Chapter 9
Fur, Wings, and Flowers: Development and Progress on Nectarivorous Bat Research in the Last 50 Years

Juan I. Moreira-Hernández, Camilo A. Calderón-Acevedo, and Nathan Muchhala

Abstract Nectarivory or the habit of feeding on nectar and pollen from flowers occurs in nearly 5% of all bat species. Nectarivorous bats are found in tropical and subtropical regions around the world and possess a suit of adaptations to find flowers, extract nectar, metabolize sugars and nutrients from nectar and pollen, and fly long distances to find enough food to meet their high metabolic demands. Quick assimilation of ingested sugars allows for fast, powered, and hovering flight. With their long-specialized tongues, bats can rapidly probe flowers and extract nectar efficiently. To find flowers in dark environments, bats rely on their elaborate echolocation system, keen sense of smell, and good vision, which is even sensitive to ultraviolet light in some cases. Some species frequently fly long-distances in agricultural landscapes or following regular migration routes, thus promoting gene flow between plant populations. In addition, nectarivorous bats provide pollination services for hundreds of economically important plant species. The intricate relationships between bats and flowers also provide educational opportunities to raise awareness about the value of bats to our diverse societies and ecosystems, fostering solutions to the conservation challenges faced by bat populations. The North American Society for Bat Research has been an important forum where much of this body

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of work has been presented during the last five decades, and we hope that it will continue to play this role in the future.

Keywords Bat pollination · Chiropterophily · Glossophaginae · Lonchophyllinae · Pteropodidae · Nectarivory

9.1   Introduction

In tropical and subtropical ecosystems bats have adopted multiple dietary niches other than insectivory. Nectarivory, feeding from nectar of angiosperm flowers, has evolved independently in distantly related groups of bats from both Old and New World. Although nectarivory in bats has been known since at least the late nineteenth century, the last several decades have seen increased research in this area. Here, we review much of this work, focusing on studies presented during the 50 years since the first meeting of the North American Society for Bat Research (NASBR).

Bats in the families Pteropodidae and Phyllostomidae account for most nectarivory in Chiroptera (Fig. 9.1). There are approximately 67 bat species from 25 genera ecologically and morphologically specialized for eating nectar (Muchhala and Tschapka 2020; Fleming et al. 2009). This is about 5% of the approximately 1400 species of bats known to date. Fifty-two species in 19 genera of specialized nectarivorous phyllostomids belong to the subfamilies Glossophaginae and Lonchophyllinae. In contrast, specialized nectarivorous pteropodids include 15 species in 6 genera in predominantly frugivorous lineages from three different subfamilies (Pteropodinae, Rousettinae, and Epomophorinae). Species from the two families share a suit of common morphological characteristics adapted for nectarivory. These include narrow and elongated rostra to probe flowers, reduced dentition, and a long tongue adapted for quick nectar extraction (Birt et al. 1997; Tschapka et al. 2015). However, dozens of species from other primarily frugivorous genera in these two families opportunistically visit flowers and eat nectar and pollen either seasonally or on a regular basis (e.g. *Phyllostomus*, *Carollia*, *Sturnira*, *Artibeus* in Phyllostomidae; *Pteropus*, *Eidolon*, *Rousettus*, *Cynopterus* in Pteropodidae; Fleming et al. 2009; Fig. 9.1). There also are two notable cases of nectarivory in the insectivorous families Vespertilionidae (*Antrozous pallidus*; Frick et al. 2009) and Mystacinidae (*Mystacina tuberculata*; Fleming et al. 2009). We consider these frugivorous/nectarivorous and insectivorous/nectarivorous bat groups as opportunistic nectarivores, because nectar and pollen are not their primary food sources. Whether specialized or opportunistic, nectarivorous bats play a major ecological role as pollinators of hundreds of plant species around the world (Fleming et al. 2009), many of considerable socioeconomic importance (Fujita and Tuttle 1991; Trejo-Salazar et al. 2016).

Here we focus on the development and progress of research on nectarivorous bats worldwide. First, we briefly discuss the early descriptions of bat pollination. Second,
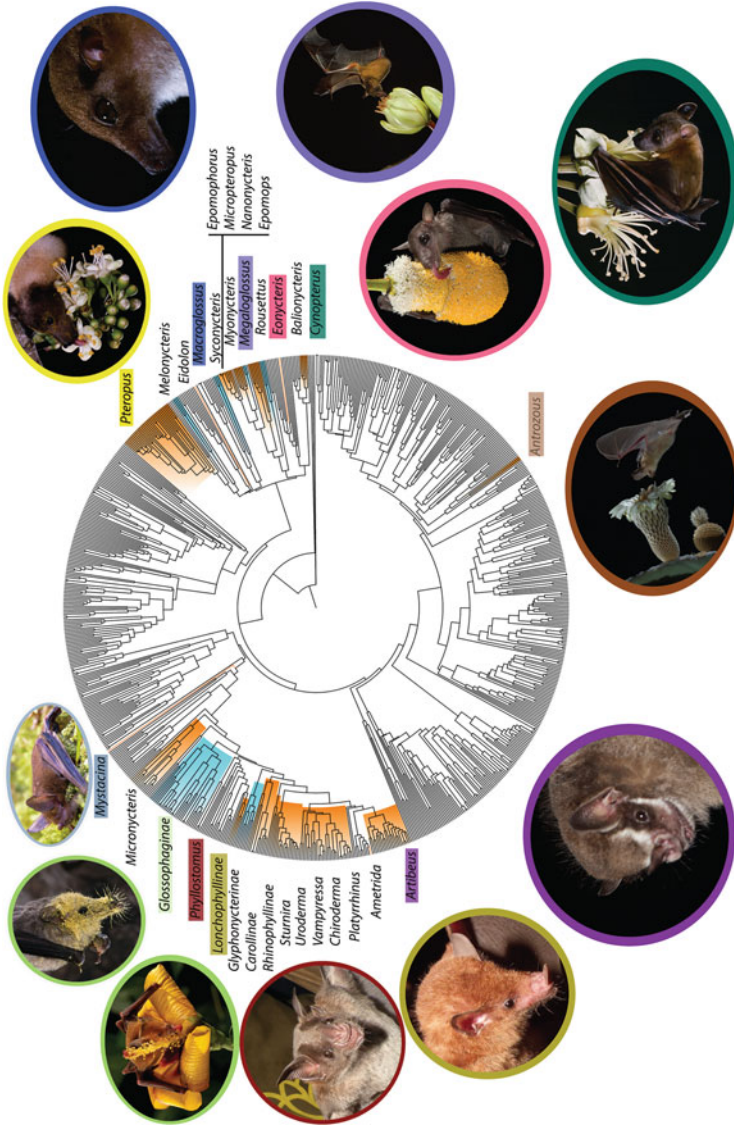
Fig. 9.1 Clades of specialized (*blue*) and opportunistic (*orange*) nectar-feeding bats superimposed on the phylogenetic tree of Chiroptera. All highlighted branches on the *left side* of the tree represent clades belonging to the New World leaf-nosed bat family (Phyllostomidae) except for the New Zealand endemic *Mystacina* (Mystacinidae). Likewise, the colored taxa on the *right side* of the tree belong to the Old World flying fox family (Pteropodidae), with the exception of the opportunistic nectar-feeding North American vesper bat *Antrozous* (Vespertilionidae). Some color-coded representative taxa are also illustrated around the tree. Photo credits: *Mystacina* by S. Parsons; *Phyllostomus* and *Artibeus* by C. Calderón-Acevedo; Lonchophyllinae by N. Muchhala; and all remaining photographs to ©MerlinTuttle.org

we show the emergence of experimental studies on nectarivorous bats that coincide with the start of NASBR. Third, we discuss those key contributions and study systems fundamental to our understanding of this aspect of bat biology. We focus on four themes: (1) physiology of nectar- and pollen-feeding; (2) sensory biology (echolocation, vision, and olfaction); (3) foraging and spatial ecology; and (4) socio-economic aspects of bat pollination and conservation. We then conclude by providing fruitful future research directions and highlighting important gaps in our knowledge.

9.2   Early Descriptions of Bat Pollination

The first publications that established the validity of the bat pollination syndrome (chiropterophily) were based on multiple records accrued since the late 1800s (van der Pijl 1961; Vogel 1969). Chiropterophilous flowers are characterized by nocturnal anthesis, predominantly dull or drab flower colors, strong musty smell, large and sturdy inflorescences and/or flower structures, copious production of pollen and hexose-rich nectar, and exposed flowers or inflorescences often growing along the main trunk and branches or suspended from long stalks away from background foliage to allow easy access by bats. Following these seminal publications, the first wave of experimental studies began in the next decade to investigate the ecological and evolutionary consequences of nectarivory in bats (see Fleming et al. 2009; Muchhala and Tschapka 2020).

9.3   Impact of NASBR on Nectarivorous Bat Research

Some of the earlier developments in research on bat-flower interactions occurred at NASBR. The first meeting in 1970 at Tucson, Arizona, had two papers focused on nectarivorous bats: population status of *Leptonycteris nivalis* in Big Bend National Park, Texas (Easterla 1972) and diet of *Leptonycteris yerbabuenae* on nectar and pollen from several flowering plants in its desert habitat (Howell 1974a). In the decades since, the number of presentations on nectarivorous bats presented at NASBR meetings has increased. To track the recent history of nectarivorous bat research, we perused the programs of 49 years of NASBR meetings (1970–2019). We selected titles that explicitly dealt with bat pollination or with aspects of bat biology linked to the nectarivorous habit. We did not include taxonomic or systematic papers, unless they explicitly addressed aspects of the ecology and evolution of bat nectarivory (e.g. evolution of feeding habits in Phyllostomidae). The resulting full list of presentations and their respective peer-reviewed publications is available online as Electronic Supplementary Material.

We found 287 oral and poster presentations on nectarivore biology at NASBR (Fig. 9.2), which have generated 124 peer-reviewed publications (as of December
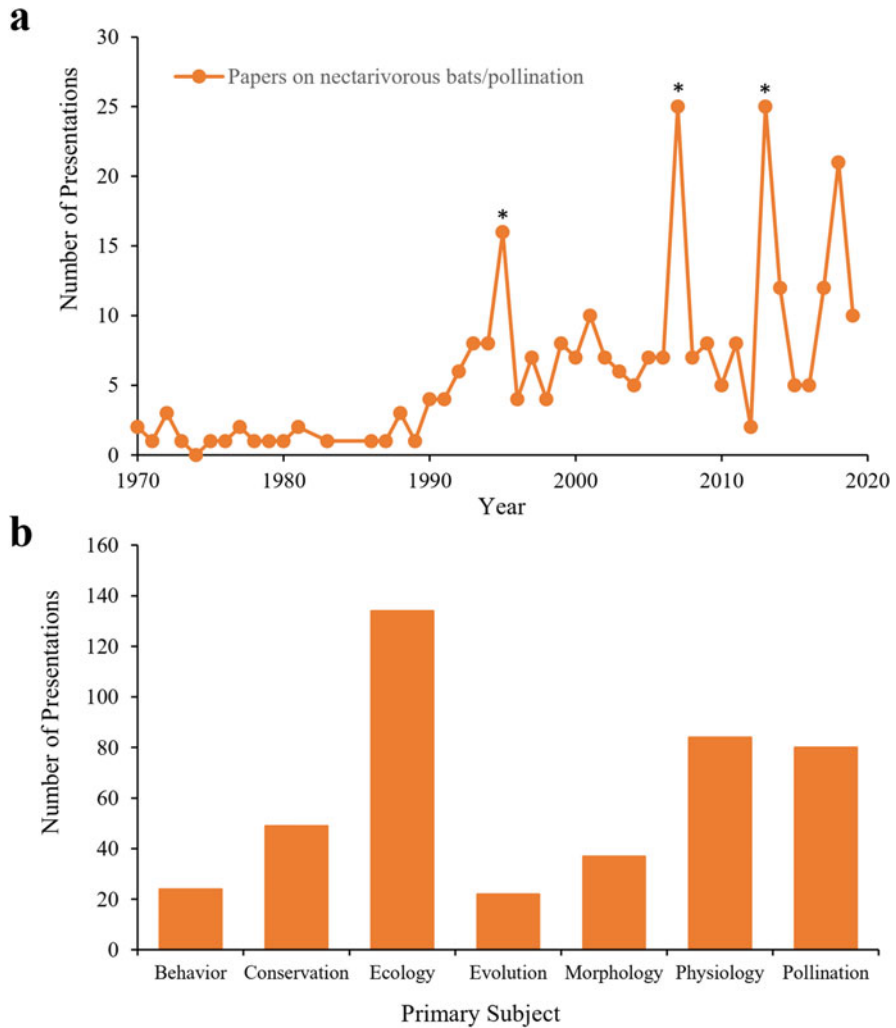
Fig. 9.2 (**a**) Number of poster and oral presentations on nectarivorous bat biology during North American Society for Bat Research (NASBR) meetings per year from 1970 to 2018. Joint NASBR meetings with the International Bat Research Conference showed a greater number of presentations and are indicated with an *asterisk* (Boston, USA 1995; Mérida, México 2007; and San José, Costa Rica 2013). (**b**) Number of poster and oral presentations on nectarivorous bat biology during NASBR meetings from 1970 to 2018 categorized by primary subject

2019). On three occasions when NASBR met with the International Bat Research Conference (Boston, USA 1995, Mérida, México 2007, San José, Costa Rica 2013), there were more oral and poster presentations about nectarivorous bat and pollination research than usual (Fig. 9.2a). There was a similar spike in the numbers of papers presented during the 2018 meeting in Puerto Vallarta, México, reflecting

many Mexican student presenters. The most common topics were ecology (e.g. foraging habits, diet, migration), followed by physiology (e.g. energetics, digestion), pollination (e.g. flower visitation, pollen transfer), and, more recently, conservation (e.g. population status, pollination services to crops; Fig. 9.2b).

We identified 74 nectarivorous bat species mentioned by papers presented at NASBR. These belong to 36 genera and all 4 bat families where nectarivory occurs. They include 29 species in 11 genera from the Old World, of which 5 species in 4 genera are specialists and 24 species in 7 genera are generalists. From the New World, 45 species have been studied, representing 25 genera, comprising 30 species of generalists in 15 genera and 15 specialists from 10 genera. Table 9.1 shows the 15 most common nectarivorous bat species from the New and Old World that were mentioned in presentations at NASBR, with New World nectarivorous phyllostomids better represented than Old World species. Those from the United States and Mexico have been the most studied and most of our examples (>80%) in the next sections are derived from presentations at NASBR, highlighting the importance of this symposium in stimulating nectarivorous bat research.

9.4 Physiology of Nectar- and Pollen-Feeding

Feeding adaptations for nectarivory encompass a set of characters that help bats use pollen and nectar as primary food sources. Finding food may mean traveling long distances, which nectarivorous bats do aided by physiological adaptations for effective energy expenditure, powering up to 80% of their hovering flight with recently ingested sugars (Fleming et al. 1993; Voigt and Winter 1999). One of the early studies on the physiological consequences of nectarivory found that nitrogen-rich pollen constitutes an important supplement to the carbohydrate-rich diet of nectarivorous bats (Howell 1974a). Pollen from bat-pollinated plants germinates in the bats' gut, which increases the amount of nutrients liberated from the grains that bats can absorb. Moreover, pollen from chiropterophilous plants has a higher concentration of nitrogen than closely related plant species pollinated by other animals, suggesting that this high nitrogen content may represent an evolutionary adaptation to encourage bat visitation.

Hovering flight has evolved in very disparate groups that rely primarily on floral resources, such as moths, hummingbirds, and specialized nectarivorous bats (Voigt and Winter 1999; Ingersoll et al. 2018). In vertebrates, this adaptation is energetically expensive and constrained by the aerobic capacity of the flight muscles that must provide lift equal to their body weight. Nectarivorous bats and hummingbirds accomplish this through physiological adaptations for rapid oxygen transport and metabolic breakdown of sugars and long-chain fatty acids in the flight muscles (Voigt and Winter 1999). This energy feeds vigorous flapping movements that generate air vortexes above and below the wings, which help the animal stay airborne. A detailed comparative study of hummingbirds and bats showed that both groups require a similar total amount of aerodynamic power per unit of mass

Table 9.1 The top 15 most-frequently studied species of specialized and opportunistic nectarivorous bats from the New and Old World based on papers presented at the North American Society for Bat Research (NASBR) meetings from 1970 to 2018

New world	Species	# Papers	Old world	Species	# Papers
Phyllostomidae			Pteropodidae		
Glossophaginae	*Leptonycteris yerbabuenae**	56		*Macroglossus minimus*	8
	*Glossophaga soricina**	32		*Syconycteris australis*	8
	*Leptonycteris nivalis**	27		*Eonycteris spelaea*	7
	*Anoura geoffroyi**	16		*Pteropus samoensis*	5
	*Choeronycteris mexicana**	16		*Pteropus vampyrus*	5
	Anoura caudifer	9		*Cynopterus brachyotis*	4
	Monophyllus redmani	9		*Pteropus poliocephalus*	4
	Erophylla sezekorni	8		*Melonycteris melanops*	3
	Glossophaga longirostris	6		*Pteropus mariannus*	3
	Leptonycteris curasoae	6		*Pteropus rufus*	3
	Phyllonycteris poeyi	6		*Rousettus aegyptiacus*	3
	Glossophaga commissarisi	5		*Rousettus amplexicaudatus*	3
Lonchophyllinae	*Lonchophylla robusta*	7		*Cynopterus sphinx*	2
Stenodermatinae	*Artibeus jamaicensis**	5		*Macroglossus sobrinus*	2
Vespertilionidae	*Antrozous pallidus**	5		*Pteropus hypomelanus*	2

Specialized nectarivorous bats are shown in bold. New World species that occur in the United States and Mexico are indicated by an asterisk

(Ingersoll et al. 2018), but they differ in the mechanism to produce lift. Hummingbirds generate this force through very fast mostly horizontal wingbeats, whereas bats drag their proportionally longer wings during extended downstrokes (Ingersoll et al. 2018). The convergence towards hovering flight among hummingbirds and bats is striking, given its high energetic costs, and implies long-term availability of abundant and spatially predictable nectar resources during the evolution of these nectarivorous taxa in the Neotropics.

Feeding habits and physiological responses have been studied in some Old World pteropodids. A good example is the specialist *Syconycteris australis*, which is highly limited by the availability of nitrogen in its diet (Law 1992). Compared to opportunistic nectarivores, such as flying foxes (*Pteropus* spp.), *S. australis* exhibits slower pollen passage time in the gut that encourages pollen germination and an efficient nitrogen uptake to meet its nightly nitrogen needs.

Some of the most remarkable adaptations of nectarivorous bats are their feeding mechanisms and the role of the tongue in facilitating rapid nectar extraction (Birt et al. 1997; Tschapka et al. 2015). Although all nectarivorous bats have elongated tongues to reach deep into flowers (Birt et al. 1997; Muchhala and Tschapka 2020), different groups exhibit distinct feeding behaviors and tongue morphology. Glossophagines have long tongues with hair-like erectile papillae at the tip, and feed using fast lapping movements during which the papillae form rows that encircle nectar before the retracting tongue carries it into the mouth (Muchhala and Tschapka 2020). In contrast, lonchophyllines have mostly hairless tongues with lateral grooves along the length where nectar is drawn towards the mouth through a combination of capillary action and dynamic tongue pumping (Tschapka et al. 2015). Lonchophyllines must keep their tongues fully extended and immersed in the nectar during this process (Tschapka et al. 2015). In specialized nectarivorous pteropodids (e.g. *Eonycteris spelaea*), tongues are often long, protractible, and covered in long filiform papillae (Birt et al. 1997). In contrast, tongues of generalist pteropodids (e.g. *Pteropus*, *Epomophorus*) are not as long, but are still longer than other frugivorous pteropodids and are covered by different types of papillae that facilitate feeding on both nectar and fruit. The physiological adaptations of nectarivorous bats remain relatively underexplored, but are crucial to understanding their ecology and evolution. This baseline information is in turn necessary to predict how nectarivorous bat populations may respond to rapid environmental change and other anthropogenic threats. For example, climate change effects on flowering phenology may decrease food availability and impose heavy physiological constraints on those bat species unable to migrate or switch to alternative food resources.

9.5 Behavior and Sensory Biology

Nectarivorous bats have a suite of behavioral and sensory adaptations to find flowers. In phyllostomids and pteropodids, foraging involves integrating multiple sensory systems in response to diverse floral stimuli. In both groups, large scale orientation is based on a combination of olfactory and visual cues, which phyllostomids further supplement with acoustic cues (Egert-Berg et al. 2018; Muchhala and Tschapka 2020). Floral volatiles containing dimethyl sulfide and other sulfuric compounds have evolved convergently in several New World bat-pollinated plant species (Pettersson et al. 2004). In contrast, Old World bat-pollinated plants seem to lack any consistent scent bouquet pattern (Pettersson et al. 2004), and experimental tests have demonstrated that dimethyl sulfide is not

preferred by pteropodid bats (Carter and Stewart 2015). Notably, the flowers from Old World populations of the pantropical bat-pollinated canopy tree *Ceiba pentandra* do not emit dimethyl sulfide (Pettersson et al. 2004), whereas its Neotropical populations do. These findings suggest that Old and New World nectarivorous bats exert different selection pressures on the floral scents of the plant species they pollinate. Research devoted to elucidate the timeline and mechanisms explaining this divergence would be useful to understand the evolution of floral scents mediated by bat pollinators.

The importance of echolocation for foraging by specialized nectarivorous Phyllostomidae was first observed decades ago. Glossophagine and lonchophylline bats use typical low-intensity, short-duration, broadband, multi-harmonic, and frequency-modulated echolocation calls that are efficient for orientation in cluttered environments (Muchhala and Tschapka 2020). However, different nectarivorous species rely on floral resources to varying degrees, and some even shift almost entirely to insectivory or frugivory for part of the year. The echolocation capabilities of different nectarivorous phyllostomids have only been directly compared in one study that exposed four species to a standardized test of wire array avoidance in a flight room (Howell 1974b). This study found that the seasonally insectivorous *A. geoffroyi* and *G. soricina* were able to detect and avoid wires as thin as those detected by insectivorous bats. In contrast, *L. yerbabuenae* performed poorly on this test and performance of *Choeronycteris mexicana* was intermediate between the extremes.

Glossophagines use their echolocation to detect distinctive echoes reflected by flowers (von Helversen and von Helversen 1999; Simon et al. 2011). Conspicuous acoustic properties of a bat-pollinated flower were first described for the legume liana *Mucuna holtonii*. Freshly-opened flowers in this species possess a small concave petal directly above the nectar opening and this "acoustic guide" produces high amplitude echoes conspicous to bats flying nearby (von Helversen and von Helversen 1999). Removing these signals from flowers in the field reduced bat visitation from 88 to 21%. Other plants have modified leaves subtending their flowers with echo-reflecting properties that effectively make them acoustic beacons. Such is the case of the woody vine *Marcgravia evenia*, in which disk-shaped leaves displayed on top of the inflorescences exhibit strong and invariant acoustic signatures (Simon et al. 2011). In controlled experiments with *G. soricina*, the removal of these disk-shaped leaves doubled the time it took the bats to find the flowers. In other bat-pollinated plants lacking obvious acoustic beacon structures, the whole flower itself may likely be the unit of attraction. Glossophagine bats utilize the acoustic properties of flowers during foraging and readily integrate this information with input from other sensory systems according to context and background complexity (Muchhala and Serrano 2015). We expect lonchophyllines and opportunistic nectarivorous phyllostomids to similarly rely on acoustic signals, although there is little research to date in these groups.

Pteropodids are mainly nocturnal, do not have ultrasonic laryngeal echolocation, and have large, conspicuous eyes with tapeta lucida that reflects light. Some roost in dark locations such as hollow trees, caves, and mines. In contrast to phyllostomids,

pteropodids had been assumed to orient by vision, except for *R. aegyptiacus* which echolocates with tongue clicks (Yovel et al. 2011). The lingual echolocation by *R. aegyptiacus* is sophisticated and well developed even though it was originally considered rudimentary. It remains to be seen if any pteropodid other than *R. aegyptiacus* uses echolocation for foraging.

The role of night vision in foraging by nectarivorous bats remains largely unexplored. Ultraviolet light detection has been demonstrated for *G. soricina* (Winter et al. 2003). Studies of gene function of UV-sensitive opsins across bats suggest ultraviolet vision in other glossophagines (e.g. *Anoura caudifer*, *L. yerbabuenae*) and some pteropodids (e.g. *Cynopterus sphinx*), but it was apparently lost in obligate cave roosters (e.g. *Lonchophylla mordax*; Kries et al. 2018). Ultraviolet light detection might be advantageous for foraging in dim light conditions such as during twilight hours, or while approaching ultraviolet-reflecting flowers with dark vegetation or a night sky in the background (Winter et al. 2003; Fleming et al. 2009).

9.6   Foraging and Movement Ecology

The physiology, feeding habits, and movement ecology of nectarivorous bat are highly interdependent. For example, *L. yerbabuenae* is the main pollinator of several *Agave* species and readily exploit the clumped distribution of these plants in space and time (Howell and Roth 1981). Similarly, the temporally aggregated blooming of various columnar cacti species in the spring and several *Agave* species in autumn along the Pacific coast of Mexico forms a veritable nectar corridor for these bats that matches their seasonal migration patterns (Fleming et al. 1993). These corridors are crucial for the endangered *L. yerbabuenae*.

More recently, Medellín et al. (2018) showed that *L. yerbabuenae* can travel up to 100 km in a single night. They applied fluorescent powder to bats from a large colony of lactating females, and recaptured marked individuals hours later at two sites about 40 and 50 km away. The bats travelled this far to reach large aggregations of the night-blooming and bat-pollinated columnar cacti, *Carnegiea gigantea*. These 100 km round trips represent the greatest foraging distances that have been accurately determined for any nectarivorous bat.

Spatial movement patterns have also been studied for some species of nectarivorous pteropodids. In Africa, *Megaloglossus woermanni* is the only obligate nectarivore bat species. Weber et al. (2009) showed that *M. woermanni* uses forests as daytime roosts and readily forages in agricultural plantations during the nighttime. The study also showed that females in agricultural landscapes have foraging ranges twice the size of those of males. Frequent use of agricultural landscapes is common in pteropodids in areas with abundant fruit crops, which unfortunately puts these bats in conflict with farmers and expose them to hunting (Frick et al. 2019).

Today, the miniaturization of GPS trackers and acoustic recorders is accelerating the study of movement patterns and foraging behavior. Using these new methods,

Egert-Berg et al. (2018) found that *L. yerbabuenae* and *R. aegyptiacus* do not forage in groups, although they do interact with conspecifics in their feeding grounds. This result suggests that nectarivorous bats do not need to forage collectively to find resources that are relatively predictable in space and time, such as flower nectar and pollen. The rapid improvements in bat tracking technologies will surely open many more windows into the movement ecology of nectarivorous bats.

9.7 Nectarivorous Bat Conservation and Pollination Services to Crops

Many studies documenting the economic importance and ecological value of bat pollination have been presented at NASBR. One inspiring conservation success story involves bat pollination of agaves. The glossophagines *L. nivalis*, *L. yerbabuenae*, and *C. mexicana* are the main pollinators of *Agave tequilana* and many other commercially important agave species from which tequila, mezcal, and pulque are obtained (Howell and Roth 1981; Sánchez and Medellín 2007). Rapid expansion of agave cultivation, combined with farming practices that prevented the plants from flowering before harvest, deprived vast agricultural landscapes of food resources for the bats (Trejo-Salazar et al. 2016). This contributed to the low population densities and endangered status that the Mexican populations of these bats have had for many decades (Sánchez and Medellín 2007). Joint efforts by bat biologists, tequila farmers, and conservationists established a program called "bat-friendly tequila", where farmers allow 5% of agave stems per hectare (~222 inflorescences) to flower during the six-month plant reproductive season. Models predicted that this would allow 89 bats to meet their nightly food requirements (Trejo-Salazar et al. 2016). "Bat-friendly tequila" is the first conservation program of its kind and has been highly successful.

In the Old World, there are similar tight relationships between nectarivorous pteropodids and socioeconomically important plants (Fujita and Tuttle 1991). Well-known examples include the Southeast Asian fruit crops of durian (*Durio zibethinus*; Malvaceae) and the legumes *Parkia speciosa* and *P. timoriana* (Fabaceae). These crops are pollinated by multiple pteropodid species, but especially by the specialist nectarivore *E. spelaea* (Stewart and Dudash 2017). Other bat-pollinated plant species in the Old World have multiple uses. For example, the leaves of *Oroxylum indicum* are cooked and eaten, the bark, roots, seeds and leaves are used in traditional medicine, and its fruits and bark are the source of a valuable black dye for coloring baskets (Fujita and Tuttle 1991). Another multiuse species is the bat-pollinated African shea butter tree (*Butyrospermum parkii*), whose seeds provide oil used for cooking, soap-making, and cosmetics (Fujita and Tuttle 1991). A final example are the mangrove species in the genus *Sonneratia* (Sonneratiaceae), which are pollinated by *Macroglossus* and *Eonycteris* bats (Stewart and Dudash 2017). *Sonneratia* species are structurally dominant in mangrove forests across Southeast Asia,

providing an important source of timber and charcoal, and help to buffer coastal regions against the effects of severe tropical storms (Fujita and Tuttle 1991; Stewart and Dudash 2017).

Despite the substantial conservation value of pollination services provided by nectarivorous bats, these animals still face many threats. Throughout the world, populations are threatened by habitat loss and fragmentation, pesticide use, direct persecution as pests or for bushmeat hunting, predation by nonnative predators (e.g. brown tree snake preying on *Pteropus mariannus* in Guam), and lack of awareness among the general public (Frick et al. 2019). However, as exemplified by the "bat-friendly tequila" program, these threats can be mitigated through conservation and education efforts that foster interactions among local stakeholders, scientists, and decision-makers.

9.8 Conclusions and Future Directions

In the last 50 years we have learned much about the many fascinating aspects of nectarivorous bat biology. Specialized nectarivore bats are exquisitely adapted to their dietary lifestyle and display an impressive array of physiological, sensory, and behavioral adaptations to exploit floral resources. They quickly process nectar and pollen to obtain energy to sustain their high metabolism, find flowers in the dark using scent, vision, and acoustic cues, and pollinate hundreds of plant species. Several other generalist nectarivorous species also contribute to pollination services, further demonstrating the complex and intricate nature of bat-plant interactions.

There are, however, still many exciting research avenues and knowledge gaps that need to be addressed. For example, the importance of bat pollinators relative to other floral visitors has been poorly explored, yet it is crucial to understand how plant species first evolved to become adapted to bats from ancestors relying on other groups of pollinators. These comparisons should include visitation rates, but also estimates of the quality and quantity of the pollen transferred by the bats and other pollinators. Bats often carry large amounts of pollen in their fur and it is likely that this pollen represents a large pool of donor plants more genetically diverse compared to that transported by other pollinators such as birds or insects. If so, pollen deposited by bats could lead to higher fruit and seed production or result in more vigorous seed germination and seedling growth.

Taxonomically speaking, the species that have been most studied tend to be the most abundant and widespread, resulting in important information gaps concerning basic natural history and ecology of some recently described Neotropical genera (e.g. *Xeronycteris*, *Hsunycteris*) and many poorly-studied pteropodid taxa (e.g. *Melonycteris*, *Notopteris*, *Lissonycteris*, *Micropteropus*). In terms of geographic coverage, medium and high elevation Neotropical phyllostomids have been less studied than their low elevation counterparts, whereas in the Old World much more research has been done on Southeast Asia and Australo-Pacific nectarivorous species than on those from Africa.

Aspects of physiology, sensory ecology, and spatial ecology offer many exciting new research possibilities with the increasing sophistication of GPS trackers, echolocation recording devices, temperature sensors, and other technology. The role of night vision and UV detection during foraging deserves attention, and efforts are also needed to examine the echolocation capabilities of pteropodids. Spatial patterns of foraging and seasonal migration must also be further explored. Bats readily use spatially aggregated floral resources, but they are also capable of long-distance flight. So to what extent do they trapline scattered food plants versus utilizing local resource-rich patches? Other than *Leptonycteris* and some pteropodids, we still know little about the movement patterns of nectarivores. This information is becoming increasingly urgent to address the effects of habitat fragmentation on bat and plant populations. Another important gap concerns those species that utilize different habitat types seasonally (e.g. along elevational gradients). In this regard, dietary studies are still needed for many species to understand how nectarivorous bats supplement their diets with other resources such as insects and fruit, and the extent to which different species can switch to alternative foods during periods of scarcity. Climate change may affect floral resource availability across many scales, which can jeopardize bat populations and the provisioning of their pollination services.

Finally, much needs to be done for the conservation of this important bat guild. The fascinating stories of bats and their flowers are powerful educational tools that can help raise awareness on the importance of nectarivorous bats specifically, and of all bats more generally. Effective conservation efforts involving local communities, farmers, scientists, and decision-makers can be inspired by these stories, giving bats everywhere a chance to continue servicing our ecosystems and societies. We are confident that NASBR will continue playing a pivotal role in the successful exchange of scientific research and innovative conservation initiatives to address the challenges that bats face in our rapidly changing world.

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