	7	10	10	3	50
LWF	Trinidad	12	0	5	5	6	28
MMF	Costa Rica	11	3	24	10	3	51
MMF	Brazil	5	9	16	6	1	37
H	Costa Rica	4	2	4	9	0	21
Total (proportion)		79 (0.267)	38 (0.128)	96 (0.324)	54 (0.182)	29 (0.098)	296

[a] Habitat designations as in Table 1.
* Includes columnar cacti.
Sources of data: Arizmendi and Ornelas (1990), Brown and Kodric-Brown (1979), Buzato *et al.* (2000), Cotton (1998b), Fleming (1988), Fleming *et al.* (1996), Muchhala and Jarrin-V. (2002), Nassar *et al.* (1997), Sazima *et al.* (1999), Snow and Snow (1972), Tschapka (1998), and Wolf *et al.* (1976).
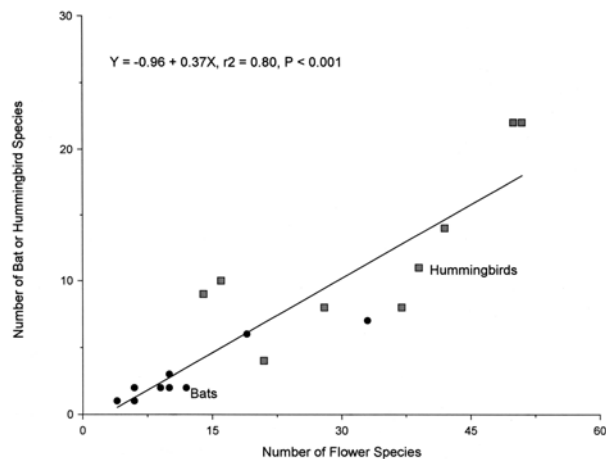
Fig. 7. Relationship between the local species richness of bats and hummingbirds and the local species richness of their flowers. Sources of data: Arizmendi and Ornelas (1990), Buzato *et al.* (2000), Fleming (1988), Fleming *et al.* (1996), (Karr 1990), Muchhala and Jarrin-V. (2002), Murray *et al.* (2000), Nassar et al. (1997), Sazima et al. (1999), Snow and Snow (1972), Stiles (1985a, b), Timm and LaVal (2000), Tschapka (1998), and Wolf *et al.* (1976).

Fig. 8. Relationship between average jaw or bill length and average flower length at five nectar-bat sites (A) and eight hummingbird sites (B). Sources of data: Arizmendi and Ornelas (1990), Brown and Kodric-Brown (1979), Buzato et al. (2000), Cotton (1998b), Fleming *et al.* (1996), Muchhala and Jarrin-V. (2002), Nassar *et al.* (1997), Sazima et al. (1999), Snow and Snow (1972), and Wolf *et al.* (1976).

flowers (means of the site means) in these communities differed significantly (Mann-Whitney U test, $z = 2.34$, $P = 0.019$). Bat flowers were nearly twice as long as hummingbird flowers: 47.0 ± 7.6 mm ($n = 5$ sites) *vs.* 28.1 ± 1.5 mm ($n = 8$ sites).

The special case of islands. Both species richness (S) and morphological diversity (MD) of West Indian nectar-feeding bats and hummingbirds differ from the mainland situation. Whereas S of hummingbirds is about four times higher than S of bats in mainland communities, on West Indian islands the two groups have statistically indistinguishable mean values of S (Table 1) (paired $t = 1.84$, $df = 8$, $P = 0.10$). Maximum S in both nectar-bat and hummingbird communities in the West Indies is 3-4 species per island —a value much closer to mainland nectar-bat communities than mainland hummingbird communities.

In terms of morphology, island nectar-bats are not random draws from their species pools whereas hummingbirds are (Fig. 9). West Indian nectar-bats belong to two subfamilies: the two species of *Monophyllus* are glossophagines and are closely related to *Glossophaga*; species of *Phyllonycteris* and *Erophylla* belong to a sister group to the glossophagines, the West Indian endemic subfamily Phyllonycterinae
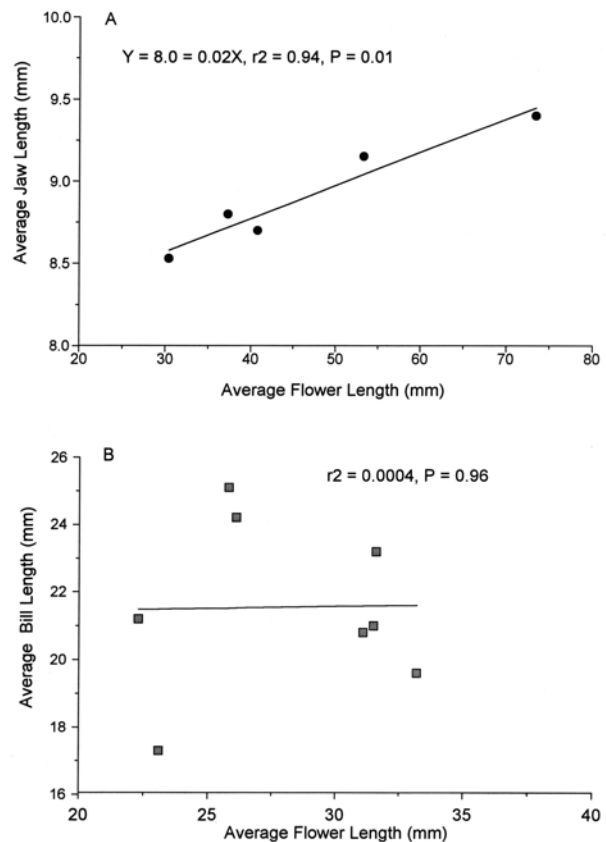
(Simmons and Wetterer 2002). Each of the five West Indian nectar-bats has a longer forearm (*i.e.*, is larger) than the median value for all nectar-bats; four of five species have jaws that are $\leq$ the median value for all bats (Fig. 9A). Phyllonycterines are among the largest of all nectar-bats but are short-jawed.

West Indian hummingbirds also represent more than one phylogenetic lineage (Bleiweiss, 1998b) and fall into two morphological groups: (1) a group of eight species that are smaller in overall size and bill length than median values for the entire family and (2) a group of eight species that are larger in overall size and bill length than median values (Fig. 9B). This distribution does not differ significantly from chance expectations ($X^2 = 3.44$, $df = 3$, $P = 0.33$).
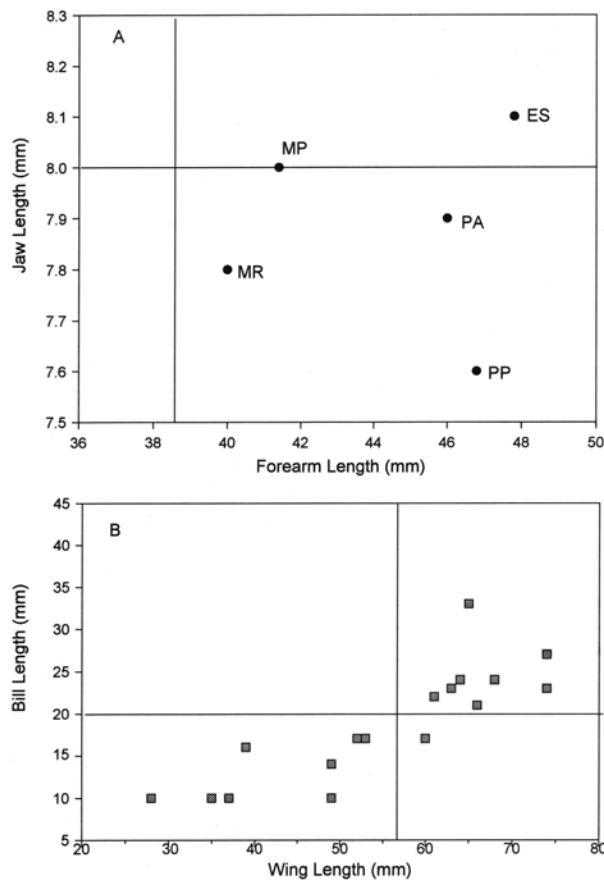
Fig. 9. Ordination of West Indian species of nectar-bats (A) and hummingbirds (B) in morphological space in relation to median values (the vertical and horizontal lines) in the entire morphological datasets of bats and hummingbirds. The species of bats are *Erophylla sezekorni* (ES), *Monophyllus plethodon* (MP), *M. redmani* (MR), *Phyllonycteris aphylla* (PA), and *Phyllonycteris poeyi* (PP). Sources of data: Lack (1973), Rodriguez-Duran and Kunz (2001) plus our morphological datasets.

Compared to nectar-bats, West Indian hummingbirds occupy a broader range of total morphological space, and the distribution of species among the four size quadrants in Fig. 9 differs significantly in bats and hummingbirds ($X^2 = 12.38$, $df = 3$, $P = 0.006$). West Indian hummingbirds are either small-sized and small-billed or large-sized and large-billed whereas most West Indian nectar-bats are large-sized and small-jawed. As indicated by Lack (1973) and Kodric-Brown *et al.* (1984), among others, individual islands in the West Indies are occupied by 1-2 species of hummingbirds from each of the two size groups.

Processes behind the patterns

The original question motivating this study was, To what extent are community patterns and processes similar or different in phyllostomid nectar-bats and hummingbirds? Have these two groups of specialized vertebrates evolved along similar trajectories? If not, why not? Based on our results, which are summarized in Table 6, the number of differences between these two taxa substantially outnumbers the number of similarities. It appears that the evolutionary/ecological trajectories of nectar-bats and hummingbirds have been quite different. What are the processes behind these similarities and differences?

Species diversity. Total species richness of nectar-bats is only one-tenth that of hummingbirds. At the community level, peak species richness of nectar-bats is only about one-quarter that of hummingbirds. Why are there more species of hummingbirds than species of nectar-bats regionally and locally? Two possible explanations, which are not necessarily mutually exclusive, for this include (1) differences in evolutionary ages of the two groups and/or (2) differences in the opportunities for speciation and adaptive radiation in these groups. Perhaps there are more species of hummingbirds than nectar-bats simply because the Trochilidae is older than the Phyllostomidae. Given similar rates of speciation and extinction, an older group will always contain more species than a younger group. While the Trochilidae likely is older than the Phyllostomidae, the adaptive radiations of extant members of both families probably date from the Miocene, beginning about 18 Mya. Thus, modern taxa in both groups have been evolving for about the same length of time, and it is unlikely that difference in species richness of these two groups is solely the result of differences in their evolutionary ages.

There is one way in which being geologically older has enabled the Trochilidae to produce more species than the Glossophaginae and Phyllonycterinae. Family Trochilidae contains two subfamilies, Phaethornithinae (hermits) and Trochilinae (nonhermits), whose evolutionary origins undoubtedly predate the Miocene (Bleiweiss 1998a). Possibly reflecting this early evolutionary divergence, these two groups differ substantially in their species richness, habitat affinities, and foraging/mating strategies. The hermits include many fewer species (34 *vs.* 294 species), many of which have long, curved bills and

Table 6. Summary of major similarities and differences in the evolutionary/ecological trajectories of phyllostomid nectar-bats and hummingbirds.

A. Similarities

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1. Trends in regional diversity are similar in both groups.
2. Local diversity (S) increases with increasing rainfall in both groups.
3. Seasonal latitudinal and altitudinal migrations occur in some species in both groups.
4. Abundance (biomass) and S of nectarivores in both groups is < that of frugivores.
5. The number of bat- or hummingbird-pollinated flowers varies among habitats in a similar way.
6. Bats and hummingbirds fall on the same regression line relating their S to local diversity of flowers.
7. Bats and hummingbirds have similar low values of S on West Indian islands.
8. Island bats and hummingbirds are not random draws from their total species pools in terms of morphology or coexistence patterns.

B. Differences

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1. S does not vary among habitats in bats but does in hummingbirds.
2. Peak S is four times higher in hummingbirds than in bats.
3. S decreases faster with elevation in bats than in hummingbirds.
4. An extensive montane radiation has occurred in trochiline hummingbirds but not in bats.
5. Beta (between habitat) diversity is higher in hummingbirds.
6. Wing and bill lengths are more variable in hummingbirds.
7. The correlation between jaw or bill length vs. forearm or wing length is stronger in bats.
8. Bats are 2.6 times heavier than hummingbirds, on average.
9. Bats living in xeric habitats are larger than those living in mesic habitats; this trend is much weaker in hummingbirds.
10. Average size decreases with increasing rainfall in bats; the opposite trend occurs in hummingbirds.
11. Growth forms of plants producing bat-flowers differs from that of hummingbirds.
12. Average jaw length strongly correlates with average flower size in bat communities but not in hummingbird communities.
13. Island bats occupy a different portion of wing-jaw morphospace than hummingbirds.

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are specialized for visiting flowers in the Zingiberales (*e.g.*, species of *Heliconia* and Costaceae) in the understory of lowland tropical forests. Hermits frequently forage via trap-lining, and many species have lek mating systems. They have not been successful in colonizing most islands in the West Indies or temperate North America (Bleiweiss 1998b). In contrast, nonhermits include many straight-billed species that forage in the canopy of lowland tropical forests as well as in a wide variety of open or disturbed habitats at all elevations. Many trochilines vigorously defend feeding territories and seldom trapline; they often have promiscuous mating systems that do not involve leks (Stiles 1981). Finally, compared with hermits, nonhermits have been much more successful in colonizing upland tropical habitats, the West Indies, and temperate North America. The rather profound evolutionary and ecological differences between hermits and nonhermits suggests that these two groups have had separate evolutionary histories for a long time. This separation undoubtedly has helped increase the overall diversity of hummingbirds by creating two hummingbird guilds in lowland tropical forests: an understory hermit guild and a canopy nonhermit guild (Feinsinger and Colwell 1978; Stiles 1981). A simi-

larly extensive set of parallel radiations has not occurred in the Glossophaginae, although it has in frugivorous phyllostomids (Bonaccorso 1979; Fleming 1986).

More important than differences in evolutionary ages, however, is that evolutionary opportunities for adaptive radiation in these two groups since the Miocene have been significantly different. Basically, there are more hummingbirds than nectar-bats both regionally and locally because there are more kinds of hummingbird flowers distributed over a broader range of habitats than there are nectar-bat flowers. *The regional and local diversity of appropriate flowers controls the diversity of nectar-feeding bats and birds.* This conclusion is strongly supported by the tight correlation between the number of nectar-bat or hummingbird flowers at a site and the number of nectar-bats and hummingbirds at that site (Fig. 7). At many sites in the neotropics, the number of hummingbird flowers outnumbers the number of bat flowers by a factor of 3-5 to one (Table 5; also see Kress and Beach (1994) and Murray *et al.* (2000)). At many sites, the number of species of hummingbirds outnumbers the number of nectar-bat species by a similar factor.

Thus, the key to understanding why there are more species of hummingbirds than nectar-bats in the New World lies in understanding why there are more species of hummingbird flowers than nectar-bat flowers. We propose that there are more hummingbird flowers because plants can more easily evolve flowers that attract hummingbirds than they can evolve flowers that attract nectar-bats. A major reason for this is that it probably takes relatively few morphological/biochemical changes for flowers to evolve from pollination by diurnal insects – the likely ancestral pollination condition for most vertebrate-pollinated plants — to pollination by diurnal hummingbirds (Bradshaw *et al.* 1995; Grant 1993; Schemske and Bradshaw 1999). Additional reasons include:

(1) Hummingbirds exploit flowers from a wider range of plant growth forms than bats. Hummingbirds pollinate 'herbaceous flowers' much more frequently and 'tree flowers' much less frequently than nectar-bats (Table 5). Since there are more species of animal-pollinated herbaceous flowers in the world than animal-pollinated tree flowers (as inferred from the significantly higher speciation rates of herbs compared with trees (Levin 2000)), the evolutionary base for potential hummingbird flowers is much larger than that for nectar-bat flowers. The contrast between the growth forms of plants visited by hummingbirds and bats is particularly striking at the northern range limits of these two groups in western North America. Nearly all of the 129 species of plants that provide food for eight species of migrant hummingbirds are herbaceous rather than woody (Grant 1994). In contrast, plants supporting migrant nectar-bats (*i.e.*, *Leptonycteris curasoae*, *L. nivalis*, and *Choeronycteris mexicana*) in the southwestern United States are woody and include two species of columnar cacti and several species of paniculate agaves.

(2) Hummingbirds often visit flowers with much smaller nectar rewards than nectar-bats. Hummingbirds frequently visit "insect" flowers (*e.g.*, Feinsinger 1976; Stiles 1981), but, to our knowledge, nectar-bats seldom do. In the Sonoran Desert, for example, hummingbirds often visit bee-pollinated flowers of mesquite (*Prosopis* spp.), palo verde (*Cercidium* spp.), and ironwood (*Olneya tesota*) in addition to hummingbird-adapted flowers of ocotillo (*Fouquieria splendens*) and the columnar cactus *Stenocereus alamosensis* as well as bat-adapted flowers of the cacti *Carnegiea gigantea*, *Pachycereus pringlei*, and *Stenocereus thurberi* (THF, pers. observations). In the same habitat, the lesser long-nosed bat visits flowers of only the latter three species plus flowers of *Agave subsimplex* (Horner *et al.* 1998 and unpubl. data). There are many more 'stingy' flowers, originally attracting insects with very small nectar rewards (*i.e.*, a few μL), in the world than 'generous' flowers producing $\geq$ 1 mL of nectar — typical values for bat-pollinated cacti (Cruden *et al.* 1983; Feinsinger 1987; Fleming 2002; Opler 1983). For example, at least 38% (n = 276 species) of the flowering plants in lowland wet forest at La Selva, Costa Rica, are pollinated by large or small bees compared with 15% that are pollinated by hummingbirds and 4% that are pollinated by bats (Kress and Beach 1994). Similarly, in montane moist forest at Monteverde, Costa Rica, about 36% of 2056 flowering plants are bee-pollinated compared with 9% that are hummingbird-pollinated and 2% that are bat-pollinated (Murray *et al.* 2000). We suggest that these differences indicate that it is easier (cheaper?) for plants to evolve flowers that attract hummingbirds than those attracting nectar-bats.

An especially conspicuous difference in the species richness of nectar-bats and hummingbirds occurs at mid-elevations in the mountains of the neotropics. Here, an extensive radiation of trochiline hummingbirds has taken place whereas no such radiation has occurred in nectar-bats. Again, the most likely explanation for this involves the ease of evolving diurnal hummingbird flowers compared to nocturnal nectar-bat flowers. As discussed by Cruden (1972) and Stiles (1978, 1981), the cool, cloudy conditions of mid-elevation sites reduce the activity of bees but not hummingbirds. Thus, ectothermic bees are less reliable pollinators under montane climatic conditions than endothermic (or heterothermic) hummingbirds. Night time conditions are even cooler at montane sites, and nocturnal nectar secretion rates are likely to be substantially lower than diurnal secretion rates (Stiles 1978). Because they are constantly endothermic (McNab 1982) and weigh at least twice as much as hummingbirds, nectar-bats, regardless of elevation, will have larger daily energy budgets than hummingbirds and will require larger energy rewards per flower to make visits profitable. Differences in the energy demands of nectar-bats and hummingbirds should increase with elevation. At montane sites, therefore, it should be

much cheaper for plants to produce hummingbird flowers than nectar-bat flowers. Hence, low flower diversity should strongly constrain the evolution of nectar-bats at montane sites.

Differences in the beta diversity of nectar-bats and hummingbirds also contribute to the greater overall species richness of the latter group. Beta diversity of hummingbirds is substantially higher than that of nectar-bats because, on average, the geographic ranges of hummingbirds are smaller than those of nectar-bats (see data in Rahbek and Graves (2000) and Santos and Arita (2002)). As a result of higher rates of between-habitat turnover, more species of hummingbirds occur in a given region than species of nectar-bats. While the reasons why hummingbirds have smaller geographic ranges than nectar-bats are not totally clear, we speculate that they likely involve differences in degree of habitat and dietary specialization with hummingbirds being more specialized, on average, than nectar-bats.

Relative abundances and seasonal changes in species richness. Although communities of nectar-bats and hummingbirds differ strongly in species richness, they are similar in terms of the unequal distribution of abundances among species and seasonal changes in species composition. The former pattern is ubiquitous in nature: all communities contain a few common species and many uncommon species. As discussed by Brown (1984) and Gaston (1996), a species' relative abundance in a local community is strongly affected by (1) size of its geographic range and (2) where that community is located within a species' geographic range. Species with large geographic ranges tend to be more common locally than species with small geographic ranges, and species tend to be more common in the central portion of their geographic range than at the edges. The first of these two generalizations appears to hold for nectar-bats and hummingbirds. Most of the taxa that we have identified as "core" (= abundant) members of their communities (*e.g. Glossophaga* and *Anoura* bats, *Phaethornis* and *Amazilia* hummingbirds) have large geographic ranges. Whether or not the local abundance of nectar-feeding bats and birds systematically decreases away from the centers of their ranges requires further study.

Seasonal movements among different communities are common in fruit- and/or nectar-feeding vertebrates (Fleming 1992; Levey and Stiles 1992). This mobility basically reflects the relatively "volatile" nature of their food supplies. In virtually all communities that have been studied, the availability of flowers and nectar varies seasonally. There are two flower peaks in many tropical sites – one in the dry season and another in the wet season (*e.g.* Cotton 1998b; Feinsinger 1976, 1978; Heithaus *et al.* 1975; Stiles 1975). In the Sonoran Desert, in contrast, a single flowering peak occurs in late spring (Fleming *et al.* 1996). Nectar-feeding bats and birds respond to these resource fluctuations in different ways. In arid regions, certain nectar-bats (*e.g.*, *Leptonycteris curasoae*) migrate whereas others (*e.g.*, *Glossophaga longirostris*) are sedentary and switch to eating fruits when flower availability declines (Sosa and Soriano 1993). *Glossophaga soricina* also switches seasonally from visiting flowers to eating fruit rather than migrating in lowland dry forests (Heithaus *et al.* 1975). Hummingbirds generally do not switch from feeding at flowers to feeding on fruit. Instead, many species of trochilines move from one community to another in response to changes in flower availability (Feinsinger 1976, 1978; Feinsinger and Colwell 1978; Stiles 1980, 1981). Many of these movements involve altitudinal migrations (Ornelas and Arizmendi 1995; Stiles 1980). The composition of many hummingbird communities is thus very fluid. Seasonal movements are likely to occur in tropical nectar-bat communities (*e.g.* Tschapka 1998), but they have not been as carefully documented.

Morphological diversity. Morphological diversity, particularly in jaw or bill size and shape, differs substantially between nectar-bats and hummingbirds and clearly reflects overall differences in species richness in the two groups. The adaptive radiation of bill size and shape in hummingbirds is especially impressive and indicates that bird bills are evolutionarily much more plastic than bat jaws (Stiles 1978). This plasticity has allowed hummingbirds to evolve specialized relationships with their flowers, which, in turn, has favored a more extensive adaptive radiation in both hummingbirds and their food plants than has occurred in nectar-bats and their food plants.

Interestingly, the greater degree of feeding specialization seen in hummingbirds provides an explanation for the differences between nectar-bats and hummingbirds seen in Fig. 8. That Figure shows that average jaw or bill length is strongly correlated with average flower length only in nectar-bat communities. We interpret these results to mean that nectar-bats feed in a much more fine-grained fashion than

hummingbirds. That is, each species of bat is likely to visit most kinds of bat-flowers in its community. Hummingbirds, on the other hand, are much more likely to be feeding specialists and hence feed in a much more coarse-grained fashion. Each species of hummingbird likely visits only a subset of the flowers in its community – only those flowers to which it is morphologically adapted for efficient nectar extraction (Cotton 1998a; Snow and Snow 1980; Stiles 1981). If nectar-bats are fine-grained feeders and hummingbirds are coarse-grained feeders, then jaw size in bats, but not in hummingbirds, should reflect average flower size in their community.

Only one morphological trend appears to be similar in both groups: species of nectar-bats and (a few) hummingbirds living in dry habitats tend to be larger and to have longer jaws or bills than species living in more mesic habitats, presumably because they forage at large flowers. This trend is much stronger in bats than in hummingbirds (compare Figs. 5 and 6), mainly because arid-dwelling hummingbirds of western North America all belong to the same clade of "bee" hummingbirds (Bleiweiss 1998a). On their breeding grounds and for most of their migration, these species feed on herbaceous plants whose flowers have converged on the same small size and tubular shape (Brown and Kodric-Brown 1979; Grant and Grant 1968).

Mainland vs. islands. Species richness in most groups of organisms is lower on islands than on the adjacent mainland, and nectar-bats and hummingbirds are no exception to this trend. For example, although Cuba is over twice as large as Costa Rica (114.5×10^3 km^2 *vs.* 50.0×10^3 km^2), it currently contains only three species of nectar-bats and two species of hummingbirds compared with 12 species of nectar-bats and 51 species of hummingbirds in Costa Rica (Rodriguez-Duran and Kunz 2001; Stiles 1983; Wilson 1983). Most islands in the West Indies contain only 1-2 species of nectar-bats and 2-3 species of hummingbirds (Lack 1973; Rodriguez-Duran and Kunz 2001). Reasons for this low diversity likely include low flower diversity on these islands, and, in the case of hummingbirds, the effects of interspecific competition and plant-pollinator coevolution.

If the species richness of island communities of nectarivores follows the same "rule" that appears to control species richness of mainland communities (*i.e.*, nectarivore diversity is controlled by flower diversity), then we expect island communities of nectar-bat and hummingbird flowers to be depauperate. Based on the regression shown in Fig. 7, for example, we would expect to find islands supporting three species of nectar-bats and three species of hummingbirds to contain 2-15 species of bat- or bird-adapted flowers (based on the 90% confidence limits around the regression). Data from Cuba and Puerto Rico support this prediction. Cuba has three species of nectar-bats, and Silva Taboada (1979) reported that these species visit the flowers of 6-10 bat-adapted plants (plus additional exotic species or non-bat-adapted flowers such as palms). Similarly, Kodric-Brown *et al.* (1984) reported that three species of hummingbirds in southwestern Puerto Rico visited a total of 13 species of hummingbird-adapted flowers. While additional data from Caribbean islands would be valuable, we tentatively conclude from these observations that the mainland "rule" also holds for West Indian islands.

Lack (1973) and Kodric-Brown *et al.* (1984) have pointed out that membership in local communities of hummingbirds in the West Indies is influenced strongly by interspecific competition for nectar resources. This competition, which often involves interspecific aggression, prevents similar-sized species from living in sympatry. Relatively large-billed species can coexist with small-billed species because they visit different sets of flowers. On Puerto Rico, for example, small species (bill length ≤ 14 mm) visit short-tubed flowers (corolla length < 22 mm) whereas large species (bill length > 22 mm) visit long-tubed flowers (corolla length > 29 mm). Kodric-Brown *et al.* (1984) suggest that the non-random distribution of bill and corolla lengths on Puerto Rico reflects coevolution between hummingbirds and their food plants.

The extent to which interspecific competition for food and coevolution between nectar-bats and their food plants has occurred in the West Indies is currently unknown. Flower-visiting glossophagines are generally much less aggressive around food sources than hummingbirds, and territorial behavior has rarely been reported in these bats (*e.g.*, Lemke, 1984). Thus, it is unlikely that interspecific aggression has played a major role in structuring either mainland or island communities of nectar-bats. No one, to our knowledge, has carefully studied flower choice and foraging behavior of West Indian nectar-bats, so the degree to which these species have coevolved with

their food plants is poorly known. The fact that West Indian glossophagines and phyllonycterines have shorter jaws than many mainland species of comparable size (Fig. 9) suggests to us that these bats are unlikely to be closely matched morphologically with specific species of flowers. Instead, it is likely that the skull morphology of these bats reflects generalized, rather than specialized, food habits. In Cuba, for example, *Monophyllus redmani*, *Erophylla sezekorni*, and *Phyllonycteris poeyi* are known to eat fruit and insects in addition to visiting flowers (Silva Taboada 1979). In general, frugivorous phyllostomids have much shorter jaws than nectarivorous phyllostomids (Freeman 1988, 1995), and it is likely that the relatively short jaws of West Indian species reflect a compromise between strong nectarivory and strong frugivory. No such compromise is likely to occur in hummingbirds.

Conclusions

Although hummingbirds and nectar-bats are often considered to be each other's temporal analogues, these two groups of flower-visiting vertebrates differ in many interesting ways. Differences in size, physiology, and morphological plasticity have profoundly influenced their community ecology. Hummingbirds are energetically cheaper pollinators and have a much more malleable trophic apparatus (bill) than nectar-bats. In addition, hummingbirds have both color and UV vision (Stiles 1978) and thus are perhaps more easily manipulated visually by plants and their flowers than bats. Consequently, a wider array of plants in a wider array of habitats have evolved hummingbird flowers, which, in turn, has favored an impressive adaptive radiation of these dynamic birds. The adaptive radiation of nectar-bats, in contrast, has been much more constrained. Although regional and local diversity of hummingbirds is much greater than that of nectar-bats, the same "rule" seems to determine local diversity in both groups: local diversity of nectarivores is controlled by the local diversity of their food plants. This rule appears to operate both on the neotropical mainland and in the West Indies. Because of their morphological plasticity, hummingbirds have evolved much more specialized feeding relationships, on average, with their food plants than have nectar-bats. Overall, ecological differences between nectar-bats and hummingbirds appear to outnumber their similarities. This is not surprising, given their very different evolutionary backgrounds. Nonetheless, both groups are likely to play important roles as pollinators and dispersers of plant genes for hundreds of species of plants in tropical, subtropical, and temperate habitats (Stiles 1981; Helversen 1993). Both groups thus are strong interactors with their food plants and deserve strong conservation protection. Don Bernardo's *Leptonycteris "yerbabuenae"* and its kin, including its diurnal allies, the hummingbirds, must not be allowed to go extinct.

Acknowledgments

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Appendix 1

Summary of the nectar-bat data from 29 mainland New World sites. Negative latitudes are south of the equator. CV = Coefficient of Variation.

Site	Country	Habitat*	Latitude	Elevation (m)	Annual rainfall (mm)	Number of bat species	Mean forearm length (mm)	CV of forearm length	Mean jaw length (mm)	CV of jaw length
Bahia de Kino, SON	Mexico	D	28.8	5	200	1	51.8		9.4	
Chamela, JAL	Mexico	LDF	19.5	250	748	5	40.1	0.19	8.8	0.26
Los Tuxtlas, VER	Mexico	LWF	18.5	350	4900	3	34.5	0.05	7.3	0.01
Tehuacan Valley, PUEB	Mexico	D	18.2	1300	380	3	51.1	0.11	10.1	0.11
Lacandona, CHIA	Mexico	LMF	16.5	300	2500	3	34.5	0.05	7.2	0.04
Santa Rosa	Costa Rica	LDF	10.8	300	1600	2	40.9	0.15	9.4	0.31
Santa Rosa	Costa Rica	LDF	10.7	0	1617	2	35.2	0.05	7.3	0.00
La Selva	Costa Rica	LWF	10.5	85	3994	6	35.6	0.13	7.4	0.17
La Pacifica	Costa Rica	LDF	10.3	100	1562	4	34.3	0.04	7.2	0.03
Palo Verde	Costa Rica	LDF	10.3	45	1562	1	36.5		7.3	
Monteverde	Costa Rica	MMF	10.2	1500	2500	5	36.0	0.11	7.7	0.13
Sherman	Panama	LWF	9.2	5	3000	1	36.5		7.3	
BCI	Panama	LMF	9.1	100	2600	3	38.2	0.14	8.0	0.20
Rodman	Panama	LDF	8.6	50	1750	1	36.5		7.3	
Imataca	Venezuela	LDF	7.5	200	1631	3	34.1	0.07	7.1	0.05
Paracou	French Guiana	LWF	5.2	20	3200	5	34.7	0.07	7.4	0.16
Puerto Triunfo	Colombia	LWF	5.1	250	3000	3	39.3	0.11	8.6	0.15
Sainte-Eugene	French Guiana	LWF	4.5	50	3000	3	34.7	0.08	7.8	0.14
Iwokrama	Guyana	LMF	4.5	70	2250	4	36.7	0.12	8.0	0.15
San Fransisco	Ecuador	MMF	3.6	1900	2156	2	40.0	0.10	9.2	0.05
BDFFP	Brazil	LMF	2.2	80	2101	3	34.7	0.07	7.4	0.11
Guajalito	Ecuador	MMF	-0.1	2000	2500	2	40.0	0.10	9.2	0.05
Otonga	Ecuador	MMF	-0.3	2200	2500	2	40.0	0.10	9.2	0.05
Manaus	Brazil	LMF	-3.1	48	2101	5	34.7	0.07	7.4	0.16
Jenaro Hererra	Peru	LMF	-4.6	130	2521	5	35.1	0.06	7.7	0.10
Pakitza	Peru	LMF	-11.6	356	2080	5	35.1	0.06	7.6	0.12
Panga	Brazil	LDF	-19.1	800	1847	3	38.8	0.09	8.5	0.13
Campos do Jordao	Brazil	MMF	-22.4	1530	1401	1	37.2		8.8	
Caraguatatuba	Brazil	LMF	-23.4	45	2526	3	38.8	0.09	8.5	0.13

[a]Habitat designations as in Table 1.

Sources of data: Ascorra *et al.* (1993, 1996), Bernard (2001), Cosson *et al.* (1999), Espinosa (2000), Findley (1993), Fleming (1988), Fleming *et al.* (1972, 1996), Jarrín-V. (2000), Kalko *et al.* (1996), Medellín (1994), Munoz (1987), Ochoa (2000), Pedro and Taddei (1997), Reis and Peracchi (1987), Sazima *et al.* (1999), Simmons and Voss (1998), Smith and Kerry (1996), and Valiente-Banuet *et al.* (1997).

Appendix 2

Summary of the hummingbird data from 32 mainland New World sites (including Trinidad). Negative latitudes are south of the equator. CV = Coefficient of Variation.

Site	Country	Habitat*	Latitude	Elevation (m)	Rainfall (mm)	No. species	Mean wing length (mm)	CV of wing length	Mean bill length (mm)	CV of bill length
White Mountains, AZ	USA	MDF	33.8	2400	524.6	4	44.1	0.09	17.3	0.10
Pinacate, SON	México	D	32.0	1000	100	3	46.1	0.07	18.8	0.05
Madera Canyon, AZ	USA	MDF	31.5	1600	480	11	52.2	0.20	20.0	0.20
Bahia de Kino, SON	México	D	28.5	0	200	3	42.2	0.06	17.2	0.03
Álamos, SON	México	LDF	27.0	410	643.5	10	57.4	0.17	23.0	0.25
Sierra Fria, AGS	México	MDF	22.2	2500	675.6	6	54.3	0.18	20.1	0.18
Palapita, NAY	México	LDF	21.2	580	600	6	57.4	0.09	24.5	0.38
Las Joyas, JAL	México	MMF	19.4	1990	1600	21	51.9	0.22	20.6	0.31
Chamela, JAL	México	LDF	19.4	300	748	9	51.6	0.22	21.0	0.43
Nepantla, MEX	México	MMF	18.6	1996	1000	10	57.1	0.19	21.2	0.17
Los Tuxtlas, VER	México	LWF	18.3	500	4900	13	58.9	0.21	24.2	0.33
Tehuacán, PUE	México	D	17.5	1300	400	7	49.7	0.23	21.4	0.16
Omiltemi, GRO	México	MMF	17.3	2200	1246.5	15	57.6	0.23	20.3	0.26
Sn. Gabriel Mixtepec, OAX	México	LMF	16.1	700	1880	11	54.2	0.18	21.9	0.42
La Sepultura, CHIS	México	MMF	16.0	1600	1530	17	57.1	0.21	21.6	0.34
El Triunfo, CHIS	México	MMF	15.4	2200	2000	28	56.6	0.21	20.5	0.32
La Encrucijada, CHIS	México	LMF	15.0	1000	2500	9	59.0	0.21	24.4	0.33
La Montura	Costa Rica	LWF	10.7	1000	3000	22	57.9	0.20	21.7	0.36
Palo Verde	Costa Rica	LDF	10.6	100	1770	10	54.2	0.20	21.7	0.29
Arima Valley	Trinidad	LMF	10.4	200	2450	8	57.4	0.17	25.1	0.37
La Selva	Costa Rica	LWF	10.3	90	3940	22	57.1	0.19	23.3	0.38
Monteverde	Costa Rica	MMF	10.1	1380	2429	21	57.1	0.22	22.9	0.35
Cerro de la Muerte	Costa Rica	H	9.3	3100	2530	4	60.4	0.21	21.2	0.30
Las Cruces	Costa Rica	LWF	8.8	1000	3988	22	57.8	0.20	22.1	0.33
Matamata	Colombia	LWF	-3.5	100	3377	16	56.7	0.18	24.2	0.32
Cerro Fonté	Colombia	MMF	-4.0	2450	2000	11	61.5	0.20	28.1	1.09
Cerro Carare	Colombia	MMF	-5.0	2400	2000	12	61.0	0.20	21.0	0.37
Togui	Colombia	MMF	-5.0	1700	2000	8	54.2	0.16	21.6	0.45
Campos de Jordao	Brazil	LMF	-22.4	1500	1400	6	54.7	0.21	20.8	0.36
Cunha	Brazil	LMF	-23.1	1000	2120	8	47.4	0.20	19.6	0.35
Caraguatatuba	Brazil	LMF	-23.3	100	2526	11	48.5	0.22	23.2	0.33
Achala	Argentina	MDF	-31.4	2000	850	3	50.4	0.20	21.3	0.38

ªHabitat designations as in Table 1.

Sources of data: Arizmendi and Ornelas (1990), Brown and Kodric-Brown (1979), Buzato *et al.* (2000), Coates-Estrada and Estrada (1985), Cotton (1998a), Escalante (1988), Gomez de Silva *et al.* (1999), González-Domínguez (1998), González-García (1993), Miatello *et al.* (1999), Navarro (1992), Ornelas and Arizmendi (1995), Russell (2000), Sazima *et al.* (1996), Snow and Snow (1972, 1980), Stiles (1983, 1985a), Toledo (1975), and Wolf *et al.* (1976).