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Large Old World Fruit Bats on the Brink of Extinction: Causes and Consequences

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Keywords

flying fox, island conservation, keystone species, *Pteropus*, hunting, climate change

Abstract

Large Old World fruit bats (LOWFBs), species of *Pteropus*, *Acerodon*, and related genera of large bats in the pteropodid subfamily Pteropodinae, play important roles as agents of dispersal and pollination across the Paleotropics. LOWFBs are also collectively the most threatened group of bats in the world, with 71% of extant species assessed as threatened by International Union for Conservation of Nature. As highlighted here, contrary to other bats, the vast majority of LOWFBs face multiple simultaneous threats. Most importantly, biological and ecological traits, in particular life history characteristics, diet, movement, social ecology, and physiology, intensify threats and accelerate species declines. Furthermore, we demonstrate that LOWFBs are to be considered keystone species and express concern about the erosion of this role and the cascading effects expected on native ecosystems. In response to this alarming situation, we advance general recommendations and identify overarching research and conservation actions.

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1. INTRODUCTION

1.1. Large Old World Fruit Bats: A Definition

It is nearly 50 years since hunting of the endemic little Marianas fruit bat (*Pteropus tokudae*) for human consumption on the Pacific Island of Guam extirpated the species (Wiles 1987). Over the following 15 years (1975–1989), trade in flying foxes (species of *Pteropus*) from other islands in Micronesia, Polynesia, and Papua New Guinea to meet demand in Guam resulted in such catastrophic population declines that by 1990, all species of *Pteropus* and the related *Acerodon* were listed on Appendix I (11 species) or II (68 species) of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Further attention to the plight of flying foxes, particularly those restricted to islands, was raised in an International Union for Conservation of Nature (IUCN) action plan (Mickleburgh et al. 1992) and a US Department of Fish and Wildlife Services conference (Wilson & Graham 1992). Despite these decades-old warnings and more recent alerts (Vincenot et al. 2017a), *Pteropus* and the related species that we collectively refer to as large Old World fruit bats (LOWFBs) remain the most threatened group of bats in the world (Section 1.2). Not only is this of intrinsic concern, but as populations continue to decline, so too do the ecosystem services they provide to native and economic plants as pollinators and seed dispersers, particularly on islands.

Flying foxes (*Pteropus* spp.) belong to a large family of plant-eating bats restricted to the Paleotropics and subtropics, the Pteropodidae (202 species) (Simmons & Cirranello 2023). Here, we extend consideration to include other large-bodied (0.1–1.6 kg) members of the pteropodid subfamily Pteropodinae to which *Pteropus* belongs and refer to these 81 species (75 extant) collectively as LOWFBs. So, in addition to the 65 species of *Pteropus*, LOWFBs include *Acerodon* (five species), *Styloctenium* (two species), *Neopteryx frosti*, *Desmalopex* (two species), and the monkey-faced bats *Pteralopex* (five species) and *Mirimiri acrodonta*. Most species inhabit islands from Madagascar to Australia, with only four species predominantly found on continents: *Pteropus lylei* and *Pteropus medius* [assessed by the IUCN as *Pteropus giganteus*] on continental Indomalaya and *Pteropus poliocephalus* and *Pteropus scapulatus* restricted to Australia (**Figure 1**). For phylogenetic and/or geographic cohesion, we did not include large (>100 g) species from genera in other subfamilies, namely *Dobsonia*, *Boneia*, *Harpionycteris* (subfamily Harpyionycterinae), or species from Africa, namely *Eidolon* (Eidolinae), *Rousettus*, *Epomops*, and *Hypsignathus* (Rousettinae) (Almeida et al. 2020).

1.2. The Most Threatened Group of Bats Worldwide

We evaluated the conservation status of all bat species from the IUCN Red List assessments (as of January 14, 2023) and compared LOWFB species with other members of the family Pteropodidae and species in all other families (**Figure 2**). We extracted the Red List category, population trend, and number and nature of threats. Six of the nine known recent (<200 years) bat extinctions were LOWFBs from small islands (*Pteropus allenorum*, *Pteropus brunneus*, *Pteropus coxi*, *Pteropus pilosus*, *P. tokudae*, *Pteropus subniger*), and the conservation status of the 75 extant LOWFBs is clearly a major concern, with ~71% of species in the threatened categories [Critically Endangered (CR), Endangered (EN), and Vulnerable (VU)] (**Figure 2*a***). Moreover, population trends in ~71% of species are decreasing, and extirpation from individual islands is widely reported [e.g., *Pteropus rodricensis* from Mauritius (Tatayah et al. 2017) and *P. niger* from Rodrigues (Kingston et al. 2018)]. Notably, the two LOWFBs exhibiting population increases are threatened island species that have been brought back from the brink of extinction by substantial conservation efforts, namely *Pteropus voeltzkowi* (from CR to VU) on Pemba (Robinson et al. 2010) and *P. rodricensis* (from CR to

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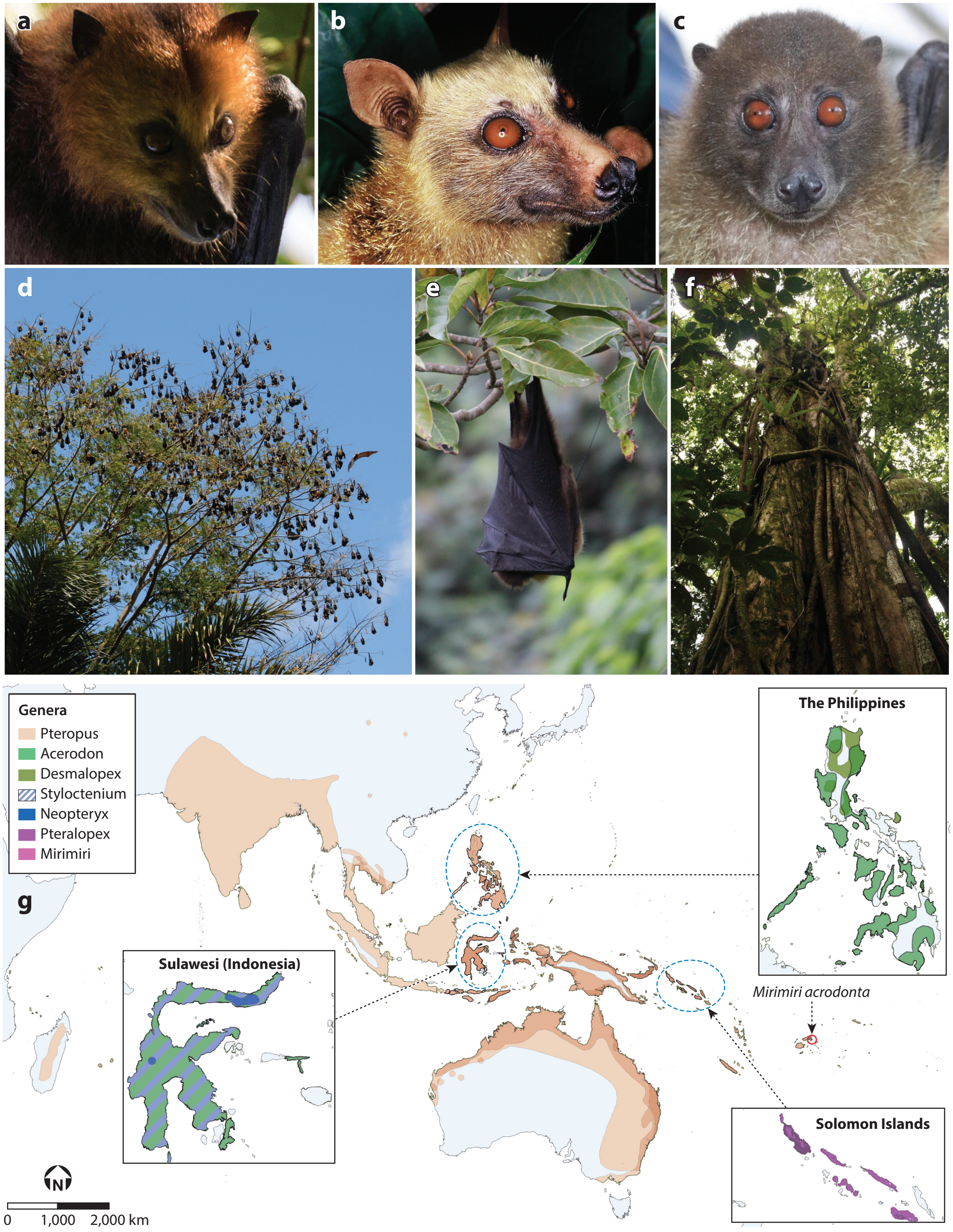

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Figure 1 (*Figure appears on preceding page*)

Large Old World fruit bats (LOWFBs), their roosting ecology, and geographical distribution. (*a*) *Pteropus niger*. (*b*) *Acerodon celebensis*. (*c*) *Pteralopex taki*. (*d*) Colonial roosting in exposed treetops. The photo shows part of a roost of several thousand *P. niger* in Mauritius. (*e*) Solitary roosting habit of *Pteropus dasymallus* in the Ryukyu Islands in Japan. (*f*) Strangler fig roost supporting small groups of monkey-faced bats (*P. taki*) in New Georgia. (*g*) Geographical distribution of the 75 extant LOWFB species across the Paleotropics. Map produced based on ranges declared in the International Union for Conservation of Nature Red List data (IUCN 2022). The number of species within a genus and area is indicated by color shading, with darker colors representing increased density. Insets illustrate distributions of non-*Pteropus* species. Photos reproduced with permission from Jacques de Spéville (panel *a*), Tigga Kingston (panels *b*, *d*), Tyrone Lavery (panels *c*, *f*), and Christian Vincenot (panel *e*).

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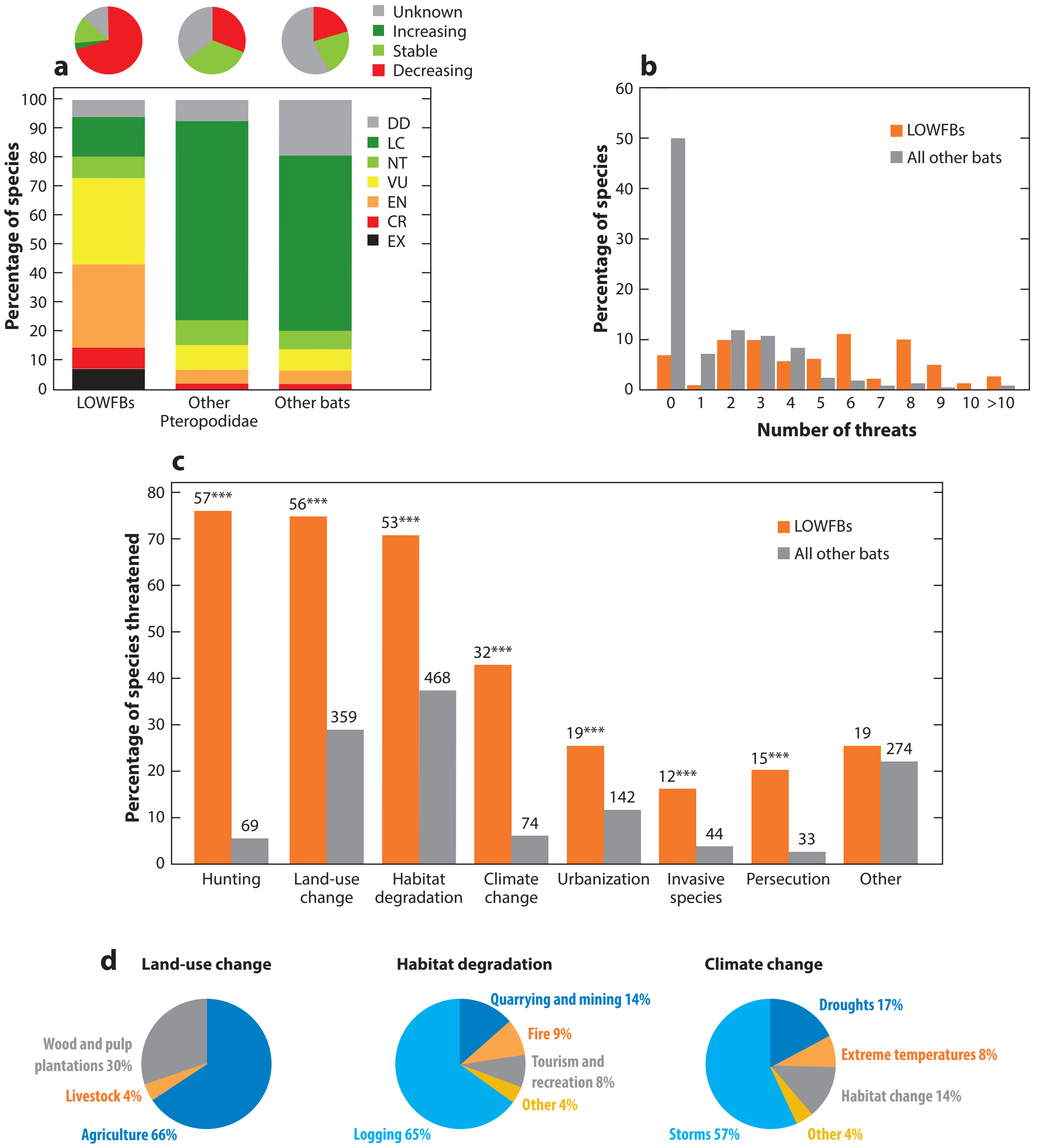

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Figure 2 (*Figure appears on preceding page*)

Conservation status, population trends, and threats to large Old World fruit bats (LOWFBs). (*a*) Red List assessment of LOWFBs, all other members of the Pteropodidae, and members of all other bat families. Pie charts indicate the proportion of species with population trends assessed as decreasing, stable, increasing, or unknown. (*b*) Number of threats per species, as a percentage of LOWFBs (*orange*) and all bat species (*gray*). (*c*) The distribution of major threats to LOWFBs (*orange*) and other bat species, including other members of the Pteropodidae (*gray*), showing the percentage of species affected. The number of species affected is shown in the text above the bars. Asterisks indicate the significance of Chi-squared tests for the hypothesis that the threat disproportionately affects LOWFBs ($^{***} = p < 0.001$). (*d*) Breakdown of threats within the major categories of land-use change, habitat degradation, and climate change. Data from International Union for Conservation of Nature Red List assessments (IUCN 2022). Readers are referred to the **Supplemental Material** for details on how the threat categories were derived from the IUCN Threat Classifications. Abbreviations: CR, Critically Endangered; DD, Data Deficient; EN, Endangered; EX, Extinct; LC, Least Concern; NT, Near Threatened; VU, Vulnerable.

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EN) from Rodrigues (Tatayah et al. 2017). The rest of the Pteropodidae and species of all other bat families are less imperiled, with ~15% and 13% of species threatened, respectively, although populations of many species are decreasing.

Supplemental Material >

1.3. Aims of This Review

We aim to identify the causes and consequences of declining populations of LOWFBs. We posit that the island distribution of many species accelerates population declines because (*a*) island populations are commonly subject to many diverse and recent threats, (*b*) life history traits and ecological characteristics both retard population recovery and intensify susceptibility to threats, and (*c*) deterministic and stochastic threats are both intensified on islands. We explore the potential consequences of population declines and extirpations for plant communities and evaluate the evidence that LOWFBs are keystone species on islands, as is frequently suggested. To conclude, we make research and conservation recommendations intended to slow declines and promote viable populations. We complement information in the IUCN Red List assessments with a literature review (for methods, see the **Supplemental Material**).

2. CAUSES: LIFE HISTORY AND ECOLOGY CONFER VULNERABILITY TO DIVERSE THREATS

2.1. A Disproportionate Diversity of Threats

The major threats to bats worldwide are hunting, land-use change, habitat degradation, climate change, invasive species, urbanization, and persecution (**Figure 2*c*,*d***; **Figure 3*a–f***) (Voigt & Kingston 2016, Frick et al. 2020). Compared to other species, LOWFBs are disproportionately affected by all major threats (**Figure 2*c***), and 67 species (83%) are subject to two or more threats, with a mode and median (of those with listed threats) of six threats per species and a maximum of 22 (**Figure 2*b***). In contrast, 50% of other bat species did not have a threat listed, and the mode and median for those with threats were 2 and 3, respectively.

2.2. Slow Recovery From Persistent or Acute Mortality Events

LOWFBs are K-selected species that are adapted to stable environmental conditions and exhibit low extrinsic mortality (Jones & Larnon 2001, McIlwee & Martin 2002). *Pteropus* spp. are large (0.1–1.6 kg) and long-lived. Their life span is generally 12–15 years in the wild, although captive *Pteropus* can live for 20–30 years (Wilkinson & South 2002), and smaller species or subspecies may have shorter life spans [e.g., *Pteropus melanotus natalis* of Christmas Island has an estimated life span of 4–6 years, although some individuals may reach 11–13 years old (C. Todd, L. Pulscher, personal communication)]. Females rarely give birth to more than one pup a year, and maturity is delayed

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Figure 3 (*Figure appears on preceding page*)

(*a–f*) Threats and (*g–i*) the ecological role of LOWFBs. (*a*) Hunting. *Acerodon celebensis* from South Sulawesi frozen for shipment to bushmeat markets in North Sulawesi. (*b*) Climate change. *Pteropus medius* clustering on the trunk of their roosting tree and panting to mitigate extreme temperatures in Pakistan. (*c*) Persecution. A wheelbarrow load of *Pteropus niger* illegally killed at a lychee orchard in Mauritius. (*d*) Invasive species. Destruction of unripe *Mimusops maxima* fruits by alien macaques from a single tree, depriving bats of one of their favorite fruits and hurting regeneration of the tree, a Mascarene endemic with a structural engineer role. (*e*) Habitat degradation and loss. Logged habitat of *Pteralopex taki* in New Georgia. (*f*) Indirect effects of invasive species. Dead and dying trees in what was a closed canopy forest in the 1930s in a protected National Park of Mauritius, illustrating the influence of encroachment of the dense undergrowth of invasive alien plants on the vegetation. (*g*) *A. celebensis* visiting a durian flower in Sulawesi. Durian is a crop of commercial importance in Southeast Asia, and exclusion experiments have demonstrated that bats are the only effective pollinators. (*h*) Small native fig seeds dispersed in *P. niger* feces in Mauritius. (*i*) Large seeds, such as this of Mauritian endemic tree *Labourdonnaisia glauca*, are not ingested by bats. Rather the seed (*right*) is dispersed with ejecta—chewed fruit material that is spat out—(*left*). Photos reproduced with permission from Sheherazade (panels *a*, *g*), Touseef Ahmed and Abdul Ali, Bat Conservation Pakistan (panel *b*), Geetika Bhanda (panel *c*), F.B. Vincent Florens (panels *d*, *f*, *h*, *i*), and Tyrone Lavery (panel *e*).

until the second or even third year, particularly on islands (Todd et al. 2018). Generation times are consequently generally long (6–8 years), and intrinsic rates of increase are low (e.g., 0.122) (Kingston et al. 2018). Sparse records for other genera suggest similar life history characteristics. Consequently, LOWFB populations are slow to recover from reductions, particularly those resulting from the direct, density-independent mortality of many individuals [i.e., mass mortality events (MMEs)]. Hunting, persecution, and extreme weather events are thus major threats to LOWFBs.

Unsustainable hunting of LOWFBs for cultural, subsistence, or commercial purposes is the most frequently reported threat to LOWFBs (**Figure 2*c***). This is of grave concern because all extinct LOWFBs were intensively hunted island species (IUCN 2022). LOWFBs are hunted for their meat, perceived medicinal value, ornaments, and even currency (Jones et al. 2010, Wiles & Brooke 2010, Mildenstein et al. 2016, Lavery & Fasi 2019, Tackett et al. 2022). Bat hunting has a long history in the insular Asia-Pacific region, dating back to prehistory, and is likely of particular importance on islands with depauperate fauna (Hand & Grant-Mackie 2012). Introduction of modern weapons through the twentieth century (Seehausen 1991) intensified hunting pressure on *Pteropus* on some islands, but even traditional methods (kites, hook lines, and nets) result in unsustainably high offtake levels, particularly given the small populations supported by islands (Struebig et al. 2007, Sheherazade & Tsang 2015, Brook et al. 2019). As human populations and access to markets have grown over the past 50 years, so too have demand and the trade networks necessary to meet demand (Wiles & Brooke 2010). Although CITES successfully disrupted trade from Pacific islands to Guam and the Northern Mariana Islands, it does not preclude illegal trade and cannot regulate trade within countries. Trade to support consumption in North Sulawesi, for example, presents a very similar scenario to that of Guam 40 years ago. Local depletion of populations in North Sulawesi has encouraged hunting in new areas throughout Sulawesi and imports from other Indonesian islands to meet demand (**Figure 3*a***) (Sheherazade & Tsang 2015, 2018).

Persecution that directly results in species mortality is listed as a threat to 11 species and is primarily driven by perceived economic losses of fruit crops to raiding bats (**Figure 3*c***) and loss of amenity when large colonies roost near villages and in urban and peri-urban habitats. Persecution can be widespread across the population and in some cases is intense enough to precipitate rapid population declines. Government culls of the Mauritian *Pteropus niger* exceeded 30% of the population and pushed the species from VU to EN (Kingston et al. 2018). Even nonlethal harassment of colonies using, for example, noise agents, can impact population growth, as the physiological stress may induce abortion events (Mo et al. 2022).

Extreme weather events include heatwaves (extreme heat events), which have proven lethal to *Pteropus* in parts of India (Dey et al. 2015) and Pakistan (**Figure 3*b***) and have occasioned MMEs

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in the tens of thousands in Australia (Welbergen et al. 2008). For example, it is estimated that >72,000 *P. poliocephalus* died from extreme heat events over a single summer (2019–2020) (Mo et al. 2021). As might be expected, continental LOWFBs have been disproportionally affected by extreme heat events. Island species are, however, regularly impacted by cyclones, resulting in MMEs as individuals are battered by high winds or blown from islands, resulting in population declines that can exceed 90% (for reviews, see Wiles & Brooke 2010, Scanlon et al. 2018). Even in Australia, cyclones reduce both the survival and reproduction of *Pteropus conspicillatus*, with an estimated sixfold increase in monthly mortality and a reduction in recruitment by approximately one fifth in the subsequent breeding season (Westcott et al. 2018). Extreme weather events are projected to increase in frequency, intensity, and duration (Rahmstorf & Coumou 2011) and are likely to result in increasing numbers of MMEs from which LOWFB populations are intrinsically unable to recover even in the best of conditions (Ratnayake et al. 2019). Moreover, conditions are worsening, with novel mortality hazards such as power lines that can electrocute bats (Vincenot et al. 2017b, Tella et al. 2020) and resource loss and shortages that compromise reproductive success and recruitment.

2.3. Dependence on Year-Round Supply of Fruits and Flowers

All species of Pteropodidae are predominantly frugivorous and/or nectarivorous and rely on year-round availability of fruits or flowers; this reliance confers vulnerability to habitat loss and climate-related food shortages and brings LOWFBs into conflict over fruit crops and urbanization. LOWFBs have some of the highest basal metabolic rates among bats, and metabolic rates increase up to 15–16 times during flight (Speakman & Thomas 2003), so food shortages quickly lead to starvation. Therefore, although LOWFBs tend to rely on a diversity of native plant species, particularly on islands (Banack 1998, Florens et al. 2017a, Lavery et al. 2020a), they are nonetheless very vulnerable to habitat loss and degradation (**Figure 3*e***), as well as food shortages associated with cyclones and other extreme weather events such as drought or heavy rain. Moreover, many LOWFBs time lactation to coincide with the greatest availability of resources (i.e., the peak of fruiting seasons) (Banack & Grant 2003), so shortages or even phenological shifts in flowering or fruiting induced by climate change (Butt et al. 2015) may reduce reproductive success, limiting recruitment and eroding fitness. Resource loss from habitat conversion and bottlenecks from climate change–induced phenology shifts and extreme events are exacerbated on islands where there are few alternate foods and limited or no migratory options.

There is growing evidence that forest degradation has consequences for *Pteropus* populations. Secondary forests in Fiji provide less than half of the fruit resources used by bats, compared with primary forests, and 10% fewer flower resources (Scanlon et al. 2018). Similarly, forests invaded by nonnative weeds in Mauritius suppress the flowering and fruiting of the native trees upon which fruit bats rely (Baider & Florens 2006, Monty et al. 2013). Monkey-faced bats are closely associated with old-growth lowland and/or montane forest (Fisher & Tasker 1997) and are particularly sensitive to deforestation and logging (Lavery et al. 2020b). In Australia, loss of large tracts of eucalypt forests has greatly reduced the availability of critical winter nectar resources for *Pteropus* spp. Consequently, periodic failure of flowering in forest remnants related to El Niño events results in acute food shortages, with consequences for body condition, reproduction, and even spillover of Hendra virus (Eby et al. 2022).

Food shortages resulting from cyclones on islands have been widely documented. Potential pteropodid food trees in flower or fruit on the Vava'u Islands were down by 85% six months after Cyclone Waka (McConkey et al. 2004). Similarly, in the 12 months following Cyclone Tomas (2010) in Fiji, tree-borne flowers and fruits used by bats decreased by 49% and 53%, respectively, in primary forest, and fruits in secondary forest decreased by 35%, compared to the 12 months before the cyclone. The diverse diets of many island flying foxes may confer some resilience to the reduction in resources attributable to cyclones, as not all plants are affected equally (Scanlon et al. 2018), and populations may rely on robust species immediately post cyclone (Wiles & Brooke 2010). However, as natural forest areas are reduced or degraded, the buffer afforded by dietary diversity is compromised, as suggested by the break-up of colonies following cyclones (Brooke et al. 2000).

With the loss of natural food resources and the generalist frugivorous habit of many species, LOWFBs are increasingly attracted to orchards of commercial fruit crops, as well as backyard fruit and urban landscaping trees or weeds (Williams et al. 2006, Tella et al. 2020, Yabsley et al. 2022). This can result in considerable human–bat conflicts ranging from outright persecution (Aziz et al. 2016) (**Figure 3*c***) to accidental deaths in nets and fences (e.g., Charerntantanakul et al. 2023). The perceived losses of both commercial and backyard lychee were the major driver of the government culls of *Pteropus niger* on Mauritius, where <5% of native habitat remains (Kingston et al. 2018). Yet, losses may in some cases be largely misattributed to bats, as shown on Okinawa (Charerntantanakul et al. 2023), or damages caused by bats may be exaggerated, as shown in Mauritius (Florens & Baider 2019). In Australia, *Pteropus* spp. were historically nomadic, following the ephemeral pulses of flowering eucalypts (Roberts et al. 2012). As populations have become increasingly dependent on urban and peri-urban resources (Meade et al. 2021, Eby et al. 2022), the noise, smell, and concerns about disease spillover associated with large permanent camps bring them into conflict with their human neighbors (Currey et al. 2018).

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2.4. Ecophysiology and Temperature Extremes

Extreme heat events are causing MMEs for continental species of LOWFBs. Many species roost colonially in large tree roosts that are directly exposed to the sun, and in combination with their large body size, this habit means that they live at the edge of thermal tolerance (**Figure 1*d***). They have diverse behavioral thermoregulatory mechanisms to cope when ambient temperatures exceed the thermal neutral zone, such as wing fanning to force convection and seeking shade. Once ambient temperature exceeds body temperature, they may also spread saliva on wrist, thumb, chest, and wing membranes; dip their belly in streams and rivers; and pant to increase evaporative cooling or clump together to reduce convective gains (Bartholomew et al. 1964, Ochoa-Acuña & Kunz 1999, Welbergen et al. 2008) (**Figure 3*b***). Yet, during extreme temperatures these efforts at heat dissipation are costly for water balance and insufficient to counteract the physiological traits typical of bats that make them particularly sensitive to heat stress, such as thick, dark-colored fur; lower thermoregulation capability in the young (Bartholomew et al. 1964); synchrony between pup rearing and the hottest days (Snoyman et al. 2012); and overall reproductive phenology (Mo et al. 2021). Thus, in Australia, temperatures in excess of 42°C are potentially lethal events (Welbergen et al. 2008). Attempts to forage during hot nights to offset food and water losses may compound the situation; metabolic rates during flight are 2–3 times higher than in similar-sized exercising mammals (Thomas 1975), and severe hyperthermia during flight in *P. poliocephalus* was recorded in ambient temperatures as low as 25°C (Carpenter 1985). Research on nectarivorous bats in the Neotropics indicates a reliance on exogenous carbohydrates to sustain the high energetic requirements of flight (Voigt & Speakmann 2007), and the same may be assumed for LOWFBs, which furthermore rely on fruits for their water supply. Quick energy depletion and dehydration are expected in these species. Conversely, LOWFBs do not tolerate very cold temperatures well. Consequently, changes in mean temperature induced by climate change may be attracting LOWFBs into regions with fewer frosted nights but a higher risk of episodic heat waves, as shown in the distribution shift of *Pteropus alecto* in Australia (Welbergen et al. 2008).

2.5. Movement Ecology and Migration Challenges

Several species of continental pteropodids migrate long distances (up to 6,000 km), tracking the availability of food resources [e.g., *P. poliocephalus*, *P. alecto*, and *P. scapulatus* in Australia (Spencer et al. 1991, Webb & Tidemann 1996, Welbergen et al. 2020)] or increase their foraging range in response to seasonal variability or unanticipated food shortages. This high mobility can be seen as an asset to counter disturbances (clearcutting, fires, hunting, etc.), efficiently exploit resources, and avoid genetic drift. Yet at the same time, it may well put LOWFBs in a challenging position, as it does other migratory species, when patchy and distant resources suddenly disappear, precipitating resource stress (Eby et al. 2022). Aerial migrations, even over short distances, expose bats to increased risks (predation, navigation, energy exhaustion, etc.), as exemplified by *Pteropus dasymallus*, which has been found dehydrated at sea by fishermen while performing interisland summer migrations in the Ryukyu Islands, Japan (C.E. Vincenot, personal communication). In addition, some migratory species, such as *Pteropus vampyrus*, are exposed to a lack of legal protection and to hunting on part of their transnational home range, which threatens populations regionally despite isolated conservation efforts by some countries (Epstein et al. 2009).

2.6. Social Ecology and Increased Vulnerability

Many *Pteropus* and *Acerodon* species are colonial, roosting in aggregations of dozens to tens of thousands in mature, tall trees (**Figure 1*d***), and commonly exhibit high fidelity to their preferred roost sites. These highly conspicuous camps are readily located by hunters, allowing for rapid depletion of populations across years (Struebig et al. 2007). Suitable large roost trees are often limited in degraded habitats and can also be the target of harvesting operations, greatly limiting the availability of large trees as roosts in secure locations and leaving colonies vulnerable to hunters (e.g., Ibouroi et al. 2018). In urban and peri-urban settings, the noise, smell, guano deposition, and damage to trees generated by the activity of large colonies, coupled with various mostly unfounded fears triggered by bats (Kingston 2016, Low et al. 2021), frequently give rise to persecution ranging from forced relocations and habitat clearances to outright culls.

Populations of colonial species may be gregarious depending on the season [e.g., *Pteropus pselaphon* (Sugita et al. 2009)] or geographical location [e.g., *Pteropus samoensis* (Russell et al. 2016)], and several species roost in a solitary or semisolitary manner [e.g., *Pteropus nitendiensis* and *Pteropus tuberculatus* (Lavery et al. 2020a) and *P. dasymallus* (Vincenot et al. 2017b)] (**Figure 1*e*,*f***). Roosting solitarily or with few conspecifics does not always reduce predation avoidance and hunting pressure. For instance, *Pteralopex* spp. typically roost singly or in small groups (1–10 individuals in tree hollows and strangler figs) (**Figure 1*e***). Although this makes them less conspicuous to hunters, ad hoc hunting is often successful, as the bats are easily captured by reaching into the roost hollows, especially as some species seem reluctant to bite (Fisher & Tasker 1997).

Finer aspects of the social ecology of LOWFBs, such as social structure and group dynamics, remain largely unknown for most species (but for detailed ethograms of the continental species *P. medius* and *P. alecto*, see Neuweiler 1969, Markus & Blackshaw 2002). Mating systems, for instance, seem to vary depending on species, and they range from vertical hierarchical structures reflected by height position in trees in *P. alecto* (Neuweiler 1969) to more complex female defense polygyny, with bats grouping face-to-face into ball-shaped clusters of females each controlled by a male, in *P. pselaphon* (Sugita & Ueda 2013). Clustering or, on the contrary, distancing behavior serves at the same time as a thermoregulatory mechanism against cold [in *P. scapulatus* and *P. pselaphon* (Bartholomew et al. 1964, Sugita & Ueda 2013)] or heat [e.g., in *Pteropus hypomelanus* (Ochoa-Acuña & Kunz 1999)]. All the foregoing social aspects of the ecology of LOWFBs have great implications for antipredator responses, resource exploitation, demographic growth, gene

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flow, and overall survival both in the wild and in captive breeding programs. Most importantly, because populations on islands may be inherently small or greatly reduced by human activities, selective mating systems facilitate inbreeding and genetic drift, ultimately leading to lower demographic growth and a higher extinction probability (Martínez-Ruiz & Knell 2017). Many species present only in small colonies or switching to a solitary lifestyle, depending on environmental conditions, may be additionally prone to greater inbreeding (e.g., Taki et al. 2021) and a possible Allee effect (Angulo et al. 2018).

2.7. Insular Settings and Intensified Challenges

The ranges of all but four LOWFB species consist largely or exclusively of islands. Ecosystems on tropical islands are inherently fragile and functionally vulnerable to change (Brodie et al. 2013, Keppel et al. 2014). While anthropogenic activities endanger bat populations worldwide (Voigt & Kingston 2016, Frick et al. 2020), economic development pressures, limited land area and natural resources, susceptibility to climate change and biological invasions combine with inherently small populations to both diversify and intensify threats to bats on islands (Jones et al. 2010, Wiles & Brooke 2010). Many islands have undergone rapid transformation of their native vegetation into agricultural or settlement uses, with less than 5% natural habitat remaining in some Mascarene Islands (Florens 2013) and the Philippines (Brooks et al. 2002), for example, and rapid loss is still projected for larger islands (Voigt et al. 2021). These losses reduce island carrying capacity and limit roosting refugia from hunting (Cousins & Compton 2005, Ibouroi et al. 2018), disturbance, and invasive species still further. Invasive species differentially affect island bat species (Welch & Leppanen 2017) and impact LOWFBs both directly through predation and disturbance [e.g., by cats (Vincenot et al. 2017b, Oedin et al. 2021), arboreal snakes (Wiles 1987), and noxious ants (Bowen-Jones et al. 1997)] and indirectly through competition for fruit resources [e.g., from macaques (Baider & Florens 2006, Reinegger et al. 2021)] and by reducing and degrading native habitats and the resources they provide (Florens et al. 2016, 2017b). Climate change is a major concern for Paleotropical islands (Taylor & Kumar 2016). Although the greatest threat posed by climate change to island bat species is the projected increases in the severity and frequency of cyclones (Rahmstorf & Coumou 2011), floods are forecast to affect bats living on low-lying islands and atolls, while sea level rise threatens to extirpate subspecies and even species [e.g., *Pteropus aldabrensis* on Aldabra where 60% of the atoll lies at or below 1 m above sea level. (Waldien & Bunbury 2020)]. Governance and regulation of natural resources on islands may be complicated by land tenure, the challenge of local enforcement of federal regulations and laws on distant islands (e.g., in Indonesia, which consists of more than 19,000 islands dispersed east–west across 2,210 km), limited capacity for governance and enforcement, and island poverty that drives overexploitation of natural resources (Brodie et al. 2013).

3. CONSEQUENCES: LARGE OLD WORLD FRUIT BATS AS KEYSTONE SPECIES

Keystone species disproportionally influence biotic communities in ways that have been likened to the role of the keystone of an arch. Removal of the keystone changes the structure and function of the arch quickly and substantially as the other stones tumble to new positions or the arch collapses. Apex predators or pathogens are good examples of keystone species, and LOWFB species have long been regarded as such, too (Cox et al. 1991, Fujita & Tuttle 1991, Banack 1998). Indeed, a diet that includes floral resources like nectar conceivably promotes pollination. This, together with their predominantly frugivorous diet and the ability to disperse a wide range of seeds from fleshy-fruited plants (Scanlon et al. 2014), sometimes over considerable distances (Roberts et al. 2012),

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suggests that LOWFBs may play important roles in plant reproduction. The role of LOWFBs as seed disseminators on oceanic islands also appears to be relatively large because of the natural depauperate fauna characteristic of these ecosystems. But to what extent can this keystone role be generalized more broadly, and could such a role be changing?

LOWFBs are often considered important pollinators, but not all flower visitors that are attracted to flowers are pollinators. Pollen may be picked up but not transferred, and flower visitors may be nectar robbers, consuming nectar without effecting pollination (Irwin et al. 2010). Even worse, a flower may be eaten, leading to the ultimate harmful effect of a flower visitor (e.g., Bissessur et al. 2019). Several studies have convincingly demonstrated that LOWFBs do serve as pollinators (Scanlon et al. 2014, Aziz et al. 2017b, Sheherazade et al. 2019) (**Figure 3*g***). However, at times, pollinator status is only suggested or implied, not demonstrated. For example, Nyhagen et al. (2005) is often cited to support a pollinating role for *Pteropus niger*. However, this work merely showed the presence of 18 pollen types on the fur, something that may even have come about by florivory for all we know. Furthermore, some of the pollen types found could have been from invasive alien species, and any pollination of these species would thus have been more detrimental than beneficial to the island's biodiversity.

The important role of LOWFBs as seed disseminators (**Figure 3*h*,*i***), however, is more widespread and convincingly demonstrated (e.g., McConkey & Drake 2006; Oleksy et al. 2015, 2017). This role is amplified when the bats disseminate seeds of canopy or fig trees, which is often the case, because these plants in turn play important ecological roles that help support populations of myriad species. Canopy trees, for instance, play important roles as physical ecosystem engineers in forests (Jones et al. 1997), whereas figs, through their year-round fruiting, are particularly important as famine food that support frugivores through seasons of fruit scarcity. Some studies have shown that LOWFBs can eat the fruits of many fleshy-fruited species and plants (e.g., conservatively, a quarter of all fleshy-fruited species and over half of all woody plants of a given forest) and were estimated to contribute to the maintenance of two thirds of the woody plant biomass of the forest sites studied (Florens et al. 2017a).

Human activities are, however, interfering with the important ecological roles of LOWFBs in varied ways, sometimes enhancing and sometimes reducing their importance through direct or indirect mechanisms. Global extinction is the ultimate cancellation of the ecological role of a LOWFB, and six species have been driven extinct already. Local extinction has similar effects where the populations have been extirpated. However, even when a species or population is not extinct, functional extinction may loom if the population size becomes too small for the ecological role to remain significant. This is particularly true for LOWFBs, owing to their specific foraging ecology whereby their seed dissemination role is lost even before they become rare (McConkey & Drake 2006).

The relative role of LOWFBs as seed disseminators may also be altered through the extinction and introduction of other frugivores, as has been widespread and common in recent centuries, particularly on islands. For example, the extinction on Mauritius of at least partly frugivorous species like dodos, giant tortoises, large parrots, and other species has artificially increased the seed dissemination role of *P. niger* (Hansen & Galetti 2009), turning it into the last species capable of disseminating larger-seeded native plants. Similarly, the introduction by humans of new frugivores on islands may conceivably diminish the relative seed disseminating role of LOWFBs, particularly because such alien species often achieve very high densities relative to natives. However, it appears that introduced frugivores may not be able to compensate for the loss of endemic frugivores as far as seed dissemination service is concerned, as was recently shown on Mauritius (Heinen et al. 2023).

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Introduced frugivores may also influence the seed dissemination role of LOWFBs in more indirect ways. One good example comes from Mauritius, where the long-tailed macaque (*Macaca fascicularis*) was introduced in the early seventeenth century. The macaque has a diverse omnivorous diet that includes native fleshy fruits. However, it virtually always attacks fruits when they are still unripe and have nonviable seeds (e.g., Baider & Florens 2006). Even worse, these fruits are almost never actually eaten but rather plucked, bitten into (**Figure 3*d***), and discarded, such that satiation does not limit the number of fruits that the macaque destroys during a visit. Macaques are known to destroy over 95% of the fruit crop of endemic trees (Baider & Florens 2006). They thus preempt bats from disseminating seeds of the majority of fruits of virtually all larger-fruited species everywhere on the island, rendering the seed dissemination role of the bats insignificant. Furthermore, this behavior of the macaques selectively reduces the regeneration of those same trees, driving regeneration deficit (Florens 2008) and rarefaction of the larger-seeded, fleshy-fruited species over the centuries of sustained macaque influence.

A final mechanism by which the seed dissemination role of LOWFBs is being inexorably eroded is through the influence of invasive alien plants. These are particularly prevalent on oceanic islands where they have been documented to influence native plants, in particular by reducing flowering intensity and frequency, as well as the number of fruits produced per plant (Monty et al. 2013, Krivek et al. 2020), thereby reducing the main foraging opportunities through which LOWFBs deliver their seed dissemination roles. Here too, longer-term influences of invasive alien plants are further weakening the role of LOWFBs. For example, on Mauritius, short-term population studies have shown invasive alien plants to increase the mortality of native trees (e.g., Florens 2008), and long-term studies of forest community structure have shown that the density of larger trees, for the most part fleshy-fruited species whose fruits *Pteropus* eats, have halved within protected areas in 68 years (Florens et al. 2017b). Furthermore, the spread of invasive alien plants in native habitats may itself be promoted when LOWFBs feed on their fruits, thereby making the seed dissemination role of LOWFBs entail harmful consequences for native biodiversity.

4. CONCLUSION

Despite warnings 50 years ago, LOWFBs remain the most threatened group of bats in the world; populations are declining, and many species are on the brink of extinction. Although the types of threats faced by LOWFBs are comparable to those experienced by other bat species, the island context of most species interacts with their life history and ecology to intensify the threats posed and subjects many species to multiple threats. Tackling threats to species in isolation is consequently unlikely to secure populations and species for the long term. Long-term conservation strategies need to characterize the nature and relative intensity of threats faced by species or populations of concern, as well as the interactions among them, and adopt a multi-faceted approach. By contrast, continental species, which were abundant and generally of little conservation concern 50 years ago (IUCN 2022), are now facing repeated MMEs due to climate change, increasing conflict with people, and losses of critical habitat needed for population stability and recovery.

The pressures on LOWFBs are not only precipitating declines and losses of populations and reducing the role they play as keystone species, spatially and numerically, but also functionally disrupting the ecological interactions that make up this keystone role through, for example, habitat degradation and the influence of invasive alien species. As a consequence, given the predominantly mutualistic relationship between LOWFBs and the plants that they service, it is reasonable to expect the emergence of an additional longer-acting and self-amplifying threat in the form of a positive feedback loop leading to gradual weakening of the plant–LOWFB mutualism. Declining or disappearing populations of LOWFBs would weaken plant reproduction (Albert et al. 2020, 2021), which would in turn lower foraging habitat quality for LOWFBs. So, we must be vigilant in conserving not just the keystone species but also the interactions that comprise their keystone role, and we should thus broaden the focus of attention as far as possible to the bat's entire ecosystem.

5. FUTURE DIRECTIONS

Many threats facing LOWFBs, like hunting and persecution, are stark and direct and legitimately attract the greatest attention. However, certain more insidious threats are also starting to emerge, such as the influence of invasive alien plants and animals, which is disrupting the mutualism between LOWFBs and plants. Those threats appear to be emerging predominantly from small oceanic islands like Mauritius. Whether this is mere idiosyncrasy or constitutes a threat set to broaden its geographical scope is yet to be seen but deserves study; globally, invasion by alien plants and animals continues to increase, approaching the extreme levels already prevailing in Mauritius. More complete and robust quantification of LOWFBs' ecological roles as pollinator and seed disseminator is also warranted, including through the use of exclusion experiments and greater exploitation of natural experiments comparing the evolution of plant communities between sites where LOWFBs are extant and others where they are extinct (e.g., Albert et al. 2021).

LOWFBs are distributed across thousands of islands belonging to more than 85 countries. The nature and strength of threats faced by any given species or population thus vary across localities and need to be determined for effective conservation. Although we have highlighted commonalities of biology and ecology that derive from a fairly conserved body plan and confer vulnerability, species differ in diet and ecological specialization, roosting ecology, social structure, movement and gene flow among populations, and tolerance of human disturbance, even when in sympatry (Russell et al. 2016, Lavery et al. 2020b). Yet, except for the Australian species, LOWFBs have been little studied. Basic information on population size, population trends, ecology, and life history are lacking for many species, and the lack of local data prompts extrapolation from other species or populations, which may compromise conservation management. The monkey-faced bats (*Pteralopex* spp. and *M. acrodonta*) are a particularly high priority, as all are threatened and poorly characterized. Three species are assessed as CR (*Pteralopex flanneryi*, *Pteralopex pulchra*, and *M. acrodonta*), two are EN (*Pteralopex atrata* and *Pteralopex anceps*), and one is VU (*P. taki*) (IUCN 2022). Populations are decreasing for all six species. Here, we highlight priority actions that make up a multi-faceted approach to halt or reserve declines of LOWFBs and ensure that their keystone role is preserved.

5.1. Protect and Restore Native Habitats

Protection of foraging and roosting resources can allow these habitats to support larger populations, buffer populations in times of food shortage, provide refugia from disturbance, and generally keep bats separate from people to minimize conflict. Effective protection requires knowledge of diets and roost site selection, as well as the movements of bats among resources, and this knowledge is lacking for most species. Movement studies have demonstrated that many bats travel long distances on islands each night (Oleksy et al. 2015, 2019), so patches of forests and foraging resources can be connected into a distributed network, although monkey-faced bats are likely to need large tracts of unmodified forest (Lavery et al. 2020b). The habitat quality of patches can be restored by removing invasive species that directly threaten bats, compete with them, or compromise food availability. Because of the role of LOWFBs as seed dispersers and pollinators, healthy bat populations have the potential to promote habitat recovery and improvements.

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5.2. Monitor and Model Population Trends and Recovery

Population estimates, trends, and models to assess the current and future status of species and populations and evaluate the potential and actual success of interventions are urgently needed (e.g., Oedin et al. 2019). For poorly known species, or those on islands that have not been (recently) surveyed, collection of basic data on distributions is a crucial first step. Similarly, life history data are required for models of population trajectories under different disturbance or conservation regimes. The paucity of survivorship and fecundity data means that population models to date have tended to use estimates of life history characteristics drawn from studied Australian species (e.g., *P. poliocephalus*, *P. alecto*, *P. scapulatus*). However, these continental species differ in many aspects of their biology from island species and so too do key life history parameters used in models of population growth (e.g., Sugita et al. 2009, Todd et al. 2018, Brook et al. 2019).

5.3. Implement Multi-Faceted Campaigns to (Re)Set Attitudes and Alter Specific Conservation-Relevant Behavior

Ultimately, sustainable outcomes for LOWFBs will be secured only through the engagement and participation of local communities (Scheffers et al. 2012, Ardoin et al. 2020). Behaviors that directly threaten bat populations, such as hunting and persecution, often derive from attitudes and norms that can be difficult to change. It is critical that conservation campaigns not be based on assumptions about people's motivations and perceptions, but rather work to characterize them first (Cousins & Compton 2005, Vincenot et al. 2015, Kingston 2016, Aziz et al. 2017a, Straka et al. 2021). Multi-faceted campaigns should therefore clearly identify the behavior of concern, the group(s) performing the behavior, and the drivers of the behavior as the foci of action. Furthermore, people may wrongfully accuse LOWFBs of a variety of offenses (e.g., damaging fruit, causing sickness). Thus, blame assigned to bats should not be assumed to be valid before conclusive investigation. Initiatives that raise awareness of scientific knowledge and of the keystone role of LOWFBs and their importance to the viability of local plant populations and ecosystems can be an integral part of such campaigns.

5.4. Strengthen Legislation and Enforcement

Legal protection for LOWFBs varies from country to country and is generally very limited. In some locations, protection is afforded if the species is recognized as a nationally threatened species (e.g., in the Philippines, Mauritius, US territories, Indonesia, India, Japan). For such countries, working to get threatened LOWFBs legally recognized as threatened is an important, but extremely challenging, first step. Even when protective legislation exists, people may not be aware of it, and legislation may not be enforced (Scheffers et al. 2012). Enforcement resources and capacity are often limited and stretched thin by the geographical extent of LOWFB populations and focus on charismatic species deemed of more immediate concern. In some places, hunting is seasonal and/or for immediate local consumption, further confounding enforcement. Even if a species is effectively protected, its critical habitat often is not protected, and legislation does not always lead to effective conservation plans to recover species (Preble et al. 2021).

5.5. Consider Captive Breeding

Although in situ conservation is the priority, captive breeding may be needed as part of a multi-faceted action plan for some species, particularly when numbers are very low, as small populations on islands are especially vulnerable to demographic and environmental stochasticity and to threats that are inescapable (e.g., rising sea levels, total loss of habitat). The potential for captive breeding to contribute to species conservation is illustrated by *P. rodricensis*, a threatened endemic from the Mauritian island of Rodrigues. The population was reduced to ~70 known individuals in the wild by hunting, habitat loss, and several cyclones, but captive breeding efforts have since resulted in holdings of >900 bats in 44 zoological institutions (Species360 2020), with much of the genetic diversity conserved (O'Brien et al. 2007). That said, to date, no captive-bred individuals have been released to the wild, so the contribution of captive breeding as a strategy to maintain populations in the wild is untested.

5.6. Build and Network Research Capacity

Bat research expertise and the capacity to implement recommendations are very limited. LOWFBs are predominantly found in low-income countries, and in the Pacific, most are also Small Island Developing States (SIDS). SIDS must address many conservation challenges with few resources and many logistical constraints. Nonetheless, there are significant hotspots of expertise and experience throughout the range of LOWFBs, and conservation research networks can accelerate capacity building through the rapid transfer of expertise from existing knowledge hotspots to countries or islands with limited prior experience. Networks also provide an important source of community support and encouragement, allow for coordinated conservation of species distributed across multiple countries, and facilitate priority setting activities (Kingston et al. 2016). Development of a multinational LOWFB Network is strongly recommended.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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