**Crumbling Island Keystones: Threat Diversity and Intensification on Islands Push Large Island Fruit Bats to the Brink**

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**Abstract**

Large island fruit bats (LIFB), species of *Pteropus, Acerodon,* and related genera in the pteropodid subfamily Pteropodinae, are keystone species for island conservation in the Palaeotropics, playing critical roles as agents of dispersal and pollination of native island plant communities. This keystone role is crumbling because LIFB are collectively the most threatened group of bats in the world. Six species (7.4%) have gone extinct in the last 200 years and ~66% of extant species are assessed as threatened by the IUCN. Life history characteristics, long lives, and low reproductive rates, elevate vulnerability and species are commonly subject to multiple threats. Here we review the primary threats to LIFB, namely unsustainable hunting, habitat degradation and loss, urbanisation, climate change, invasive species, and persecution. We highlight how the island context intensifies and accelerates population and species declines. We make specific recommendations in response to the major threats and identify overarching research needs to support conservation action. Specifically, research is needed that addresses: (1) population sizes and trends; (2) life history and social ecology; (3) dietary, roosting and movement ecology; (4) human attitudes and behaviors towards LIFB; (5) island-specific threats to LIFB; (6) distributions, populations and ecology of non-*Pteropus* species. Although there is great complexity of threats and contexts, five key conservation actions emerge that have the collective potential to secure LIFB populations throughout their ranges: (1) protect and restore native habitats; (2) improve attitudes and behaviours towards LIFB; (3) strengthen protective legislation and enforcement; (4) captive breeding of species at immediate risk of extinction; (5) build and network research and conservation capacity.

*Key words*: flying fox, monkey-faced bat, island conservation, keystone species, *Pteropus, Acerodon,* hunting, habitat loss, climate change.

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**I. INTRODUCTION**

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, 1987a). Over the following 15 years (1975-1989), demand in Guam reduced the other native *Pteropus* species, *P. mariannus*,to less than 100 animals and led to imports of more than 220,000 bats of ten *Pteropus* species from other islands in Micronesia, Polynesia, and Papua New Guinea (Wiles, 1992). The trade in flying foxes (species of *Pteropus*), resulted in such catastrophic population declines that by 1989 the focal species were listed under Appendix I of CITES and all other species of *Pteropus* and *Acerodon* on Appendix II.

In 1992, the International Union for Conservation of Nature (IUCN) published an action plan for the conservation of Old World fruit bats (family Pteropodidae) with emphasis on species of *Pteropus* or “flying foxes'' (Mickleburgh, Hutson, & Racey, 1992). Two years prior, the US Fish and Wildlife Service (USFWS) organised a Pacific Island Flying Fox Conference (Wilson & Graham, 1992) that produced seminal works highlighting both the conservation plight of flying foxes on islands across the Palaeotropics and their critical contribution as seed dispersers and pollinators to island ecosystems (Cox *et al.*, 1991; Fujita & Tuttle, 1991). Because of island colonization history and anthropogenic extinctions, island flying foxes are often the only remaining vertebrates on islands capable of dispersing large seeds (Entwistle & Corp, 1997a; Banack & Grant, 2002; Meehan, McConkey, & Drake, 2002; Hansen & Galetti, 2009; McConkey & Drake, 2015) and travelling the long-distances needed to connect fragmented plant populations through seed dispersal and pollination (Nakamoto, Kinjo, & Izawa, 2009; Oleksy, Racey, & Jones, 2015; McConkey & Drake, 2015). Focused studies have confirmed the disproportionate importance of flying foxes as keystone species to island ecosystems throughout their distribution (Fisher & Tasker, 1997; Entwistle & Corp, 1997a; Banack, 1998; Bollen & Van Elsacker, 2002; McConkey & Drake, 2006, 2015; Fall, Drezner, & Franklin, 2007; Staddon, Compton, & Portch, 2010; Chen *et al.*, 2017; Florens *et al.*, 2017a) as well as the ecosystem collapse that can follow their extinction (Heinen *et al.*, 2018; Albert, Flores, & Strasberg, 2020). Consequently, the status of island flying fox species is not only of intrinsic conservation concern but has direct implications for the long-term viability of island plant communities, many of which comprise numerous threatened endemics (Bollen & Van Elsacker, 2002; Fall *et al.*, 2007; Kier *et al.*, 2009; Caujapé-Castells *et al.*, 2010; Scanlon *et al.*, 2014a), and the faunal assemblages they support (Vincenot, Florens, & Kingston, 2017b). Furthermore, flying foxes are important pollinators of island plants of local or economic importance (Scanlon *et al.*, 2014a; Aziz *et al.*, 2017a; Sheherazade, Ober, & Tsang, 2020).

Ninety-five percent of all global mammal extinctions over the past 500 years have occurred on islands (Loehle & Eschenbach, 2012) and bats are no exception. Six of the nine known recent (<200 years) bat extinctions (*Pteropus allenorum, P. brunneus, P. coxi, P. pilosus, P. tokudae, P. subniger*) were island flying foxes (IUCN 2020). In addition, populations of extant species have been extirpated from individual islands within their historical range (e.g., *P. melanotus* from Enggano, Indonesia (Hutson *et al.*, 2008), *P. rodricensis* from Mauritius (Tatayah *et al.*, 2017)*. P. niger* from Rodrigues (Cheke & Hume, 2010) or are probably extinct (*P. ocularis* from Ambon, Indonesia (Tsang, 2016a), *Pteropus aruensis* from the Aru Islands, Indonesia (Tsang, 2016b), *Pteralopex flanneryi* from several of the Solomon Islands (Lavery, 2017), or in imminent danger of local extinction (e.g., *P. pselaphon* from Haha-jima (Vincenot, 2017)). Here we evaluate the current status of and major threats to island flying foxes and extend consideration to include related large-bodied genera, that we collectively describe as LIFB.

All LIFB are members of the pteropodid subfamily Pteropodinae, which comprises three tribes. The tribe Pteropodini is made up of *Pteropus* (65 species), *Acerodon* (five species)*, Styloctenium* (two species), and *Neopteryx frosti.* The tribe Pteralopini comprises *Pteralopex* (5 species), *Desmalopex* (2 species), *Mirimiri acrodonta* (Almeida, Simmons, & Giannini, 2020). Melonycterini is a new tribe hosting small (< 0.06 kg), nectarivorous species of Least Concern (IUCN 2020) restricted to the Bismark Archipelago (*Melanycteris melanops*) and Solomon Islands (*Nesonycteris* spp.). The Melonycterini is not considered further in this review and all reference to Pteropodinae hereafter refers only to the Pteropodini and Pteralopini - large (up to 1.6 kg) fruit bats that typically play disproportionately important ecological roles on islands. Of these, 75 are extant and six *Pteropus* are extinct. The genera are restricted to the Old World tropics, with *Pteropus* distributed predominantly on islands from Madagascar to Australia, *Acerodon* in the Philippines and Sulawesi (Indonesia) and *Neopteryx frosti* and *Styloctenium* spp. known only from Sulawesi. The two *Desmalopex* spp. are only found in the Philippines, and the rare, and poorly known, monkey-faced bats are recorded only from Fiji (*Mirimiri acrodonta*) and the Solomon Islands (*Pteralopex* spp.) (Fig. 1). In our consideration of large *island* fruit bats, we excluded the eight *Pteropus* species (*P. alecto, P. conspicillatus, P. medius* [as *P. giganteus* in the Red List]*, P. intermedius, P. lylei, P. poliocephalus, P. scapulatus, P. vampyrus*) that are extensively or exclusively distributed on continental Indomalaya or Australia.

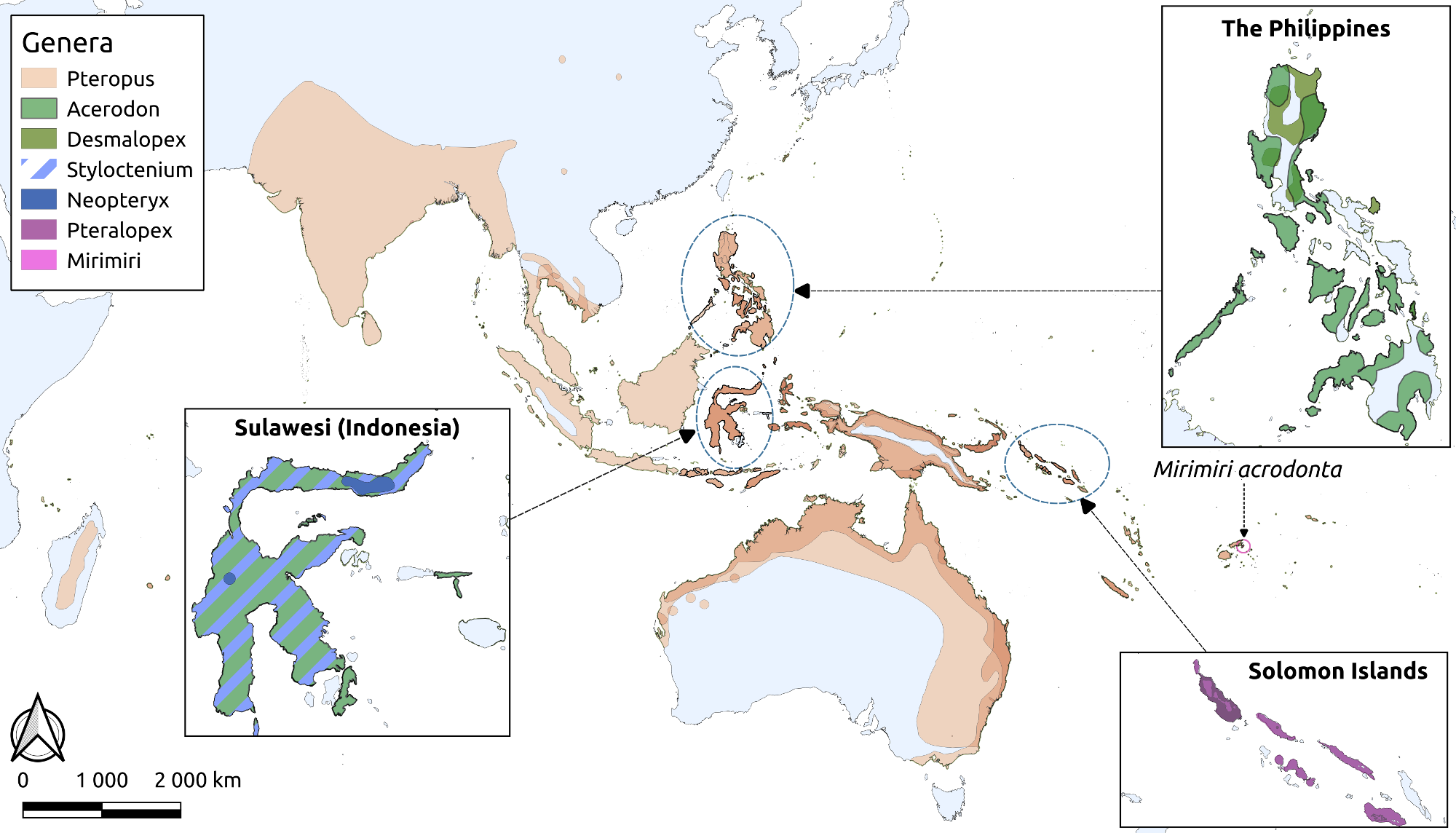
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Fig. 1. Geographical distribution of the 75 extant large island fruit bats species (tribes Pteropodiniand Pteralopiniof the subfamily Pteropodinae) across the Palaeotropics. Map produced based on ranges declared in the IUCN Red Data List. Number of species within a genus and area is coded through colour shading (from light to dark by increasing density). Insets illustrate distributions of non-*Pteropus* species.

We posit that the island context accelerates population declines of large island fruit bats. LIFB are particularly vulnerable because: (1) life history traits and ecological characteristics both retard population recovery and intensify susceptibility to threats; (2) island populations are commonly subject to many diverse threats; and (3) both deterministic and stochastic threats are intensified on islands.

**II. METHODS AND DATA**

We evaluated the conservation status of all bat species from the IUCN Red List assessments (as of 21st December 2020). We extracted the Red List category, population trend, number and type of threats. For the LIFB, we further reviewed each assessment for any pertinent ecological and conservation information. The number of threats per species was assessed at the lowest level of classification provided by the assessment (usually level 2 or 3). For example, a count of 3 threats might come from a record in the assessment of 5.3, 5.1.2, 7.2.10. To describe the types of threats, we renamed or pooled IUCN threat types into seven categories most relevant for bat conservation as follows: hunting – IUCN threat classification 5.1.1; habitat degradation – IUCN classifications 1.3, 5.3, 5.2, 7.1, 7.2.2, 7.2.8, 7.3; land-use change – 2.1, 2.2, 2.3, 7.2.10, 7.2.11; climate change – 11; urbanisation – 1.1, 1.2, 4.1, 4.2, 4.4; invasive species – 8; other – 3.2, 3.3, 5.1.2, 6.1, 6.2, 6.3, 9.0, 10; persecution -- 5.1.3. (IUCN 2012). Population trends are assessed as decreasing, stable, increasing or unknown.

We reviewed the scientific literature returned by the Web of Science from a search parameterized thus: TOPIC: (Flying fox\* OR Pteropus OR Acerodon OR Styloctenium OR Neopteryx OR Pteralopex OR Mirimiri OR Monkey-faced) AND TOPIC: (ecology OR conservation OR threat\* OR diet OR roost) AND TOPIC: (island\* OR Philippines OR Indonesia OR Malaysia OR Solomon OR New Guinea OR Madagascar OR Mauritius OR Mascarene OR Seychelles OR Fiji OR Reunion OR Pacific OR Micronesia OR Polynesia OR Melanesia OR Pemba OR Rodrigues) Timespan: 1900-2020. Indexes: SCI-EXPANDED, SSCI (final search -- 02 Dec 2020). This resulted in 204 documents of any type spanning 1990-2020. We reviewed all documents for information on the biology, ecology and threats of the species, paying particular attention to information that would support or refute points (1)-(3) above. Of these, 131 held relevant information. Where appropriate, we drew on additional literature about mainland *Pteropus* spp., bats, island conservation, and social science practices known to us, or cited by or citing literature returned from the search. Based on our findings, we make specific recommendations for conservation research and action.

**III. CONSERVATION STATUS**

Despite their ecological importance, large island fruit bats are the most threatened group of bats in the world and their status continues to worsen (Vincenot *et al.*, 2017b) (Fig. 2). Seventy-three species of LIFB have been assessed by the IUCN (Dec 21 2020 - *D. leucopterus not in the system*), 67 of which are extant. Sixty-eight percent of species are currently assessed as extinct or threatened, falling in threat categories Extinct (EX), Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) (Fig. 2a), whereas only 13% of all other bat species are threatened or extinct (Fig. 2b) (IUCN 2020). Furthermore, information on 10% of living species of Pteropodinae is so scarce that their status could not be assessed (DD). The populations of 45 species (55.6%) are decreasing, and stable or increasing populations known for only ten (12.3%) and two species (2.5%) respectively. The two increasing populations are both of species brought back from the brink of extinction by substantial conservation effort, namely *Pteropus voeltzkowi* (VU) on Pemba (Robinson *et al.*, 2010), and *P. rodricensis* (EN) from Rodrigues (Tatayah *et al.*, 2017).

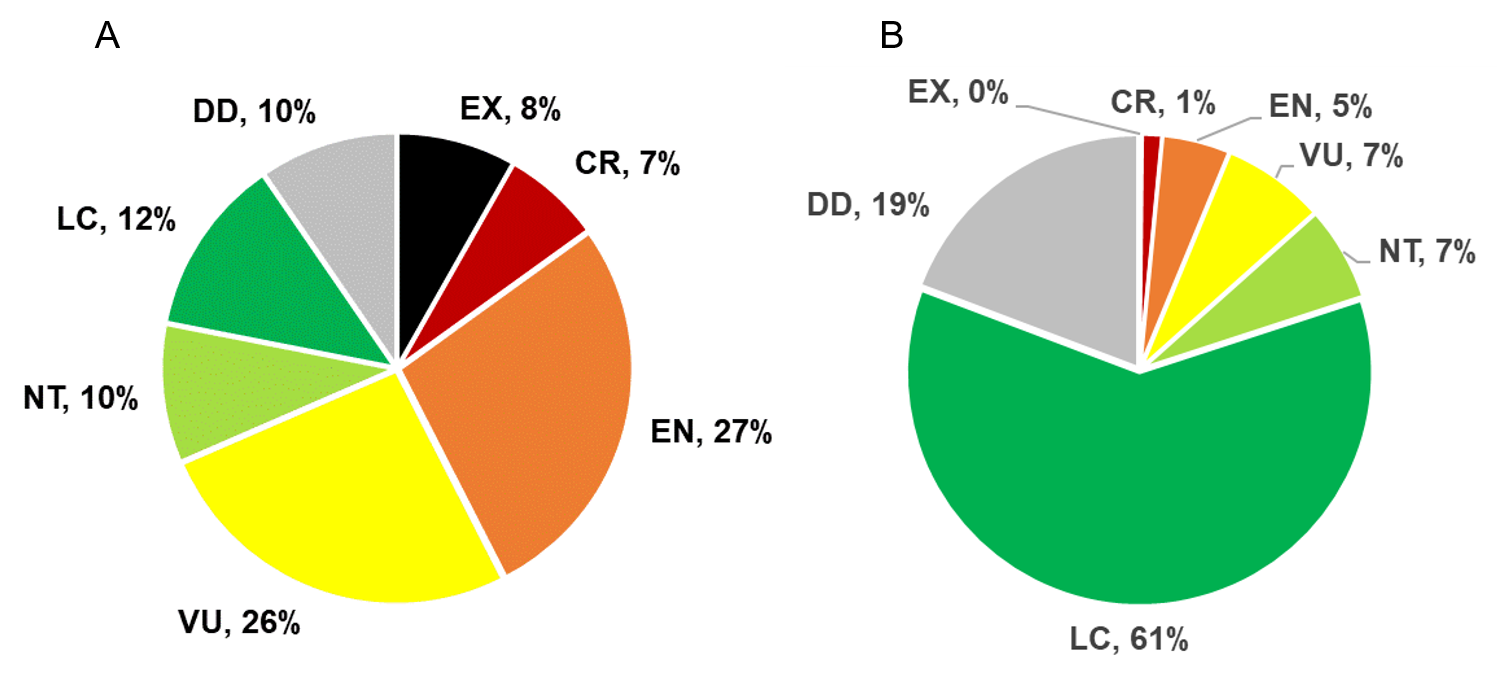


Fig. 2. Red list status of 67 LIFB (A) and the 1231 other bats (B). Abbreviations correspond to IUCN Red List categories EX--Extinct, CR--Critically Endangered, EN--Endangered, VU--Vulnerable, NT--Near Threatened, LC--Least Concern, DD--Data Deficient.

**III. LIFE HISTORY CONFERS VULNERABILITY**

Island Pteropodinae are K-selected species adapted to stable environmental conditions and exhibit low extrinsic mortality (Jones & Larnon, 2001; McIlwee & Martin, 2002). *Pteropus* spp. are large (up to 1.6 kg) and long-lived. Lifespan is generally between 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 lifespans (e.g., *Pteropus melanotus natalis* of Christmas Island has an estimated lifespan of 4-6 years, although some individuals may reach 11-13 years old -- Christopher Todd, Laura Pulscher *pers. comm.*). Females rarely give birth to more than one pup a year and maturity is delayed 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), so populations are slow to recover from reductions (e.g., (Craig, Trail, & Morrell, 1994). The sparse records for other genera suggest similar life history characteristics.

**IV. THREAT DIVERSITY AND INTENSIFICATION**

Ecosystems on tropical islands are inherently fragile and functionally vulnerable to change (Brodie, Pikacha, & Tuiwawa, 2013; Keppel *et al.*, 2014), so the impact of human disturbance is significantly greater on islands than on mainland regions (Kier *et al.*, 2009). While anthropogenic activities endanger bat populations worldwide (Voigt & Kingston, 2016; Frick, Kingston, & Flanders, 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; Conenna *et al.*, 2017). Moreover, governance and regulation of natural resources may be complicated by land tenure, the challenge of local enforcement of federal regulations and laws on distant islands (e.g., Indonesia, which comprises more than 19,000 islands dispersed E-W across 2,210 km), limited capacity for governance and enforcement and island poverty that drives overexploitation of natural resources (Brodie *et al.*, 2013).

We found that 57 LIFB species are subject to two or more threats in the Red List threat classification scheme, and 36 species experience four or more threats (Fig. 3a). Compared to other species, LIFB are disproportionately affected by all major threats (Fig. 3b).

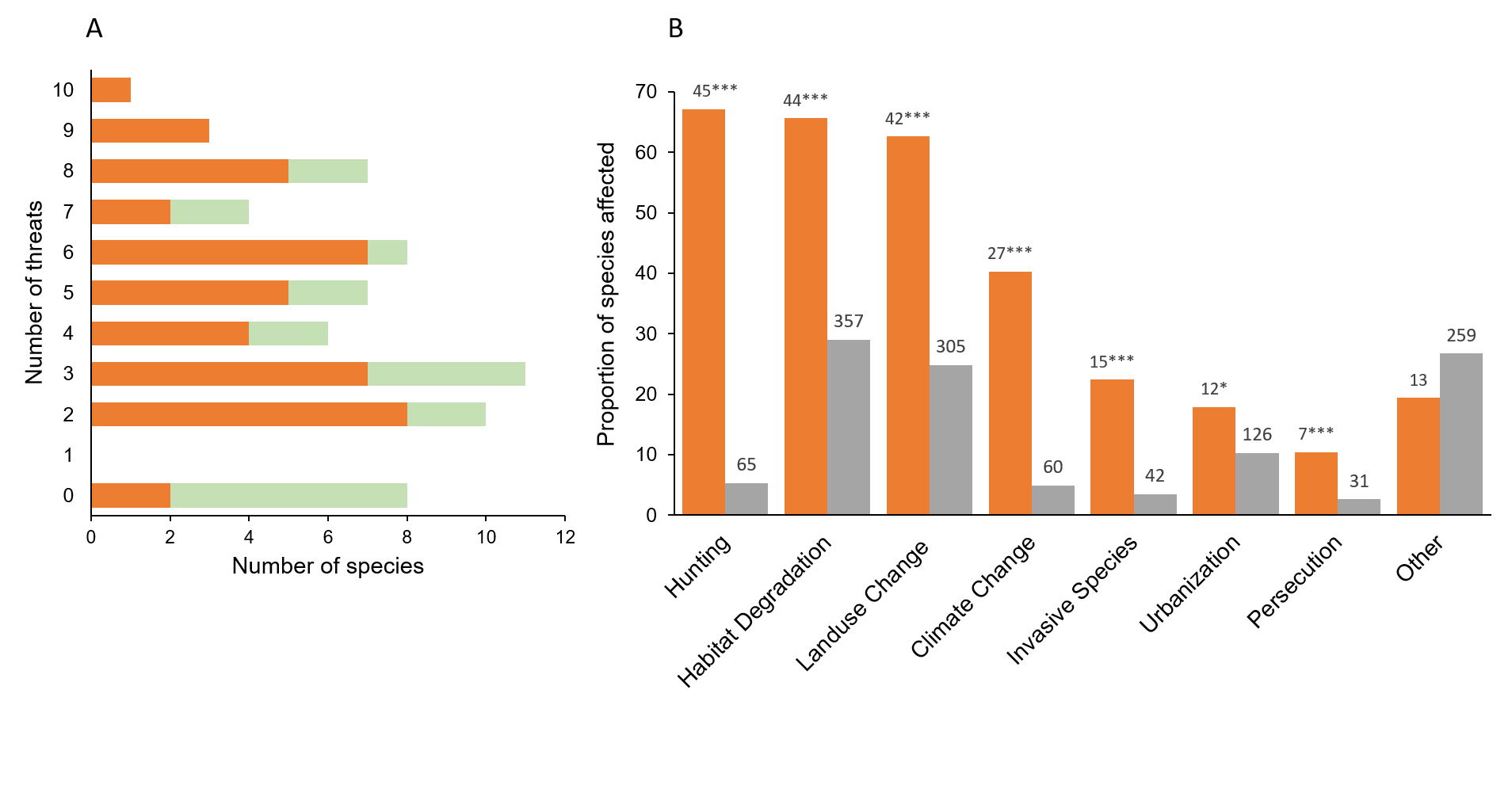


Fig. 3. Diversity and intensity of major threats to LIFB. (A) Number of threats listed for LIFB in the Red List assessments. Data – IUCN 2020 downloaded 21 Dec 2020. Orange = threatened species (those assessed as CR, EN, VU), green = non-threatened species (NT, LC, DD). (B) The distribution of major threats to LIFB (orange) and other bat species (grey), as proportions of species affected. Number of species affected is shown as text above the bars. Asterisks indicate significance level of Chi-squared tests that the threat disproportionately affects LIFB (\*\*\* < 0.001; \*\*< 0.01; \* < 0.05).

**(1) Hunting**

Unsustainable hunting of large island fruits bats for cultural, subsistence or commercial purposesis the most frequently reported threat to LIFB (Fig. 3b). This is of grave concern because all extinct LIFB were intensively hunted (IUCN 2020). Flying foxes and their relatives are hunted for their meat, perceived medicinal value, and for ornaments and even currency (Jones *et al.*, 2010; Wiles & Brooke, 2010; Mildenstein, Tanshi, & Racey, 2016; Lavery & Fasi, 2019). Many *Pteropus* species are colonial, and commonly exhibit high fidelity to preferred roost sites, where they aggregate in large numbers to form highly conspicuous camps that are readily located by hunters across years. In contrast, *Pteralopex* spp. typically roost in small groups (1-10 individuals in tree hollows and strangler figs). Although this makes them less conspicuous to hunters, adhoc 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). Notably, the now globally extinct *Pteropus subniger* was hunted in a similar fashion on Mauritius (Cheke & Hume, 2010).

Bat hunting has a long history in insular Asia-Pacific, dating back to prehistory and likely of particular importance on islands with depauperate fauna (Hand & Grant-Mackie, 2012; Hawkins, O’connor, & Kealy, 2016). Introduction of modern weapons through the 20th Century (Seehausen, 1991; Wiles, 1994; Entwistle & Corp, 1997b) 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 trade networks to meet demand (Wiles & Brooke, 2010). Although CITES successfully disrupted trade from Pacific islands to Guamand 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 throughout Sulawesi and imports from other Indonesian islands to meet demand (Sheherazade & Tsang, 2015, 2018; Latinne *et al.*, 2020).

Roost selection by hunted LIFB is typically determined by the relative safety from humans provided by inaccessible areas (Entwistle & Corp, 1997b; Brooke, Solek, & Tualaulelei, 2000; Brooke, 2001; Cousins & Compton, 2005; Sheherazade & Tsang, 2018) including mangroves (Tsang, Wiantoro, & Simmons, 2015; Latinne *et al.*, 2020). However, refuges on islands are limited by extensive changes in land use and loss of roosting habitat (Cousins & Compton, 2005; Ibouroi *et al.*, 2018b). Moreover, although religious taboos attach to hunting of some species (e.g., *P. voeltzkowi* in Pemba graveyards -- (Entwistle & Corp, 1997b), most species fall outside the core geographic distribution of Buddhism and associated protection in monasteries often seen on continental Indo-Malaya (Ravon *et al.*, 2014).

**Recommendations:** Hunting emerges from social, cultural and economic imperatives. Hence, socio-economical and anthropological studies focused on understanding perception and utilitarian values of bats, and the social norms reinforcing hunting behaviour, are crucial. Drivers of hunting can be evaluated using bespoke conceptual frameworks, such as the Theory of Planned Behavior (Ajzen, 1991; Kingston, 2016; St. John *et al.*, 2018), to identify components for intervention. Based on situation assessment, appropriate mitigation measures that suit the particular context (e.g., following the Theory of Change (Rice, Sowman, & Bavinck, 2020)) can be inferred and explored. For example, subsistence hunting may occur to satisfy protein intake, in which case interventions might focus on how to make alternative protein sources available. If hunting is driven by economic needs, prosed mitigations might focus on ecotourism, conservation or other alternative livelihoods, whereas if it is the product of a cultural norm, solutions should aim to rely on local leaders (e.g., Sheherazade & Tsang, (2015)).

Regulated hunting should align with periods of traditional use (Oedin *et al.*, 2019) but take place outside of mating and maternity seasons. In any case, the sustainability of current and projected offtake must be rigorously and regularly reassessed. This task should include population size estimations, monitoring, and hunter surveys as well as market surveys. As for the latter, optimally, the nationwide supply market should be mapped to account for any outflows from regions of interest (see Latinne *et al.*, (2020)). Finally, effective measures to enforce quotas must be seen as a strict necessity (e.g., such as is done in New Caledonia).

**(2) Habitat degradation and land-use change**

Many islands have undergone rapid transformation of their native vegetation into agricultural or settlement uses, as well exemplified by Mauritius (< 5% natural habitat remaining), Rodrigues (Florens, 2013), La Reunion (Strasberg *et al.*, 2005), Comoros (2% native forest cover left), Eastern Melanesian Islands (< 11% unmodified forest (Sloan *et al.*, 2014)). Some islands have a high percentage of built-up areas and environmentally sensitive areas are under threats of further peri-urban expansion (Hammond *et al.*, 2015). Natural habitat that remains is often relatively accessible and lacking in protection, so projections of land-cover change by 2100 are greater on islands than mainland areas (Kier *et al.*, 2009), a situation worsened by rising sea-levels caused by climate change (Wetzel *et al.*, 2012).

Loss of native habitats, particularly forests, is a dual threat to island fruit bat populations, reducing foraging grounds that can provide year-round supply of fruits and flowers, and the availability of large trees as roosts in secure locations (e.g., Daniel *et al.*, (2017); Ibouroi *et al.*, (2018b)). Moreover, there is growing evidence that forest degradation has consequences for *Pteropus* populations. Secondary forests in Fiji provide less than half the fruit resources used by bats than primary forests, and 10% fewer flower resources (Scanlon *et al.*, 2018). Similarly, forests invaded by non-native weeds in Mauritius suppress flowering and fruiting of native trees upon which fruit bats rely (Baider & Florens, 2006; Monty, Florens, & Baider, 2013). Ultimately, habitat degradation may necessitate dietary shifts, as seen in *P. rufus* in response to loss of forest cover in Madagascar (Reuter *et al.*, 2016), and *P. dasymallus* to urbanisation in the Ryukyus (Nakamoto, Kinjo, & Izawa, 2007, 2015).

Monkey-faced bats are closely associated with old-growth lowland and/or montane forest (Fisher & Tasker, 1997) and so are particularly sensitive to deforestation. For example, *Pteralopex taki* has only been found within 5 km of primary forest, and capture rates were negatively related to logging intensity over a 23 year period in the Solomon Islands (Lavery *et al.*, 2020b). Roosts are typically canopy or emergent trees large enough (Fisher & Tasker, 1997) to provide hollows of sufficient size to shelter groups of up to 10 individuals and allow roost-sharing with larger *Pteropus* species (e.g., *P. admiralitatum*). *Pteropus anceps* is similarly found in hollows of large rosewood (*Pterocarpus indicus*)and fig trees (Bowen-Jones *et al.*, 1997).

In addition to the loss of inland native forests, loss of mangrove ecosystems is widespread due to commercial logging and overexploitation (e.g., for firewood) by local communities and conversion to aquaculture/agriculture (Valiela, Bowen, & York, 2001; Brodie *et al.*, 2013; Thomas *et al.*, 2017). Mangroves provide important food resources and roosting refuges for some flying fox species (Entwistle & Corp, 1997a; Lee *et al.*, 2009), especially on islands with hunting (Tsang *et al.*, 2015; Sheherazade & Tsang, 2018).

**Recommendations:** Unsurprisingly, remedies rely mainly on the protection of natural habitats supporting bat populations, and significant, individual roost trees. The principal tools for protection are laws and sometimes cultural or religious rules (e.g., in case of bats roosting in sacred places). Research is, however, critical to undertake upstream. Movement and dietary studies are necessary to identify key food resources and patches that can ensure year-round foraging and roosting sites. Since tracking studies suggest that many large island fruit bats fly long distances (e.g. (Oleksy *et al.*, 2015, 2019), connectivity of patches can be seen as less important than quality of the habitat itself (e.g., tree species composition including preferred food sources, absence of human disturbance, predators or competitors, especially invasive species). Habitat quality should be improved whenever possible. For instance, experiments undertaken in Mauritius demonstrated that targeted weeding of exotic species was highly beneficial to the Mauritian flying fox (Krivek *et al.*, 2020). Similarly, roost trees should be characterized, mapped and shielded from anthropogenic disturbance (especially hunting) through remote telemetry (i.e. spatial tracking) studies and collaboration with local stakeholders. The creation of artificial roost trees to attract bats to secure locations is also a promising research topic. Finally, we suggest that large benefits are attainable with limited resources by focusing on protecting a few high-value sites that might have disproportionate, positive effects on bats while requiring minor time investment in terms of protection (e.g., temples, cemeteries, mangroves).

**(3) Urbanisation - of people and bats**

The proportion of human populations in urban areas on islands has been steadily increasing since the middle of the last century and is projected to range from 30% (Melanesia), 50% (Polynesia) to 70% (Oceania) by 2050 (Anon., n.d.). Globally, studies of urban landscapes report declines in overall bat diversity and activity compared to more natural areas (Jung & Threlfall, 2016), and urbanisation appears to affect large island fruit bats through two routes. First, urban development removes natural habitats and hence food and roosts, and introduces novel hazards, particularly power lines that can electrocute bats (Cheke & Dahl, 1981; Vincenot, Collazo, & Russo, 2017a; Tella *et al.*, 2020). Second, urban areas appear to attract some large island fruit bats that commonly roost near human settlements (e.g., P. *dasymallus* in Japan, *P. hypomelanus* on Tioman Island, Malaysia (Aziz *et al.*, 2017b), *P. s. comorensis* on the Comoros Islands (Ibouroi *et al.*, 2018b)) if they are not persecuted or hunted. Increasing urbanisation of flying foxes may be driven by a combination of loss of natural habitat and resources and provision of food resources by plantings (especially of fruit trees) in and around urban and village areas (Williams *et al.*, 2006; Tait *et al.*, 2014; Tella *et al.*, 2020). Urban and peri-urban fruit bats exploit both native and non-native fruit trees (Lee *et al.*, 2009; Lim *et al.*, 2018a), and through seed dispersal may create a feedback loop ultimately increasing the availability of food resources in urban and peri-urban habitats. Interestingly, although *P. s. comorensis* roosts in proximity to villages and roads on the Comoros Islands, it forages in natural forest. Similarly, Tioman Island (Malaysia) retains tracts of undisturbed forest, suggesting other motivations for roosting of *P. hypomelanus* near people (Tait *et al.*, 2014; Aziz *et al.*, 2017b).

Increasing proximity to people has several consequences. Large colonies can be a source of inconvenience through noise, odour and faeces, and may feed on backyard fruit trees and orchards. Both bring bats into conflict with people (Cousins & Compton, 2005; Aziz *et al.*, 2017b; Anthony, Tatayah, & De Chazal, 2018; Florens & Baider, 2019) and can expose populations to persecution and hunting, even in areas where hunting was previously uncommon or reduced (Kingston *et al.*, 2018; Ibouroi *et al.*, 2018b). Proximity to people also increases concerns about possible transmission of diseases from bats to people (Basri *et al.*, 2017). Centrally, greater use of urban and village areas and crop raiding by bats can lead to the perception that populations are more abundant than they are, undermining support for conservation initiatives (Vincenot *et al.*, 2017a; Florens & Baider, 2019). Urbanisation of human populations can also erode experience and awareness of the value of biodiversity in general (Miller, 2005; Brodie *et al.*, 2013) resulting in negative or apathetic attitudes towards wildlife in conflict situations. Such attitudes may even be made worse when authorities opt to pursue non- or contra-evidence-based policies (Florens & Baider, 2019).

**Recommendations**: Research on tropical urban bat ecology is in its infancy and very limited on islands. That said, there is a rich seam of research from Australia where urban and peri-urban *Pteropus* populations have been increasing for decades. In some cases, urban camps even establish outside of the bats’ historic geographical range (van der Ree *et al.*, 2006; Williams *et al.*, 2006). Research on island bats should focus on the ecology of urbanisation, addressing urban use (e.g., roosting, foraging (McDonald-Madden *et al.*, 2005)) through tracking and dietary studies, that might identify drivers of urbanisation that could be mitigated, through protection of natural roosts and foraging sites, for example. Once established, mainland urban *Pteropus* spp. show high fidelity to their urban roosts, suggesting the importance of establishing and mitigating drivers early in the urbanisation process. Peaceful coexistence with urban fruit bat populations will require effective methods to protect backyard and public spaces (particularly fruit trees), management of roost trees, and research on the best methods to manage valuation and perception of bats through outreach, education, social marketing and similar campaigns across all stakeholders. Evidence-based assessment and management of conflicts including those concerned with disease risk are warranted.

**(4) Climate change**

Climate change threatens several of the world’s biodiversity hotspots and is a major concern for palaeotropical islands (Taylor & Kumar, 2016). Floods are forecast to affect bats living on low-lying islands and atolls while sea level rise threatens to extirpate subspecies such as *P. pelagicus pelagicus* in the Mortlock islands (Buden, Helgen, & Wiles, 2013) and *P. aldabrensis* on Aldabra where 60% of the atoll lies at or below 1 m a.s.l. (Waldien & Bunbury, 2020). Heatwaves, which have proven lethal to *Pteropus* in parts of India (Dey, Roy, & Chattopadhyay, 2015) and have occasioned die-offs of near-biblical scale in Australia (Welbergen *et al.*, 2008; Welbergen, Booth, & Martin, 2014), have so far been reported only on continents. Yet, as their increase in frequency and intensity is predicted to further endanger flying foxes (Ratnayake *et al.*, 2019), they might become a subject of concern also on islands.

The greatest threat posed by climate change to island bat species is the projected increase in severity and frequency of cyclones (Tsuboki *et al.*, 2015). Cyclones are a source of direct mortality as individuals are battered by high winds or blown from islands, resulting in population declines that can exceed 90% (see (Wiles & Brooke, 2010; Scanlon *et al.*, 2018) for review).

Furthermore, cyclones can cause extensive damage to natural habitats and the food and roosts they provide (Craig *et al.*, 1994). All species of Pteropodidae are predominantly frugivorous and/or nectarivorous and rely on year-round availability of fruits or flowers, although leaves, and in some species insects, are consumed when fruit or nectar are scarce (Raheriarisena, 2005; Scanlon, Petit, & da S. Sternberg, 2013). They are thus very vulnerable to food shortages that arise from disruption of fruiting or flowering associated with cyclones and other extreme weather events such as drought or heavy rain. 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. Several species of mainland pteropodids migrate long distances (up to 6,000 km) (e.g., *Pteropus poliocephalus, P. alecto* and *P. scapulatus* in Australia (Spencer, Palmer, & Parry-Jones, 1991; Welbergen *et al.*, 2020), *Eidolon helvum* in Africa (Thomas, 1983; Richter & Cumming, 2005), or increase their foraging range (Fahr *et al.*, 2015) in response to seasonal variability or unanticipated food shortages, but this is not an option on small islands. The diverse diets of many island flying foxes (Banack, 1998; Lee *et al.*, 2009; Florens *et al.*, 2017a; Lavery *et al.*, 2020a) may confer some resilience to 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 break up of colonies following cyclones (Stinson, Glass, & Taisacan, 1992; Brooke *et al.*, 2000). Models from Australia suggest cyclones reduce both survival and reproduction (Westcott *et al.*, 2018).

Extreme weather events are projected to increase in frequency, intensity and duration (Knutson *et al.*, 2010; Rahmstorf & Coumou, 2011; Westra *et al.*, 2014), resulting in more frequent and pronounced unpredictable resource shortages (Maron *et al.*, 2015), but climate change also brings changes in the spatial and temporal distribution and occurrence of temperature and precipitation with consequences for the phenology of fruit and flower resources (Butt *et al.*, 2015). As many island fruit bats time lactation to coincide with the greatest availability of resources (i.e. peak of fruiting seasons) (Banack & Grant, 2003), changes in fruiting phenology may result in a phenological mismatch between bat reproduction and fruit availability, reducing reproductive success and eroding fitness. Climate change may also break mutualisms central to the persistence of key bat resources e.g., loss of pollinating fig wasps and hence figs (Harrison, 2000). The response of large island fruit bats to climate change thus fits a “press-pulse” framework (Harris *et al.*, 2018) whereby stresses of long-term change combine catastrophically with those of extreme weather events. Resource 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.

**Recommendations:**  Given the pervasive, yet locally unpredictable consequences of climate change, the single most effective mitigation is to protect and restore diverse, high quality foraging areas to buffer post-cyclone food shortages and other climate-driven failure of foods through time. Hunting moratoria following extreme weather events, or sustained food shortages, are also recommended to allow populations to recover from high mortality rates or diminished reproductive success, for species not threatened with extinction. Monitoring and surveillance are likely needed to detect some climate effects (e.g., dehydration deaths in the Ryukyus) so distributed community-based surveillance and reporting systems should be established. Rising sea levels currently directly only affect a few species, but research into the options for rescue and relocation, and the conservation value and outcomes of such actions are needed.

**(5) Invasive species**

Islands are infamously susceptible to invasion by alien species, frequently with devastating consequences for native island biodiversity (Vitousek, 1988; Reaser *et al.*, 2007; Corlett, 2010; Bellard, Cassey, & Blackburn, 2016), including bats (Welch & Leppanen, 2017). Invasive species threaten large island fruit bats directly through predation, competition and disease (see earlier review in Wiles & Brooke, (2010)), and indirectly through degradation of native forest resources.

Invasive predators are key drivers of global biodiversity loss and endemic island faunas are especially vulnerable (Doherty *et al.*, 2016). Large size, flight and a tree-roosting habit protect large island fruit bats from predation to some extent, but introduced cats are known to take *P. melanotus natalis* on Christmas Island (Tidemann, Yorkston, & Russack, 1994), and both cats and dogs are reported to take *P. dasymallus* on Ryukyu islands (Vincenot *et al.*, 2017a), and *P. ornatus* and *P. vetulus* in New Caledonia (Palmas *et al.*, 2017),among others. Cat predation typically occurs when the bats forage close to the ground, which can limit the population impact, although individual cats may specialize on bat hunting and predation pressure is likely to increase as populations of feral and abandoned domestic predators increase on islands (Vincenot *et al.*, 2017a). Arboreal predators present more immediate threats, exemplified by the accidental introduction of the brown tree snake (*Boiga irregularis*) to Guam in the 1940s. The large (up to 3 m), arboreal, nocturnal snake proved adept at exploiting non-volant young of the native flying fox (*Pteropus mariannus*) left behind at tree colonies while mothers foraged, hindering population recruitment and exacerbating declines from human hunting (Wiles, 1987b). Noxious invasive arboreal ants (e.g., the yellow crazy ant (*Anoplolepis gracilipes*), little fire ant (*Wasmannia auropunctata*)) can also reach roosting bats, with consequences for roosting patterns (Bowen-Jones *et al.*, 1997), behaviour, and possibly energy budgets that may impact fitness (Dorrestein *et al.*, 2019).

The potential for competitive interactions to impact large island fruit bats has been little appreciated, but is becoming increasingly apparent on Mauritius, where the alien long-tailed macaque (*Macaca fascicularis*) consumes or damages native tree fruits important to bats before they ripen (Reinegger *et al.*, 2021). For example, about 95 % of fruits of the *Sideroxylon grandiflorum*, a canopy tree, are destroyed before maturity by monkeys (Baider & Florens, 2006), denying the bats a large proportion of their natural food. Rats have been introduced to most islands and also reduce fruit availability. Even introduced insects can compete for fruit on some islands (e.g., scarab beetles, *Protaetia orientalis,* eating breadfruit on Guam) (Wiles & Brooke, 2010).

There have been several anecdotal reports of localized mass die-offs or high-mortality epidemics of *Pteropus* species that are likely attributable to the accidental introduction of novel pathogens (e.g., *P. ualanus* on Kosrae Island (Micronesia) in 1927 (Coultas, 1931), *P. ornatus* on New Caledonia in the 1960s(Flannery, 1995), *P. rayneri* in Bougainville and Buka in 1987 (Flannery, 1989) and Choiseul Island (Solomons) in 1994 (Bowen-Jones *et al.*, 1997)) and even deliberate introduction of avian cholera in the mid-1890s to eradicate populations of *Pteropus* on the Samoan island of ‘Upolu to reduce bat damage to fruit crops (Spennemann & Wiles, 2001).

Of long-term concern is the potential for indirect effects of invasive species to compromise large island fruit bat populations, primarily by reducing and degrading native habitats and the resources they provide. For example, on Mauritius alien plant species are progressively invading native habitats to reach high densities and replace native species and hence food sources (Florens *et al.*, 2016), even in protected areas where a halving of larger trees occured in 68 years (Florens *et al.*, 2017b). Alien plants can also suppress reproductive output (flowering and fruiting) of native trees (Monty *et al.*, 2013), and further reduce plant fitness by slowing growth and even elevating tree mortality rates (Florens, 2008). Invasive insects and pathogens also cause direct mortality of plants of importance to bats. Flowers of coral trees (*Erythrina* spp.) are visited for their nectar and pollen by *Pteropus* spp. across the Palaeotropics but are being destroyed by the invasive erythrine gall wasp *Quadrastichus erythrinae* throughout their range (Wiles & Brooke, 2010). Whereas the relationship between native fruit bats and their food plants are usually mutualistic, invasive feral pigs (*Sus scrofa*), goats (*Capra hircus*), deer (*Rusa marianna*), macaques, and rats are often predators of seeds and/or saplings, reducing recruitment and compromising regeneration of natural habitats and diversity of food species important to bats (Wiles & Brooke, 2010). In summary, invasion by alien species result in two distinct blows to fruit bats: (1) There is a lower availability of flowers and fruits per individual tree in invaded forests; and (2) There is a decreasing number of fruit trees useful to bats per unit area of forest.

**Recommendations**: Eradication or control of invasive species is central to conservation plans for many islands, and removal of predators and competitors would clearly benefit large island fruit bats. Research on the specifics of the interaction between bats and the invasive species is needed, and experimental evidence of the effectiveness of proposed mitigations are critical because mitigation is often costly. Control of invasive alien plants has been shown to improve foraging habitat quality of *P. niger* on Mauritius by increasing native fruit production, resulting in greater bat foraging rates (Krivek *et al.*, 2020). Nutritional stress is likely a contributor to susceptibility to novel pathogens, so again, retaining and expanding high-quality foraging habitats would help protect bats.

**(6) Persecution**

Persecution of large island fruit bats is listed as a direct threat to seven species (*Acerodon jubatus, Pteropus dasymallus, P. macrotis, P. niger, P. nitendiensis, P. pselaphon, P. tuberculatus*), and is primarily driven by perceived economic losses in the agricultural sector. Loss of income and consumption of fruits from domestic backyard trees compounds the issue in some regions (Zimmermann, Macdonald, & Kingston, 2020a). Island *Pteropus* are frugivorous generalists and often visit fruit orchards in their quest for food. While farmers may benefit from the pollination services or seed shadows provided in the process (Scanlon *et al.*, 2014a; Aziz *et al.*, 2017c), fruit growers most often focus on fruit losses (see global review in Aziz *et al.*, (2016)). Losses attributable to bat damage may be overestimated if other sources of loss are not quantified (e.g., birds, rats, wind, fungus) or may be deliberately exaggerated (Florens & Baider, 2019; Oleksy *et al.*, 2021). Crop damage concerns sometimes compound with fear of zoonotic disease spillover from bat saliva and faeces contaminating fruits, a significant transmission pathway demonstrated in several instances (e.g., Fogarty *et al.*, (2008), Rahman *et al.*, (2012); Henry *et al.*, (2018)).

Various means are used to kill bats, including shooting, hooking with kites, poisoning and netting, and are most often employed as part of local, sometimes secretive, initiatives by individuals or citizen groups (Robinson *et al.*, 2010; Vincenot, Koyama, & Russo, 2015b; Aziz *et al.*, 2017b; Sheherazade & Tsang, 2018). Large-scale government-sponsored campaigns or culls are rare, but culling is an emerging threat expected to increase with land conversion for agriculture and urbanisation (e.g., Luskin, (2010); Weber *et al.*, (2015)). Coordinated culls are particularly destructive (e.g., over 30% population cull of *P. niger* in Mauritius and still counting over five government culls (Kingston *et al.*, 2018; Florens & Vincenot, 2018; Zimmermann *et al.*, 2020a); and are most often activated as a political response to agricultural damages, despite their proven ineffectiveness (Florens & Baider, 2019) and the existence of simple, non-lethal crop protection measures (e.g., netting, decoy trees, natural repellents, biocontrol agents) (Van Mele, Camara, & Vayssieres, 2009; Raharimihaja *et al.*, 2016; Tollington *et al.*, 2019; Oleksy *et al.*, 2021). Other destructive management policies include the preemptive destruction of entire patches of forests in order to “relocate” bat colonies (Vincenot & Petit, 2016). For more “minor offenses” (e.g., nuisances to the neighbourhood), mechanical deterrents (e.g., scaring or smoking out, loud noise playback, bright lights, automated water sprinklers directed at roosting bats; see review in (Aziz *et al.*, 2016) are preponderant. These solutions, on top of negatively impacting bats and non-target wildlife, may favor epidemic outbreaks by triggering a stress-induced increase in viral load in urine and spreading infectious bats to new locations (Edson *et al.*, 2015).

**Recommendations**: Fighting persecution calls for similar solutions as for hunting. Sources of human-bat conflicts must first be exhaustively identified through perception studies (e.g., Vincenot *et al.*, (2015a)) to understand not only the practical issues at stake but also what is predominantly shaping the attitude towards bats (Dickman, 2010; Vincenot *et al.*, 2017a). Targeted investigations on identified socio-economic or cultural drivers should then follow. In the case of bat-farmer conflicts, assessing objectively the effective extent of damages to orchards is a critical step to consider, as past studies have shown that bat damage can be significantly lower than perceived by farmers, and that bats are not always the only or even primary agent of fruit loss (Florens & Baider, 2019; Oleksy *et al.*, 2021). Pre-existing negative attitudes towards “crop-raiding” bats may be impervious to such knowledge, and the misperception of risk is a common feature of human-wildlife conflicts (Dickman, 2010), but it is still important when considering the costs and benefits of mitigation strategies (Zimmermann *et al.*, 2020a).

In many cases, crops can be effectively protected with wildlife-friendly netting, but financial, technical and attitudinal barriers to uptake need to be explicitly investigated and overcome (Dickman, 2010). Certification schemes that reward farmers following bat-friendly practices, such as the use of netting, should be explored, particularly for crops exported to markets responsive to “green-labelling”. For minor, controllable conflicts or, on the contrary, situations that would require disproportionate, impracticable measures to mitigate (e.g., netting of hectares of pineapples), alternative approaches should be researched (e.g., use of repellents or decoys instead of nets (Aziz *et al.*, 2016)). Costs of mitigation should also be evaluated versus the financial costs of the damages themselves, as in some modest cases government subventions to cover losses might be the simplest solution. In all instances of persecution, the conflict must be regularly monitored to detect notable detrimental situations and prevent the emerging issues from escalating by reacting promptly, for example to changes in attitude or rises in crop damages and/or bat fatalities. If the issue escalates to a deep-rooted conflict, in which stakeholders attach social identity to the conflict or feel that values are threatened, staged conflict resolution efforts involving neutral third parties to relieve tensions and guide the debates, and identify solutions that can be effectively implemented, may be needed (Dickman, 2010; Zimmermann *et al.*, 2020a; Zimmermann, McQuinn, & Macdonald, 2020b).

**V. OVERARCHING RESEARCH NEEDS**

Large island fruit bats have been little studied. Basic information on population size, population trends, ecology, and life history are lacking for many species. Of note is that, despite the fairly conserved body plan, species differ in diet and ecological specialization, roosting ecology, social structure, movement and gene flow among islands, and tolerance of human disturbance, even when in sympatry (Trewhella *et al.*, 2001; Russell *et al.*, 2016; Lavery *et al.*, 2020b). The implications of these differences for conservation management are only now starting to become apparent, and we caution practitioners to beware situations where lack of local data prompts extrapolation from other species or populations. Here we highlight priority research directions needed for effective conservation that are applicable to most species and support the recommendations in response to the individual threats.

**(1) Population sizes and trends -- long-term monitoring and population modeling.**

Population estimates and trends are needed to assess the current and future status of species and populations and evaluate the success of interventions (e.g., Robinson *et al.*, (2010). For poorly known species, or on islands that have not been (recently) surveyed, at minimum basic data on distributions and abundance are a crucial first step (e.g., in the Andaman and Nicobar Islands (Aul *et al.*, 2014), western Pacific (Lavery *et al.*, 2020a)). Diurnal and nocturnal walked line transects can also be used to estimate roosting and feeding densities (Lee *et al.*, 2009; Lavery *et al.*, 2020a) and roost inventories. Direct and emergence counts provide the basis for population estimates and/or trend detection of colonial-roosting species (Utzurrum *et al.*, 2003; Westcott & McKeown, 2005). However, estimating population size is challenging if roosts are inaccessible, or unknown, and if populations are widely distributed with frequent movement among roosts (as shown in (Oleksy *et al.*, 2019). Roosts may also comprise more than one species making species-specific counts difficult. Solitary species are especially difficult to locate, but in at least some cases remain faithful to specific branches or trees (Brooke *et al.*, 2000). Despite these difficulties, the value of population data is high, and every effort should be made to estimate populations, and to monitor the population at regular intervals (e.g., Woinarski *et al.*, (2014)). State-space models, which incorporate seasonal and stochastic processes, may also improve the detection and characterization of population trends (Westcott *et al.*, 2018); and weather radar have been used to estimate colony sizes in Australia (Meade *et al.*, 2019).

Broad trends can also be inferred from historical vs. contemporary assessment of roost occupancy (Mohd-Azlan, Zubaid, & Kunz, 2001; Oedin *et al.*, 2019), or from measured or reported counts from hunters or hunting licences (Struebig *et al.*, 2007; Epstein *et al.*, 2009). Age distributions can be constructed from histological analysis of tooth *cementum annuli* and used to parameterize population models, although this requires capture and anesthesia for tooth extraction so works best in conjunction with research that already requires handling (Brook *et al.*, 2019). Tissue samples from captured bats can also be used to estimate effective population size (Ne) using RADseq techniques (Andrews *et al.*, 2016; Nunziata & Weisrock, 2018). For cryptic species, remote non-invasive sampling (through faeces, pellets or bitten fruits collection) provides sufficient DNA for population genetics studies (e.g. gene flow estimation) (Taki *et al.*, 2021). Population genetic studies can also identify management units, based on the degree of structure and gene flow (e.g., Brown *et al.*, (2011), Okada *et al.*, (2014), Russell *et al.*, (2016), Ibouroi *et al.*, (2018a)).

**(2) Life history and social ecology**

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., *Pteropus poliocephalus, P. alecto, P. scapulatus*) (but see Todd *et al.*, (2018); Brook *et al.*, (2019)). However, these continental species differ in many aspects of their biology from island species, with likely consequences for life history. Recent characterization of the life history of *Pteropus melanotus natalis* suggests that the substitution of mainland species’ data may compromise population models and inference. For example, female *P. m. natalis* reach reproductive maturity at approximately 24 months, rather than the 11 months of *P. poliocephalus (Todd et al., 2018)*. Similarly, adult survival rates in *P. rufus* on Madagascar may be as low as ~0.5, substantially lower than the ~0.9 estimated for continental Australian species (McIlwee & Martin, 2002). Although many species are seasonally monoestrous, asynchronous parturition is seen in others (Sugita, Inaba, & Ueda, 2009). Thus, reproductive phenology should be adequately characterized to quantify models, identify appropriate times for population counts or hunting bans, and to investigate the potential for viral shedding during lactation.

Even less is known about the variability in mating systems and social ecology. There is a tendency to think of LIFB as colonial in terms of roosting and foraging. Yet, many species forage or roost in a solitary or semi-solitary manner (e.g., *Pteropus nitendiensis*, *P.* *tuberculatus* and *P. dasymallus*; see resp. (Lavery *et al.*, 2020a), *ibid*.,). Furthermore, some populations may be more or less gregarious depending on season (e.g., *P. pselaphon*, Sugita et al. 2009) or geographical location (e.g., *P. samoensis,* (Russell *et al.*, 2016)). Similarly, unexpected plasticity in foraging timing has been observed for some LIFB to range from partial to full diurnality, depending on species and predation pressure (Cox, 1983; Tidemann, 1987; Vincenot, 2017). Finer aspects of the social ecology of LIFB, such as social structure and group dynamics, remain largely unknown for most species (but see (Neuweiler, 1969) and (Markus & Blackshaw, 2002) for detailed ethograms of of the mainland species *P. giganteus* and *P. alecto*). Mating systems, for instance, seem to vary depending on species and span from vertical hierarchical structure 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 behaviour serves at the same time as a thermoregulatory mechanism against cold (in *P. scapulatus* and *P. pselaphon* (Bartholomew, Leitner, & Nelson, 1964; Sugita & Ueda, 2013)) or heat (e.g., in *P. hypomelanus*; (Ochoa-Acuña & Kunz, 1999)). All the foregoing social aspects of the ecology of LIFB have great implications for anti-predator response, resource exploitation, demographic growth, gene flow, and *in fine* survival both in the wild and in captive breeding programs.

**(3) Dietary, roosting and movement ecology**

Protection of critical foraging and roost resources is a priority conservation action on many islands. This requires knowledge of diets and roost site selection, as well as movements of bats among resources, that is lacking for most species (e.g., Tsang & Wiantoro, (2019)). Dietary studies can also evaluate the nutritional content of food sources, identify periods of resource stress, and indicate the contribution of cultivated fruit crops to bat diets, a measure of the potential for conflict with fruit growers and/or the role that crops and introduced plants play in sustaining bat populations when forest is reduced (Long & Racey, 2007; Gérard *et al.*, 2015). Information on diet can also contribute to island-specific education campaigns by highlighting the role of local bat species as pollinators and seed dispersers of island plants known to the public.

Diets can be assessed through identification of plant remnants, seeds, and pollen in feces and rejecta at roosts, foraging sites, or from captured bats (Entwistle & Corp, 1997a; Banack, 1998; Bollen & Van Elsacker, 2002; Stier & Mildenstein, 2005). Molecular approaches (e.g., DNA metabarcoding) have also recently been applied to determine fruit bat diets and allow for detection of species missed by morphological methods, provided comparable material is available in reference databases or a site-specific collection (Aziz *et al.*, 2017c; Lim *et al.*, 2018b; Chan *et al.*, 2021). GPS, satellite and radio telemetry provide insights into bat movement ecology e.g., (Banack & Grant, 2002; Mildenstein *et al.*, 2005; de Jong *et al.*, 2013; Oleksy *et al.*, 2015, 2017, 2019) that can pinpoint foraging grounds and roosting sites and highlight nightly and seasonal changes in both that can be important for conservation and management.

**(4) Human attitudes and behaviours towards large island fruit bats.**

Characterizing knowledge and perceptions of large island fruit bats and understanding drivers of human behaviours towards them are a critical foundation for conservation interventions and outreach that address hunting, persecution, and urbanisation (**Conservation Rec. 2**) (Cousins & Compton, 2005; Barnes, 2013; Vincenot *et al.*, 2015a; Aziz *et al.*, 2017b). Historically, the significance of human attitudes and behaviours towards large island fruit bats largely centred on understanding drivers of hunting. Increasingly, habitat loss, increase in fruit crop production, and urbanisation bring LIFB into possible conflict with islanders (Aziz *et al.*, 2017b). However, not all attitudes towards LIFB are negative. Cultural beliefs and connections to LIFB that place them in a more favorable light are important to identify, as these may provide opportunities for positive messaging that can support conservation action. Studies should be based in informative conceptual frameworks and employ appropriate methods and are often most effectively designed and implemented in collaboration with experts in social science research (T. Straka, J. Coleman, E. Macdonald, T. Kingston *in revision*).

**(5) Island-specific threats to large island fruit bats**

LIFBs 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 will thus vary among localities and need to be established for effective conservation. Ideally, studies should evaluate the strength of threats in terms of their direct impact on populations (e.g., offtake from hunting, kills arising from persecution), or their indirect influence on fitness and hence population declines (e.g., habitat loss and degradation). Wherever possible, population information should be presented in terms that can assist the Red List assessment process (e.g., providing estimates of population size; past, current, and future declines in populations or critical habitat; updating the distribution of the species). To guide interventions, it is important to identify the social, economic, or policy drivers of threats, pinpoint barriers to change, and encompass perspectives from a diversity of stakeholders. Interventions should be designed to provide evidence of their success or otherwise (www.conservationevidence.com).

**(6) Distributions, populations and ecology of non-*Pteropus* species***.*

The monkey-faced bats (*Pteralopex* spp. and *Mirimiri acrodonta*) are a particularly high priority as all are poorly-known and threatened. Three species are assessed as Critically Endangered (*P. flanneryi, P. pulchra* and *M. acrodonta*), two Endangered (*P. atrata*, *P. anceps*) and one Vulnerable (*P. taki*). Populations are decreasing for all six species.

**VI. CONSERVATION ACTIONS**

**(1) Protect and restore native habitats**

A recurrent recommendation in response to individual threats is the protection of foraging and roosting resources that can support larger populations, buffer populations in times of food shortage, provide refugia from disturbance, and generally keep bats separate from people to minimize conflict. The habitat quality of patches can be restored by removing invasive species that directly threaten bats, compete with them, or compromise food availability. Movement studies have demonstrated that many bats move around islands, so patches of forests and foraging resources can be connected into a distributed network. Because of the role of LIFB as seed dispersers and pollinators, they are likely to promote habitat improvements. However, monkey-faced bats are likely to need large tracts of unmodified forest.

**(2) Implement multi-faceted campaigns to (re)set attitudes and alter specific conservation-relevant behaviour**

Behaviours that directly threaten bat populations, such as hunting and persecution, often derive from attitudes and norms that can be difficult to change. Multi-faceted campaigns should clearly identify the behaviour of concern, the group(s) performing the behaviour(s) and the drivers of the behaviour as the focus of action. Some drivers are most suited to interventions that seek to change social norms, for example through social marketing (Guenther & Shanahan, 2020). Others may be better targeted with practical solutions (e.g., netting of fruit crops) or alternatives to the behaviour (alternative livelihood projects to provide protein sources). Likely, many campaigns may need to incorporate several approaches responsive to multiple stakeholders. Regardless, it is important that action is not based on assumptions about people’s motivations and perceptions, but on research that has identified them (**Research Rec. 4)**

Broader outreach and education initiatives that raise awareness of the contribution of LIFB to the viability of local plant populations and ecosystems can be an integral part of such campaigns (e.g., Trewhella *et al.*, (2005)) and can also aim to tackle particular misperceptions (e.g., on bats and diseases, blood sucking), or more local prejudices typical of the region that would have been identified through prior perception studies. For example, *P. niger*, a species known to dip into seawater,has been accused of stealing fish by fishermen, see (Seegobin & Probst, 2020). Such initiatives may be especially powerful if initiated before any conflicts or issues arise or intensify as prior attitudes influence responses to conflict situations (Guenther & Shanahan, 2020). Pre-emptive campaigns could create or enhance positive attitudes and develop strategies to mitigate any prevailing negative associations, providing a better starting position for future conservation actions should need arise. Ultimately, sustainable outcomes for LIFBs will only be secured through engagement and participation of local communities (Scheffers *et al.*, 2012; Aul *et al.*, 2014; Ardoin, Bowers, & Gaillard, 2020)

**(3) Strengthen legislation and enforcement**

Legal protection for LIFBs varies from country to country and is generally very limited. In some, protection is afforded if the species is recognised as a nationally threatened species (e.g., the Philippines, Mauritius, US territories, Indonesia, India, Japan). For such countries, working to get threatened LIFB legally recognised as threatened is an important, but extremely challenging, first step. For example, Indonesian law recognises just three of the 23 LIFB species found in the country (*Neopteryx frosti* EN*, Acerodon humilis* EN, *Pteropus pumilus* NT) as “Protected Species” although 11 species are listed as threatened by the IUCN (IUCN 2020). Hunting and trade of the remaining 20 species is allowed under permit (Law Number 5 year, 1990; Law Number 20 year, 2018; Government Act Number 8 year, 1999). It is notable that the three selected species have very limited range in Indonesia. In India, although decades of campaigning secured protection for some threatened bat species, the Endangered *Pteropus faunulus* of the Nicobar Islands remains on Schedule V --“vermin” -- of the Indian Wildlife Act 1972.

There is global concern that legal protection for wildlife is being eroded (Florens, 2016; Abessa, Famá, & Buruaem, 2019). In Mauritius, the Native Terrestrial Biodiversity and National Parks Act 2015 weakened the protection of *Pteropus niger* previously afforded under the Wildlife and National Park Act of 1993 that it replaced. Clause 36 of the new law allows treatment of any native species as a pest that can then be controlled through culling. This provision has allowed for five government culls of the *P. niger*, implemented by the Special Mobile Force, with targets ranging from ~10,000 to > 30,000 each year. Though still officially protected by the Act from actions of the general public, hunting and persecution by the public has increased without consequences for perpetrators.

Even when protective legislation exists, several related problems exist. (1) Not all people are aware that the species is protected. (2) The legislation is not enforced (Scheffers *et al.*, 2012; Husen *et al.*, 2017). Enforcement resources and capacity are often limited and stretched thin by the geographical extent of LIFB 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. (3) Although a species may be protected, its critical habitat often is not protected. (4) Legislation does not always lead to effective conservation plans to recover species (Preble, Ohte, & Vincenot, 2020).

**(4) 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, or if threats are inescapable (e.g., rising sea levels, total loss of habitat). Seventeen species of *Pteropus* are currently held in recognised zoological institutions, of which 10 are LIFB (Species360 2020). Breeding success is variable across species and institutions, but the potential for captive breeding to contribute to species conservation is illustrated by *Pteropus 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. In the late 1970s the Durrell Wildlife Conservation Trust initiated a captive breeding program and brought twenty-seven wild-caught individuals into captivity, of which 23 could potentially breed. Genetic diversity was largely conserved (O’Brien *et al.*, 2007) and by 2020 there were 928 bats in 44 zoological institutions, with 91 births recorded in the preceding 12 months (Species360 2020).

To date, no captively 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. It is challenging to maintain the capacity for sustained flight in captive populations, and enclosures suitable for one species may not work for others (Bell *et al.*, 2019). If appropriate candidates for release are identified, advances in telemetry appropriate for LIFB (GPS and satellite transmitters) mean that the behaviour and fate of reintroduced individuals could be tracked, if suitable wild contexts are identified. Given the susceptibility of LIFB to extinction, and the relative success of captive breeding to date, captive breeding should be given serious thought for species recognised as Critically Endangered or Presumed Extinct in the Wild (if they are discovered) if the threats they face cannot immediately be mitigated. The monkey-faced bats fit these criteria, but knowledge of their biology and ecology that could support a captive breeding program is limited (Palmeirim *et al.*, 2007; Scanlon, Petit, & Bottroff, 2014b).

**(5) Build and network research capacity.**

Bat research expertise and capacity to implement recommendations are very limited. Large island fruit bats 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 (Weeks & Adams, 2018). Nonetheless, there are significant hotspots of expertise and experience throughout the range of LIFBs. For example, in the Philippines flying fox roosts have been monitored for close to 20 years, and a nationwide action plan is in development by the Department of Environment and Natural Resources. Researchers and conservationists on Mauritius and Reunion have experienced all aspects of *Pteropus* conservation, from successful captive breeding to bring *P. rodricensis* back from the brink of extinction, to the disastrous government culls of the Endangered endemic *P. niger.*  Methods to quantify hunting and trade and characterize trade networks have been implemented, with depressing results, in Sulawesi (Sheherazade & Tsang, 2015; Latinne *et al.*, 2020) and New Caledonia (Oedin *et al.*, 2019). Conservation research networks can accelerate capacity building through 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 Large Island Fruit Bat network is strongly recommended.

**VII. CONCLUSION**

1. Large fruit bats are keystone pollinators and dispersers on palaeotropical islands.
2. Large island fruit bats are the most threatened bats in the world. Although the types of threats faced by LIFB are comparable to those experienced by other bat species, the island context intensifies threats 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 will need to characterize the nature, relative intensity of threats faced by species or populations of concern, as well as the interactions among them, and adopt a multi-faceted approach.
3. Knowledge of basic LIFB biology and ecology needed to develop and evaluate conservation programs is limited. Human capacity to implement such programs is also very limited, and there is an urgent need to increase and network research capacity.
4. Despite these complexities and challenges, immediate habitat protection and restoration, coupled with interventions to reduce hunting and persecution, would slow or reverse population declines on many islands. Both require urgent attention; these are truly bats on the brink and inaction will push many more species to ecological extinction or extinction.

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