Published by Associazione Teriologica Italiana
Volume 29 (1): 33–39, 2018
OPEN ACCESS
Hystrix, the Italian Journal of Mammalogy
SPECIAL SECTION: BAT DIVERSITY AND ECOLOGY IN OPEN AREAS
Edited by Maria João Ramos Pereira, Damiano G. Preatoni, Lucas A. Wauters and Danilo Russo
Available online at:
`http://www.italian-journal-of-mammalogy.it`
doi:10.4404/hystrix-00036-2017

Research Article

Nectar Bat-Plant Interactions in North American Deserts

Theodore H. FLEMING[1,2,*], J. Nathaniel HOLLAND[3]

[1] *University of Miami, Coral Gables FL 33124, USA*
[2] *Current address: 6211 N Camino de Corozal, Tucson AZ 85704, USA*
[3] *Dept. of Biology and Biochemistry, University of Houston Science & Research 2, Rm 369, 4800 Calhoun Rd., Houston, Texas 77204, USA*

Keywords:
agavaceae
cactaceae
mutualism
nectarivore
stable isotopes

Article history:
Received: 14 March 2017
Accepted: 17 August 2017

Acknowledgements
Our research on desert bat-plant interactions was funded by Bat Conservation International, the National Geographic Society, and the U.S. National Science Foundation. We thank A. Tejedor for conducting the stable isotope analyses in the lab of L. Sternberg (University of Miami); the editors of this special issue for inviting us to write this review; J. Nassar and T. Hernández-Hernández for discussion; and an anonymous reviewer for useful comments and suggestions.

Abstract

The deserts and arid regions of North, Central, and South America are unique in the world because of the frequent dependence of their often-dominant plants (Cactaceae, Agavaceae) on nectar-feeding bats (Phyllostomidae: Glossophaginae and Lonchophyllinae) for pollination. In no other deserts have such specialized nectar bat-flowering plant mutualisms evolved. Three lineages of morphologically specialized phyllostomid nectar bats (*Leptonycteris*, *Choeronycteris*, and *Platalina*) are involved in this mutualism: the former two genera occur in Mexico, southwestern United States, and, in the case of *Leptonycteris*, northern South America whereas the latter genus occurs in the central Andes of South America. In this paper we describe the importance of *Leptonycteris* and *Choeronycteris* as pollinators of columnar cacti and paniculate agaves in North American deserts, discuss the evolutionary history of these interactions, and briefly compare these interactions with those in other Neotropical arid regions. We point out that because of their wide-ranging foraging and migratory behavior *Leptonycteris* bats are critical for maintaining genetic connectivity among populations of their food plants. Recent phylogenetic studies indicate that nectar bats have also been an important factor behind the high diversification rates of columnar cacti and paniculate agaves in the past 10 million years. Because of the unique ecological and evolutionary importance of these bats, their conservation should be a high priority.

Introduction

Plant communities in many arid Neotropical regions are dominated by two charismatic groups of plants: columnar cacti (Cactaceae) and paniculate agaves (Agavaceae; now considered to be a subfamily of Asparagaceae)(e.g., Anderson, 2001; Gentry, 1982; Yetman, 2007). In addition to their striking morphology, these plants are notable because of their use of nectar-feeding bats, in some cases nearly exclusively, for pollination of their flowers (Valiente-Banuet et al., 1996). In the Cactaceae, for example, about 22% genera contain bat-pollinated species compared with about 15% of genera in 67 other angiosperm families with bat pollination (Fleming et al., 2009). Valiente-Banuet et al. (1996) estimated that about 60% of the 70 species of columnar cacti in the tribe Pachycereeae in Mexico are likely to be bat-pollinated. This mutualistic relationship is unique in the world. In no other arid regions are conspicuous groups of plants highly dependent on bats as their major pollinators (Fleming and Kress, 2013). In this paper, we will review this nectar bat-plant mutualism in North American deserts, first by putting this interaction into a community and trophic context before describing this interaction in detail and reviewing its phylogenetic history. Finally, we briefly compare the North American situation with arid regions in northern and northwestern South America. Our overall goal here is to describe the unique coevolutionary consequences of the interactions between nectar-feeding bats and two groups of their food plants in New World deserts and other arid habitats.

The structure of a Sonoran Desert bat community

Before describing the ecological and evolutionary consequences of this mutualism in detail, we will place it into a trophic context by comparing the diets of insectivorous and nectarivorous bats at one of our study sites in the Sonoran Desert by means of stable isotope analysis. The Sonoran Desert of northwestern Mexico and southern Arizona is the biologically richest desert in the world. It contains approximately 3500 species of plants and 187, 500, and 130 species of reptiles, birds, and mammals, respectively (Phillips and Comus, 2000). Dominant plants in terms of biomass in this desert include several genera of trees in Fabaceae (e.g., *Cercidium*, *Olneya*, *Prosopis*) as well as several species of columnar cacti (e.g., *Carnegiea gigantea*, *Pachycereus pringlei*, and *Stenocereus thurberi*). About 20 species of *Agave* also occur in this desert and are especially common in Baja California (Turner et al., 1995). How dependent are nectar bats in this habitat on columnar cacti and agaves for food?

Bat communities or assemblages in the Sonoran Desert contain at least 14 species in three families (Tab. 1). Most of these species are insectivorous but three are known to visit and pollinate flowers of columnar cacti and paniculate agaves. *Leptonycteris yerbabuenae* and *Choeronycteris mexicana* (Phyllostomidae: Glossophaginae) are strongly adapted morphologically for visiting the large flowers of columnar cacti. They have moderately (*Leptonycteris*) or greatly (*Choeronycteris*) elongated snouts and long, brush-tipped tongues (Fig. 1A, B). In contrast, *Antrozous pallidus* (Vespertilionidae) lacks these features, reflecting its strongly insectivorous ancestry (Fig. 1C), but is still an effective pollinator of cactus flowers (Frick et al., 2013).

We used stable isotope analysis of feces collected from 11 species of bats captured at Organ Pipe Cactus National Monument (ORPI) in southwestern Arizona to document the trophic structure of this

---

[*] Corresponding author
Email address: `tedfleming@dakotacom.net` (Theodore H. FLEMING)

Hystrix, the Italian Journal of Mammalogy ISSN 1825-5272

`doi:10.4404/hystrix-00036-2017`
7th March 2018

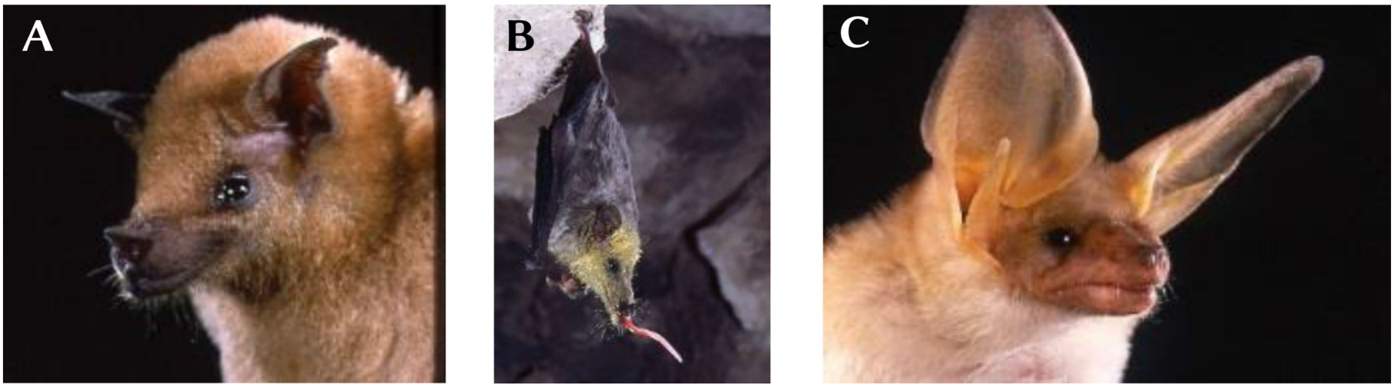

Figure 1 – Three Sonoran Desert bats that visit cactus flowers: (A) *Leptonycteris yerbabuenae*; (B) *Choeronycteris mexicana*; and (C) *Antrozous pallidus*. Photo credit: M. Tuttle, Bat Conservation International.

assemblage of Sonoran Desert bats (see Appendix for methods). Carbon stable isotopes, expressed in δ^{13}C notation, allow us to distinguish between two plant-based carbon pools in this desert: low values of this ratio (ca. <-20) come from C3 plants (the most common plants in most habitats, e.g. Fabaceae) and high values (ca. >-15) come from CAM plants (uncommon in most non-arid habitats, e.g. Agavaceae, Cactaceae). Two columnar cacti, *C. gigantea* and *S. thurberi*, are common at ORPI. Delta nitrogen values (δ^{15}N) increase with increasing trophic position; carnivores or insectivores have higher δ^{15}N values than herbivores. The nectar bat *L. yerbabuenae* is clearly an outlier in this assemblage because of its strong dependence on CAM plants (i.e., cacti and agaves) for carbon that it acquires from nectar and pollen (Fig. 2). *A. pallidus*, the other cactus– and agave–flower visitor for which we have data, differs from most other vespertilionids in its relatively high value of δ^{13}C. At other Sonoran Desert sites it is even more strongly CAM in its carbon composition than at ORPI (Herrera et al., 1993; Frick et al., 2014). In Baja California Sur, for example, its δ^{13}C values in January (about -19.0) are similar to those of sympatric insectivorous bats, but in May when columnar cacti are flowering they are intermediate (about -15.5) between those of other insectivores (about -20.0) and two nectar bats (*C. mexicana*, -11.6; *L. yerbabuenae*, -12.1) (Frick et al., 2014). Results of these stable isotope studies clearly emphasize the strong trophic dependence of Sonoran Desert nectar-feeding bats on CAM plants. This trophic specialization, in turn, suggests that these bats and their food plants are likely to be coevolutionary partners. Pollinator exclusion experiments described below provide us with insight into how symmetrical this relationship is. Nectar bats are clearly strongly dependent on columnar cacti and paniculate agaves for food. But how dependent are these plants on these bats as pollinators?

Whereas they are common members of Sonoran Desert plant communities, columnar cacti are absent from the Chihuahuan Desert of north-central Mexico and adjacent southwestern United States, but paniculate agaves are common there (Gentry, 1982). Another species of *Leptonycteris*, *L. nivalis*, is the major nectar-feeding bat in this desert, and its diet is strongly dependent on flowering agaves (Moreno-Valdez et al., 2004; Sanchez and Medellin, 2007). In arid regions of south-central Mexico, *L. yerbabuenae* is the major pollinator of columnar cacti and agaves in the Tehuacan Valley and surrounding areas in the states of Puebla and Oaxaca. *C. mexicana* and a few additional species of phyllostomid bats (e.g., *Glossophaga soricina* and *Artibeus jamaicensis*) also visit cactus flowers in this region, which is characterized by an exceptionally high abundance and diversity of columnar cacti (Valiente-Banuet et al., 1996; Yetman, 2007).

Morphologically specialized phyllostomid nectar bats are also major pollinators of columnar cacti and agaves in arid regions of northern South America. In northern Venezuela, the Netherland Antilles, and arid enclaves in Colombia, *Leptonycteris curasoae*, the sister species to *L. yerbabuenae*, is the most important pollinator of cacti in the genera *Pilosocereus*, *Stenocereus*, and *Subpilocereus* (Nassar et al., 1997; Petit, 1998). *Glossophaga longirostris* also pollinates these cacti. On the western slope of the central Andes another morphologically specialized species, *Platalina genovensium* (Phyllostomidae: Lonchophyllinae), pollinates columnar cacti, including species of *Haageocereus* and *Weberbauerocereus* (Maguiña and Amanzo, 2016; Sahley, 1996).

Glossophagine bats as pollinators of North American columnar cacti and agaves

Bat-cactus interactions have been studied in detail using experimental methods in the Sonoran Desert and Tehuacan Valley. Results of

Table 1 – Sonoran Desert bats captured in spring 1997 at Organ Pipe Cactus National Monument, Arizona. Forearm length is a general measure of size in bats. Abbreviations in parentheses are used in Fig. 2.

Family	Species	Forearm length (mm)	Number of captures	General diet
Phyllostomidae	*Macrotus californicus* (Mac)	51	8	Insects, often gleaned from vegetation
	*Choeronycteris mexicana**	45	-	Nectar, pollen, fruit
	Leptonycteris yerbabuenae (LY)	53	29	Nectar, pollen, fruit
Vespertilionidae	*Antrozous pallidus* (AP)	54	6	Insects, often gleaned from the ground; nectar
	Corynorhinus townsendii (CT)	44	8	Insects
	Eptesicus fuscus (EF)	46	19	Insects
	*Lasiurus cinereus**	52	-	Insects
	Myotis californicus (MyC)	33	9	Insects
	M. velifer (MyV)	42	60	Insects
	Pipistrellus hesperus (PH)	30	26	Insects
Molossidae	*Eumops perotis**	77	-	Insects
	E. underwoodi (EU)	71	2	Insects
	Nyctinomops femorosaccus (NF)	47	2	Insects
	Tadarida brasiliensis (TB)	41	27	Insects

* Not captured but known to occur at this site (T. Tibbetts, *pers. comm.*)

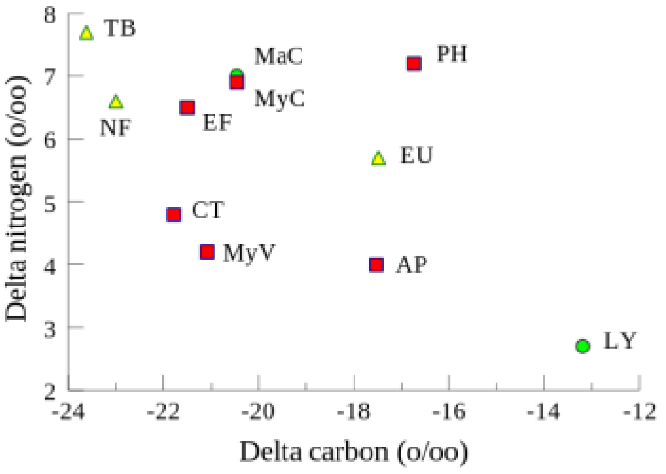

Figure 2 – Ordination of 11 species of Sonoran Desert bats by their mean stable isotope values. Delta carbon (in ‰) indicates the importance of CAM plant (mean δ^{13}C=-12.6‰) or C3 plant (mean δ^{13}=-26.4‰) carbon in the diets of these bats. Plant values come from Fleming et al. (1993). Delta nitrogen (in ‰) indicates the approximate trophic position (from herbivores to carnivores) of these bats. Species abbreviations are shown in Tab. 1. Symbols: solid circle = Phyllostomidae; solid triangle = Molossidae; solid square = Vespertilionidae.

pollinator exclusion experiments in the Tehuacan Valley indicate that bats, primarily *L. yerbabuenae*, are the nearly exclusive pollinators of several species of columnar cacti (e.g., *Neobuxbaumia macrocephala*, *N. mezcalaensis*, *N. tetetzo*, *Pachycereus weberi*, and *Pilosocereus chrysacanthus*) (Valiente-Banuet et al., 1996, 1997a,b). In contrast, similar experiments in the Sonoran Desert indicate that this bat is a minor pollinator of three columnar cacti (*C. gigantea*, *Pachycereus pecten-aboriginum*, and *Stenocereus thurberi*) but is the major pollinator of *P. pringlei* (Fleming et al., 1996, 2001; Molina-Freaner et al., 2004). Birds are the major pollinators of the first three species, particularly for *C. gigantea* whose flowers open later in the evening and close later the next day than the other three species.

Radio-tracking studies and genetic analyses indicate that *Leptonycteris* bats are wide-ranging foragers that likely move plant genes via pollination frequently among cactus populations. In the Bahia de Kino area of Sonora, Mexico, for example, many females of *L. yerbabuenae* roost in one or more maternity colonies on Isla Tiburon in the Sea of Cortez (Gulf of California) and commute nightly 25–30 km to the Mexican mainland to feed. Their foraging areas on the mainland are large (up to 250 ha), and they sometimes fly 5–10 km between patches of columnar cacti to feed (Horner et al., 1998). Similar long-distance commuting flights by this bat have also been reported in other parts of the Sonoran Desert and southeastern Arizona (Buecher and Sidener, 2012; Ober and Steidl, 2004). This bat clearly has the potential to be a long-distance (i.e.,10s of kilometeres) pollinator of its cactus food plants.

Species of *Leptonycteris* are unusual among glossophagine bats for at least two reasons: (1) they are highly gregarious and often roost in colonies containing tens of thousands of individuals and (2) they are long-distance fliers on both a nightly and a seasonal basis. In addition to their long nightly foraging flights, some of these bats undergo substantial seasonal migrations. Many females of *L. yerbabuenae*, for example, mate in November and December in Jalisco, Mexico, and fly up to 1000 km north in the spring to form large maternity colonies in the Sonoran Desert as far north as southwestern Arizona (Fleming, 2004). Large body size, high aspect ratio wings, and efficient flight physiology are adaptations in these bats that permit cheap long-distance flight (Sahley et al., 1993).

Results of genetic analyses based on starch gel electrophoresis indicate that populations of vertebrate-pollinated Sonoran Desert columnar cacti exhibit low levels of genetic subdivision as measured by Wright's F_{ST} or G_{ST} values. These values, which range from 0 (in totally panmictic populations) to 1 (in totally subdivided populations), measure the degree to which observed levels of genetic subdivision (or differentiation) differ from values expected in randomly mating populations. Values of G_{ST} range from 0.075 to 0.128 in three species of Sonoran Desert columnar cacti (*C. gigantea*, *P. pringlei*, and *S. thurberi*) (Hamrick et al., 2002). In contrast, the moth-pollinated *Lophocereus schottii* there was 0.242. Similarly, low values of G_{ST} of 0.043–0.126 occur in three species of bat-pollinated Venezuelan columnar cacti (Nassar et al., 2003a). In contrast, values of G_{ST} in two non-columnar cacti — bee-pollinated *Pereskia guamacho* and hummingbird-pollinated *Melocactus curvispinus* — were 0.112 and 0.189, respectively (Hamrick et al., 2002). While more comparative data are needed, it is likely that long-distance pollinators such as species of *Leptonycteris* bats play an important role in maintaining the genetic integrity of populations of their food plants.

As mentioned above, many females of *L. yerbabuenae* migrate north and form maternity colonies in the Sonoran Desert in the spring. At this time of the year, up to four species of columnar cacti are flowering, and the flowering seasons of three of them (*C. gigantea*, *P. pringlei*, and *S. thurberi*) overlap broadly in April and May — a situation that could potentially result in significant interspecific competition for pollinators (Fleming et al., 1996). At the very least, it is likely that (randomly) foraging bats — the first pollinators to visit these night-blooming cacti — regularly deposit heterospecific pollen on the stigmas of cactus flowers. If flowers of these self-incompatible cacti receive only heterospecific pollen (i.e., the “wrong” pollen), they are likely to abort, an example of the negative consequences of interspecific competition for pollinators. But, more likely, cactus flowers often receive a mixture of conspecific (the “right” pollen) and heterospecific pollen delivered by (randomly) foraging bats, which might not have negative consequences depending on the amount of conspecific pollen delivered relative to heterospecific pollen.

To examine the possible consequences of receiving the wrong pollen, Fleming (2006) conducted a series of controlled hand pollinations to mimic the behavior of randomly foraging *Leptonycteris* bats. These experiments involved placing either conspecific or heterospecific pollen on the stigmas of flowers of two cacti with overlapping flowering seasons, *P. pringlei* and *S. thurberi*. Results for *P. pringlei* were straightforward: flowers receiving conspecific pollen set fruit whereas those receiving heterospecific pollen aborted. Results for *S. thurberi* were surprising: flowers receiving both kinds of pollen set fruit. Flowers receiving only *P. pringlei* pollen produced mature fruit containing mature-looking seeds, but closer examination revealed that these seeds lack embryos and are sterile. A survey of open-pollinated flowers of *S. thurberi* indicated that in the period early April to mid-May, many fruit were the products of heterospecific pollination (Fleming, 2006). The production of sterile fruit is another negative consequence of interspecific competition for pollinators, so it should be strongly selected against. But, as discussed by Fleming (2006), there may be reasons why *S. thurberi* “tolerates” the receipt of the wrong pollen in some situations. One of these reasons may reflect selection for early flowering (which results in broad interspecific flowering overlap) caused by long-distance pollinator-mediated gene flow from populations of S. *thurberi* that do not co-occur with populations of *P. pringlei*. Whatever the explanation, pollination by *Leptonycteris* bats has had interesting consequences for this Sonoran Desert cactus. Whether or not other species of *Stenocereus* can set fruit with heterospecific pollen is not yet known.

The pollination biology of only two species of Sonoran Desert Agaves, *A. angustifolia* and *A. subsimplex*, have been studied in detail. The former species is widely distributed in the coastal lowlands and mountains of Mexico and Central America; the latter species occurs in a few scattered populations in the lowlands of Sonora (Gentry, 1982). Both species are self-incompatible and flower in late winter and spring. A variety of pollinators, including *Leptonycteris* bats, several species of birds, and hawkmoths and honeybees, visit flowers of both species. Pollinator exclusion experiments indicate that *A. angustifolia* relies almost exclusively on bats for effective pollination whereas *A. subsimplex* relies on both nocturnal and diurnal pollinators for its fruit set (Molina-Freaner and Eguiarte, 2003). *Agave palmeri*, which occurs in upland grasslands and pine-oak forests of southeastern Arizona, is an important food plant for *L. yerbabuenae* and *C. mexicana* in the late summer (Ober and Steidl, 2004). The results of pollinator exclusion experiments, however, indicate that, as in the case of certain night-blooming Sonoran Desert columnar cacti, nectar-feeding bats are minor pollinators of this species (Slauson, 2000). In central Mexico, however, Rocha et al. (2005) reported that bats, including *L. yerbabuenae*, *C. mexicana*, and *G. soricina*, were the most common visitors to flowers of four of five species of *Agave* subgenus *Littea*, This is similar to the situation in columnar cacti in which bats are more important pollinators of tropical species than most Sonoran Desert species.

Historical roots of this interaction – phylogeny of the bats and plants

Arid habitats in North and South America, including its deserts, savannas, shrublands, and grasslands, are the products of major climatic and geological changes that occurred during the Miocene and more recent geological epochs. Andean uplift, volcanism, and decreases in global air temperature, precipitation, and CO_2 levels were major drivers behind the evolution of Neotropical arid ecosystems and their succulent flora (reviewed in Arakaki et al., 2011 and Hernández-Hernández et al., 2014). Cactaceae is the older of the two plant families considered in this paper. It evolved in Late Eocene-Early Oligocene (about 35 Ma [millions of years ago]) in the Andes of Chile, Argentina, and Bolivia, but its major radiations occurred in the Late Miocene, 10–5 Ma. These radiations occurred in three major areas: in the central Andes (the "TCB" tribes Trichocereeae, Cereeae, and Browningieae of subfamily Cactoideae), in eastern Brazil (tribe Cereeae), and in North America (the "PHB" tribes Pachycereeae, Hylocereeae, and Browningieae) (Wallace, 2002). Columnar members of these tribes are young, evolving 8–6 Ma (Arakaki et al., 2011). Agaves are North American in origin. These plants first evolved 26–22 Ma; the genus *Agave* is about 10 million years old; and agaves underwent two pulses of diversification, 8–6 Ma and 3.5–2 Ma (Good-Avila et al., 2006; Rocha et al., 2006).

The New World bat family Phyllostomidae likely first evolved in North America (judging from the geographic distribution of its oldest living members, the genus *Macrotus*, which occurs in the Greater Antilles, southwestern United States, Mexico, and Guatemala) in the Middle Eocene, about 42 Ma. Basal members of this family date from Late Eocene/Early Oligocene (35–32 Ma), and many extant lineages emerged in the Oligocene and Miocene (29–20 Ma) (Datzmann et al., 2010; Dumont et al., 2012; Rojas et al., 2016). Two clades of nectar-feeding phyllostomids are currently recognized: Glossophaginae and Lonchophyllinae. The Glossophaginae, which occurs in the Greater Antilles (e.g., *Monophyllus*) as well as throughout the mainland Neotropics, dates from about 22 Ma; the *Leptonycteris-Glossophaga* clade dates from about 14 Ma; and the *Hylonycteris-Choeronycteris-Musonycteris* clade dates from about 11 Ma (Rojas et al., 2016). The subfamily Lonchophyllinae is mostly South American in distribution and contains the morphologically specialized Andean cactus visitor *Platalina genovensium*; it dates from about 13 Ma. The current species richness of these bats is shown in Tab. 2.

Table 2 – Summary of the species richness of phyllostomid bats that are known to pollinate flowers of columnar cacti and agaves in arid regions of the New World tropics and subtropics. Data come from Simmons (2005).

Subfamily	Genus	Number of species	Geographic distribution
Glossophaginae	*Anoura*	5	southern Mexico to northern Argentina
	Choeronycteris	1	southwestern United States to Honduras
	Glossophaga	5	northern Mexico to northern Argentina
	Monophyllus	2	West Indies
	Leptonycteris	3	southwestern United States to Guatemala; northern Venezuela, Colombia, and Netherland Antilles
Lonchophyllinae	*Platalina*	1	west coastal and montane Peru

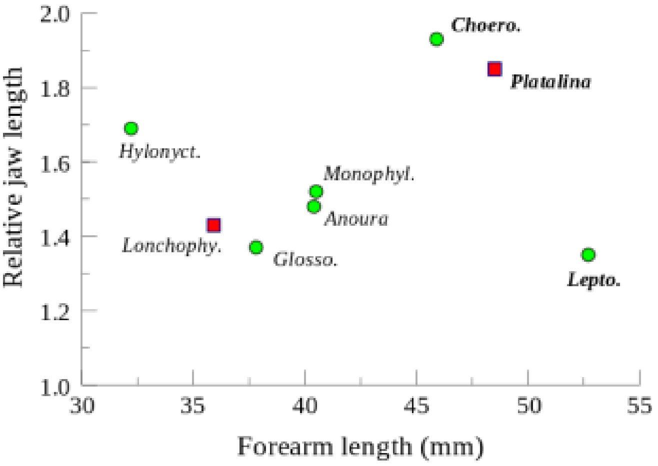

Figure 3 – Ordination of several genera of nectar-feeding phyllostomid bats by size (forearm length) and relative jaw length (maxillary tooth row/molar breadth); modified from Fleming and Nassar (2002). Genera that are frequent visitors to cactus flowers are indicated in bold. Abbreviations: Choero. = *Choeronycteris*; Glosso. = *Glossophaga*; Hylonyct. = *Hylonycteris*; Lepto. = *Leptonycteris*; Lonchophy. = *Lonchophylla*; Monophyl. = *Monophyllus*. Symbols: circles = Glossophaginae; squares = Lonchophyllinae.

Cactus-visiting phyllostomids of the two nectar bat subfamilies are substantially larger and generally have longer snouts than their forest-dwelling relatives (Fig. 3). The glossophagine *Leptonycteris* is much larger but has a similar (relative) snout length to that of its close relative *Glossophaga*; *Choeronycteris* is much larger and longer-snouted than its relative *Hylonycteris*; and the lonchophylline *Platalina* is also much larger and longer-snouted than its relative *Lonchophylla*. Interestingly, not all cactus-visiting nectar bats are large and long-snouted. Taxa that are not true desert-dwellers (e.g., *Glossophaga*, *Monophyllus*, and *Anoura*) sometimes visit cactus flowers but are generally small (Arizmendi et al., 2002; Rivera-Marchand and Ackerman, 2006) (Fig. 3). Large size and long snouts have been selectively favored in very arid habitats for two reasons: (1) generally low plant densities and substantial seasonal changes in the locations of rich food patches (e.g., in the Sonoran Desert) favor large size to reduce nightly and annual (migratory) flight costs (Sahley et al., 1993); and (2) arid zone cactus flowers are generally larger than bat-pollinated flowers in moister habitats, which favors longer snouts and tongues (Fleming et al., 2005).

The ages of the bat-pollinated plant lineages and nectar bats that we discuss here are summarized in Fig. 4. Both plant families predate the evolution of nectar-feeding bats, and insect pollination is ancestral in both families (e.g., Good-Avila et al., 2006; Hernández-Hernández et al., 2014). But the major radiations in these plant families occurred after the evolution of flower-visiting bats, and Good-Avila et al. (2006) and Hernández-Hernández et al. (2014) have postulated that a switch to bat (and bird) pollination has been a major driver in the diversification of Agaves and columnar cacti, respectively. In Cactaceae, a columnar growth habit and pollination by vertebrates and hawkmoths are coevolved traits that likely first evolved in tropical dry forests where selection favored tall growth forms (Cody, 2002; Hernández-Hernández et al., 2014; Yetman, 2007). Large plants can produce large flowers containing enough nectar to attract flower-visiting bats and birds. These two traits — a columnar growth habit and vertebrate-adapted flowers — opened up new reproductive niches for cacti and ultimately led to higher diversification rates than in other growth forms in this family.

Similar selection pressures for taller plants with paniculate (derived) rather than spicate (ancestral) inflorescences that attracted vertebrate pollinators also occurred in Agavaceae (Good-Avila et al., 2006). Thus, although Cactaceae and Agavaceae are very distantly related, they likely underwent parallel adaptive radiations and coevolution in

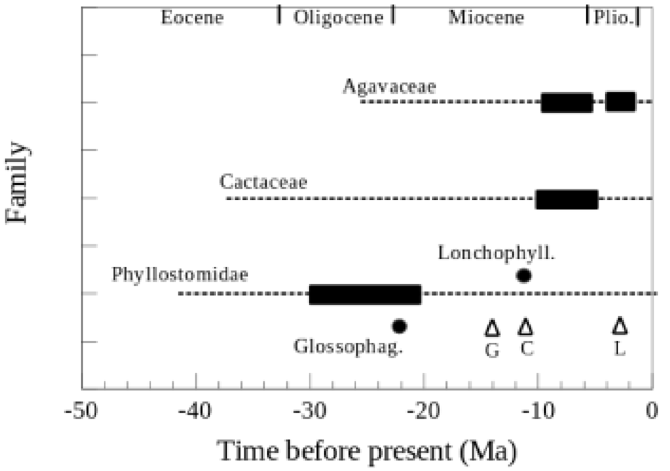

Figure 4 – Summary of the timing of evolution in one bat family (Phyllostomidae) and two plant families (Agavaceae, Cactaceae) based on data in Arakaki et al. (2011); Datzmann et al. (2010), and Good-Avila et al. (2006). Dashed lines indicate the known time lines for each family. The hashed boxes indicate periods of high rates of radiation (of columnar cacti in Cactaceae). In Phyllostomidae, the solid circles indicate the estimated times of origin of two subfamilies: Glossophaginae and Lonchophyllinae; empty triangles indicate estimated times of origin of three glossophagine genera (C = *Choeronycteris*; G = *Glossophaga*; L = *Leptonycteris*). Ma = millions of years.

arid New World habitats with nectar-feeding bats being major drivers behind floral evolution and diversification in tall-statured plants in both families.

Hernández-Hernández et al. (2014) reported that diversification rates in the vertebrate-pollinated TCB and PHB cactus clades (see above) are much higher than those of bee-pollinated clades. This may seem paradoxical initially because we have ample evidence that nectar bats are long-distance gene dispersers and that genetic subdivision in populations of their food plants is generally low. All else being equal, low levels of genetic subdivision should lead to reduced rates of genetic divergence among populations and, ultimately, low rates of allopatric speciation, the most common speciation mode in angiosperm plants. But diversification rates are the net effects of rates of speciation and extinction. It may well be that long-distance gene (and seed) dispersers also play an important role in reducing rates of extinction in species with low-density and widely scattered populations, two conditions that occur frequently in arid habitat species. Strong flying nectar-feeding (and seed-dispersing) bats such as species of *Leptonycteris* can thus be viewed as important ecological "glue" that holds populations of their food plants together genetically and prevents them from undergoing high rates of extinction. Of course, these nectar bats do not have infinite flying and foraging abilities and so there are limits to how far they can disperse plant genes. Two conditions — widely scattered roosts and topographic heterogeneity, e.g in the form of mountains — could easily result in restricted gene flow among populations of bat-pollinated columnar cacti and agaves. Both of these conditions are common in New World arid habitats. *Leptonycteris* bat roosts usually occur at low densities (Fleming, 2004; Fleming and Nassar, 2002), and many species of columnar cacti and paniculate agaves are montane in distribution (see maps in Gentry, 1982 and Yetman, 2007). These two conditions should result in reduced gene flow among populations, geographic isolation, and ultimately high rates of speciation in these plants.

Comparisons with other Neotropical arid zone nectar bat-plant interactions

Bat-pollinated columnar cacti also occur in many arid regions in northern South America. This pollination mutualism has been best-studied in northern Venezuela and Curaçao where pollinator exclusion experiments indicate that bats, primarily *L. curasoae* but also *Glossophaga longirostris*, are the nearly exclusive pollinators of species such as *Cereus repandus*, *Pilosocereus lanuginosus*, and *Stenocereus griseus* (Nassar et al., 1997; Petit, 1995). Genetic analyses indicate that populations of these plants, like their Sonoran Desert counterparts, exhibit low levels of genetic subdivision (G_{ST} values of 0.043–0.126) in northern Venezuela and that *L. curasoae* also shows low levels of genetic subdivision (F_{ST}=0.167) in the same area (Nassar et al., 2003b; Newton et al., 2003). Confirming that *L. curasoae* is a wide-ranging bat, individuals of this species are known to fly between the Caribbean islands Aruba, Bonaire, and Curaçao and between Aruba and Bonaire and the Venezuelan mainland (Simal et al., 2015). Stable isotope analyses indicate that, like Sonoran Desert *L. yerbabuenae*, *L. curasoae* is strongly CAM in its carbon composition and feeds heavily on cactus and agave nectar and pollen (Nassar et al., 2003a). Finally, Ruiz et al. (1997) reported that *G. longirostris* is an important pollinator of columnar cacti in the inter-Andean valleys near La Tatacoa, Colombia.

Little is known about the population biology and foraging behavior of *Platalina genovensium*, the most morphologically specialized nectar bat in South America. In the Andes of southern Peru, it is an important pollinator of the cactus *Weberbauerocereus weberbaueri* in some years but not in others when two species of hummingbirds are more important (Sahley, 1996). In response to strong year-year changes in local cactus flower production, this bat likely migrates among resource patches (Sahley and Baraybar, 1996). In the arid lowlands near Lima, it pollinates flowers of two species of *Haageocereus* cacti (Maguiña and Amanzo, 2016).

Elsewhere in South America, putatively bat-pollinated cacti in the genus *Pilosocereus* are diverse in the cerrados of eastern Brazil, but little is known about their pollination biology (Yetman, 2007; Zappi, 1994). If they are bat-pollinated, their chiropteran visitors are likely to be members of the glossophagine genera *Anoura* and *Glossophaga*, which are both relatively small bats (Fig. 3). Large, long-snouted bats have not evolved in arid regions in northeastern Brazil. *P. royenii* occurs in tropical dry forest in Puerto Rico and has apparently bat-adapted flowers. A two-year study of its pollination biology, however, revealed that the small glossophagine, *Monophyllus redmani* (Fig. 3), was a rare flower visitor and that *Xylocopa* bees were its most effective pollinators (Rivera-Marchand and Ackerman, 2006). Other southern South American night-blooming columnar cacti in the genera *Cereus*, *Echinopsis*, and *Trichocereus* appear to be mostly moth-pollinated and are not visited by bats (de Viana et al., 2001; Ortega-Baes and Saravia, 2011; Silva and Sazima, 1995).

Conclusions

A diverse array of species of bat-pollinated columnar cacti and paniculate agaves occurs in the deserts and other arid regions of North and South America. These plants have coevolved with two clades of nectar- and pollen-feeding phyllostomid bats, beginning in Late Miocene. On the plant side, this coevolution involves the timing of flower anthesis and flower size and its nectar and pollen rewards (Fleming, 2002). On the bat side, it involves many morphological, behavioral, and physiological traits (Fleming and Nassar, 2002).This plant-animal mutualism is unique to New World deserts, and dependence on bats (and birds) for pollination has led to high rates of diversification in these plants. Relatively few species of bats, some of which are quite specialized morphologically, are involved in this interaction. Until recently, at least two of them (*L. yerbabuenae* and *L. nivalis*) have been classified as "endangered" in the United States and Mexico (Medellin, 2016a,b). This makes this interaction of special conservation concern (Fleming, 2004; Nabhan and Fleming, 1993; Santos and Arita, 2002). Anything that threatens the continued existence of bats such as species of *Leptonycteris* and *Choeronycteris mexicana*, and *Platalina genovensium* also threatens the reproductive success of many of their food plants, which are often abundant and ecologically important members of their plant communities (Kunz et al., 2011). Conservation of these bats and their food plants should thus be a high priority in arid ecosystems.

References

Anderson E.F., 2001. The cactus family. Timber Press, Portland, Oregon.

Arakaki M., Christin P.A., Nyffeler R., Lendel A., Eggli U., Ogburn R.M., Spriggs E., Moore M.J., Edwards E.J., 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. Proc Nat Acad Sci USA 108: 8379–8384.

Arizmendi M.D., Valiente-Banuet A., Rojas-Martinez A., Davila-Aranda P., 2002. Columnar cacti and the diets of nectar-feeding bats. In: Fleming T.H., Valiente-Banuet A. (Eds.) Columnar cacti and their mutualists: ecology, evolution, and conservation. University of Arizona Press, Tucson AZ. 264–282.

Buecher D.C., Sidener R., 2012. Long distance commutes by lesser long-nosed bats (*Leptonycteris yerbabuenae*) to visit residential hummingbird feeders. In: Gottfried G.J., Follliott P.F., Gebow B.S., Eskew L.G., Collins L.C. (Eds.). Proc of the Madrean Arch Conf Biodiv III.

Cody M.L., 2002. Growth form variations in columnar cacti (Cacti: Pachycereeae) within and between North American habitats. In: Fleming, T.H., Valiente-Banuet A. (Eds.). Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson AZ. 164–188.

Datzmann T., Von Helversen O., Mayer F., 2010. Evolution of nectarivory in phyllostomid bats (Phyllostomidae Gray, 1825, Chiroptera: Mammalia). BMC Evol Biol 10(165).

de Viana M.L., Baes P.O., Saravia M., Badano E.I., Schlumpberger B., 2001. Flower biology and pollinators of *Trichocereus pasacana* (Cactaceae) in Los Cardones National Park, Argentina. Rev Biol Trop 49: 279–285.

Dumont E.R., Dávalos L.M., Goldberg A., Santana S., Rex K., Voigt C., 2012. Morphological innovation, diversification and invasion of a new adaptive zone. Proc Royal Soc B - Biol Sci 297: 1797–1805.

Fleming T.H., 1995. The use of stable isotopes to study the diets of plant-visiting bats. In: Racey P.A., McDonnell U., Swift S. (Eds.). Bats: ecology, behaviour, and evolution. Oxford University Press, Oxford. 99–110.

Fleming T.H., 2002. The pollination biology of Sonoran Desert columnar cacti. In: Fleming T.H., Valiente-Banuet A. (Eds.). Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson. 207–224.

Fleming T.H., 2004. Nectar corridors: migration and the annual cycle of lesser long-nosed bats. In: Nabhan P. (Ed.). Conserving migratory pollinators and nectar corridors in western North America. University of Arizona Press, Tucson, AZ. 23–42.

Fleming T.H., 2006. Reproductive consequences of early flowering in organ pipe cactus, *Stenocereus thurberi*. Int J Plant Sci, 167: 473–481.

Fleming T.H., Kress W.J., 2013. The ornaments of life: coevolution and conservation in the tropics. University of Chicago Press, Chicago, IL.

Fleming T.H., Geiselman C.K., Kress W.J., 2009. The evolution of bat pollination: a phylogenetic perspective. Ann Bot 104(6): 1017–1043.

Fleming T.H., Muchhala N., Ornelas J.F., 2005. New World nectar-feeding vertebrates: community patterns and processes. In: Sanchez-Cordero V., Medellin R.A. (Eds.) Contribuciones mastozoologicas en homenaje a Bernardo Villa. Instituto de Biologia y Instituto de Ecologia, Universidad Nacional Autonoma de Mexico. 161–184.

Fleming T.H., Nassar J., 2002. Population biology of the lesser long-nosed bat, *Leptonycteris curasoae*, in Mexico and northern South America. In: Fleming T.H., Valiente-Banuet A. (Eds.). Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson AZ. 283–305.

Fleming T.H., Nunez R.A., Sternberg L.S.L.,1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia 94: 72–75.

Fleming T.H., Sahley C.T., Holland J.N., Nason J.D., Hamrick J.L., 2001. Sonoran Desert columnar cacti and the evolution of generalized pollination systems. Ecol Monogr 71: 511–530.

Fleming T.H., Tuttle M.D., Horner M.A., 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. Southw Nat 41: 257–269.

Frick W.F., Price R.D., Heady P.A. III, Kay K.M.,2013. Insectivorous bat pollinates columnar cactus more effectively per visit than specialized nectar bat. Am Nat 181(1): 137–144.

Frick W.F., Shipley J.R., Kelly J.F., Heady P.A., Kay K.M., 2014. Seasonal reliance on nectar by an insectivorous bat revealed by stable isotopes. Oecologia 174: 55–65.

Gentry H.S., 1982. Agaves of continental North America. University of Arizona Press, Tucson AZ.

Good-Avila S.V., Souza V., Gaut B.S., Eguiarte L.E., 2006. Timing and rate of speciation in *Agave* (Agavaceae). Proc Nat Acad Sci USA 103: 9124–9129.

Hamrick J.L., Nason J.D., Gaut B.S., Eguiarte L.E., 2002. Genetic diversity in columnar cacti. In: Fleming T.H., Valiente-Banuet A. (Eds.) Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson AZ. 122–133.

Hernández-Hernández T., Brown J.W., Schlumpberger B., Eguiarte L.E., Magallon S., 2014. Beyond aridification: multiple explanations for the elevated diversification of cacti in the New World succulent biome. New Phytol 202: 1382–1397.

Herrera G.M., Fleming T.H., Findley J.S., 1993. Geographic variation in the carbon composition of the pallid bat, *Antrozous pallidus*, and its dietary implications. J Mammal 74: 601–606.

Horner M.A., Fleming T.H., Sahley C.T., 1998. Foraging behaviour and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). J Zool 244: 575–586.

Kunz T.H., Braun de Torrez E., Bauer D., Lobova T., Fleming T.H., 2011. Ecosystem services provided by bats. Annals NY Acad Sci 1223: 1–38.

Maguiña R., Amanzo J., 2016. Diet and pollinator role of the long-snouted bat *Platalina genovensium* in Lomas ecosystem of Peru. Tropical Conservation Science, 9: 1–8.

Medellin R.A., 2016a. *Leptonycteris yerbabuenae*. The IUCN Red List of Threatened Species: eT11697Z22126172.

Medellin R.A., 2016b. *Leptonycteris nivalis*. The IUCN Red List of Threatened Species: eT136659A21988965.

Molina-Freaner F., Eguiarte L.E., 2003. The pollination biology of two paniculate agaves (Agavaceae) from northwestern Mexico: contrasting roles of bats as pollinators. Amer J Bot, 90: 1016–1024.

Molina-Freaner F., Rojas-Martinez A., Fleming T.H., Valiente-Banuet A., 2004. Pollination biology of the columnar cactus *Pachycereus pecten-aboriginum* in north-western Mexico. J Arid Environ 56: 117–127.

Moreno-Valdez A., Honeycutt R.L., Grant W.E., 2004. Colony dynamics of *Leptonycteris nivalis* (Mexican long-nosed bat) related to flowering agave in northern Mexico. J Mammal 85: 453–459.

Nabhan G.P., Fleming T.H., 1993. The conservation of mutualisms. Cons Biol, 7: 457–459.

Nassar J., Ramirez N., Linares O., 1997. Comparative pollination biology of Venezuelan columnar cacti and the role of nectar-feeding bats in their sexual reproduction. Amer J Bot 84: 918–927.

Nassar J.M., Beck H., Sternberg L.S.L., Fleming T.H., 2003a. Dependence on cacti and agaves in nectar-feeding bats from Venezuelan arid zones. Journal of Mammalogy 84: 106–116.

Nassar J.M., Hamrick J.L., Fleming T.H., 2003b. Population genetic structure of Venezuelan chiropterophilous columnar cacti (Cactaceae). Amer J Bot 90: 1628–1630.

Newton L.R., Nassar J.M., Fleming T.H., 2003. Genetic population structure and mobility of two nectar-feeding bats from Venezuelan deserts: inferences from mitochondrial DNA. Mol Ecol 12: 3191–3198.

Ober H.K., Steidl R.J., 2004. Foraging rates of *Leptonycteris curasoae* vary with characteristics of *Agave palmeri*. Southw Nat, 49: 68–74.

Ortega-Baes P., Saravia M., 2011. Reproductive biology of *Echinopsis terscheckii* (Cactaceae): the role of nocturnal and diurnal pollinators. Plant Biol, 13: 33–40.

Petit S., 1995. The pollinators of two species of columnar cacti on Curacao, Netherlands Antilles. Biotrop., 27: 538–541.

Petit S., 1998. The effectiveness of two bat species as pollinators of two species of columnar cacti on Curacao. Haseltonia, 6: 22–31.

Phillips S.J., Comus P.W., (Eds), 2000. A natural history of the Sonoran Desert. Arizona-Sonora Desert Museum Press, Tucson AZ.

Post D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718.

Rivera-Marchand B., Ackerman J.D., 2006. Bat pollination breakdown in the Caribbean columnar cactus *Pilosocereus royenii*. Biotrop., 38: 635–642.

Rocha M., Good-Avila S.V., Molina-Freaner F., Arita H.T., Castillo A., Garcìa-Mendoza A., Silva-Montellano A., Gaut B.S., Souza V., Eguiarte L.E., 2006. Pollination biology and adaptive radiation of Agavaceae, with special emphasis on the genus *Agave*. Aliso 22(1): 329–344.

Rocha M., Valera A., Eguiarte L.E., 2005. Reproductive ecology of five sympatric *Agave Littaea* (Agavaceae) species in Central Mexico. Amer J Bot 92(8): 1330–1341.

Rojas D., Warsi O.M., Davalos L.M., 2016. Bats (Chiroptera: Noctilionoidea) challenge a recent origin of extant Neotropical diversity. Syst Biol, 65: 432–448.

Ruiz A., Santos M., Cavelier J., Cadena A., 1997. Relaciones mutualisticas entre el murcielago *Glossophaga longirostris* y las cactaceas columnares en la zona arida de La Tatacoa, Colombia. Biotrop 29: 469–479. [in Spanish]

Sahley C.T., 1996. Bat and hummingbird pollination of an autotetraploid columnar cactus, *Weberbauerocereus weberbaueri* (Cactaceae). Amer J Bot, 83: 1329-1330.

Sahley C.T., Baraybar L., 1996. The natural history of the long-snouted bat, *Platalina genovensium* (Phyllostomidae: Glossophaginae), in southwestern Peru. Vida Silv Neotrop, 5: 101–109.

Sahley C.T., Horner M.A., Fleming T.H., 1993. Flight speeds and mechanical power outputs of the nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae). J Mammal 74: 594–600.

Sanchez R., Medellin R.A., 2007. Food habits of the threatened bat *Leptonycteris nivalis* (Chiroptera : Phyllostomidae) in a mating roost in Mexico. J Nat Hist, 41: 1753–1764.

Santos M., Arita H.T., 2002. Priority areas for the conservation of New World nectar-feeding bats. In: Fleming T.H., Valiente-Banuet A. (Eds.). Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson, AZ. 342–363.

Sealy J.C., van der Merwe N., Lee Thorp J.A., Lanham J.L., 1987. Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. Geochim Cosmochim Acta 51: 2707–2717.

Silva W.R., Sazima M., 1995. Hawkmoth pollination in *Cereus peruvianus*, a columnar cactus from southeastern Brazil. Flora, 190: 339–343.

Simal F., de Lannoy C., García-Smith L., Doest O., de Freitas J.A., Franken F., Zaandam I., Martino A., González-Carcacía J.A., Peñaloza C.L., Bertuol P., Simal D., Nassar J.M., 2015. Island-island and island-mainland movements of the Curacaoan long-nosed bat, *Leptonycteris curasoae*. J Mammal 96 (3): 579–590.

Simmons N.B., 2005. Order Chiroptera. In: Wilson D.E., Reeder D.M. (Eds.). Mammal species of the world, a taxonomic and geographic reference. Johns Hopkins Press, Baltimore MD. 312–529.

Slauson L.A., 2000. Pollination biology of two chiropterophilous agaves in Arizona. Amer J Bot, 87: 825–836.

Turner R.M., Bowers J.E., Burgess T.L., 1995. Sonoran desert plants. University of Arizona, Tucson, AZ.

Valiente-Banuet A., Arizmendi M.D., Martinez-Rojas A., Dominguez-Canesco L., 1996. Geographical and ecological correlates between columnar cacti and nectar-feeding bats in Mexico. J Trop Ecol 12: 103–119.

Valiente-Banuet A., Rojas Martinez A., Arizmendi M.C., Davila P., 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, Central Mexico. Amer J Bot 84: 452–455.

Valiente-Banuet A., Rojas-Martínez A., Casas A., Arizmendi M., Dávila P., 1997b. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacan Valley, central Mexico. J Arid Environ 37(2): 331–341.

Wallace R.S., 2002. The phylogeny and systematics of columnar cacti: an overview. In: Fleming T.H., Valiente-Banuet A. (Eds.). Columnar cacti and their mutualists: evolution, ecology, and conservation. University of Arizona Press, Tucson, AZ. 42–65.

Yetman D., 2007. The great cacti. University of Arizona Press, Tucson, AZ.

Zappi D.C., 1994. *Pilosocereus* (Cactaceae): the genus in Brazil. In: Hunt D., Taylor N. (Eds.) Succulent plant research. Roy Botan Gard, Kew, London, 3: 1–160.

Associate Editor: D. Russo

Appendix: A Sonoran Desert bat community

We documented the taxonomic and trophic structure of a Sonoran Desert bat community at Organ Pipe Cactus National Monument, Pima County, Arizona (31°57′ N, 112°52′ W) from April through June 1997. Two species of bat-pollinated columnar cacti, *Carnegiea gigantea* and *Stenocereus thurberi*, occur at this site (Fleming et al., 2001). We captured 11 species of bats at seasonal water holes, a permanent pond, and a swimming pool using one 6 m mist-net on each of 17 nights for a total of 60 h (Tab. 1). We recorded species, sex, age, reproductive status, forearm length (to nearest 0.5 mm), and mass (to nearest 0.5 g) for 196 bats and collected fecal samples for dietary analysis from 110 of them.

We examined the trophic structure of these bats using carbon and nitrogen stable isotopes from the fecal samples (Sealy et al., 1987). Isotopic ratios were expressed in δ notation, i.e. parts per thousand or δ^{13}C (‰) and δ^{15}N (‰) (see Fleming et al., 1993 and Fleming, 1995 for isotope methods and standards). The Sonoran Desert contains two major carbon pools, CAM plants (cacti and agaves) that have an average δ^{13}C value of -12.63‰ and C3 plants (non-succulents) that have an average δ^{13}C value of -26.41‰ (Fleming et al., 1993). Stable isotope analyses indicate that this bat assemblage uses both sources of carbon but that individual species obtain most of their carbon from one or the other of the two carbon pools (Fig. 2). Because fecal samples from the nectar bat *L. yerbabuenae* contained only pollen and water, we report its nitrogen value (not measured here) as 3.4‰ lower than the average value of insectivorous bats in this study (see Post, 2002).