The cover features four bats in flight against a black background. One bat is in the top left, another in the top right, one in the middle left, and one in the bottom right. The title 'Phyllostomid Bats' is centered in purple, with 'Bats' being significantly larger than 'Phyllostomid'. Below the title is the subtitle 'A Unique Mammalian Radiation' in a smaller, gold-colored font. At the bottom, the editors' names are listed in a green font.

Phyllostomid Bats

A Unique Mammalian Radiation

*Edited by Theodore H. Fleming,
Liliana M. Dávalos, and Marco A. R. Mello*

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“Phyllostomid Bats is an excellent, comprehensive compendium of the latest research on this fascinating group. The book reflects how this incredibly diverse clade can be a model system for advancing our understanding of fundamental aspects of evolution and ecology of not just bats, but also of other organisms. The language is accessible to both budding biologists and veteran researchers looking to dip their toes into a new field, and it will surely be an indispensable volume to bat researchers everywhere.”

—Susan M. Tsang, research associate, Department of Mammalogy, American Museum of Natural History

“An outstanding book. The diversity of detailed information is exceptional. The book’s twenty-four chapters provide an in-depth look at these astonishing bats. The book will be an exceptional addition to the libraries of bat biologists, evolutionary biologists, and those who are intrigued by diversity. I am glad that I have already ordered my copy.”

—M. Brock Fenton, Department of Biology, University of Western Ontario (Canada), coeditor of *Bat Ecology* and coauthor of *Bats: A World of Science and Mystery*

“These are timely and eagerly anticipated reviews of the huge volume of research carried out in recent decades on this diverse and fascinating family of bats.”

—Paul Racey, Regius Professor of Natural History (Emeritus), University of Aberdeen, Scotland

“Phyllostomid Bats is certainly worthwhile, as we have learned a good deal about this family in the last forty years or so (since the previous review of the whole family). From interesting speculation on the correlation between sexual dimorphism and mating systems in bats to a very nice summary of conservation threats and more importantly, perhaps, a good overview of some of the actions being taken in response, this book will serve the bat community well, and will be used by anyone studying this family in the future.”

—Don E. Wilson, curator emeritus of vertebrate zoology, National Museum of Natural History, Smithsonian Institution

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Phyllostomid Bats

A Unique Mammalian Radiation

Edited by

Theodore H. Fleming,

Liliana M. Dávalos, and

Marco A. R. Mello

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*We dedicate this book to past, present,
and future students of this fascinating group
of mammals*

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The Ecology and Evolution of Nectar Feeders

Introduction

As detailed in this book, New World leaf-nosed bats have undergone a rapid and extensive diversification, in terms of both species richness and the niches they occupy. One trophic niche particularly important to the ecology of New World ecosystems is the nectar-feeding specialists, which many plants have evolved to depend on for their pollination services (Fleming et al. 2009; Garibaldi et al. 2012). Nectar provides an especially carbohydrate-rich food source that is relatively easy to digest (Baker et al. 1998), and many phyllostomids occasionally include nectar in their diets. This is particularly common among primarily frugivorous genera such as *Artibeus*, *Sturnira*, and *Carollia* and omnivores such as *Phyllostomus* (Giannini and Kalko 2004; Heithaus et al. 1975; Szazima 1976). However, only a handful of phyllostomid genera have evolved adaptations for a diet composed primarily of nectar. In this chapter, we review the ecology and evolution of these bats, as well as the flowers with which they have coevolved.

Evolution of Nectarivory

Nectarivore specialists occur in the subfamilies Glossophaginae and Lonchophyllinae. Glossophaginae comprises 14 genera and 36 species, and Lonchophyllinae 5 genera and 20 species (table 16.1); thus, in total, nectarivores make up about one-quarter (26%) of the 216 known species of phyllostomids (Cirranello et al. 2016; chap. 4, this vol.). These species share a suite of traits that adapts them to their nectarivorous lifestyle, including reduced dentition, elongated snouts, long, extensible tongues with hairlike papillae, and the ability to hover in front of flowers while extracting nectar (Freeman 1995; Norberg et al. 1993; von Helversen and Winter 2003). Early phylogenetic work based largely on morphology suggested that the two subfamilies were sister clades (e.g., Slaughter 1970), which implies that nectarivory

Table 16.1. Classification scheme for the 52 known species of nectarivorous phyllostomid bats (following Cirranello and Simmons, chap. 4, this vol.)

Subfamily	Tribe	Subtribe	Genus	Species	
Glossophaginae	Brachyphyllini	Brachyphyllina	<i>Brachyphylla</i>	<i>B. cavernarum</i> , <i>B. nana</i>	
		Phyllonycterina	<i>Erophylla</i>	<i>E. bombifrons</i> , <i>E. sezekorni</i>	
			<i>Phyllonycteris</i>	<i>P. aphylla</i> , <i>P. poeyi</i>	
	Choeronycterini	Anourina	<i>Anoura</i>	<i>A. aequatoris</i> , <i>A. cadenai</i> , <i>A. carishina</i> , <i>A. caudifer</i> , <i>A. cultrata</i> , <i>A. fistulata</i> , <i>A. geoffroyi</i> , <i>A. latidens</i> , <i>A. luismanueli</i> , <i>A. peruana</i>	
		Choeronycterina	<i>Choeroniscus</i>	<i>C. godmani</i> , <i>C. minor</i> , <i>C. periosus</i>	
			<i>Choeronycteris</i>	<i>C. mexicana</i>	
			<i>Dryadonycteris</i>	<i>D. capixaba</i>	
			<i>Hylonycteris</i>	<i>H. underwoodi</i>	
			<i>Lichonycteris</i>	<i>L. degener</i> , <i>L. obscura</i>	
			<i>Musonycteris</i>	<i>M. harrisoni</i>	
			<i>Scleronycteris</i>	<i>S. ega</i>	
		Glossophagini	...	<i>Glossophaga</i>	<i>G. commissarisi</i> , <i>G. leachii</i> , <i>G. longirostris</i> , <i>G. morenoi</i> , <i>G. soricina</i>
				<i>Leptonycteris</i>	<i>L. curasoae</i> , <i>L. nivalis</i> , <i>L. yerbabuena</i>
	<i>Monophyllus</i>		<i>M. plethodon</i> , <i>M. redmani</i>		
Lonchophyllinae	Hsunycterini	...	<i>Hsunycteris</i>	<i>H. cadenai</i> , <i>H. dashe</i> , <i>H. pattoni</i> , <i>H. thomasi</i>	
	Lonchophyllini	...	<i>Lionycteris</i>	<i>L. spurrelli</i>	
			<i>Lonchophylla</i>	<i>L. bokermanni</i> , <i>L. chocoana</i> , <i>L. concava</i> , <i>L. dekeyseri</i> , <i>L. fornicata</i> , <i>L. handleyi</i> , <i>L. hesperia</i> , <i>L. inexpectata</i> , <i>L. mordax</i> , <i>L. orcesi</i> , <i>L. orienticollina</i> , <i>L. peracchii</i> , <i>L. robusta</i>	
			<i>Platalina</i>	<i>P. genovensium</i>	
			<i>Xeronycteris</i>	<i>X. vieirai</i>	

evolved only once in the family. A detailed analysis of hyoid and lingual morphology, however, led Griffiths (1982) to suggest that lonchophyllines and glossophagines represented independent origins of nectarivory. This caused some controversy, with further analyses arguing for a single origin of nectarivory (Baker et al. 1981; Haiduk and Baker 1982; Smith and Hood 1984; Wetterer et al. 2000) or giving equivocal results (Carstens et al. 2002). The latest molecular work now strongly supports the conclusion of Griffiths (1982) that the Glossophaginae and Lonchophyllinae are not, in fact, sister clades (Baker et al. 2016; Datzmann et al. 2010; Rojas et al. 2011, 2016). Morphological and behavioral evidence further supports independent origins of nectarivory: while lonchophyllines and glossophagines are superficially similar in their elongated snouts and tongues and in their ability to hover, differences in tongue musculature, papillae arrangement, and feeding behavior suggest these similarities are examples of convergent evolution (Datzmann et al. 2010; Griffiths

1982; Tschapka et al. 2015; Winter and von Helversen 2003; see "Morphological Adaptations to Nectarivory" below). Interestingly, among these two nectar-feeding radiations, there appears to be one instance of a shift to a frugivorous diet, in the genus *Brachyphylla*. The two species in this genus possess extensible tongues with papillae, yet are more similar to frugivorous phyllostomids in skull (Freeman 1995) and tooth morphology (Griffiths 1985), and limited dietary studies suggest they do in fact feed primarily from fruits (Lenoble et al. 2014; Silva Taboada and Pine 1969; Swanepoel and Genoways 1983a, 1983b).

What ancestral feeding mode did the nectar-feeding phyllostomids evolve from? While initially it was thought that nectarivory evolved from frugivory, which in turn evolved from insectivory (Ferrarezzi and Gimenez 1996), more recent phylogenetic reconstruction of ancestral diets suggests that each plant-feeding specialization has evolved independently from primarily insectivorous ancestors (Baker et al. 2012; Rojas

et al. 2011). The idea that insectivory could shift directly to nectarivory is supported by the fact that an insectivorous bat (*Antrozous pallidus*) from a highly insectivorous family (Vespertilionidae) was recently discovered to supplement its diet with nectar from cactus flowers (Frick et al. 2009, 2013). However, it can be difficult to reliably reconstruct ancestral states, particularly if there has been extensive extinction of less-specialized ancestral taxa. An alternate hypothesis is that the ancestral species that gave rise to the nectar-feeding clades were in fact omnivores that fed on insects, fruits, and nectar. In support of this scenario, the less-derived taxa among extant species of glossophagines tend to be particularly generalized (Fleming and Kress 2013), including taxa such as *Phyllonycteris*, *Erophylla*, *Brachyphylla*, and *Glossophaga soricina*, relative to other species of *Glossophaga*. In the same way that *Antrozous pallidus* suggests that shifts directly from insectivory to nectarivory may be possible, the unusual New Zealand endemic *Mystacina tuberculata* (Mystacinidae) may support the possibility of a shift through an omnivorous intermediate; it feeds on insects and fruits but also visits flowers and possesses distinct adaptations to nectarivory, such as a long tongue and reduced dentition (Arkins et al. 1999; Carter and Riskin 2006). Overall, given phylogenies and current diets, it seems likely that the ancestral nectarivores had a generalized diet that was supplemented at least by insects and possibly by fruits as well.

Dietary Breadth

While phyllostomid nectar-feeding bats possess specialized morphologies, as outlined above, the majority have relatively flexible diets in that they will feed occasionally on insects and/or fruits. The three bats with the most extreme adaptations to nectarivory include the glossophagines *Anoura fistulata* and *Musonycteris harrisoni* and the lonchophylline *Xeronycteris vieirai*. While most nectar bats can extend their tongues to approximately 60% of their body length, *A. fistulata* has a tongue extension of 150% of its body length, longer than any other mammal and exceeded only by chameleons among vertebrates (Muchhala 2006a). A glossal tube extends back from the jaw and houses the base of the tongue in the rib cage, allowing a much greater resting tongue length. Despite this specialized morphology, *A. fistulata* also feeds on insects (Muchhala, unpublished data). *Musonycteris harrisoni* also has a re-

markable tongue extension; it does not possess a glossal tube, so houses the resting tongue entirely in its mouth but has an extremely long snout (20 mm), longer than any other nectar bat (Gonzalez-Terrazas et al. 2012; Tellez and Ortega 1999). It feeds nearly exclusively on flowers from a wide variety of species, although insects have also been found in its feces (Tschapka et al. 2008). Finally, *Xeronycteris vieirai* is notable for having the greatest reduction in dentition (in terms of smaller teeth and larger gaps between them) among nectar bats. Given their increased reliance on a liquid diet, teeth are less important for nectar feeders and are much less robust than in other phyllostomids (Freeman 1995); *X. vieirai* takes this trend to an extreme, with many typical tooth structures absent or greatly reduced (Gregorin and Ditchfield 2005).

At the opposite end of the specialization spectrum, *G. soricina* is a widespread, abundant bat with a relatively short rostrum and a highly opportunistic diet. It is distributed from Mexico to Argentina, encompassing nearly the entire distribution of glossophagines (Alvarez et al. 1991), and is known to feed primarily on insects and fruit for large portions of the year in parts of its range (Clare et al. 2014; Hobson et al. 2001; Howell 1974b; Zortéa 2003). Dietary data on many other nectar bat species suggest they regularly supplement their floral diet with insects and fruit, which has led some authors to argue that they (and phyllostomids in general) should be considered opportunistic omnivores (Rex et al. 2010). For instance, *Glossophaga commissarisi* in a Costa Rican rainforest was found to switch to frugivory for several months of the year when nectar is scarce, with up to 30% of the individuals per month showing no pollen at all in the fur (Tschapka 2004). While species of *Anoura* in cloud forests are rarely found to consume fruits (Muchhala and Jarrín-V. 2002; Muchhala et al. 2005), in the Brazilian Cerrado, seeds are regularly found in their feces (Zortéa 2003). In fact, for *Anoura geoffroyi*, Zortéa (2003) estimated that pollen/nectar represented only 13% of their diet, while fruit parts represented 45% and insect parts represented 42%. Other records of fruit feeding among nectar bats include *Choeronycteris mexicana* and *Leptonycteris yerbabuena* in Mexican deserts (Godinez-Alvarez and Valiente-Banuet 2000), *L. curasoae* and *Glossophaga longirostris* in Venezuelan shrublands (Sosa and Soriano 1993), and *Erophylla sezekorni* and *Monophyllus redmanii* in Puerto Rican moist forests (Soto-Centeno

and Kurta 2006). Records of insectivory are even more common than those of frugivory; in fact, in all studies we have reviewed where feces of nectar bats were analyzed, at least some proportion of the samples contained insect parts (citations in this paragraph, and Barros et al. 2013; Goyret and Yuan 2015; Petit 1997; Rex et al. 2010; Sánchez and Medellín 2007; Sazima 1976; Sperr et al. 2011; Willig et al. 1993). The extent to which this represents aerial hunting remains unclear, as many of these insects may have been gleaned from flowers or other surfaces; however there are also records of nectar bats actively capturing flying insects in hawking bouts (Clare et al. 2014; Howell 1974b).

Morphological Adaptations to Nectarivory

The evolution of elongated mouthparts to facilitate access to nectar in flowers, arguably the most important physical adaptation to a nectar-feeding lifestyle, is common across the nectar-feeding members of various animal groups, including moths, flies, butterflies, and birds (Fenster et al. 2004). For phyllostomids, elongated jaws (see plate 4) allow bats to house longer tongues (Bolzan et al. 2015; Freeman 1995), which in turn allows for longer tongue extension and the ability to extract nectar from flowers with deep floral tubes (Gonzalez-Terrazas et al. 2012; Muchhala 2006a; Winter and von Helversen 2003). However, this does come with a trade-off: the longer the jaw, the greater the out-lever of the jaw system, and thus the weaker the bite force (Aguirre et al. 2002; Nogueira et al. 2009; Santana 2015; Santana et al. 2012), which may limit the ability to eat hard-bodied insects and tougher fruits or to defend against predators.

With an increasing degree of specialization, the jaw becomes less important as a tooth-bearing structure and more important for supporting the tongue (Freeman 1995). In correspondence with a predominantly fluid diet, there is a tendency toward reduction of the dentition within nectar-feeding phyllostomids. Bats with increased morphological specialization show a gap between the lower incisors (e.g., *Monophyllus* spp.) or have even have lost them entirely (e.g., *Anoura*; fig. 16.1), probably to maximize space for tongue movements (Carstens et al. 2002; Freeman 1995). In more derived species, there are also large gaps (diastemas) between the comparably small molars, as seen in *X. vieirai* (Gregorin and Ditchfield 2005) and *M. har-*

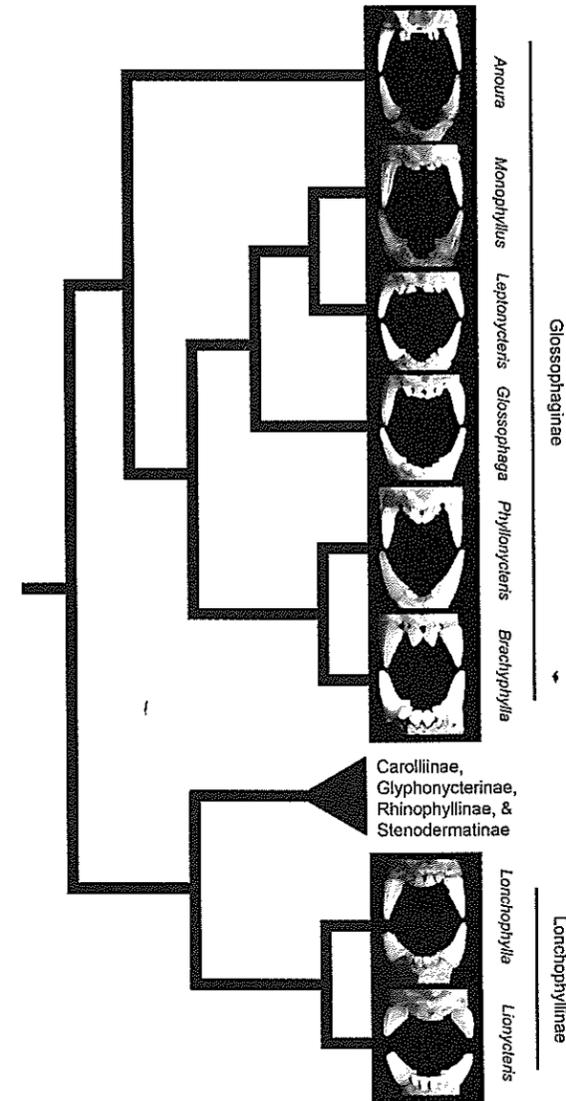


Figure 16.1. Upper and lower incisor morphology for select nectarivorous phyllostomids, showing the frontal gap through which the tongue is exerted, with phylogenetic relationships for the species. Adapted from Carstens et al. (2002), using the phylogeny of Rojas et al. (2016); images kindly provided by B. Carstens.

risoni (Tellez and Ortega 1999). Interestingly, canine teeth remain well developed across nectarivores (fig. 16.1), suggesting an important role. Freeman (1995) hypothesized that nectarivores brace upper and lower canines against each other to support the jaw during rapid tongue movements, citing patches of wear on the teeth where they contact each other. Canines may also function in “scraping” nectar off of the tongue’s papillae as it moves past, or alternatively, they may primarily be used for defense or intraspecific aggression.

Tongue length is correlated with jaw length across

species of phyllostomid nectarivores (Winter and von Helversen 2003) and seems to depend on the degree of specialization on a nectar diet. In many species, animals maintain the tongue protruding slightly from the tip of the snout while not feeding. While less-derived nectarivores such as *Glossophaga* spp. can extend their tongues ca. 4 cm, more specialized species with particularly long jaws such as *C. mexicana* or *M. harrisoni* can extend them to 7–8 cm (Winter and von Helversen 2003). As in all mammals, tongues of nectar-feeding bats are muscular hydrostats, that is, they have a constant volume and are moved through complex bundles of muscles that allow elongation, shortening, bending, and torsion (Harper et al. 2013; Kier and Smith 1985). As in other mammals, the tongue initiates at the base of the oral cavity but differs in having a tongue retractor muscle that attaches much farther back, to the xiphoid process of the rib cage (plate 5b). *Anoura fistulata*, as mentioned above, provides a remarkable exception to this pattern in that the base of the tongue is shifted back into the thoracic cavity, close to the sternum (Muchhala 2006a; plate 5a). *Anoura* spp. are among the most insectivorous of the nectar-feeding bat species; it is possible that selection favored this solution for *A. fistulata* rather than elongation of the rostrum because it conserved the bite force necessary to feed successfully on insects.

Although Glossophaginae and Lonchophyllinae both evolved long tongues with papillae, closer inspection reveals profound differences in their morphologies, consistent with their independent evolution of nectarivory. While glossophagines have brush-like tongues with numerous filamentous papillae at the tip, lonchophyllines are characterized by papillae-lined grooves along the lateral sides of the tongue (Griffiths 1982; Howell and Hodgkin 1976). Recent studies of glossophagine feeding show that, as tongues approach maximum extension, the papillae on the tip become hydraulically erected through blood infusion and actively aid in collecting nectar (Harper et al. 2013). Glossophagine tongues perform sinusoidal lapping movements, alternating between dipping into the nectar and retracting into the mouth. In contrast, the extended lonchophylline tongue stays immersed in the nectar fluid throughout flower visits (Tschapka et al. 2015). Nectar rises along the canals into the mouth cavity, probably due to a combination of active peristaltic pumping and capillary forces in the small canals.

Interestingly, the efficiency of these two very different and independently evolved drinking methods are quite similar in terms of nectar extraction per unit of time, at least while feeding from artificial flowers (Tschapka et al. 2015; Muchhala, unpublished data). These differences in nectar extraction might offer advantages at flower types that differ in nectar amount and presentation: the lonchophylline pumping mechanism may work better at flowers with a larger nectar volume concentrated in one spot (e.g., *Ochroma pyramidale*—Malvaceae), while the glossophagine “nectar mop” may be better-adapted for the extraction of small and diffusely distributed droplets from smaller flowers (e.g., *Capanea grandiflora*—Gesneriaceae; *Merinthopodium neuranthum*—Solanaceae). Regardless, for both lonchophyllines and glossophagines, the amount of nectar they can extract within a certain time span (extraction efficiency) decreases sharply when they have to reach deeper into flowers, possibly due to greater time needed for tongue extension, increased leakage during tongue retraction, and/or decreased pumping power at longer extensions (Tschapka et al. 2015). Flower depth can vary widely across bat-visited flowers, from openly presented nectar in species such as *Cleome spinosa* (Capparaceae) to long-tubed species such as the columnar cactus *Pachycereus pecten-aboriginum*, with its 9-cm-deep corollas (Tschapka et al. 2008).

Another key to efficiently visiting flowers is nectar-feeding bats’ ability for extended hovering flight. Extracting nectar without needing to support their weight on the flowers during visits allows bats to exploit flowers of less-robust plants, which likely expanded their possible dietary spectrum. In slow flight, and particularly while hovering, glossophagine bats reverse the hand wings during the upstroke to generate thrust and a small amount of lift (Håkansson et al. 2015; Norberg and Winter 2006). In contrast, hummingbirds rotate the entire wing around the shoulder joint and thus are able to produce even more lift during the upstroke (Warrick et al. 2005).

Physiological Adaptations to Nectarivory

Nectar is primarily an aqueous sugar solution that is very easy to digest. Stomachs of nectar-feeding bats are therefore relatively simple compared to those from other dietary habits. Bats match their feeding behavior to nectar sugar content, increasing food uptake in re-

sponse to lowered sugar concentration (Ayala-Berdon and Schondube 2011). This ability to compensate likely has a lower limit due to the physiology of hydrolysis and water processing from extremely dilute sugar solutions (Ramírez et al. 2005). The enzyme sucrase in the digestive system of the glossophagine *Leptonycteris nivalis* was found to have a much higher affinity for sugars than that of its sister species *L. yerbabuena*, which might translate into a more efficient energy uptake that may have permitted it to expand into higher, colder altitudes (Ayala-Berdon et al. 2013).

The high energetic needs of nectar-feeding bats, a product of a high basal metabolic rate and a feeding ecology requiring visitation to many flowers, translate into enormous food requirements. Small species such as *G. soricina* regularly consume up to 150% of their body weight per night when feeding on 17% sugar water (Winter and von Helversen 2003). This extremely high liquid uptake requires a particularly efficient water management physiology. Through regulation of glomerular filtration rate, urination is tightly coupled to liquid uptake, and excess water is shed by reducing renal water reabsorption. Nectar-feeding phyllostomids, like their frugivorous counterparts, need to excrete water while conserving electrolytes and they have a relatively well-developed renal cortex compared to their insectivorous ancestors (Casotti et al. 2006).

The constant influx of sugar may lead to extremely high glucose concentrations in the blood. In contrast to most other mammals that mobilize required energy from previously built-up fat stores, flight activity of glossophagine bats is largely fueled directly by their incoming carbohydrates, a physiological adaptation that they share with hummingbirds (Voigt and Speakman 2007). Although extended periods of high blood glucose concentration are detrimental to the health of most mammals, nectar-feeding bats do not appear to suffer such costs, either due to specialized physiological adaptations or because they are able to regulate high glucose levels through high physical activity (Kelm et al. 2011). This corresponds to experiments showing that glossophagines fly longer each night than necessary, based solely on their foraging needs (e.g., Horner et al. 1998). The consequence is a daily energy expenditure that is kept within a narrow range (von Helversen and Winter 2003). Energy turnover in glossophagines is extremely high, and in fact most of the body fat built up during a night of foraging (ca. 1 g for *G. soricina*) is consumed

over the course of the following day (von Helversen and Winter 2003). In situations where available resources do not cover daily energy requirements, glossophagines have been found to use diurnal torpor. In contrast to non-phyllostomid bats using torpor, glossophagines do not lower their body temperature close to ambient temperature but try to maintain the highest levels possible, given the energetic resources available to them (Kelm and von Helversen 2007). To date, torpor in nectar-feeding phyllostomids has only been investigated in laboratory experiments; the extent to which they actually use this strategy in nature remains unknown.

While in the majority of cases nectar bats visit flowers primarily for their nectar, after visits they will groom and consume the pollen that collects on their fur (Álvarez and González Quintero 1970; Herrera and Martínez del Río 1998; Howell 1974a). There are even occasional records of bats directly feeding on pollen during visits, for example, from *Pachira aquatica* (Hernández-Montero and Sosa 2015) or the nectarless, wind-pollinated species of *Cecropia* (Tschapka 2004). In captivity, they will actively consume dry pollen provided in dishes (NM and MT, pers. obs.). The exine of pollen grains is extremely tough and probably cannot be digested by bats. However, the stomach of nectar-feeding bats primarily contains a warm sugar solution that promotes the germination and emergence of the pollen tube from the exine shell and allows it to be digested (Howell 1974a; von Helversen 1995). Pollen is nearly always detected in nectar bat feces (e.g., Álvarez and González Quintero 1970), and, as might be expected, nectar bats that have been tested to date (*L. yerbabuena*, *A. geoffroyi*, and *Brachyphylla nana*) are physiologically much more efficient at extracting the nutritious contents of pollen grains than other phyllostomids, even those known to opportunistically include pollen in their diets (Herrera and Martínez del Río 1998; Mancina and Balseiro 2005).

Sensory Ecology

Echolocation

While searching for flowers, nectar-feeding phyllostomids use a combination of active echolocation and passive perception of scent and other floral cues. Based on this foraging mode and their habitat, they can be classified as members of the “narrow space passive/

active-gleaning” forager guild (Denzinger et al. 2016). Their echolocation calls correspond largely to the usual phyllostomid pattern, with very short (1–2 ms), multi-harmonic FM calls of low intensity. Traditionally, phyllostomids have been considered to be “whispering” bats because call recordings typically register low intensities. However, recent work shows their calls can be quite loud but are emitted with high directionality and thus can be difficult to record (Brinkløv et al. 2009; Kalko 2004). When flying in the open, the nectar-feeding bats *Phyllonycteris poeyi* and *Leptonycteris yerbabuena* also use longer calls (up to 8 ms), with the highest energy in the first harmonic (Mora and Macías 2007; Gonzalez-Terrazas, pers. comm.). These open space calls are easily recorded from over 10 m away. The same species, however, emit typical phyllostomid calls when flying in more confined environments, such as a flight cage (Gonzalez-Terrazas, Koblitz et al. 2016), indicating a high flexibility in echolocation behavior.

Echolocation not only is used for orientation and obstacle avoidance during distance flight, but it also plays an important role for flower recognition and approach coordination. Glossophagine bats are able to recognize minute surface structures by echolocation, to a resolution of 0.38 mm (Simon et al. 2014). Additionally, they have been shown to recognize similar shapes despite varying sizes, demonstrating that they can generalize shape cues (von Helversen 2004). A few flowers have been shown to exploit these echolocation capabilities, and it is probable that even more will be recognized as acoustically conspicuous (see “Bat-Pollinated Flowers” for more details).

Olfaction

Scent is clearly an important sensory modality for phyllostomid nectar bats, as suggested by the fact that their olfactory bulbs and associated brain regions are relatively large (Bhatnagar and Kallen 1974; Stephan and Pirlot 1970). Accordingly, Neotropical bat-pollinated flowers typically produce strong, musky scents to attract their pollinators. Traditionally, scent has been viewed as a long-distance attractant that can guide bats to the general vicinity of bat-adapted plants before they switch to relying on echolocation (and perhaps vision) to locate specific flowers. However, recent flight cage experiments show that floral scent also plays a role at short distances (Gonzalez-Terrazas, Martel et al. 2016).

Scented flowers are consistently located faster than unscented flowers, and odor seems to be particularly important when locating flowers in structurally more complex environments (Muchhala and Serrano 2015).

As in most mammals, olfaction in nectar bats is important not only for locating food but also in interspecific interactions. Relatively few studies have explored mating systems of nectar bats, but those that have point to a central role for odor cues. For example, *Erophylla sezekornii* males produce garlic-scented secretions above their eyes, which they use along with wing movements to attract females to lek mating sites (Murray and Fleming 2008). Similarly, during its mating season, male *L. yerbabuena* smear an odoriferous mixture of various body fluids on their backs, which may provide females with a cue to mate quality given that less-scented males have been found to have higher parasite loads (Muñoz-Romo et al. 2011, 2012; Rincón-Vargas et al. 2013). The similarity between these odors and those of bat-adapted flowers suggests a possible link, in that flowers may be exploiting a preference that originally evolved for interspecific communication.

Vision

The role of vision in nectar-feeding bats still seems to be rather unexplored. As in other phyllostomids, nectar feeders are relatively flexible and may switch between different sensory modalities for different activities. There are older reports that *A. geoffroyi* relied on visual over echolocation cues during escape behavior (Chase 1983), although bats of this species never stop echolocating throughout. Laboratory tests with *G. soricina* that have investigated its spectral sensitivity in choice experiments showed that it cannot distinguish between different parts of the color spectrum and therefore has to be considered color blind, at least for the scotopic (low-light) conditions used in this study (Winter et al. 2003). Interestingly, the same experiments also showed sensitivity at extremely short wavelengths, that is, in the ultraviolet range, which may be an adaptation to enhance visual contrast of ultraviolet-reflecting flowers that could increase their flower search efficiency. The physiological basis for this short wave sensitivity includes the fact that, unlike the visual systems of most diurnal mammals, both their cornea and lens transmit ultraviolet light (Müller et al. 2009), which can then be perceived by both rods (due to the beta-band in rod opsins;

Winter et al. 2003) and cones (due to shortwave-sensitive opsins; Müller et al. 2009). There are several night-blooming flowers, including chiropterophilous ones, that reflect short wavelengths (Biedinger and Barthlott 1993); however, the actual role of ultraviolet perception during foraging remains to be investigated.

Eye sizes vary distinctly between species of nectar bats. While rain forest species such as *Hylonycteris underwoodi* have small eyes, the desert-dwelling *L. yerbabuena* has relatively large eyes (plate 6). Given the distinct differences in the structure of their habitats, this could indicate an adaptation to visual landmark orientation, for example, the outlines of mountains against the horizon during the long-distance flight of the latter in relatively open habitats, which probably plays a lesser role for most rain forest bats. So far, there are no experimental data on the use of vision during identification of flowers as food resources. It is conceivable that, in relatively open habitats such as dry forests or deserts, detection of the silhouettes of flowers may be important, especially at dusk or against a moonlit sky, while relatively closed habitats such as the understory of a rain forest may not provide sufficient light for this. Deserts also tend to have comparably bright flowers, such as those of columnar cacti (e.g., species of *Carnegiea*, *Pachycereus*, and *Stenocereus*), which may provide visual cues from short distances by maximizing contrast between flower and stem.

Spatial Memory

While most fruits or insects can be consumed only once, most flowers produce nectar over a period of several hours or even days, and nectar-feeding bats frequently visit the same floral resource repeatedly throughout the course of a night. In this sense, it is likely more energy-efficient for nectarivores to remember the precise location of past resources than to constantly search for new ones. Because their main nectar resources are renewable, selection likely favors high spatial memory abilities among nectarivores relative to frugivores and insectivores. Accordingly, spatial memory seems to be more important than other sensory cues for relocating previously visited flowers (Carter et al. 2010; Thiele and Winter 2005; Toelch et al. 2008; Winter and Stich 2005). Likely in response to such well-developed spatial memory, individual bat-adapted plants typically flower for months while presenting only one or few

open flowers each night ("steady-state flowering," *sensu* Gentry [1974]) in certain habitats. For instance, plants of the bat-adapted rain forest species *M. neuranthum* will remain in bloom for up to 10 months (Tschapka 2004). Many species of the primarily bat-pollinated rain forest bromeliad genus *Werauhia* cue into bat's spatial memory at an even finer scale: flower buds originally orient outwards from two opposite sides of a flowering stalk, yet all reorient to face in the same direction just before opening, which results in an inflorescence that may be visited from the same side over its entire flowering duration of several weeks (Tschapka and von Helversen 2007). In contrast, bat-pollinated desert columnar cacti have shorter, cornucopia (*sensu* Gentry 1974) flowering seasons (Fleming 2002; Nassar et al. 1997) that could still favor well-developed spatial memory. Trapline foraging, that is, the repeated visitation of a circuit of flowers by the same individual, is likely and has been mentioned repeatedly as a strategy used by nectar-feeding bats (e.g., Fleming 1982; Sazima et al. 1999; von Helversen, 1993). However, actual observational proof of it in the field is still lacking. Advances in modern GPS-based tracking techniques may allow elucidation of such foraging patterns, particularly in species with large home ranges.

Nectar Bat Communities

Phyllostomid nectar bats form guilds (*sensu* Root 1967) that contain more specialized species than bat guilds in other parts of the world (Fleming and Muchhala 2008). Numbers of species in a guild are not easy to access from the literature. It can be difficult to differentiate rare but permanent members of the local guild, which will be shaped by more deterministic assembly processes, from the stochastic occurrence of transient species. The only way to differentiate these is by monitoring the community at a site over extended periods for several years. Species lists from field stations do not necessarily reflect the actual ecological communities, as they have a tendency to accumulate species over time, through stray individuals from neighboring habitats as well as through misidentification of species. The minute diagnostic differences in dentition among species of *Glossophaga*, for example, make nectar-feeding bats in this context a particularly problematic group.

Local guilds of nectar bats usually contain one to six species (Fleming and Muchhala 2008; Fleming

et al. 2005). Additionally, often a smaller number of generalist phyllostomids feed from the locally available flower resources. These species, such as the omnivorous *Phyllostomus* spp. or the frugivorous *Carollia perspicillata* and *Artibeus jamaicensis*, are typically less capable at hovering and only use the few plant species that provide large amounts of easily accessible nectar, such as *Ochroma pyramidale* or *Ceiba pentandra* (Kays et al. 2012). Drier or more seasonal habitats also seem to promote nectar feeding among bats not specialized on flower visitation (MacSwiney G. et al. 2012; Tschapka and Dressler 2002). Most commonly, the core of lowland nectar-feeding guilds is formed by species of *Glossophaga*, although in South America these are sometimes replaced by small lonchophyllines such as *Hsundaycteris thomasi*, while in montane habitats species of *Anoura* are often the most abundant nectar specialists (Fleming et al. 2005). Species that are more specialized morphologically, such as *M. harrisoni*, *H. underwoodi*, *A. fistulata*, and *Choeronycteris mexicana*, are in general far less abundant than the less-derived species, such as *G. soricina*.

Neotropical nectar bat communities are highly dynamic because the species depend on seasonally changing flower resources. Consequently, communities possess a core of resident species that are consistently present year-round, while other species fluctuate in numbers or are simply absent for part of the year (Sperr et al. 2011; Tschapka 2004). A seasonal presence at a location can be the consequence of long-distance migration or of more local resource-tracking movements, such as altitudinal migrations. It is feasible that there is a continuum between seasonal local movements and long-distance migration that so far is not very well understood. Long-distance migration is observed at the northern extreme of the distribution of phyllostomid bats, where the relatively large species *Leptonycteris yerbabuena*, *L. nivalis*, and *C. mexicana* track seasonal flowering peaks (e.g., of *Agave* spp. or columnar cacti such as *Carnegiea gigantea*) in the deserts between Mexico and the United States (Moreno-Valdez et al. 2004; Penalba et al. 2006; Scott 2004). The well-studied migrations of *L. yerbabuena* in Mexico provide an especially interesting case, and there is evidence of two distinct migration patterns with different reproductive timing on the Mexican mainland (Fleming and Nassar 2002). While about half of the females migrate northwards during early spring and give birth in the

Sonoran Desert, the remaining half remain in central and southern Mexico and give birth in December/January (Fleming et al. 1993; Stoner et al. 2003). These different behavioral modes do not represent genetically distinct groups but probably reflect individual decisions by females concerning where to roost (Newton 2002). Males largely remain relatively sedentary and likely provide genetic connectivity between populations of more mobile females. Body size is probably a key trait in migration, as larger species are capable of storing the energy necessary for buffering long-distance flight (Winter and von Helversen 2001), while small species are probably restricted to more local movements, for example, altitudinal migration along mountain slopes.

Patterns of resource partitioning by nectar bats and the underlying plant traits that shape their guilds are still relatively unexplored. Territoriality is only rarely observed among nectar-feeding bats. When nectar bats gather at plants with high resource density, such as *Mucuna holtonii* (Fabaceae) or at *Quararibea cordata* (Malvaceae), animals are occasionally observed chasing each other from the flowers, and the typical distress calls of *Glossophaga* spp. or *Lonchophylla robusta* can be heard during these occasions. Similar observations can be made at artificial feeders, which offer an extremely rich and long-lasting resource. However, this behavior seems to be restricted to especially profitable resources, in marked contrast to the frequent occurrence of territoriality in the ecologically similar hummingbirds (Fleming et al. 2005). This may reflect differences in the sensory systems used by bats, in that echolocation functions over a much shorter distance than vision (Kalko 2004) and may not allow bats to detect competitors entering a territory in time to prevent consumption of resources. Defense of a foraging territory therefore may only be feasible at plants offering very high resource density—that is, a substantial amount of food concentrated in a very small area that can be easily defended. Correspondingly, field observations of resource defense by glossophagine bats come from plant species offering many flowers at large inflorescences, such as *Agave desmettiana* (Agavaceae) (Lemke 1984) or *Calyptrogyne ghiesbreghtiana* (Arecaceae). At the latter species, *G. commissarisi* defends access not only against conspecifics but also against small *Artibeus* spp. and katydid insects (Orthoptera: Ensifera) (Tschapka 2003). In most situations, however, community structuring by competition likely reflects exploitative rather

than interference competition. This may have selected for small body size in glossophagines since smaller species have lower energy requirements (Winter and von Helversen 2001). Additional benefits of being small include increased maneuverability, which facilitates access to flowers. In turn, smaller size and lower energetic requirements may have facilitated the evolution of bat-adapted flowers in the New World. In line with this, trees provide the majority of flowers in the Old World, while a diversity of growth forms (vines, herbs, epiphytes, and trees) provide bat-adapted flowers in the New World (Fleming et al. 2005).

There is evidence that bats make foraging choices based on the energy density of floral resources, in terms of nectar volume, sugar concentration, number of flowers, and density of plants. In a Costa Rican lowland guild of four nectar bat species, *Lichonycteris obscura* and *L. robusta* visited the study site only during the main flowering season and favored plants with high energy density that permitted very efficient foraging (Tschapka 2004). Among the permanent residents at that study site, the common and less-specialized *G. commissarisi* favored plants offering high feeding efficiency for part of the year and then switched to feeding on abundant fruit when these were no longer available. The morphologically more specialized nectar-feeder *H. underwoodi* visited flowers year-round, including those with lower nectar density that required a higher flight effort per night.

Differences in wing characteristics support the idea

of resource partitioning based on foraging efficiency. Compared to differences between bat families (Findley et al. 1972), the differences in wing proportions among nectar-feeding phyllostomids are subtle, yet they may reflect adaptations to different spatial foraging strategies. One can quantify wing proportions by calculating the aspect ratio index and wing tip index, indices that reflect basic flight characteristics of bats (Findley et al. 1972). The aspect ratio index assesses relative antero-posterior width of the wing, with high values indicating narrow wings, which allow for rapid flight. The wing tip index measures the length of the wing tip relative to the forearm; relatively long tips also aid with high flight speeds and are found in hovering species. Data on these wing proportions compiled for nine nectar bat species from Costa Rica and Mexico reveal some interesting patterns (fig. 16.2). Within the La Selva guild, the specialized *H. underwoodi* has wings with both a higher aspect ratio index and higher wing tip index than the generalized *G. commissarisi*, which may be an adaptation to their efficient visitation to the more scattered low nectar density plants. Among all species in fig. 16.2, the highest aspect ratio indexes were found in *Anoura geoffroyi* and *Anoura cultrata*. Species of *Anoura* are characteristic inhabitants of montane forests. Perhaps the high aspect ratio index, indicating an adaptation to fast long-distance flight, in combination with their relatively large body size allows these species to occupy more flexible niches in montane habitats. While based at a permanent roosting cave, they may quickly reach

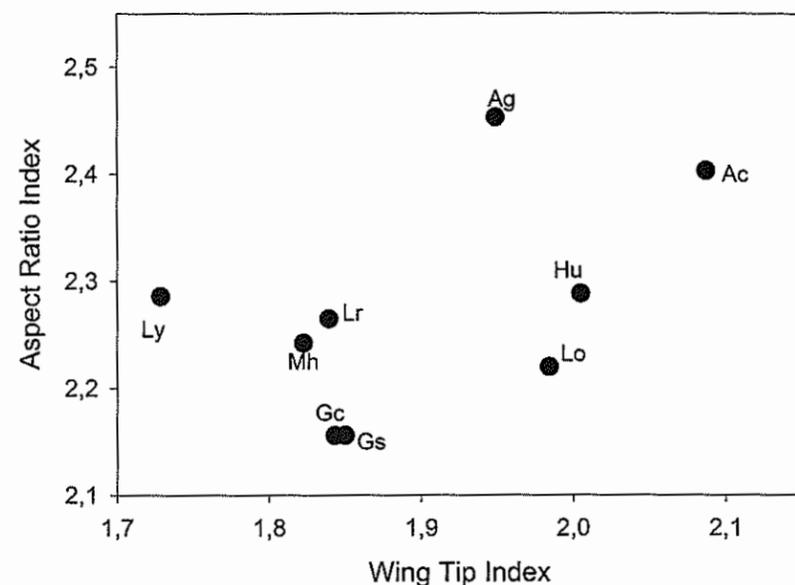


Figure 16.2. Wing proportions of nectar-feeding bats. *Anoura geoffroyi* and *A. cultrata* show a higher aspect ratio index than all other species. Species abbreviations and sample sizes: Ac: *A. cultrata* (4), Ag: *Anoura geoffroyi* (22), Gc: *Glossophaga commissarisi* (276), Gs: *G. soricina* (175), Hu: *Hylonycteris underwoodi* (41), Lo: *Lichonycteris obscura* (27), Lr: *Lonchophylla robusta* (71), Ly: *Leptonycteris yerbabuenae* (124), Mh: *Musonycteris harrisoni* (46).

foraging habitats in different altitudes with different floral resources, allowing these bats to track temporal shifts in local floral resource availability along mountain slopes.

Habitats with low nectar density will be unable to support large populations of nectar-feeding bats, particularly for those species that only rarely use alternative resource classes (fruits and/or insects). Small population size may ultimately also restrict mating behavior, in that species occurring at low densities will have fewer mating opportunities (see chap. 13, this vol.). The flexible diet of *Glossophaga* spp. allows the occurrence of large populations with roosts containing up to hundreds of individuals. In contrast, the largest colony reported of the more nectar-dependent *H. underwoodi* contained only eight individuals (LaVal and Fitch 1977), so mating opportunities should be more limited in this species. Although *G. commissarisi* and *H. underwoodi* are similar in size (body mass 8.8 g vs. 7.6 g, respectively; Tschapka 2004), maximum testis size differs by a factor of two (fig. 16.3). Testis size is a morphological correlate for the occurrence of sperm competition (Wilkinson and McCracken 2003; chap. 13, this vol.). The comparatively large testes of *G. commissarisi* suggest that sperm competition plays a more important role for it than for *H. underwoodi*. A female *Glossophaga* may easily encounter and mate with several males, who therefore compete with each other for paternity, while multiple matings should be much less frequent in the uncommon *H. underwoodi*. The small

testes of *Hylonycteris* and several other highly specialized and rare species, such as *M. harrisoni* and *L. obscura*, may therefore be an anatomical representation of a mating system adapted to low population densities in nectar-poor habitats.

Species of *Leptonycteris* (especially *L. curasoae* and *L. yerbabuenae*) are the largest glossophagines and differ from all other nectar-feeding phyllostomids by living in colonies containing tens of thousands of individuals (Fleming and Nassaar 2002). When feeding on the flowers of columnar cacti, these strong-flying bats commute long distances from their day roosts to their foraging areas (e.g., up to 90 km one-way; Y. Yossel, pers. comm.). Their large size (up to ca. 30 g) and high aspect ratio wings result in efficient long-distance commute flights (Sahley et al. 1993).

Bat-Pollinated Flowers

Despite the recent appearance of nectar-feeding phyllostomid bats (ca. 20 mya; Baker et al. 2012) relative to other pollinating animals, a substantial number of tropical and desert plants have adapted to bat pollination in the New World, including more than 500 species from 67 families (Fleming et al. 2009). Flowers of these plants typically share a suite of traits, termed the chiropterophilous pollination syndrome, that adapt them to pollination by bats. In many cases, chiropterophily has evolved from ornithophilous ancestors, specifically pollination by hummingbirds (Fleming et al. 2009;

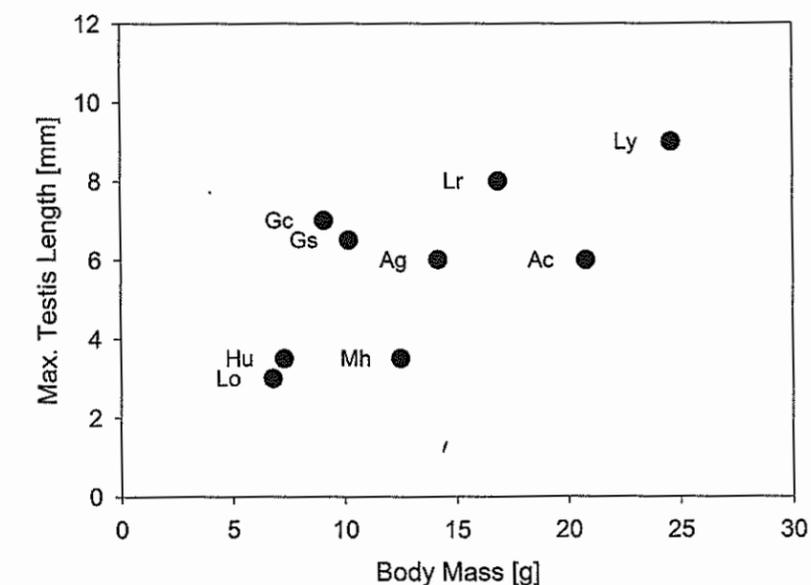


Figure 16.3. Testis size in nectar-feeding bats. Maximum testes length is plotted to account for the seasonal changes in testicle size. *Musonycteris harrisoni*, *Hylonycteris underwoodi*, and *Lichonycteris obscura* show remarkably small testicles for these species' overall size, suggesting a low level of sperm competition. Species abbreviations as in figure 16.2 (with sample sizes in parentheses): Ag (9), Ac (2), Gc (133), Gs (32), Hu (18), Lo (9), Lr (15), Ly (105), Mh (22).

Knox et al. 2008; Martén-Rodríguez et al. 2009; Tripp and Manos 2008).

Botanists have long recognized that different types of pollinators lead to convergent evolution on different suites of traits, and began to formalize descriptions of these pollination syndromes in the middle of the twentieth century (Baker 1961; van der Pijl 1961; Vogel 1954, 1969). For chiropterophily, these traits traditionally include (1) nocturnal anthesis, (2) whitish or drab colors, (3) large and sturdy flowers, (4) large amounts of nectar and pollen, (5) “unfresh” smell, and (6) well-exposed flowers positioned outside of the foliage (van der Pijl 1961; Vogel 1969). Since these initial descriptions, our understanding of the variety and evolutionary significance of these traits has progressed as bat pollination has been documented in more plants (Dobat and Peikert-Holle 1985; Fleming et al. 2009) and as the interaction between these mutualists has been studied in more detail.

The majority of chiropterophilous traits can be readily understood as outcomes of selective pressures imposed by relatively large nocturnal animals; these include nocturnal anthesis, large flower size, and the production of copious amounts of nectar. Given their exceptionally high metabolic rates, phyllostomid nectar bats require large quantities of nectar to satisfy their nightly energy needs. However, the copious nectar that bat flowers produce tends to be dilute compared to that of other flowers, typically with less than 20% sugar content (Perret et al. 2001; Roces et al. 1993; Sazima et al. 1999; von Helversen 1993). This is initially surprising, given that bats provided with options of different concentrations prefer higher sugar levels, up to a threshold of 60% (Roces et al. 1993; Rodríguez-Peña et al. 2007). This apparent discrepancy resolves when one considers that flowers have access to a set amount of sugar to dispense and thus can either increase quantity (more water, lower concentration) or quality (less water, higher concentration). Bats prefer both the greatest quantity and the highest quality per flower, but their ability to distinguish differences in either decreases at higher amounts. An elegant combination of experiments and computer simulations (Nachev et al. 2017) demonstrated that this leads to a preferred balance of quantity and quality involving moderate amounts of dilute nectar, close in concentration levels to that found in nature.

Along with relatively low overall sugar concentrations, bat-adapted flowers tend to have higher levels of

hexoses (fructose and glucose) than sucroses in their nectar, in contrast to the sucrose-dominated nectar of insect- and bird-adapted flowers (Baker and Baker 1990; Baker et al. 1998; Rodríguez-Peña et al. 2016). However, bats actually prefer sucrose over hexose when given the choice (Aguirre et al. 2002; Herrera 1999) or fail to show any preference (Rodríguez-Peña et al. 2007). Thus, bats do not seem to select for hexose, and the evolutionary significance of high hexose levels in bat flowers remains a mystery.

Due to the relatively large size of phyllostomids and their rough handling of flowers during visits (compared to birds and insects), the petals and pedicels/peduncles of chiropterophilous flowers tend to be particularly sturdy. While hummingbirds and insects typically do not displace flowers during visits, bats either hover throughout visits, displacing them as they quickly enter and exit corollas (visits usually last only 0.3–0.6 s), or they cling briefly, hooking onto petals with their thumb claws and pulling the flowers down under their weight (Voigt 2004). Aside from sturdiness, the fit between bat and flower is another important aspect of floral size and shape. Two main morphologies can be found among chiropterophilous flowers: a “shaving brush” shape, with open flowers/inflorescences and multiple projecting stamens, and a “cup” or “bell” shape with petals forming a relatively wide tube that fits around the head of the bat. The former is more common among Old World flowers pollinated by pteropodids (Fleming and Muchhala 2008), including species of *Sonneratia* (Nor Zalipah et al. 2016) and *Syzygium* (Law 2001); they can also be seen in phyllostomid-pollinated New World species such as *Pseudobombax ellipticum* (Dobat and Peikert-Holle 1985). Tubular flowers are much more common in the New World (see plate 7) and range from the long tubes of *Pitcairnia* (Muchhala and Jarrín-V. 2002) and *Centropogon nigricans* (Muchhala 2006a) to the bell shapes of *Werauhia gladioliflora* (Tschapka and von Helversen 2007) and *Burmeistera* (Muchhala 2006b) to the conical shapes of cacti such as *Weberocereus tunilla* (Tschapka et al. 1999) and *Pachycereus* spp. (Fleming et al. 2001). For these tubular flowers, the width of the opening is particularly important to properly guide bats’ heads and thus maximize contact with the flower’s reproductive parts (Muchhala 2007). Chiropterophilous flowers tend to be wider than ornithophilous flowers, which are narrower to fit birds’ bills (Castellanos et al. 2004) and sphingoph-

ilous flowers, which are particularly narrow to fit the hawkmoths’ probosces (Johnson et al. 2016). There are also instances of bat-adapted flowers that cannot be easily classified as either shaving brush or tubular, such as the papilionaceous flowers of *Mucuna* (von Helversen and von Helversen 2003) or the candelabra-like inflorescences of *Marcgravia* (Tschapka et al. 2006). For additional photographs and illustrations of the various shapes of bat-adapted flowers, please see Dobat and Peikert-Holle (1985).

Along with aspects of floral morphology to withstand and effectively transfer pollen during bat visits, selective pressures on chiropterophilous flowers will also favor traits that maximize attraction of their bat pollinators. As discussed above, vision, olfaction, and echolocation likely all play roles in nectar bat foraging. Of these, vision is arguably the least important, given the low light availability at night. While hummingbird and insect flowers are marked by a diversity of vibrant colors, bat flowers tend to be unsaturated (dull colored), reflecting the fact that bats are presumed to be color blind (Winter et al. 2003). In the Old World, despite low saturation, the flowers adapted to pteropodid fruit bats often display high brightness (e.g., white or cream coloration; Baker 1961), which likely reflects a heavier reliance on vision among the nonecholocating pteropodids (Liu et al. 2015; von Helversen 1993). In the New World, flowers adapted to phyllostomid nectar bats typically display both low saturation and low brightness, and shades of green or purple are the most common (although there are exceptions such as the bright cactus flowers of North American deserts). This marks a strong contrast with nocturnal flowers adapted to moth pollination, which are typically bright white (Grant 1983). In fact, the darker shades of some Neotropical bat flowers have been hypothesized to reflect an evolutionary tactic to “hide” the flowers from moths or other unwanted pollinators (von Helversen 1993). Experimental studies have shown that hawkmoths prefer white flowers under dim conditions, likely due to their high contrast and visibility (Goyret et al. 2008; Goyret and Yuan 2015). Given that hawkmoths typically do not contact stamens/stigmas during visits to bat-adapted flowers (Ibarra-Cerdeña et al. 2005; Machado et al. 1998), selection may favor darker colors to deter hawkmoth visits and conserve nectar for bats.

Chemical attractants are universally used for pollinator attraction, and bat-pollinated flowers are no

exception. The smell of bat-pollinated flowers has been described as unpleasant, for example, garlicky, musky, or cadaver-like (Dobat and Peikert-Holle 1985). Interestingly, many Neotropical species share the presence of sulfurous compounds, which are only rarely found among floral attractants (Bestmann et al. 1997; Knudsen and Tollsten 1995). Experiments in a captive colony with naive bats showed that the compound dimethyl disulphide is an innate attractant for the nectar-feeding bat *G. soricina* (von Helversen et al. 2000). This substance is found in a number of Neotropical bat-pollinated flowers, but Old World bat plants seem not to use it at all (Pettersson et al. 2004). In fact, flowers of *Ceiba pentandra* in the New World contain dimethyl disulphide while those in the Old World do not (Pettersson et al. 2004; von Helversen et al. 2000). Supporting this, flight cage experiments found that the Old World nectar-feeding bat *Eonycteris spelaea* is not attracted to it (Carter and Stewart 2015).

Aside from scent and vision, phyllostomid bats also rely on echolocation while foraging. As in almost all bat families, echolocation is critical to their orientation at night (Gonzalez-Terrazas, Koblitz et al. 2016; Gonzalez-Terrazas, Martel et al. 2016). It has been recently discovered that some chiropterophilous plants have evolved to exploit this sensory system, providing highly conspicuous echoacoustic signals to guide bats. Von Helversen and von Helversen (1999) demonstrated that the concave upper petals (vexillum) of *M. holtonii* flowers function as acoustic “mirrors” for *Glossophaga*, concentrating and strongly reflecting their echolocation calls and thus signaling the presence of ripe flowers. Newly opened flowers offer the greatest reward, yet are hard to exploit because bats must land in a certain way to trigger the explosive pollination mechanism. Vexillae are common to all Fabaceae flowers, and in this case selection by nectar bats appears to have optimized it as a specialized echo reflector, maximizing successful visitation and thus pollen transfer (von Helversen and von Helversen 1999, 2003). *Marcgravia evenia* exhibit a similar phenomenon: specialized dish-shaped leaves positioned above their inflorescences provide consistently strong and invariant echoes over wide angles of incidence (Simon et al. 2011). Flight cage experiments have demonstrated that the presence of these leaves greatly reduce search times for flowers (Simon et al. 2011). The ubiquity of such echoacoustic “beacons” among bat-adapted flowers is still unclear, although

it has been suggested that the bell-shaped corollas of many flowers may function in a similar fashion and that the waxy petals common to many bat flowers also serve to increase echo reflectance (Holderied and von Helversen 2006; von Helversen et al. 2003). Even in the absence of explicit beacons, chiropterophilous flowers can facilitate their detection by echolocating animals by reducing the presence of background obstructions that would otherwise lead to acoustic “clutter echoes.” The well-exposed nature of chiropterophilous flowers noted early on in descriptions of pollination syndromes (*sensu* van der Pijl [1961, 51]: “a peculiar position outside of the foliage”) may represent an adaptation to do this (Winter and von Helversen 2001). Different bat-adapted flowers accomplish this exposure differently, whether through flagelliflory (hanging inflorescences), cauliflory (inflorescences on trunks), or long pedicels (floral stems). Across the primarily bat-pollinated genus *Burmeistera*, the only species that does not possess long pedicels, *B. ceratocarpa*, instead has very small terminal leaves near its flowers, which likely provides an alternate solution to increasing floral exposure by minimizing clutter echoes from these leaves (Muchhala 2006b). Experimental work supports the idea that reducing background clutter aids in detection: in the absence of a complex background of leaves, bats readily located artificial flowers with or without odor cues, while with the leaf background they relied significantly more on odor cues (Muchhala and Serrano 2015). An alternate approach to reducing clutter echoes, rather than eliminating background plant structures, would be to provide background plant structures that are particularly effective at absorbing sound. In a possible example of this, flowers of the columnar cactus *Espostoa* emerge from an apical region that is covered by a cephalium, an area of dense, wooly hairs. These hairs may provide an acoustically nonreflective backdrop, thus enhancing the conspicuousness of echoes from emerging flowers (Schöner et al. 2016; von Helversen et al. 2003). The bat’s sensory system may therefore exert selection on plants not only for ultrasound reflecting but also for nonreflecting surfaces.

Different pollinator types can also exert differing selection pressures on pollen, in terms of the amount produced per flower, its morphology, and its presentation schedule, that is, the manner in which it is made available to pollinators over the life of a flower (Castel-

lanos et al. 2006; Thomson et al. 2000). An extensive comparison of pollen morphology of flowers adapted to bats versus other pollinators, however, found no consistent differences in shape or exine ornamentation, although bat-adapted pollen tended to be larger by around 10% (Stroo 2000). This likely represents a by-product of the larger size of bat flowers, rather than a specific adaptation to bats, since a strong correlation between style length and pollen size was also detected. Although morphological differences are not great, chiropterophilous flowers tend to produce much larger quantities of pollen (Faegri and van der Pijl 1979; Skog 1976). For example, among species in an Ecuadorian cloud forest, bat flowers were found to produce sevenfold more pollen on average than hummingbird flowers (Muchhala and Thomson 2010). Flight cage experiments comparing pollen transfer by bats and hummingbirds found a strong positive linear relationship between the amount of pollen bats picked up from one flower and subsequently delivered to a second flower. However, the same relationship for hummingbirds leveled off quickly; that is, there was an upper limit to how much pollen an individual hummingbird could carry (Muchhala and Thomson 2010). This may be due to behavioral differences or because fur can be loaded with pollen to a greater extent than can feathers. These results suggest that a shift to bat pollination will favor an evolutionary increase in pollen production, as flowers that produce more pollen will sire more seeds, while there is an upper limit to the profitability of increased investment in pollen production among hummingbird flowers. Bats may also select for greater pollen production because of the importance of pollen in their diet, although as mentioned previously, they have only rarely been documented to consume pollen directly from flowers during visits.

In the same way that phyllostomid frugivores, insectivores, and nectarivores do not always exclusively feed from their preferred resource, flowers often do not strictly conform to their pollination syndromes (Ollerton et al. 2009; Waser et al. 1996). Flowers are often visited and pollinated by taxa other than what would be predicted by their floral traits. Chiropterophily is actually one of the best-defined pollination syndromes in terms of the traits that characterize it and its predictive power (Rosas-Guerrero et al. 2014), likely due to the large differences in the size, behavior, and sensory

systems of bats relative to more typical insect and hummingbird pollinators. The traits that adapt a flower to bats probably impose heavy trade-offs, decreasing the effectiveness of other pollinator types, as has been shown for floral width (Muchhala 2007). Even so, there are several well-documented cases of bat-visited flowers also relying on other pollinator types. For instance, bats, bees, and hawkmoths contribute to pollination of *Pachira aquatica* (Hernández-Montero and Sosa 2015), and both bats and hummingbirds can effectively pollinate *Siphocampylus sulfureus* (Sazima et al. 1994), *Aphelandra acanthus* (Muchhala et al. 2009), various Antillean *Gesneria* and *Rhytidophyllum* (Martén-Rodríguez et al. 2009), and several species of columnar cacti (Dar et al. 2006; Fleming et al. 2001).

For their part, nectarivorous phyllostomids will also stray on occasion from flowers that conform to their pollination syndrome. There are records of bats visiting insect- or wind-pollinated flowers (Hernández-Montero and Sosa 2015; Sperr et al. 2011; Tschapka 2004), which they probably do not pollinate effectively and are thus essentially parasitizing floral resources adapted to other pollinators. It is possible that the high energy turnover and associated food requirements of nectar-feeding bats selected for a high degree of inquisitiveness and opportunism in their foraging behavior. Further evidence of their inquisitiveness can be seen in their rapid acceptance of hummingbird feeders across the Neotropics, structures that bear neither visual nor olfactory resemblance to the chiropterophilous syndrome (Tschapka 2003).

Within chiropterophily, there exists very little further specialization in terms of specific bat-flower interactions. All nectar-feeding phyllostomids in a particular habitat tend to visit all bat-adapted flowers available to them; although there often are distinct differences in intensity of use, typically there is almost complete overlap in terms of the floral species in their diets (Muchhala and Jarrín-V. 2002; Tschapka 2004). This is true even for *M. harrisonii*. Although it has the longest jaw of any nectar bat, no flowers are known to be adapted exclusively to its pollination (Tschapka et al. 2008). The only known exceptions to this rule are two species in the diet of *A. fistulata*. *C. nigricans* (Muchhala 2006a; Muchhala and Thomson 2009) and *Marcgravia williamsii* (Muchhala, unpublished data) have flower/nectary depths that prevent other bats from accessing their nectar

and are exclusively pollinated by *A. fistulata*. The fact that bat flowers do not typically specialize on different phyllostomid species comes with a fitness cost: bats regularly carry the pollen of multiple flowers on their fur (Muchhala and Jarrín-V. 2002; Tschapka 2004), losing pollen to foreign flowers and clogging stigmas with foreign pollen (Muchhala and Thomson 2012). In response to this cost, different bat flowers in a given habitat or clade will often place their pollen on different parts of bat bodies (Howell 1977; von Helversen 1995). For species with less precise pollen placement, this partitioning is relatively coarse, as in species of *Marcgravia* (Tschapka et al. 2006), which will use either the ventral or the dorsal surfaces of bat bodies and wings. *Burmeistera* flowers represent the opposite extreme because they pick up and deposit pollen from a precise spot on bats’ heads, and multiple species can coexist with limited pollen mixing by varying this location from the end of the snout to between the shoulder blades (Muchhala 2008; Muchhala and Potts 2007).

Conclusions

Nectar-feeding bats are a large and diverse group of phyllostomid species that have enlisted plant partners in all major habitats of the Neotropics, from the deserts of Mexico and South America to Amazonian rainforests, up to the cloud forests of Central American cordilleras and the Andes. Nectarivory has evolved twice among phyllostomids, in the Glossophaginae and Lonchophyllinae. Species in these two subfamilies all possess elongated tongues and rostrums and the ability to hover, yet they differ in details of tongue morphology and feeding behavior. While the nectar of the coevolved flowers constitutes their main resource, for many species insects and fruits play an important role seasonally or even year-round. It is likely that the high energetic requirements for these animals selected for an extreme dietary flexibility and the ability to use many accessible resources. For plants, this flexibility results in a continuum ranging from coevolved mutualisms with highly efficient pollination (e.g., *M. neuranthum*, *C. gigantea*, *Crescentia alata*, *C. nigricans*) to parasitism where the bats are mere consumers of floral resources without providing benefits for the plants (e.g., insect- or wind-pollinated plants). This wide range of interactions offers interesting possibilities for studying evolutionary

trade-offs because fitness consequences of bat-plant interactions are relatively easy quantified. Energetic benefits for bats can be estimated in kilojoules content of the nectar, while benefits of plants can be estimated by percentage of seed set.

While we have greatly improved our understanding of nectar bat biology over the past several decades, particularly in terms of physiology and behavior, much remains to be explored. We still do not fully understand nectar bat foraging behavior, in terms of what cues they rely on to find flowers, the importance of these cues when locating and approaching flowers, and typical movement patterns throughout nights and years. Some particularly interesting questions that we would like to highlight include the following. (1) Do nectar-feeding bats perform traplining, moving in predictable circuits each night? (2) Do they migrate, either locally or regionally, through the year? (3) Do they perceive colors at dusk/dawn, and what is the role of ultraviolet vision in movement and foraging? (4) To what extent do they actively hunt insects? (5) How do lonchophylline tongues extract nectar? (6) How do communities of nectar bats partition resources, and to what extent do they compete, either directly (territoriality/aggression) or indirectly (exploitative competition)? (7) Why are bat flowers hexose rich?

Finally, relatively little work has been done on conservation of nectar-feeding bats. As for most phyllostomids, nectar-feeding bats suffer from habitat loss and habitat fragmentation, which changes plant species composition and therefore also affects their native food resources. However, in contrast to, for example, most of the gleaning animalivores (chap. 14, this vol.), many nectar-feeding bats can also persist in largely anthropogenically transformed habitats. They roost in abandoned houses, sewer canals, and shacks and may use some cultivated or native species that thrive in disturbed areas. For instance, *Glossophaga* spp. are frequently observed in banana (*Musa* spp.) plantations. Although the cultivated forms of banana do not require pollination for fruit production, the inflorescences offer rich, year-round nectar sources that are readily accepted by bats. The long-term consequences for these bats of such a year-round uniform diet remain largely unexplored, as do the potential impacts of agrochemicals used in the plantations.

The potential impacts of global warming on nectar-feeding phyllostomids are also poorly understood. For

instance, *L. yerbabuenae* colonies use the flowering and fruiting season of several columnar cactus species in the Sonoran Desert to be able to establish their maternity colonies there. The impacts of warming on these bats in the already extreme conditions of these deserts merits further study, especially given that this is a particularly sensitive period of their annual cycle. Finally, besides offering many intellectually stimulating scientific questions as well as urgent conservation challenges, the interaction between flower bats and bat-adapted flowers is also a particularly charismatic one, a fact which can and should be exploited to find more human friends for bats!

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The Frugivores

Evolution, Functional Traits, and Their Role in Seed Dispersal

Introduction

Most bats are insectivorous, but two families—the Old World Pteropodidae (with about 186 species) and New World Phyllostomidae (with about 216 species)—contain species that consume fruits and disperse the seeds of hundreds of species of tropical and subtropical plants. These two families are only distantly related and differ in their evolutionary ages and in many aspects of their morphology, sensory biology, and foraging ecology. Despite these differences, frugivorous bats of both families, along with fruit-eating birds, primates, and a variety of other mammals, play important functional roles in the maintenance and dynamics of tropical and subtropical terrestrial ecosystems worldwide (Fleming and Kress 2013).

Although some species of primarily insectivorous or carnivorous phyllostomids occasionally eat fruit (chap. 14, this vol.), this dietary specialization is concentrated mostly in two morphologically derived subfamilies, Carollinae and Stenodermatinae, whose evolutionary ages are approximately 18–20 million years (Ma). Carollines are much less species rich than stenodermatines (chap. 4, this vol.) and forage for fruit mainly in forest understories. Stenodermatines, in contrast, are the most species-rich phyllostomid clade and have diversified extensively in the last 10 Ma; they forage for fruit mainly in forest canopies (Dumont et al. 2012; Rojas et al. 2012, 2016; Saldaña-Vázquez et al. 2013).

Reflecting their relatively long evolutionary history of interacting with frugivorous bats, tropical fruits whose seeds are dispersed by bats (hereafter “bat fruits”) have a series of morphological and nutritional characteristics that distinguish them from fruits dispersed by other kinds of vertebrate frugivores (e.g., birds and monkeys). Based on his knowledge of Old World pteropodid bats and their food plants, van der Pijl (1982) characterized bat fruits as drab in color sometimes musky smelling, often large and juicy, and sometimes displayed outside plant canopies via flagellicarpy (fruits on long pedicels) or caulicarpy (fruits directly on branches or trunks). Pteropodid fruits