


REVIEW

The threat of invasive species to bats: a review

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ABSTRACT

1. Biological invasions are a major driver of biodiversity loss, but no study has described the scope of threats to bats (Chiroptera) by invasive species.
2. We reviewed the literature for negative effects of invasive species to bats and summarised threats according to four categories: predation, disease, competition, and indirect interactions. We identified threats of 37 invasive species to 40 bat species. Ten bat species were threatened by more than one invasion pathway.
3. About 38 percent of cases are speculative and 18 percent circumstantial, many attributed to overlapping ranges, and most accounts do not quantify effects needed to forecast bat population impacts.
4. Evidence of cat predation is frequently cited, constituting the greatest incidence of observational data. Other direct and indirect impacts were documented from goats, dogs, brown tree snake, rainbow lorikeet, rose-ringed parakeet, yellow crazy ant, giant centipede, palm, burdock, avian cholera, and white-nose syndrome. Circumstantial evidence suggests impacts by rats, stoats, coqui frog, common wolf snake, little fire ant, kudzu, and *Lantana camara*. Other impacts by giant centipede, yellow crazy ant, cats, goats, rats, and avian cholera are speculative, as are those from pigs, deer, white eye, common starling, house sparrow, rock dove, barn and little owls, brush-tailed possum, honeybee, wasp, phytophagous insects, tamarisk, *Cinnamomum verum*, and *Tabebuia pallida*.
5. Over 60 percent of bat species reviewed are island-dwelling, corresponding with evidence indicating that most extinctions occur on islands and invasive species' impacts are worse for island than mainland populations.
6. Although appreciable bat population reductions owing to invasive species are often unproven, invasions are likely to exacerbate effects of other vulnerabilities. Multiple invaders and synergistic interactions may ultimately lead to species losses.
7. Managers should exercise the precautionary principle by taking action against non-native species when first detected, even if new species do not appear to be detrimental.

INTRODUCTION

Numbering nearly 1400 species (N. Simmons 2017, personal communication), bats (Chiroptera) are the second most species-rich mammalian order after rodents (Rodentia). Nearly 15% of bat species are threatened

according to the International Union for Conservation of Nature (IUCN), signifying that they are at a high risk of extinction (Anonymous 2015). An additional 17% of species, designated as Data Deficient, lack assignment to a Red List threat category owing to insufficient knowledge about their abundance and/or distribution.

Habitat destruction, catastrophic weather events, over-hunting, persecution, and pesticides are consistent threats to bats (Racey & Entwistle 2003). Bats are especially susceptible to imperilment because they have low fecundity – their average life span is 3.5 times greater than that of non-flying placental mammals of similar size, but most produce only one young per year (Wilkinson & South 2002). Although flight and nocturnality afford bats decreased mortality (Barclay & Harder 2003), failure to breed in combination with extrinsic threats can make population recovery difficult.

Biological invasions are a major driver of worldwide biodiversity loss (Vitousek et al. 1997). Invasion literature has grown rapidly (MacIsaac et al. 2011) and many population- to ecosystem-level impacts of biological invasions are recognised (reviewed by Mack et al. 2000). However, authors of reviews of challenges for bat conservation have largely ignored biological invasions (e.g. Fenton 1997, Mickleburgh et al. 2002, Weller et al. 2009). A comprehensive perspective of global bat conservation should include interactions between bats and invasive species.

In this paper, we summarise threats caused by invasive species to bats. Positive effects of invasion include exotic plants providing roosting sites (Campbell et al. 2006), food resources (Corlett 2005, Voigt et al. 2011), and heterogeneous foraging habitat (Borkin & Parsons 2010, Rodriguez-San Pedro & Simonetti 2013), and exotic fish serving as high-nutrient prey (Aizpurua et al. 2013). We restrict our review to negative effects of invasion. We provide examples of threats from each of four pathways (predation, pathogens, competition, indirect interactions), and conclude with recommendations for the detection of invasive threats.

METHODS

To identify species of interest, we performed a filtered search using the IUCN Red List of Threatened Species (hereafter, Red List; Anonymous 2015) with Chiroptera selected for the taxonomy option and invasive species selected for the threat option. We located references provided by the Red List, and then searched the Web of Knowledge data base using each bat species name as the topic, plus the search string: *invasi** OR *introduce** OR *non-native* OR *nonnative* OR *exotic* OR *alien* OR *non-indigenous* NOT *non-invasive* NOT *noninvasive*. We identified additional bat species and located further references by searching the Google Scholar data base and tracking citations provided in retrieved references. We reviewed literature written in English only; thus, we might underrepresent the total number of published cases.

RESULTS AND DISCUSSION

Using all search methods, we identified 50 bat species with apparent invasive threats, but included only 40 species in this review (Table 1). Specifically, the Red List search returned 22 bat species. For those species, Web of Knowledge and Google Scholar searches resulted in 87 and 3914 references, respectively. Subsequent searches identified 29 more bat species. However, we excluded 11 species because we could not locate sufficient corroborating literature pertaining to threats from invasive species.

Invasive threats by and large autonomously apportioned into four broad categories: predation, pathogens, competition, and indirect interactions (Table 2). We identified 36 invasive species that pose threats to bats, and ten bat species that were threatened by more than one type of invasion. We also report, in Table 2, evidence for each invasive threat categorised as observational (i.e. eye-witness report), circumstantial (i.e. correlation between invasive threats and bat numbers or behaviours), or speculative (i.e. anecdote unsupported by data).

Predation

Predation is the most severe direct consequence of invasion, and is responsible for approximately 80% of terrestrial vertebrate extinctions (Clout & Russell 2011). Predation can also have non-lethal population impacts, by causing species to change behaviours to avoid mortality. For example, bats might opt for lower quality foraging areas when predators move into preferred habitats (Lima 1998). Measuring effects of predation is difficult because bats are not usually the primary prey of invasive predators (Pitt & Witmer 2007), thus population-level impacts are variable.

Although bats experience low predation rates relative to other mammals (Tuttle & Stevenson 1982), impacts could be significant on roosting bats. Predators are lured by noise and odour emitted by congregating bats, especially to large colonies where attractants are magnified. Predator presence strongly influences roost selection and might cause bats to abandon roosts altogether (Lewis 1995). Even if roosts are not abandoned, young bats are at high risk of predation, because they are immobile (Tuttle & Stevenson 1982). Furthermore, predator presence near a maternity colony can delay bat emergence and influence how long a bat will forage, which can negatively affect a lactating bat's ability to feed her pup (Kalcounis & Brigham 1994). Ultimately, cumulative effects of actual and perceived predation risk serve as a selective pressure on bat behaviour (Lima 1998), particularly for bat species that evolved without such predatory pressure.

Domestic cats are the most highly cited predators of bats, possibly because cats often present kills to their

Table 1. Bat species discussed in this review. The IUCN Red List category abbreviations are as follows: LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; PE = Possibly Extinct. In the last column, we provide the type of corroborating evidence for each invasive species account as follows: O = observational, C = circumstantial, S = speculation.

Scientific name	Family	Common name	Red List	Threat type	Invasive species
<i>Brachyphylla cavernarum</i>	Phyllostomidae	Antillean fruit-eating bat	LC	Predation	Cat (O)
<i>Chalinolobus dwyeri</i>	Vespertilionidae	Large-eared pied bat	NT	Indirect interaction	Goat (O)
<i>Chalinolobus gouldii</i>	Vespertilionidae	Gould's wattled bat	LC	Competition	Rainbow lorikeet (O)
<i>Chalinolobus tuberculatus</i>	Vespertilionidae	Long-tailed wattled bat	VU	Predation	Cat (O), rat (C), stoat (C), little owl (S), brush-tailed possum (S)
				Competition	Common starling (S), house sparrow (S), rock dove (S), wasp (S), rat (S)
<i>Coleura seychellensis</i>	Emballonuridae	Seychelles sheath-tailed bat	CR	Predation	Barn owl (S)
				Indirect interaction	kudzu (C), <i>Cinnamomum verum</i> (S), <i>Tabebuia pallida</i> (S)
<i>Desmodus rotundus</i>	Phyllostomidae	Common vampire bat	LC	Predation	Cat (O)
<i>Emballonura semicaudata rotensis</i>	Emballonuridae	Pacific sheath-tailed bat	EN	Indirect interaction	<i>Lantana camara</i> (C)
<i>Eptesicus fuscus</i>	Vespertilionidae	Big brown bat	LC	Indirect interaction	Burdock (O)
<i>Erophylla bombifrons</i>	Phyllostomidae	Brown flower bat	LC	Predation	Cat (O)
<i>Lasiurus borealis</i>	Vespertilionidae	Eastern red bat	LC	Indirect interaction	Burdock (O)
<i>Lasiurus cinereus semotus</i>	Vespertilionidae	Hawaiian hoary bat	LC	Competition	Coqui frog (C)
<i>Lasiurus xanthinus</i>	Vespertilionidae	Western yellow-bat	LC	Indirect interaction	Tamarisk (S)
<i>Lasionycteris noctivagans</i>	Vespertilionidae	Silver-haired bat	LC	Indirect interaction	Burdock (O)
<i>Monophyllus redmani</i>	Phyllostomidae	Leach's single-leaf bat	LC	Predation	Cat (O)
<i>Mormoops blainvillei</i>	Mormoopidae	Antillean ghost-faced bat	LC	Predation	Cat (O)
<i>Myotis evotis</i>	Vespertilionidae	Long-eared myotis	LC	Indirect interaction	Burdock (O)
<i>Myotis lucifugus</i>	Vespertilionidae	Little brown myotis	LC	Indirect interaction	Burdock (O)
<i>Myotis septentrionalis</i>	Vespertilionidae	Northern myotis	LC	Disease	<i>Pseudogemnoascus destructans</i> (O)
<i>Myotis vivesi</i>	Vespertilionidae	Fish-eating myotis	VU	Predation	Cat (O), rat (C)
<i>Mystacina robusta</i>	Mystacinidae	New Zealand greater short-tailed bat	CR	Predation	Rat (C)
<i>Mystacina tuberculata</i>	Mystacinidae	New Zealand lesser short-tailed bat	VU	Predation	Cat (O), rat (C)
				Competition	Brush-tailed possum (S)
<i>Nyctalus lasiopterus</i>	Vespertilionidae	Giant noctule	VU	Competition	Rose-ringed parakeet (O)
<i>Nyctalus leisleri</i>	Vespertilionidae	Leisler's noctule	LC	Competition	Rose-ringed parakeet (O)
<i>Nyctalus noctula</i>	Vespertilionidae	Noctule	LC	Competition	Rose-ringed parakeet (O)
<i>Nyctophilus howensis</i>	Vespertilionidae	Lord Howe Island long-eared bat	CR (PE)	Predation	Cat (S), rat (S), owl (S)
<i>Pipistrellus coromandra</i>	Vespertilionidae	Indian pipistrelle	LC	Predation	Cat (O)
<i>Pipistrellus tenuis murrayi</i>	Vespertilionidae	Christmas Island pipistrelle	CR (PE)	Predation	Common wolf snake (C), giant centipede (S)
				Competition	Yellow crazy ant (O)
<i>Plecotus auritus</i>	Vespertilionidae	Brown long-eared bat	LC	Predation	Cat (O)
<i>Pteronotus parnellii</i>	Mormoopidae	Common mustached bat	LC	Predation	Cat (O)
<i>Pteronotus quadridens</i>	Mormoopidae	Sooty mustached bat	LC	Predation	Cat (O)
<i>Pteropus dasymallus</i>	Pteropodidae	Ryukyu flying fox	NT	Predation	Cat (O), dog (O)
				Indirect interaction	Palm (O)
<i>Pteropus mariannus</i>	Pteropodidae	Marianas flying fox	EN	Predation	Brown tree snake (O)
				Competition	Phytophagous insect (S)
				Indirect interaction	Goat (S), pig (S), deer (S)
<i>Pteropus melanotus natalis</i>	Pteropodidae	Christmas Island flying fox	VU	Predation	Cat (O), common wolf snake (C), giant centipede (O)
				Competition	Yellow crazy ant (S)
<i>Pteropus neohibernicus</i>	Pteropodidae	Great flying fox	LC	Disease	Unknown disease (C)
<i>Pteropus pselaphon</i>	Pteropodidae	Bonin flying fox	CR	Competition	Rat (S), white eye (S), honeybee (S)

(Continued)

Table 1. (Continued)

Scientific name	Family	Common name	Red List	Threat type	Invasive species
<i>Pteropus rayneri</i>	Pteropodidae	Solomons flying fox	NT	Disease Competition	Unknown disease (C) Little fire ant (C)
<i>Pteropus samoensis</i>	Pteropodidae	Samoan flying fox	NT	Disease Competition	Avian cholera (S) Phytophagous insect (S)
<i>Pteropus tonganus</i>	Pteropodidae	Pacific flying fox	LC	Disease Competition	Avian cholera (O) Phytophagous insect (S)
<i>Saccolaimus flaviventris</i>	Emballonuridae	Yellow-bellied pouched bat	LC	Competition	Honeybee (S)
<i>Syconycteris australis</i>	Pteropodidae	Southern blossom bat	LC	Predation	Cat (O)

Table 2. Summary of the numbers of bat species and invasive species associated with each category of invasion. We found references for 40 unique bat species; however, 10 bat species were threatened by more than one invasion pathway

Invasion category	Bat species	Invasive species	Observational	Circumstantial	Speculation
Predation	20	11	18	7	7
Disease	5	3	2	2	1
Competition	15	14	5	2	14
Indirect interaction	11	10	7	2	6

owners (Daniel & Williams 1984). Effects on bird populations have been well documented – cats are responsible for 26% of predator-related extinctions of island birds (King 1985). However, impacts to other fauna have been poorly studied (Courchamp et al. 2003). Cats are probably attracted to the sporadic movements of bats, and cats are typically agile enough to jump (P. Racey 2017, personal observation) or climb to reach flying or roosting bats, respectively.

Bats that roost or forage near human settlements are susceptible to predation by pet cats, because cats maintain their predatory nature despite receiving preferred food items (Adamec 1976). For example, video footage from collar cameras revealed that 24 of 55 free-roaming pet cats hunted wildlife (Loyd et al. 2013). In Australia, surveys over a five-year period documented injuries from cats to eight bat species (Dickman 1996). Another study conducted in Central and Northern Italy showed that approximately 29% of reported bat rescues were in response to cat attacks (Ancillotto et al. 2013). In Great Britain, where households documented outdoor pet cat kills for five months, 44% reported kills from 986 cats in total. Thirty bat species, including the brown long-eared bat *Plecotus auritus*, were among the prey items (Woods et al. 2003). Single reports illustrate cat attacks on the Indian pipistrelle *Pipistrellus coromandra* (Virkar & Shrotriya 2013), southern blossom bat *Syconycteris australis* (Phillips et al. 2001), and fish-eating myotis *Myotis vivesi* (Vázquez-Domínguez et al. 2004).

While documenting common vampire bats *Desmodus rotundus* feeding on livestock, Delpietro et al. (1994) recorded several instances of predation by cats. Cats were

kept in corrals with goats, pigs, sheep, and cattle to guard them against vampire bat attacks, which farmers said were frequent before they started keeping cats. One owner stated that his cat began catching bats at about seven months old; another said that his cat would go on the hunt at the alarm of pig cries.

Domestic cats prey on the Vulnerable New Zealand lesser short-tailed bat *Mystacina tuberculata* (Daniel & Williams 1984, Molloy 1995). Over a seven-day period, Scrimgeour et al. (2012) discovered remains of at least 102 lesser short-tailed bats in Rangataua Forest on New Zealand's North Island. A single male tabby cat was identified as the predator using DNA samples of fur found near the roost; moreover, no more dead bats were found after the cat was captured. Curiously, video recordings at the roost did not show a cat visiting, so it is unknown how bats were captured. New Zealand's long-tailed wattled bat *Chalinolobus tuberculatus*, a Vulnerable aerial insectivore (O'Donnell 2008a), is also documented prey of cats (Daniel & Williams 1984).

During an eight-month study in Culebrones Cave, Puerto Rico, remains of six bat species (*Brachyphylla cavernarum*, *Erophylla bombifrons*, *Monophyllus redmani*, *Mormoops blainvillei*, *Pteronotus parnellii*, *Pteronotus quadridens*) were found in cat scat from as many as 16 feral cats (Rodríguez-Durán et al. 2010). The most abundant bat, the Antillean ghost-faced bat *Mormoops blainvillei*, did not suffer the highest mortality due to cats; Leach's single-leaf bat *Monophyllus redmani* was caught most according to wing remains. In this case, flight behaviour might influence susceptibility to cat predation.

Feral cats might be responsible, in part, for a 35% population decline over six years (Walshe et al. 2012) in the Vulnerable Christmas Island flying fox *Pteropus melanotus natalis*, an Indo-Pacific island endemic (Hutson et al. 2001). These flying foxes are susceptible to predation by cats because they sometimes forage near the ground and are docile when approached (Tidemann et al. 1994). In fact, flying fox remains made up approximately 9% of stomach content weight in 90 cats (Tidemann et al. 1994). Curiously, cats have been present on the island since 1904, and the bat has not been extirpated (Walshe et al. 2012). Therefore, recent population declines could be influenced by a variety of suspected predators (discussed below; Walshe et al. 2012). Similarly, cats (and sometimes dogs) have been observed hunting the Ryukyu flying fox *Pteropus dasymallus* in Japan (Vincenot et al. 2015, 2017).

Described from a single sub-fossil record from Lord Howe Island (McKean 1975), the Lord Howe Island long-eared bat *Nyctophilus howensis* is listed in the Red List as Critically Endangered and may be extinct (Hall et al. 2008). It is uncertain if the bat was extinct prior to European discovery (ca. 1778; Hutton et al. 2007), or if its decline coincided with the introduction of cats (ca. 1788), arrival of rats via shipwreck (ca. 1918), or the introduction of owls to control rats (ca. 1922; Paramonov 1960). By 1958, biological surveys failed to record the bat (Recher & Clark 1974).

Three rat species (brown rats *Rattus norvegicus*, Pacific rats *Rattus exulans*, and roof rats *Rattus rattus*) have hitchhiked via human expansion, reaching over 80% of islands and all continents barring Antarctica (Atkinson 1985), and some bats share traits with species known to be vulnerable to rat predation (e.g. they are nocturnal or ground-dwelling, have low fecundity, or inhabit cavities or crevices; Towns et al. 2006). Moreover, consequences of rat invasion can be severe – rats have caused an estimated 54% of island bird extinctions (King 1985) – so even uncertain accounts must be taken seriously.

The fish-eating myotis, a Vulnerable vespertilionid endemic to small islands in the Gulf of California (Arroyo-Cabrales & Ospina-Garces 2016), is considered easy prey for rats because it roosts in rock crevices (Floyd et al. 2010). Declines in its distribution and population densities correspond with rat invasion (Samaniego-Herrera et al. 2009). Although rodents have now been eradicated from some islands (Samaniego-Herrera et al. 2011), pre- and post-eradication bat population data have not been published (W. Frick 2016, personal communication).

The most detailed accounts of rat invasion come from New Zealand, where the arrival of rats on about 142 offshore islands by the mid-1980s (Atkinson & Taylor 1992) coincides with population declines of the archipelago's three endemic bat species (Towns et al. 2006).

The New Zealand greater short-tailed bat *Mystacina robusta* is a Critically Endangered ground-forager belonging to the family Mystacinidae (O'Donnell 2008b). Fossil evidence indicates that it was once present on Stewart Island, and that numbers of bat and Pacific rat fossils are negatively correlated on Big South Cape and Solomon Island (Molloy 1995). On Big South Cape Island, the greater short-tailed bat was extirpated in about 1962, at the same time as roof rats were introduced (Towns et al. 2006). There have been no live sightings of the bat since 1967 (Molloy 1995), but the species is suspected to survive on an offshore island (O'Donnell 2010).

Between 1975 and 1983, 40 New Zealand lesser short-tailed bat skeletons with holes chewed in their skulls were retrieved from a nursery colony, though it is unknown whether roof rats killed the bats or merely scavenged their carcasses (Daniel & Williams 1984). In addition to rats, population declines in New Zealand's long-tailed wattled bat correspond with the presence of stoats *Mustela erminea* (Pryde et al. 2006). Furthermore, an eye-witness reported seeing introduced little owls *Athene noctua* unsuccessfully trying to catch the bats, and failed attempts by brushtail possums *Trichosurus vulpecula* to reach bat maternity roosts (O'Donnell 2001).

Since its introduction to the Seychelles in 1949, predation by the barn owl *Tyto alba* has presumably added to the decline of the Critically Endangered Seychelles sheath-tailed bat *Coleura seychellensis* (Gerlach et al. 2008). Throughout its native range, the barn owl is a frequent predator of insectivorous bats (e.g. Ruprecht 1979) that are functionally and morphologically similar to the Seychelles sheath-tailed bat. Although no evidence of interaction between the bats and owls has been documented, the bat falling prey to the invasive bird is not a stretch of the imagination (Gerlach 2011).

Apart from a few well-known cases, and probably owing to their secretive habits, accounts of bat predation by invasive snakes are rare. However, because many snake species are reported to take bats in their native habitats (Esbérard & Vrcibradic 2007), snake introductions portend bat susceptibility. The accidental arrival of a facultative arborealist, the common wolf snake *Lycodon aulicus capucinus*, on Christmas Island during the 1980s coincides with declines in populations of the Christmas Island flying fox (Fritts 1993) and Christmas Island pipistrelle *Pipistrellus tenuis murrayi* (Lumsden et al. 2007). Remains of flying foxes were not found in examined snake guts (Walshe et al. 2012), but pipistrelles were not recorded at detector sites immediately adjacent to three locations with snakes (Lumsden et al. 2007).

Brown tree snake *Boiga irregularis* predation is likely to have contributed to the decline of the Endangered Marianas flying fox *Pteropus mariannus* (Wiles 1987). Since

its introduction to Guam in the 1940s, only one case of predation by a brown tree snake on a bat has been documented, but the nocturnal snake probably kills young bats at roosts (Wiles 1987). Moreover, bats were extirpated from southern Guam by the 1970s as snake numbers increased (Fritts & Rodda 1998).

Owing to their abundance, giant centipedes *Scolopendra morsitans* may also pose danger to the Christmas Island pipistrelle (Molinari et al. 2005). Introduced during the 1980s, centipedes have become numerous in trees where they can encounter roosting bats, and venom allows the arthropods to capture relatively large prey (Walshe et al. 2012). Indeed, a giant centipede *Scolopendra gigantea* native to Venezuela has been reported to catch and feed on at least three bat species (Molinari et al. 2005). There has been at least one case of a Christmas Island flying fox found immobilised by a centipede, but it is unknown if centipedes increase mortality or are simply a nuisance to roosting bats (Walshe et al. 2012).

Disease

Diseases are caused by pathogens, usually microorganisms such as bacteria, fungi, and viruses. The spread of invasive pathogens and their vectors exploded during the Age of Exploration (Hulme 2009), and amid today's rapid international travel, potential pandemics are a continued concern. Invasive species that carry pathogens into novel environments can cause acute disease in similar taxa or disruptions that escalate existing disease in the native ecological community (Hickling 2011).

Much attention is afforded to zoonotic disease in bats, especially to the rabies virus, owing to its transmission to humans and domestic animals. Disease impacts on bat communities, *per se*, are largely unknown (Schountz 2014); however, infectious disease ranks lowest as the cause of multiple mortality events (except for white-nose syndrome, as discussed below; O'Shea et al. 2016). Many bats roost in large groups where close proximity increases the possibility of transmission. Moreover, some species can live very long: 34 years for *Myotis lucifugus*, 38 years for *Myotis myotis*, and 43 years for *Myotis brandti* (G. Wilkinson 2017, personal communication). Thus, an infected bat can transmit pathogens over long periods. Pathogens could also be introduced to populations if infected bats are accidentally moved long distances in shipping containers or cargo planes (reviewed by Constantine 2003), or if bats escape from captivity (e.g. Egyptian rousette *Rousettus aegyptiacus* in the Canary Islands, Nogales et al. 2006).

The most pressing threat to cave-roosting bats in North America is white-nose syndrome, caused by the invasive fungus *Pseudogymnoascus destructans* that was transmitted from its native Europe presumably via contaminated

caving equipment (Leopardi et al. 2015). Since its discovery in 2006, the fungus has spread to at least 32 states in the USA and to five Canadian provinces, infected seven species, and killed an estimated six million bats (Anonymous 2012). The list of endangered species identified for federal protection by the USA Fish and Wildlife Service now includes the northern myotis *Myotis septentrionalis* owing to disease-associated mortality (Anonymous 2016). Causes and consequences of the disease are an increasing focus of research and are reviewed by Frick et al. (2016).

During a brief period in the 1900s, infectious disease was endorsed as a means of exterminating unwanted taxa (Spennemann & Wiles 2001). Once considered a fruit pest on the Samoan island of 'Upolu, the extirpated Pacific flying fox *Pteropus tonganus* was the likely target of deliberate avian cholera introductions in the 1980s; the Samoan flying fox *Pteropus samoensis* may also have been affected (Spennemann & Wiles 2001).

Large bat die-offs without apparent cause have been attributed to introduced disease epidemics. In 1987, high fatality in the Solomons flying fox *Pteropus rayneri* occurred so suddenly in Bougainville and Buka Island populations that introduced disease was the presumed culprit (Flannery 1989). Similarly, on Manus and the Admiralty Islands, great flying foxes *Pteropus neohibernicus* became rare after suffering from 'disease' over several weeks. Our review might exclude cases of invasive disease causing mortality in bats because pathogens are not necessarily reported as having non-native origins in the literature.

Competition

Invasive species are hypothesised to be successful when they are competitively superior at acquiring resources shared with native species (Dickman 2011). Two types of competition are generally recognised: interference and exploitative. Interference competition occurs when one species prevents another from accessing a shared resource through aggression or chemical warfare (e.g. roost competition, below). Exploitative competition occurs when one species consumes a shared, limited resource before the other species encounters it (e.g. dietary competition, below).

Invasive species compete with bats for roosts, and roost availability is a primary factor in habitat selection by bats. Cavity selection is often species-specific and strongly influenced by temperature, roosting substrate, proximity to foraging areas, and disturbance (Kunz & Lumsden 2003). Because maternity colonies must be protected from predators, selection is especially important for roosting females. Competition for suitable habitat forces bats to forage in poorer quality habitat, and can be burdensome for cavity roosters that require particular tree species, tree sizes, stand ages, or tree decay (Crampton & Barclay 1998). Availability

is also important when bats need to switch roosts seasonally or accommodate microclimates (Kunz 1985); thus, fecundity or survivability could be reduced if bats are evicted or unable to occupy optimal roosts.

Feral goats often use caves as shelter at night, which could disturb bats roosting on low ceilings. Because large-eared pied bats *Chalinolobus dwyeri* abandoned a roost after disturbance by ungulates (Anonymous 2011), conservation priorities now include protecting roost sites with gates and goat population reduction within bat foraging habitat.

Roosts suitable for long-tailed wattled bats have been found occupied by common starlings *Sturnus vulgaris*, house sparrows *Passer domesticus*, rock doves *Columba livia*, wasps *Vespula* sp., and rats (O'Donnell 2001). It is not known, however, if bats were evicted by these invasive species. It would not be surprising if starlings compete with bats for roosts, because starlings do in their native range (Myczko et al. 2016).

The rose-ring parakeet *Psittacula krameri* is commonly transported for the pet trade, and subsequent releases and escapes have resulted in invasive populations (Feare 1996). Like many bat species, the parakeet nests in tree cavities (Ruczyński & Bogdanowicz 2005). In Seville, Spain, researchers showed that the giant noctule *Nyctalus lasiopterus* and parakeets prefer cavities with the same entrance size and at the same heights, and that cavity occupancy by bats was positively related to distance from a parakeet-occupied cavity (Hernández-Brito et al. 2014). Similarly, in the Netherlands, the parakeet and the noctule *Nyctalus noctula* prefer the same habitat and tree cavities (Haarsma & van der Graaf 2013). Parakeets have also been observed aggressively expelling greater noctules and Leisler's notules *Nyctalus leisleri* from cavities (Haarsma & van der Graaf 2013 and Menchetti et al. 2014, respectively). In both cases, the evicted bats died. Likewise, in Perth, Australia, a rainbow lorikeet *Trichoglossus haematodus* killed and took over the roost of three Gould's wattled bats *Chalinolobus gouldii* (Start 1998).

Feral honeybees *Apis mellifera* occupy tree cavities, excluding other roosting species for approximately three to seven years (Oldroyd et al. 1997). Established in Australia in 1822, honeybee colony distribution and abundance has increased dramatically since the mid-1930s (Paton 1996). Feral colonies might inhibit nesting by the native yellow-bellied pouched bat *Saccolaimus flaviventris* (McKenzie & Pennay 2008), as bees have been found to occupy roosts suitable for bats. Population impacts, however, are likely to depend on the availability of cavities and on the frequency of occupation by honeybees (Paton 1996).

The little fire ant *Wasmannia auropunctata* is considered the most threatening ant in the Pacific region (Anonymous 2017) because its sting has caused blindness in domesticated

dogs and cats (Fasi et al. 2009). The cavity-nesting ant was introduced to Choiseul, Solomon Islands, as a bio-control agent for nut-fall bug *Amblypelta* sp. infestation (Fasi et al. 2013), but has been observed attacking native cuscus *Phalanger orientalis* (Wetterer & Porter 2003). Similarly, ants might displace the Solomons flying fox from roosting trees (Bowen-Jones et al. 1997). According to locals interviewed in 1995, Solomons flying foxes were not present in previously occupied roosts within two to five years of the ants' arrival, a scenario that mirrors the decline of the species in Bougainville in 1987.

The yellow crazy ant *Anoplolepis gracilipes* was first introduced to Christmas Island in around 1915, but impacts on the native ecosystem were not observed until the 1990s (O'Dowd et al. 1999). Evidence of threats to bats is limited, but ants are likely to have exacerbated ongoing reductions in bat numbers. One instance of mortality was documented in a Christmas Island pipistrelle (Lumsden et al. 2007), and potential roost trees are infested by ants, probably altering vegetation and invertebrate communities (Schulz & Lumsden 2004) – changes that can scale up to affect bat carrying capacity. The Christmas Island flying fox might abandon tree canopies owing to ant swarms, and ant supercolonies probably reduce food resources for the frugivorous bat (Walshe et al. 2012). Adult bats are unlikely to be killed by ants, but are injured by acid produced by ants defending the colony.

The diet of the Critically Endangered Bonin flying fox *Pteropus pselaphon*, the only mammal endemic to the five Ogasawara (Bonin) Islands of southern Japan (Saitoh et al. 2014), includes nine endemic and 44 alien plant species. Invasive rodents damage seeds of at least one of these endemic plants *Elaeocarpus photiniifolius* (Hashimoto 2010). Although the bat's diet before plant invasion is unknown, its consumption of alien plants might signal a shortage of native plant species, which could force novel bat–plant interactions (Inaba et al. 2004). Both the Japanese white-eye *Zosterops japonicus* and the honeybee have been introduced to the islands, so they might also compete with bats for plant resources.

An introduced scarab beetle *Protaetia orientalis* is likely to consume seeded breadfruit *Artocarpus mariannensis*, a major food source of the Marianas flying fox (Wiles & Brooke 2010). Moreover, an introduced cycad scale insect *Aulacaspis yasumatsui* and the erythrina gall wasp *Quadrastichus erythrinae* attack fruit trees visited by the Marianas fruit bat and congeners *Pteropus samoensis* and *Pteropus tonganus*.

The coqui frog *Eleutherodactylus coqui* was introduced from its native Puerto Rico to Hawai'i in the late 1980s, and has reached densities of as many as 20000 frogs per hectare (Beard & Pitt 2005). Beard and Pitt (2005) reported that most of what the frogs consume are non-native

leaf litter invertebrates. However, a later analysis found a diet consisting of nearly 40% aerial insects and their larvae, including insect species in the diet of the Hawaiian hoary bat *Lasiurus cinereus semotus* (Bernard 2011), the only terrestrial native Hawaiian mammal. Moreover, the bats were shown to consume fewer beetle species when there were dense frog populations.

The New Zealand lesser short-tailed bat is the principal pollinator of the native parasitic plant *Dactyloctenium aegyptium* (Lord 1991), from which the bat consumes nectar. Invasive rats and wasps have been recorded visiting the plant, but typically leave inflorescences intact (Ecroyd 1996). However, brushtail possums, introduced from Australia and Tasmania to establish a fur industry (Pracy 1962), destroy the plant's flowers. Despite reductions in possum populations (Lloyd & McQueen 2002), however, both the bat and the plant are Endangered across their ranges and co-occur in few areas (O'Donnell 2010).

Indirect interactions

The studies about how biological invasions affect bats above have documented direct interactions. Indirect effects of invasion occur when an invasive species alters interactions between two or more native species (Strauss 1991). Although many indirect interactions have been hypothesised, causal mechanisms are difficult to detect, predict, and quantify (White et al. 2006). Because indirect effects can cross trophic levels, invasive species can disrupt interactions of entire native communities (Wootton 1994). We provide examples of indirect threats of invasion on bats through modification of habitat and food availability.

Modification of native habitat can influence bat behaviour because habitat use is partly dictated by ecomorphology, the relationship between functional morphology and ecology, which can explain diversity of bat feeding and flight patterns (Swartz et al. 2003). Bat manoeuvrability in flight is uniquely adapted to habitat complexity, as shown by the correlation between wing anatomy and neural activity (Safi & Dechmann 2005). Orientation and prey detection by echolocating bat species can be disrupted (Brigham et al. 1997) when invasive species change the three-dimensional structure of native habitats (e.g. Asner et al. 2008). For example, in fragmented forests near Chicago, USA, invasive shrub and tree removal was second only to prescribed fire in increasing bat activity (Smith & Gehrt 2010), probably owing to the removal of high understory clutter caused by invasive vegetation.

Invasive vegetation can conceal and replace bat roosts. In addition to threats described above, low counts of the Seychelles sheath-tailed bat on Silhouette and Mahé islands were attributed to invasive kudzu vines *Pueraria*

phaesoloides that overgrew some cave entrances (Bambini et al. 2006, Gerlach 2009). Anecdotal evidence suggests that the habitat of the western yellow bat *Lasiurus xanthinus* is threatened by invading tamarisk *Tamarix ramosissima* because tamarisk reduces water availability for desert fan palms *Washingtonia filifera* (Barrows 1993), the bat's preferred roost tree (Williams et al. 2006). Although the occurrence of tamarisk is not an important predictor of bat activity according to Ortiz and Barrows (2014), the authors hypothesised that as tamarisk stands mature they might reduce water available to growing palms.

Invasive vegetation also obstructs bat flight, which can result in injury. The Ryukyu flying fox, for example, reportedly becomes entangled in the leaf fibres of two introduced palms (Wiles & Brooke 2010). Invasive burdock *Arctium minus* produces large, prickly flower heads with hooked bracts that entrap bats. In 2002, Hendricks et al. (2003) discovered two mummified long-eared myotis *Myotis evotis* entangled in clusters of burdock flower heads. The authors offered past reports of bat mortality owing to burdock, including one eastern red bat *Lasiurus borealis*, one big brown bat *Eptesicus fuscus*, and several little brown myotis *Myotis lucifugus* (Hendricks et al. 2003). In Canada, two silver-haired bats *Lasiurus noctivagus* were rescued from burdock, rehabilitated, and released (Norquay et al. 2010). Burdock might be a particular threat to bats glean-ing insects from vegetation (Verts 1988), where accidental ensnarement is likely, especially for clumsy juvenile bats (Norquay et al. 2010).

Reductions in native vegetation or alterations of plant architecture can lead to changes in phytophagous insect prey of bats (Lawton 1983). On the island of Aguiguan, Northern Mariana Islands, the Endangered Pacific sheath-tailed bat *Emballonura semicaudata rotensis* was less active in a monoculture of invasive lantana *Lantana camara* than in native forests, and bat activity was correlated with the abundance of nocturnal, volant insects (Welch et al. 2016). Similarly, Seychelles sheath-tailed bat habitat invaded by *Cinnamomum serum* and *Tabebuia pallida* supports reduced numbers of phytophagous insects, especially highly preferred beetles (Gerlach 2009), but correlations with bat numbers were not explored.

Heavy browsing by invasive ungulates can indirectly affect bats through both reduction of native vegetation and alteration of habitat structure. As ungulates deplete understory vegetation, they further modify habitat by eroding and compacting soils, and altering nutrient cycling (Hobbs 1996). Invasive goats, pigs, and deer have been linked to reductions in fruit trees frequented by the Marianas flying fox (Wiles & Brooke 2010). In combination with typhoons and excessive hunting (Wiles et al. 1989), invasive ungulates exacerbate bat declines through habitat disturbance and

facilitation of the spread of invasive flora (Anonymous 2009).

CONCLUSION

Two main conclusions can be derived from these results. Firstly, over 60% of the bat species included in this review are island-dwelling. Fittingly, impacts of invasive species on island populations are considered worse than those on mainland populations (Simberloff 1995). Although less than 5% of the Earth's land mass consists of islands, island species are disproportionately threatened and most extinctions have occurred on islands (reviewed in Courchamp et al. 2003). For the bat clade, over half of the species are island-dwelling and a quarter are island endemics (Jones et al. 2009); therefore, many more bat species than reviewed here are possibly threatened by invasive species.

Secondly, some threats are refutable owing to unsubstantiated evidence – in 28 of the 73 cases provided here, negative effects of invasive species are presumed from anecdotes (Table 2). Experts sometimes suggest plausible threats to conservation groups given overlapping ranges of invasive species and bats, even if confirmation from the field is lacking. Outside of direct observation and statistics, threats on bats can be difficult to discriminate (Esler et al. 2010), especially if they vary in time or space (Parker et al. 1999). Indirect interactions are particularly difficult to ascertain, although implications for native communities are numerous (Wootton 1994). Given the diversity of roles bats perform in ecosystems (reviewed by Kasso & Balakrishnan 2013), changes to trophic pathways could conceivably end with negative consequences.

Reductions in population numbers are often the focus of impact assessments involving invasive species (Parker et al. 1999), but for bats, population-level changes are lacking even when invasive threats are demonstrable. Aside from in bat species that congregate in accessible caves, monitoring population trends is difficult. Indeed, 55% of bat species have unknown population trends (Anonymous 2015). Meyer et al. (2010) showed: (1) four surveys per site conducted biennially over 20 years were required to detect an annual population change in bats greater than or equal to 5%, and (2) temporal variation in bat abundance differs across species and monitoring locations. Therefore, other measures should be considered when determining if invasion substantially impacts bat species. Given improvements in acoustic monitoring technology and camera traps, examining shifts in habitat use could be a useful surrogate for population abundance estimates.

Although uncertainty surrounds the severity of invasion impacts on bats, the absence of clear evidence

does not negate the foundation that invasive species do threaten some bat species (Clavero & Garcia-Berthou 2005). Furthermore, multiple invaders and synergistic interactions of threats may ultimately lead to species losses (Brook et al. 2008). For example, invasive predators can take weak bats easily following severe weather (Palmeirim et al. 2007), and overhunting can exacerbate bat population declines that result from the destruction of native habitats by invasive ungulates (Worthington et al. 2001). In the wake of increasing ecosystem disruptions owing to climate change, distributions of hibernating bat species (Humphries et al. 2002) and tropical bat species (Hughes et al. 2012) could be severely restrained.

In closing, we offer suggestions for assessing the threat of invasive species on bats. Conservation managers should establish records of sites supporting high levels of bat activity, and evaluate potential threats and habitat requirements, so that deviations from baseline measurements can be calculated. For island species especially, research initiatives could assess effects of invasive species by comparing bat behaviour and ecology on islands with and without the invasion. Major roost sites should be monitored regularly, especially those used by endangered species, and if potential invasive predators are encountered their stomach contents should be examined for evidence of bats. Responses to biological invasions are rich for New Zealand, where introductions and associated extirpations received attention early (Courchamp et al. 2003). Thus, future conservation initiatives should look to experiences in New Zealand to facilitate management. Raising public awareness about local invasions and affected native bat species would also be beneficial. Moreover, citizen science programs could be developed to record bat sightings at roosts and calls during specified times of the year, much like projects led by the UK's Bat Conservation Trust (<http://www.bats.org.uk/pages/batmonitoring.html>). Most importantly, conservation managers should exercise the precautionary principle by taking action against non-native species when they are first detected (Simberloff 2001), even if new species do not first appear to be detrimental.

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