Conserving bats and their foraging habitats

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Introduction

Natural history stems from our limitless curiosity about nature and the organisms with which we share the planet. The focus of this book on the natural history of bat foraging animates our sense of wonder and fosters desire for further scientific inquiry and discovery into the adaptations and species interactions involved in bat foraging. Sadly, our appreciation of bat foraging must also include discourse on the reality of the global biodiversity crisis and an entreaty to protect bat species and their habitats. Although threats to bats vary with geographical and ecological context, by far the most pervasive threat to bats globally are land uses that destroy or degrade habitats (Voigt and Kingston, 2016; Frick et al., 2020). Bat conservation efforts are part of the broader conservation movement to protect and restore ecological integrity, recognizing the inexorable links between environmental and human well-being (Sokolow et al., 2019; Hopkins et al., 2022).

With over 1460 species, bats are diverse and their conservation needs varied. Over a third of bat species assessed by the International Union for the Conservation of Nature (IUCN) are ranked as threatened or data deficient, with 23 species currently listed as critically endangered, 85 as endangered, 113 as vulnerable, and 236 as data deficient (IUCN 2023). Generally, for bat species to thrive, they need intact foraging grounds, a healthy aerosphere, access to safe roosts, and clean surface water for drinking (Fig. 16.1). By definition, bat foraging involves species interactions, whether those interactions are predator-prey dynamics of animalivorous bats or the mutualisms of nectivorous bats pollinating flowering plants or frugivorous bats dispersing seeds. Conservation actions focused on broad-scale habitat protection and restoration are the most relevant to bat foraging.

Roost protection receives a lot of conservation attention and is a high priority for bat conservation. Bat roosts are good examples of Small Natural Features (SNFs), defined as spatially distinct habitats with potentially disproportionate importance on ecosystem function relative to their size, analogous to the concept of keystone

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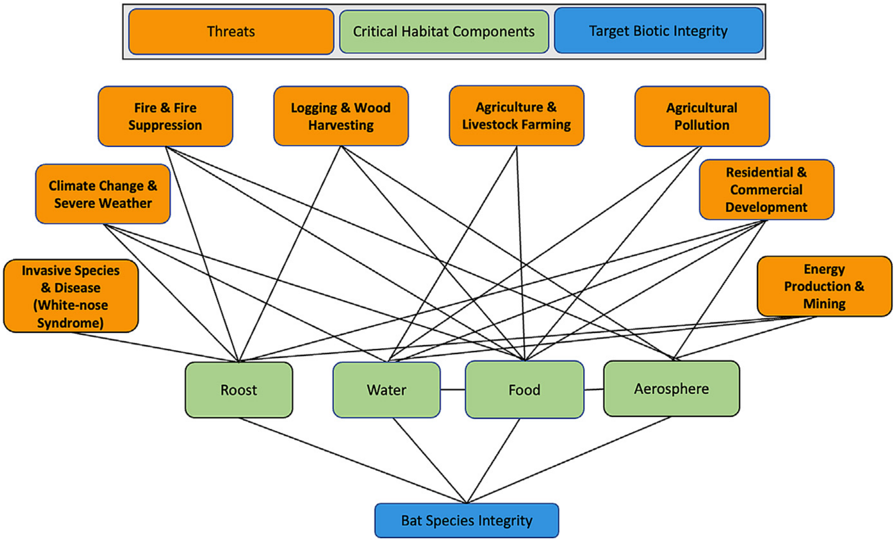

FIGURE 16.1

Conceptual metamodel showing pathways of anthropogenic threats to bats via four critical habitat components.

species (Hunter et al., 2017). From a conservation perspective, SNFs are highly attractive because they represent defined spaces to focus habitat protection or restoration activities (Davis et al., 2017; Hunter et al., 2017). Conservation practitioners must often prioritize limited resources to maximize conservation benefit. Focusing on SNFs is rational conservation planning given the potential for a high "impact-to-action" ratio, a measure of the conservation benefit relative to the level of effort the action requires (Hunter et al., 2017). Large colonies concentrated in a cave or mine are priority conservation targets given they generally have small spatial footprints relative to the value to protecting species or populations and are vulnerable to threats of disturbance or persecution (Furey and Racey, 2015; Hunter et al., 2017; Medellin et al., 2017; Frick et al., 2020). For example, protecting the last remaining cave roost for a bat species could prevent the global extinction of a species (Frick et al., 2020).

While roost protection is undeniably important for bat conservation, protecting and providing foraging habitats is also critical for supporting healthy bat populations, yet has received less attention. Sixty-two of IUCN species assessments consider the loss of foraging resources as a threat to bat species, and these are distributed across threat categories (1 critically endangered, four endangered; eight vulnerable; nine near threatened; 40 least concern) (IUCN, 2023). In most cases, the loss of foraging resources is associated with a loss of habitat generally, mostly due to anthropogenic causes (e.g., expansion of agriculture and logging). Loss of foraging resources also results indirectly from activities such as use of pesticides that reduce insect availability. In general, evidence of loss of foraging resources as a cause of species decline is indirect (habitat loss includes both roosting and foraging habitat) and is less widely available in the literature.

Identifying important foraging areas and strategies to protect foraging habitat can be more challenging than identifying roost sites given the inherent complexity to defining high-quality foraging habitat. Determining the appropriate scale and configuration for foraging habitat protection is particularly daunting given the scale of nightly movements of bats (McCracken et al., 2016; Goldshtein et al., 2020; O'Mara et al., 2021). For example, many molossid species fly over vast areas in a night, often at high altitudes (McCracken et al., 2008; Gillam et al., 2009; O'Mara et al., 2021). For these aerial insectivores, foraging primarily occurs in the aerosphere, and the direct linkages to specific terrestrial habitats may be diffuse (Kunz et al., 2008, Box 16.1). Even species that forage directly on plants can have foraging areas that are spatially disjunct from their roosting habitats. Straw-colored fruit bats typically forage for fruit approximately 35 km from their roosts and can fly over 90 km in search of nectar (Fahr et al., 2015; Calderón-Capote et al., 2020). Similarly, nectar-feeding lesser long-nosed bat (*Leptonycteris yerbabuernae*) can fly over 60 km each way from a cave roost to foraging areas for cactus nectar (Goldshtein et al., 2020).

Bats live at their energy ceilings, and many species rely on their daily foraging success to maintain positive energy balance (e.g. (O'Mara et al., 2017)). Research on conservation physiology and how energetic needs of bats relate to habitat quality

Box 16.1 Aeroecology

Thomas Kunz introduced the term aeroecology in 2008 to recognize the importance of aerial habitats for species interactions, most notably of bats, birds, and insects (Kunz et al., 2008). Aeroecology integrates ecology and atmospheric science, defining the aerosphere as habitat (Chilson et al., 2012; Diehl, 2013; Diehl et al., 2018). The concept of airspace as habitat is intuitive yet was not traditionally recognized as a habitat biome on par with terrestrial or marine biomes (Diehl, 2013). The unifying concept of aeroecology is a focus on the planetary boundary layer and lower free atmosphere (i.e., the aerosphere) and the airborne organisms that inhabit and depend upon this aerial environment for their existence (Chilson et al., 2012). Because of their ability to move over large spatial scales, volant organisms such as birds, bats, and insects contribute to the ecological integrity of ecosystems that span geopolitical boundaries linked by migration or dispersal through the aerosphere. The abundance of insects aloft is an important food source for aerial consumers, such as aerial insectivorous birds and bats (Frick et al., 2018). The scope and scale of seasonal migrations of insects is far greater than previously recognized and an important driver of aeroecological dynamics (Satterfield et al., 2020). Gary McCracken was one of the first researchers to provide insights into high-altitude aerial foraging behaviors of Brazilian free-tailed bats (McCracken et al., 2021). Use of weather radars has advanced aeroecological work by providing observational data of aloft biomass at relevant temporal and spatial scales (Chilson et al., 2012). Aeroecology and its promotion of airspace as habitat draws attention to specific threats to aeroecological integrity, including structures that cause direct mortality (e.g., wind turbines) or disrupt behaviors (e.g., light pollution) (Kunz et al., 2008; Chilson et al., 2012). Conservation attention to the aerosphere is key to protect biodiversity, global health, and ecological integrity (Kunz et al., 2008).

could provide useful information about how habitat protection and restoration actions can benefit bat conservation over broad spatial and temporal scales. With growing interest in protecting and restoring habitats to help meet global 30 by 30 targets and sustain biodiversity, a better understanding of how bat energetic needs maps to habitat use would help inform conservation planning.

Threats to bat foraging

Bats occupy the widest range of ecological niches of any mammalian order. While the majority of bat species feed on arthropods, many include fruit, nectar, and vertebrates in their diets. However, the foraging requirements for many bat species remain unknown, and nearly 20% of bat species are classified as Data Deficient by the IUCN (https://www.iucnredlist.org/). Basic information about dietary composition and diversity as well as habitat preferences to find these resources remain poorly understood for most of these species. Because of this, conservation aimed to protect bat foraging faces a range of challenges, most of which are rooted in identifying and protecting access to quality foraging habitats or resolving conflict with humans. Top ranked threats in the IUCN Red List for bat species include logging and agriculture, indicating that habitat loss is the greatest threat to bat biodiversity globally (Frick et al., 2020). Changes and degradation of land cover can negatively impact insect abundance and quality, fruit and flower availability, and drinking water access, and built infrastructure can interfere with access to foraging habitat or result in direct mortality of foraging bats.

Global declines in insect availability threaten the viability of many bat species (Thomas et al., 2004; Shortall et al., 2009; Hallmann et al., 2017; Lister and Garcia, 2018; Sánchez-Bayo and Wyckhuys 2019). The insect apocalypse is likely caused by a combination of factors including habitat loss, pesticide use, climate change, and increasing light pollution (Sánchez-Bayo and Wyckhuys, 2019). The loss of insects has far-reaching consequences, as insects and other arthropods play important roles in ecosystems, including as food sources for other animals, including the majority of bat species. Arthropods can have complex life cycles with distinct habitat needs requiring habitat protection efforts that achieve integrity of varied habitats that support entire life cycles (Arrizabalaga-Escudero et al., 2015). Given that approximately 70% of bat species are insectivores, the impacts of the insect apocalypse on bat conservation are, of growing concern (Goulson, 2019; IBPES, 2019).

Many bats, especially those that do not forage directly on nectar or fruit, need regular access to pooled drinking water. Due to their large surface area to volume ratios and uninsulated wings, water loss can range between 15% and 31% of body mass per day through evaporation (Studier, 1970; Webb, 1995). This is elevated in arid environments that hold a third of global biodiversity hotspots (Durant et al., 2012) and contain a quarter of the world's terrestrial vertebrate species, with high rates of endemism and species of highest conservation concern (Brito et al., 2014; Durant et al., 2014). Bat activity is highest around water where bats drink (Kurta et al., 1990; Mclean and Speakman, 1999), hunt for arthropods (Adams and Thibault, 2006; Rebelo and Brito, 2007; Korine et al., 2015), and cool off. Bats drink in flight and, consequently, may require a minimum surface size of water to be able to approach while flying (Laverty and Berger, 2020). Experimental reductions of desert pond size have reduced bat activity and species richness, particularly for larger, less maneuverable species (Razgour et al., 2010; Hall et al., 2016). In some arid regions, bats comprise the largest proportion of mammal diversity and partition use of water resources (Razgour et al., 2018). As climate change exacerbates drought conditions, arid environments may no longer be able to support high diversity of bat species (Adams and Hayes, 2021).

Environmental pollution threatens bat foraging by reducing insect populations (Sánchez-Bayo and Wyckhuys, 2019) as well as contaminating habitats, including water where bats drink and forage (Bayat et al., 2014; Korine et al., 2015; Oliveira et al., 2020). Agricultural pesticides can cause direct mortality in bats, or when chronically exposed, these compounds can bioaccumulate in their tissues and cause sublethal impacts that affect immune function and reproductive health (Bayat et al., 2014; Oliveira et al., 2020). Chemical spills in water sources have been linked to reduced survival in bats (Frick et al., 2007), and water quality can affect bat activity (Korine et al., 2015) and bat physiology (e.g. (Hill et al., 2016)). More studies on the effects of chemical pollutants on bats are needed, including ecotoxicology as well as population-level impacts (Bayat et al., 2014; Zukal et al., 2015; Oliveira et al., 2020). Sublethal effects or disruptions to food webs may be challenging to identify but could have cumulative or chronic effects on bat populations (Bayat et al., 2014). Bats have been suggested as useful bioindicators (Jones et al., 2009; Zukal et al., 2015), and efforts to expand global databases as well as bat monitoring programs like the North American Bat Monitoring Program (Loeb et al., 2015; Reichert et al., 2021) could be helpful in assessing the effects of pollution on habitat quality, bat health, and population trends (Russo et al., 2021).

Sensory pollutants and the effects of anthropogenic light and noise on bats is an expanding area of conservation research. Noise pollution is increasingly recognized as disruptive to bat foraging success, especially for species that use passive listening to identify prey (Barber et al., 2010; Domer et al., 2021). Light pollution has mixed effects on bat communities and can simultaneously have negative effects on bats by reducing insect populations or disrupting foraging activity (Stone et al., 2015) but can also provide enhanced feeding opportunities for some insectivorous bat species that feed effectively at artificial lights that attract moths and other phototactic insects (Voigt et al., 2021; Barré et al., 2022; Frick et al., 2023). Responses of bat species to Artificial Light at Night (ALAN) vary with foraging behavior and landscape context but could influence bat community composition and habitat use at broad scales (Cravens et al., 2018; Seewagen and Adams, 2021; Barré et al., 2022).

While many bat species exploit and use urban habitats, sensory pollutants and fragmented foraging habitats in urbanized areas likely reduce species richness and could also create chronic stressors even for species that have adapted readily to roosting in human structures (Russo and Ancillotto 2015; Voigt and Kingston 2016).

Some bats exploit urban areas for foraging (Egert-Berg et al., 2021), although whether urban areas function as ecological traps remains poorly understood for foraging (Russo and Ancillotto 2015). For example, recent work tracking Egyptian fruit bats (*Rousettus aegyptiacus*) in rural versus urban areas in Israel showed that these mobile fruit-eating bats commuted nightly into urban areas and shifted foraging behaviors to be more exploratory, including frequent switching among foraging patches in urban settings, which resulted in diversified diets (Egert-Berg et al., 2021).

Climate change is a threat to biodiversity globally (Bellard et al., 2012). For bats, climate change presents a direct mortality threat when extreme temperatures cause mass mortality events (Welbergen et al., 2008; O'Shea et al., 2016; Festa et al., 2023). Heat stress causing die-offs of flying foxes in Australia has been observed over the past decade and extreme cold temperatures caused a mass mortality event of Mexican free-tailed bats in Texas during a "big freeze" event in 2021 (McSweeny and Brooks, 2022). These major die-offs often capture media attention and raise awareness of the impact of climate change on species conservation. In a more subtle and chronic way, climate change can amplify the impacts of other anthropogenic threats (Festa et al., 2023). Certain species, foraging guilds, and biomes are more sensitive to the effects of climate change than others indicating that the effects of climate change vary across phylogeny and geography (Festa et al., 2023). Bat species that rely on closely timed migration to feed on ephemeral flowering plants are more vulnerable to effects of climate change (Gómez-Ruiz and Lacher, 2017) than those that have diverse diets or exploit human habitats and structures. Climate change heightens risks to bat foraging by intensifying drought (Adams and Hayes, 2021), increasing the strength and frequency of cyclones and hurricanes (Festa et al., 2023), and causing phenological mismatches between migrating consumers and food resources (Kubelka et al., 2022).

Conservation evidence

Effective conservation of foraging resources requires knowing the impact of potential actions, and we are currently in an evidence crisis in conservation (Sutherland et al., 2004, 2022). Misguided actions have wasted millions of dollars and continue to leave species and ecosystems vulnerable (Sutherland et al., 2022). One challenge for bat conservation is the lack of evidence for conservation actions directed to benefit bats (Frick et al., 2020; Berthinussen et al., 2021). The Conservation Evidence program (www.conservationevidence.org) summarizes available conservation actions and systematically compiles the scientific literature available to evaluate efficacy of different actions (Sutherland et al., 2022). The conservation evidence database currently lists 200 conservation actions that could potentially benefit bat populations (Berthinussen et al., 2021). However, of these 200 actions, 60% currently have no studies reporting evidence and another 22% were ranked as "unknown effectiveness" due to the limited number of studies available. Furthermore, there is a bias toward actions in the global north, whereas bat diversity peaks in the global south. Forty-seven actions are directly related to bat foraging and categorized within two themes: education and awareness and land protection and management. These actions are mostly targeted at mitigating the effects of agriculture and modification of natural systems—particularly in applications toward annual and perennial nontimber crops, modifying natural systems to accommodate human housing and urban areas, and preserving surface water. Clearly, more work directly addressing diverse approaches and challenges to bat conservation are needed.

The benefits to human well-being of protecting where bats eat

Protecting where bats forage by ensuring availability of food resources across their native ranges and across their active seasons is not only crucial for maintaining bat health but can also help to reduce human–bat conflict and risk of zoonotic pathogens spilling into humans (Plowright et al., 2021). The spillover and subsequent emergence of zoonotic pathogens—microbes transmitted from animal hosts to humans that cause disease—is most often the result of close interactions between people, domestic animals, and wildlife (Plowright et al., 2021; Shapiro et al., 2021). Reservoir hosts are the species or populations in which a pathogen naturally occurs, and the availability, abundance, and quality of foraging resources largely determine their spatial distribution, their movement and feeding behaviors, and their physiological state (e.g., nutrition, reproduction, immunity and infection status) (Plowright et al., 2017; Kessler et al., 2018; Shapiro et al., 2021). However, anthropogenic changes to ecosystems driven by land-use change (i.e., transformation of natural habitats into agricultural and urban landscapes) and climate change (e.g., frequent and extreme droughts and storms) have shown to permeate the physical and physiological barriers between reservoir hosts and humans and induce the spillover of pathogens, including some for which several bat species are reservoir hosts (e.g., Nipah virus, Hendra virus, and Rabies) (Plowright et al., 2021; Reaser et al., 2022).

Flying foxes native to Australia (*Pteropus scapulatus*, *P. alecto. P. conspicillauts, P. poliocephalus*) are natural reservoir hosts of Hendra virus, a paramyxovirus in the Henipavirus genus that has caused sporadic, often fatal, outbreaks of respiratory illness in horses and humans since the 1990s (Plowright et al., 2011; Kessler et al., 2018). Flying foxes infected with Hendra virus do not show apparent clinical symptoms of disease but can shed the virus in their saliva, urine, feces, and placental fluids (Halpin et al., 2011). Long-term empirical studies suggest nutritional stress and poor body condition in flying foxes caused by food shortages, combined with behavioral changes due to urban and agricultural resource provisioning, are key factors driving spillover of Hendra virus into horse and human populations (Plowright et al., 2021; Eby et al., 2022). Flying foxes rely on flowering trees for food, as their diet consists primarily of nectar and fruits, and they migrate long distances (up to thousands of kilometers) following seasonal food pulses provided by flowering plants (Welbergen et al., 2020; Eby et al., 2022). The progressive loss of native forests in Northeastern Australia, combined with increased frequency of climatic events that affect flowering plant phenology, has resulted in flying fox populations becoming sedentary in human-dominated landscapes, where they obtain a continuous, yet suboptimal supply of food resources (Eby et al., 2022). These agricultural and urban food resources do not meet the energetic and nutritional demands of flying foxes and can lead to immune deficiencies that increase risk of Hendra virus infection and shedding (Plowright et al., 2008; Kessler et al., 2018; Eby et al., 2022). Furthermore, these altered behaviors place flying foxes in close proximity to horses, creating opportunities for spillover of Hendra virus to horses and subsequently to humans (Kessler et al., 2018).

Flying foxes native to South and Southeast Asia are natural reservoirs of Nipah virus—another Henipavirus that has caused multiple outbreaks of respiratory disease and encephalitis in domestic animals and humans (Epstein et al., 2006). Decades of research on Nipah virus outbreaks and on the ecology of human–bat interactions in the region suggest that land-use change and agricultural and urban resource provisioning are key drivers of Nipah virus spillover dynamics (Pulliam et al., 2012; Islam et al., 2016; McKee et al., 2021). For example, the spatial overlap between commercial pig farms and agricultural production of mango in Malaysia facilitated the spillover of Nipah virus into a pig farm, where pigs consumed contaminated mango fruit that was partially eaten by local infected flying foxes (*Pteropus hypomelanus*) (Epstein et al., 2006; Pulliam et al., 2012). Infections in pigs led to subsequent transmission to pig farmers and abattoir workers and a country-wide outbreak that resulted in the death of 105 people and the culling of over one million pigs (Epstein et al., 2006; McKee et al., 2021). In Bangladesh, date palm sap, which is used to make palm wine and is obtained by tapping palm trees and collecting it in large clay pots, has become an easily accessible food resource for *Pteropus medius*. When infected *P. medius* visit date palm trees to consume this resource, they can contaminate the sap by shedding the virus through their saliva, urine, and feces, thereby transmitting the virus to people who consume the sap (Islam et al., 2016; McKee et al., 2021).

In Latin America, *Desmodus rotundus* is one of the main reservoirs of the rabies virus, and the only species of vampire bat whose primary diet includes both wildlife (both mammals and birds) and livestock (Schneider et al., 2009; Streicker and Allgeier, 2016). Rabies is a lethal neurological disease that kills thousands of livestock annually and causes sporadic outbreaks in people from rural villages (Streicker and Allgeier, 2016). The feeding behavior and prey preference of *D. rotundus* are highly variable at both individual and population levels (Streicker and Allgeier, 2016), and such variability can be largely explained by anthropogenic disturbances that affect prey availability (Stoner-Duncan et al., 2014). In Uruguay and the Peruvian and Brazilian Amazon, agricultural expansion and other resource extractive industries have led to the displacement of *D. rotundus*' natural prey and shifted this species' feeding preferences to domestic animals and even very rarely humans (Stoner-Duncan et al., 2014; Streicker and Allgeier, 2016; Botto Nuñez et al., 2020). Interestingly, in villages where livestock are present, *D. rotundus* tend to preferentially feed on livestock, as livestock represent an abundant and reliable food source (Gilbert et al., 2012; Streicker and Allgeier, 2016). This shift in feeding behavior may have significant consequences for the health of bats if they are exposed to pathogens or antibiotics in the blood of livestock and may also have economic consequences to farmers from losing livestock to rabies disease or decreasing production due to anemia (Streicker and Allgeier, 2016).

The loss of native foraging habitat and prey and the subsequent shifts in diet toward livestock and agricultural food sources has also led to conflict with livestock and fruit orchard farmers, which has resulted in the persecution and even legal culling of endangered bats (Streicker and Allgeier, 2016; Oleksy et al., 2021). For example, the Mauritian flying fox (*Pteropus niger*) is considered an agricultural pest because this species tends to feed on commercial fruit plants like mango and lychee, which have replaced the native fruit trees, causing economic losses to orchard farmers worth millions of dollars annually (Oleksy et al., 2021). Consequently, in 2015 and 2016, the Mauritian Government allowed the legal culling of almost 70,000 flying foxes in an attempt to control the damage caused in fruit orchards by *P. niger,* yet resulting in a 50% population decline of this species and its uplisting from Vulnerable to Endangered by the IUCN (Oleksy et al., 2021).

Ecological interventions that protect where bats forage (and the quality of their foraging resources), could substantially reduce conservation threats to bats while also reducing risks to human health and reducing human–bat conflict (Sokolow et al., 2019). For example, researchers found that a massive winter flowering event in eastern Australia managed to feed hundreds of thousands of flying foxes, amid a landscape that was otherwise depauperate of food for these bats, thus protecting them from Hendra virus infection and reducing risk of spillover to horses and humans (Eby et al., 2022). They suggest that in addition to conventional medical approaches for disease prevention (e.g., vaccines and treatments), landscape restoration programs focused on restoring native forests that provide winter foraging habitat would ensure the reliability of these food sources during winter and draw flying foxes away from suburban landscapes (Plowright et al., 2016; Sokolow et al., 2019). Similarly, in addition to improving technologies for rabies vaccine delivery to vampire bats, habitat restoration and wildlife protection practices aiming to preserve *D. rotundus'* native prey in the Amazon could switch vampire bat foraging back to natural feeding habits and reduce rabies transmission (Sokolow et al., 2019). Nipah virus outbreaks in pigs and humans in Malaysia have substantially decreased since the adoption of a policy that requires farmers to plant fruit trees at a minimum distance from pigsties (Pulliam et al., 2012). Prevention of Nipah virus outbreaks in Bangladesh are centered on human behavioral changes, which include placing bamboo skirts over date palm sap collection pots that prevent the sap from becoming contaminated with flying foxes' saliva, urine and feces

(Nahar et al., 2014; Sokolow et al., 2019). Likewise, covering fruit trees with nets has shown to be the most effective bat deterrent that prevents damage to fruit orchards without causing any harm to flying foxes; a practice that can be implemented alongside native forest restoration efforts and informational campaigns that address negative attitudes toward bats (Tollington et al., 2019; Oleksy et al., 2021). Reducing bat depredation on fruit orchards through netting could have an added benefit of reducing virus spillover risk at the bat-human-domestic animal interface.

The health and biodiversity impacts of land-use change and climate change go beyond zoonotic spillover risk, and these zoonotic diseases are certainly not restricted to bats as potential reservoir hosts (e.g. (Sokolow et al., 2019)). Scientists continue to adopt systems-based approaches to understanding the biodiversity, health, and economic impacts of environmental degradation and identifying sustainable solutions that can protect biodiversity and human health (e.g. (Sokolow et al., 2015, 2019; de Wit et al., 2019; Cronin et al., 2022; Hopkins et al., 2022)). The emergence of Hendra, Nipah, and rabies viruses highlight how changes to ecosystems that affect the distribution, abundance, and quality of bats' foraging resources not only represent a threat to bat populations but can also increase contact and spillover risk at the bat-human-domestic animal interface. As such, interventions that aim to protect where bats naturally forage can result in outcomes that benefit the conservation of bats and the ecosystems in which they forage (i.e., functions and services), as well as human health and people's livelihoods (e.g. (Hopkins et al., 2021)).

Conservation initiatives targeting bat foraging

Restoring and conserving healthy habitat for nectarivorous bats, agaves, and people

Conservation of bat foraging habitat can occur in both natural and human-dominated landscapes and can offer co-benefits to human communities through provisioning of ecosystem services, such as pollination. In North America, there are three nectar-feeding bats that migrate annually from Mexico to the southwestern United States and depend on flowering plants. The lesser long-nosed bat (*Leptonycteris yerbabuenae*), the Mexican long-nosed bat (*Leptonycteris nivalis*), and the Mexican long-tongued bat (*Choeronycteris mexicana*). These three species rely on approximately 50 species of flowering plants across their ranges, extending from central Mexico into the southwestern United States, consuming nectar from agaves, columnar cacti (e.g., saguaro and organ pipe), and dry forest plants like *Ceiba* and *Ipomoea* (Arroyo-Cabrales et al., 1987; Cole and Wilson, 2006; USFWS, 2016; U.S. Fish and Wildlife Service, 2018). As pollinators of plants like agave and cactus, bats support critical functioning of ecosystems and economies. Yet, anthropogenic pressures combined with climate change threaten these species foraging resources and viability.

Agave habitat is under threat from agricultural and urban expansion, grazing, drought, fire, and overharvesting (Reichenbacher, 1985; Alducin-Martinez et al., 2023). Agave plants have been used by people since pre-Colombian times and agaves continue to be used by communities throughout rural Mexico for food, fibers, construction materials, livestock fodder, medicinal uses, and distilled spirits. However, these uses involve harvesting the plant prior to blooming, thus reducing nectar availability for bats and other pollinators. Models predicting the future distribution of Mexican long-nosed bats and *Agave* species indicate the spatial overlap between these mutualistic species will be reduced by at least 75% in the next several decades (Gómez-Ruiz and Lacher, 2019).

Migration routes of *Leptonycteris* species follow a "nectar corridor" of blooming cacti and agave plants from central and southern Mexico into the Sonoran and Chihuahuan deserts of northern Mexico and the southwestern United States (Fleming et al., 1993; Gómez-Ruiz and Lacher, 2017; Frick et al., 2018). For *L. nivalis*, agaves are often the only or main chiropterophilic plant and nectar source for this species during the energetically demanding period of migration and reproduction. For *L. yerbabuenae*, the importance of agave species to the bats' diet increases in the northern portion of the migratory range. Agaves are the main nectar source for this species during mid- to late summer and fall, as well as during their fall migration southward (Cole and Wilson, 2006).

Bat Conservation International's Agave Restoration Initiative

In 2018, Bat Conservation International launched their Agave Restoration Initiative (batcon.org/agave), a binational and landscape scale effort to protect and restore critical agave foraging habitat surrounding known cave roosts and along migratory corridors for the Mexican long-nosed bat, lesser long-nosed bat, and Mexican long-tongued bat. The initiative involves dozens of partners from the United States and Mexico that span the conservation, civil, government, and business communities. BCI's Agave Restoration Initiative aims to protect and restore agaves in Mexico and the United States to create a climate-resilient "nectar corridor" that benefits both bats and local communities.

Initial efforts focused on restoring foraging habitat within a 50 km radius of known roosts of *Leptonycteris* species to reduce commuting distances bats must travel each night to find food, which is especially important for females nursing pups that must return to their cave multiple times per night (Medellin et al., 2018; Goldshtein et al., 2020). Protecting and restoring foraging habitat around known roosts may not be sufficient, given the long-distance seasonal migrations these bats make each year. Thus, the project was expanded to plant agaves in targeted areas within the migratory corridors of these species to help restore and recreate resilient foraging habitats along their migratory routes.

The program focuses on creating climate-resilient foraging habitat by planting and restoring native agave species known to thrive in particular regions. Agave species are selected to maximize blooming at different times of the year to provide longer periods of nectar availability and to support any potential shifts in the timing of bat migration or flowering phenology. In addition, targeted regions for planting and restoring agaves encompass altitudinal gradients to account for suitable habitat for a diversity of agave species, with a particular emphasis on higher elevation areas that are projected to be climate strongholds for agave species diversity (Gómez-Ruiz and Lacher, 2019). In the first 5 years of the initiative, over 80,000 agaves were planted at key sites in six U.S. and Mexican states, and over 9000 ha of land were protected for agave habitat.

Restoration of agaves is not just focused on creating resilient nectar corridors for migratory bats but also supports farmers and communities in Mexico who rely on agaves as important parts of their livelihoods and culture (Lear 2020). In desert, scrubland, and montane ecosystems of the United States and Mexico, agave plants (*Agave* spp.) function as keystone species for both natural and human systems, supporting ecosystem integrity as well as human livelihoods. Agaves are both wild-harvested and cultivated to make food and beverage products such as tequila, mezcal, *agua miel*, *pulque*, and agave syrup, and they are used for feeding livestock, controlling erosion, building fences, and supporting healthy water sources, among other uses (Lear, 2020). Agaves are especially important for many communities during periods of drought, as people harvest agaves to augment their income and diet and utilize agave as supplemental cattle feed when range forage is limited. BCI's agave restoration program directly supports local communities through investment in local community infrastructures and business opportunities (e.g., community greenhouses for growing agave seedlings prior to planting), and co-creating best-practices for sustainable agricultural and ranching techniques that aid rural communities through increasing landscape resilience through soil erosion control, improved water management, alternative sources of fodder for livestock during drought, and sustainable sources of income.

The conservation of foraging habitat for long-distance migratory species such as *Leptonycteris* bats poses several challenges that stem from the ecological aspects of the system as well as human dimensions. Creating and protecting connected patches of foraging habitat along binational migratory corridors requires a coordinated vision and the involvement of many landowners and other stakeholders. Furthermore, the exact migratory pathways remain unknown, which limits the ability to target foraging habitat conservation efforts in the most critical areas. Work is ongoing to identify potential new roosts along these corridors as well as identify associated foraging areas. Novel approaches to identifying the migratory corridors and foraging areas, such as the use of environmental DNA (eDNA), are being tested to provide cost-effective surveys to identify foraging routes. Flowers of agaves can be sampled for the presence of bat DNA from salivary cells on flowers and eDNA has recently been successfully used to detect Mexican long-nosed bats from both whole agave flowers and swabs of flowers (Walker et al., 2022). Use of eDNA surveys to identify foraging areas and migratory pathways are currently being explored.

Gardening for bats

People often inquire how to help bats with their individual actions. Bat Conservation International (www.batcon.org) and Bat Conservation Trust (www.bats.org.uk) promote the concept of gardening for bats as an engagement strategy with potential benefits to improve bat foraging conditions. The idea of "bat gardens" is to encourage gardening practices aimed to increase local insect prey abundance and diversity and improve bat foraging habitats within residential areas. Guidance includes planting night-blooming plants that attract nocturnal insects as food resources for bats. Local varieties of native plants are recommended because they are best suited for local conditions and most likely to support native insects. Replacing invasive plants with natives can make gardens more biodiversity friendly (Burghardt and Tallamy, 2015). When available, local native plant nurseries or gardening clubs can help identify suitable local plants and gardening practices.

General guidance for gardening for bats includes using plants with a diversity of floral structures, heights, and colors can help attract a diversity of insects (Bat Conservation Trust, 2015). Allowing grasses to grow long may also improve habitat value for insects and their larvae. Trees and shrubs can provide shelter for many insect larvae; hedges encourage concentrations of insects; and aquatic plants provide habitat for aquatic larvae such as mayflies (Bat Conservation Trust, 2016). Reducing or avoiding use of pesticides is recommended as best-practice for supporting local insect abundance and diversity (Frampton and Dorne, 2007). Additionally, reducing certain types of artificial light in and near gardens or garden features could reduce disturbance to some bats (Mathews et al., 2015; Seewagen and Adams, 2021). In larger gardens, features such as adding a pond or other water feature could provide drinking water for bats and may be particularly beneficial in arid climates with limited water availability. Lastly, gardens can become more bat friendly when people keep their cats indoors to prevent predation (Oedin et al., 2021), and gardens can support bat roosting habitat by protecting old trees or putting up an appropriately designed and located bat houses (Taylor et al., 2020).

Bat gardens are an opportunity to engage the public and groups interested in wildlife and supporting conservation, such as parks, schools, nature centers, and churches, in bat conservation. In addition to improving habitats in the urban environment, they offer educational tools to teach the public about the habitat needs of bats and the importance of local and global bat conservation.

Conclusion

Bats support ecological integrity through the ecological services they provide but also depend on intact habitats that can support both roosting and foraging needs to sustain viable populations. Conservation of bat foraging must be a priority for both conservation research and action to prevent further biodiversity loss and protect planetary function. We have much work to do to identify and implement strategies that can be effective at providing resilient foraging habitats for bats alongside protecting roost habitats from the effects of human disturbance or destruction. The escalating threat of climate change and how it amplifies and intensifies other threats, including intensification and expansion of agriculture and urbanization, stresses the urgency to use and build the evidence base for bat conservation to ensure our sustained progress on protecting bats and their foraging habitats around the world.

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