

**Conservation Biology of Bats:
Invasive Threats, Research Effort, and Extinction Risk**

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ABSTRACT

Global conservation for bats is needed: 15 percent of species are listed as extinct or threatened, signifying that they are at a high risk of extinction. An additional 17 percent are designated data-deficient, denoting that a threat category has not been assigned owing to insufficient knowledge on species abundance or distribution. In this dissertation, I use methods from both ecology and evolution to contribute to the study of bat conservation. Firstly, I review the impacts of biological invasion on bats, and provide examples of threats from each of four broad categories: predation, pathogens, competition, and indirect interactions. Overall, detailed accounts of invasive species threatening bats are lacking, but the most persuasive cases occur on islands. Secondly, I provide a case study of the endangered Pacific sheath-tailed bat (*Emballonura semicaudata rotensis*) to illustrate the importance of investigating indirect effects of invasion on species of conservation concern. The results imply that the impact of an invasive shrub on the persistence of the bat has been underestimated and that it is unclear how a feral ungulate alters bat habitat aside from reducing understory vegetation. Thirdly, I describe the state of academic literature for most of the bat clade, and provide ranked prioritization of bats for research based upon species vulnerability and evolutionary irreplaceability. Lastly, I use evolutionary comparative methods to identify species of conservation concern. Given simulations using important correlates of bat extinction risk, I predict that 31 data-deficient bats are threatened by endangerment. Overall, my work will benefit bat conservation by highlighting gaps in knowledge and elucidating research priorities that will be useful for directing conservation action.

TABLE OF CONTENTS

INTRODUCTION.....	1
References.....	4
CHAPTER I: The threat of invasive species to bats: A review.....	5
Abstract.....	6
Introduction.....	7
Methods.....	8
Results and Discussion.....	8
Conclusion.....	20
References.....	23
Appendix.....	35
CHAPTER II: Indirect impacts of invaders: A case study of the Pacific sheath-tailed bat (<i>Emballonura semicaudata rotensis</i>).....	41
Abstract.....	42
Introduction.....	43
Methods.....	44
Results and Discussion.....	48
Conclusion.....	50
References.....	52
Appendix A: Figures.....	56
Appendix B: Supplementary Methods.....	58
Appendix C: Supplementary Tables and Figures.....	63
CHAPTER III: Prioritizing bats for research effort.....	75
Abstract.....	76
Introduction.....	77
Methods.....	78
Results.....	80
Discussion.....	82

References.....	85
Appendix.....	88
CHAPTER IV: Predicting extinction risk for data-deficient bats.....	103
Abstract.....	104
Introduction.....	105
Methods.....	106
Results	108
Discussion.....	111
References.....	114
Appendix.....	116
CONCLUSION.....	128
VITA.....	130

LIST OF TABLES

Table I.1. Bat species discussed in the review.	35
Table II.1. SM2BAT+ acoustic detector settings.	63
Table II.2. Results from Bayesian analyses comparing bat activity and insect abundances between native forest and lantana shrub.	64
Table II.3. Bat activity correlations with site location and site weather.	65
Table II.4. Detailed results from the RDA between bat call parameters and predictor variables.	66
Table II.5. Results from the generalized linear model comparing seedling counts at forest locations given the history of goat presence.	67
Table II.6. Results from a Bayesian analysis comparing consumption of the three tree species by goats.	68
Table II.7. Correlations between bat activity and site native forest characteristics.	69
Table III.1. Sources and descriptions of data used in this study.	88
Table III.2. Proportion and number of species and articles for each Red List threat category.	90
Table III.3. Proportion and number of species and articles for each family.	91
Table III.4. Proportion and number of species and articles for each world region.	92
Table III.5. Proportion and number of full-text articles for each primary and secondary topic.	93
Table III.6. Keywords ascribed to each topic.	94
Table III.7. Regressions for single predictors of <i>number of articles</i> using two models of evolution.	95
Table III.8. Details of regressions for single predictors that are factors.	96
Table III.9. Pairwise correlations between variables used in single-predictor regressions.	97
Table III.10. Top ten priority ranking for research effort across all regions.	98
Table IV.1. Sources and descriptions of data used in this study.	116
Table IV.2. Results of single predictor phylogenetic logistic regressions predicting extinction risk in bats.	118

Table IV.3. Sample sizes for single predictor phylogenetic logistic regressions predicting extinction risk in bats.	120
Table IV.4. “Predictor-rich” model details.	121
Table IV.5. “Taxon-rich” model details.	122
Table IV.6. List of ten species at high risk of extinction according to two simulations.	123

LIST OF FIGURES

Figure II.1. Hypotheses for the indirect effects of invaders, feral goats and <i>Lantana camara</i> , on <i>Emballonura semicaudata rotensis</i>	56
Figure II.2. A map of Aguiguan Island, CNMI.	57
Figure II.3. Total bat activity at paired sites within two habitats.	70
Figure II.4. Total bat activity at each site throughout the sampling period.	71
Figure II.5. Total insect abundance at paired sites within two habitats.	72
Figure II.6. The correlations between bat call parameters and predictor variables with two canonical axes.	73
Figure II.7. Examples of bat call duration and bandwidth.	74
Figure III.1. Proportion of topic keywords for each full-text article by the year of publication.	99
Figure III.2. Number of topic keywords for full-text articles relative to row mean values.	100
Figure IV.1. Comparison of prediction intervals between models.	126
Figure IV.2. Estimated species threat for 59 species designated DD on the Red List. according to the taxon-rich model parameter estimates.	127

INTRODUCTION

Numbering over 1,300 species, bats (Chiroptera) are the second most species-rich mammal order after rodents (Rodentia) (Fenton and Simmons, 2014). Bats occur worldwide, excluding polar-regions, and have diverse life histories and morphologies, as shown by their important roles as pollinators, seed dispersers, and bioindicators of environmental stressors (Jones et al., 2009b). Bats are also significant to human-dominated areas; they provide an estimated \$3.8 billion per year in North America alone in economic benefits to agricultural systems as a natural control of pests (Boyles et al., 2011).

Global conservation for bats is needed: 15 percent of species are listed as extinct or threatened, signifying that they are at a high risk of extinction (IUCN, 2015). An additional 17 percent are designated data-deficient, denoting that a threat category has not been assigned owing to insufficient knowledge on species abundance or distribution. Bats are susceptible to imperilment owing to their long life spans and low fecundity; the average life span of bats is 3.5 times greater than that of non-flying placental mammals of similar size and most have only one young per year (Wilkinson and South, 2002). Thus, failure to breed in combination with extrinsic threats can make population recovery difficult

Habitat destruction, catastrophic events, overhunting, persecution, and pesticides are consistent threats to bats (Racey and Entwistle, 2003). In the wake of increasing ecosystem disruptions owing to climate change, the distribution of hibernating and tropical bat species could be further restricted. Biological invasion is a major driver of biodiversity loss across the globe; however, no study has described the scope of impacts on bats by invasive species.

In Chapter I, Christy Leppanen and I review the impacts of biological invasion on bats, and provide examples of threats from each of four broad categories: predation, pathogens, competition, and indirect interactions. Overall, detailed accounts of invasive species threatening bats are lacking, but the most persuasive cases of invasion affecting bats occur on islands. Fittingly, invasion devastates isolated islands more than mainlands, because island biota evolved with few predators, pathogens, and vertebrate herbivores (D'Antonio and Dudley, 1995). In addition, bats are an oddity among mammals in that roughly a quarter of species are island endemics (Jones et al., 2009), making them

important members of island communities. Given their vulnerability to novel interactions and their significant contribution to island diversity, research on the interactions between invasive species and island bats is a conservation priority.

In Chapter II, Dan Simberloff, Jim Fordyce, and I consider the conservation of *Emballonura semicaudata rotensis* to illustrate impacts of invasion on island bats. *E. s. rotensis* is a small, endangered insectivore, formerly distributed across limestone islands of Guam and the Commonwealth of the Northern Mariana Islands (CNMI) but now present only on the uninhabited island of Aguiguan (Wiles et al., 2011). Two ubiquitous invasive species, *Lantana camara* and feral goats, also occur on Aguiguan. We describe pathways by which both invasive species could indirectly threaten *E. s. rotensis* by reducing of the bat's native resources. However, we argue that management of *L. camara* is most important for the longevity of the bat population. Proudly, these results have contributed to the petition to list *E. s. rotensis* on the United States Endangered Species Act.

The discovery of echolocation has accelerated scientists' ability to study bats, but still, 55 percent of species have unknown population trends—the evidence traditionally used to caution species imperilment (IUCN, 2015). An inclusive understanding of all taxa would aid bat conservation, but the magnitude of the crisis limits the resources available to invest in species research. For other taxa, biologists have begun to describe patterns of research effort, by approximating the number of relevant peer-reviewed publications referenced in research databases (Lawler et al., 2006). Studies show that research effort has not been distributed evenly according to species imperilment, nor have taxa been researched equally across the tree of life. Furthermore, spatial biases pervade research effort.

In Chapter III, I describe the state of academic literature for most of the bat clade, indicate factors correlated with research effort, and suggest popular research topics. I found that threatened species and species that occur in the Asia-Pacific region have low research effort, and topics that likely inform on bat population trends are understudied. I finish by providing ranked prioritization of bats for research based upon species vulnerability and evolutionary irreplaceability. These results and additional analyses will contribute directly to conservation planning by the nonprofit organization Bat Conservation International.

Owing to limited conservation resources and lack of information on bats, approaches that can inform species risk of extinction are vital. Advances in phylogenetic methods and access to large datasets of species traits have accelerated the use of comparative methods to address these needs (Fisher and Owens, 2004). Because extinction risk is non-random across the phylogeny (Purvis et al., 2000), one can predict extinction risk for a given species provided appropriate traits and degree of relatedness to a species with known risk. Using the first comprehensive phylogeny for bats, Jones et al. (2003) assessed the biological correlates of extinction risk, and showed that biological correlates can predict known extinction risk.

In Chapter IV, Jeremy Beaulieu and I build on this and other previous studies by re-assessing correlates of bat extinction risk given a well-resolved, genetically based phylogeny. We then develop two models of extinction risk to illustrate trade-offs between model complexity and data availability. We end by providing binary estimates of extinction risk for bat species designated as data-deficient or not evaluated on the IUCN Red List.

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CHAPTER I

The threat of invasive species to bats: A review

Abstract

Biological invasion is a major driver of biodiversity loss across the globe, but no study has described the scope of invasion impacts on bats, the second largest mammal clade. We summarize negative impacts of invasive species on bats according to four broad categories: predation, pathogens, competition, and indirect interactions. We show that most accounts are anecdotal and do not provide direct evidence of population declines. However, pressures of invasion might exacerbate bat species vulnerability to other threatening factors. Our main conclusions are that the majority of cases of invasive species threatening bats occur on islands, but conclusive evidence of invasion impacts on bat populations is lacking.

Introduction

Numbering nearly 1,400 species (N. Simmons, 2017, personal communication), bats (Chiroptera) are the second most species-rich mammal order after rodents (Rodentia). Nearly 15 percent 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 percent are designated data-deficient, denoting that a threat category has not been assigned owing to insufficient knowledge on species abundance or distribution.

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

Biological invasion is a major driver of biodiversity loss across the globe (Vitousek et al., 1997). An invasive species is an organism that has been introduced into a novel environment, reproduced and spread (reviewed in Mack et al., 2000). Although the invasion literature has grown rapidly since the publication of Charles Elton's 1958 book on *The Ecology of Invasions by Animals and Plants* (MacIsaac et al., 2008) and the Rio Convention on Biological Diversity in the early 1990s, no study has described the scope of impacts on bats by invasive species.

In this paper we summarize impacts of biological invasion on bats. Some positive effects of invasion on bats include exotic plants providing roosting sites (Campbell et al., 2006), food resources (Corlett, 2005, Voigt, 2001), and heterogeneous foraging habitat (Borkin and Parsons, 2010, Rodriguez-San Pedro and Simonetti, 2013), and exotic fish serving as high-nutrient prey (Aizpurua et al., 2013). Here, we restrict our review to negative effects of invasion. We provide examples of threats from each of four threat types, and conclude with recommendations for the detection of impacts associated with invasion.

Methods

To identify species of interest, first 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, regardless of Red List assessment year. Then we located references provided by the Red List for each species identified in the filtered search. We also performed a literature search of the Web of Knowledge database using each bat species name as the topic and the search string: *invasi** OR *introduce** OR *non-native* OR *nonnative* OR *exotic* OR *alien* OR *nonindigenous* NOT *non-invasive* NOT *noninvasive*. We located additional references by tracking citations and performing keyword searches using the Google Scholar database.

Results and Discussion

The Red List search returned 22 bat species identified with invasive threats, however, bats for which we could not locate sufficient corroborating literature were excluded. Using all search methods, we retrieved article references for 36 bat species (Table I.1.). We apportioned invasive threats into four broad categories: predation, pathogens, competition, and indirect interactions.

Predation

Worldwide, non-native predators have been introduced for sport hunting and companionship, as biological controls, and unintentionally as hitchhikers with human commerce. Predation is the most severe direct consequence of invasion and is responsible for approximately 80 percent of terrestrial vertebrate extinctions (Clout and Russell, 2011). Predation can also have non-lethal effects on populations, 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 population-level impacts of predation is difficult because bats are not usually the primary prey of invasive predators (Pitt and Witmer, 2006).

Although bats experience low predation rates relative to other mammals (Tuttle and Stevenson, 1982), predation on roosting bats has been observed. Predators are lured by noise and odour emitted by congregating bats, especially to large colonies where

attractants are magnified. Presence of predators strongly influences roost selection and may cause bats to abandon roosts altogether (Lewis, 1995). Even if roosts are not abandoned, newly volant bats are at high risk of predation because they are immobile (Tuttle and 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 bats' ability to feed her pup (Kalcounis, 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, but now face a novel predator.

Cats are the most highly cited predators of bats, possibly because cats often present kills to their owners (Daniel and Williams, 1984). Cats were widely introduced for rodent control after domestication 3,000 years ago (Barun and Simberloff, 2011), and as opportunistic hunters, cats prey on a variety of wildlife weighing less than 400 g (Pearre and Maas, 1998). Effects on bird populations have been well documented—cats are responsible for 26 percent of predator-related extinctions of island birds (as cited in Pitt and Witmer, 2006). However, impacts on other fauna have not been well studied (Courchamp et al., 2003). Cats are likely attracted to the sporadic movements of bats and 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 most 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). One Australian survey indicated that 248 out of 421 households had pet cats that captured mammals, and a single wildlife shelter reported injuries of eight bat species owing to cats (as cited in Dickman, 1996). Another study conducted in Central and Northern Italy showed that approximately 29 percent of reported bat rescues were in response to cat attacks (Ancillotto et al., 2013). In Great Britain, where households documented kills of outdoor pet cats for five months, 44 percent reported kills from 986 cats. A total of 30 bats, including the 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 and Shrotriya, 2013) and the eastern blossom bat (*Syconycteris australis*) (Phillips et al., 2001).

In an effort to document common vampire bats (*Desmodus rotundus*) feeding on livestock on small farms, Delpietro et al. (1994) recorded several instances of cat predation. Interestingly, cats were kept in livestock corrals with goats, pigs, sheep, and cattle to guard them against vampire bat attacks, which farmers said were frequent before keeping cats. One owner stated that his cat began catching bats at about seven months old; another said his cat would go on the hunt at the alarm of pig cries.

During an eight-month study in Culebrones Cave, northern Puerto Rico, remains of six bat species (*Brachyphylla cavernarum*, *Erophylla bombifrons*, *Monophyllus redmani*, *Mormoops blainvillei*, *Pteronotus quadridens*, and *Pteronotus parnellii*) were found in cat scat belonging to as many as 16 different cats (Rodríguez-Durán et al., 2010). Interestingly, the most abundant bat occupying the cave, the Antillean Ghost-faced bat (*Mormoops blainvillei*), did not have the highest mortality by cats; Leach's single-leaf bat (*Monophyllus redmani*) was caught most according to wing remains. This suggests that bat flight behaviour might influence its susceptibility to cat predation.

Cats might be responsible, in part, for a 35 percent population decline over six years (Walshe et al., 2012) in the vulnerable Christmas Island flying fox (*Pteropus melanotus*), an Indo-Pacific island endemic (Hutson et al., 2008). Flying foxes are susceptible to cat attacks because the bats sometimes forage near the ground and are docile when approached (Tidemann et al., 1994). In fact, flying fox remains made up approximately nine percent of stomach content weight in 90 feral cats (Tidemann et al., 1994). Cats have, however, been present on the island since 1904 (Walshe et al., 2012). Therefore, recent population declines of the bat could be influenced by a variety of suspected predators (discussed below) (Walshe et al., 2012).

Domestic cats prey on the vulnerable lesser short-tailed bat (*Mystacina tuberculata*) (Daniel and Williams, 1984), one of three native terrestrial New Zealand mammals. While performing seasonal counts of bats in Rangataua Forest on New Zealand's North Island, Scrimgeour et al. (2012) discovered remains of at least 102 lesser short-tailed bats over a seven-day period. 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 at the roost

after the cat was captured. Curiously, video recordings at the roost do not show a cat visiting, so it is unknown how the bats were captured. New Zealand's long-tailed bat (*Chalinolobus tuberculatus*), a vulnerable, aerial insectivore (O'Donnell, 2008a) is also documented as prey of cats (Daniel and William, 1984).

The fish-eating bat (*Myotis vivesi*), a vulnerable vespertilionid endemic to small islands in the Gulf of California (Arroyo-Cabrales and Ospina-Garces, 2016), is considered easy prey because it roosts in rock crevices (Floyd et al., 2010). Fish-eating bat predation by cats was confirmed in 1998 (Vazquez-Domingues et al., 2004), and surveys conducted in 2005 documented no bats where historical records previously noted the species. In cases like this, the influence of cats on bat populations may be confounded by the presence of other invasive predators, such as rats (described below).

Three species of rat (brown rats (*Rattus norvegicus*), Pacific rats (*Rattus exulans*), and ship rats (*Rattus rattus*)) have hitchhiked via human expansion, reaching 90 percent of islands and all continents barring Antarctica (as cited in Towns et al., 2006). The negative effects of rat invasion on native species include reduced recruitment, local extirpations, and total extinctions (reviewed in Towns et al., 2006). Correlation between rat predation and species declines is often unsupported by direct observation, but where their distributions overlap, rats likely threaten roosting bats. For instance, predatory rats have caused an estimated 54 percent of island bird extinctions (as cited in Pitt and Witmer, 2006), and following rat eradication native ecosystems show definitive recovery (Towns et al., 2006).

Known from a single sub-fossil record, the Lord Howe long-eared bat (*Nyctophilus howensis*) is listed as critically endangered and possibly extinct (Hall et al., 2008). The loss of the bat occurred after European arrival (ca. 1778, as cited in Hutton et al., 2006) to Lord Howe Island in the Tasman Sea, but it is unknown if ship rats were responsible because they invaded later, in 1918 (Hutton et al., 2006). Complicating matters, in the 1920s "several kinds" of owls were released intentionally on the island as rat control (as cited in Paramonov, 1958), so owl predation may have further reduced the bat population. According to a biological survey published in 1974, no resident mammals occurred on Lord Howe, but two non-breeding bat species were recorded (Recher and Clark, 1974). The Lord Howe long-eared bat was either extremely rare by that time or already extinct, and a single skull fossil is known from 1972 (Hall et al., 2008).

Declines in the distribution and population density of the fish-eating bat (*Myotis vivesi*) across barren Mexican islands correspond with ship 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 bats are the only endemic mammals. Pacific rats were likely introduced first by way of Polynesian rafts (ca. 1280, Towns et al., 2006), brown rats arrived in the late 1700s, and ship rats appeared in the 1950s (Towns and De Lange, 2011). Rats had reached about 142 offshore New Zealand Islands by the mid-1890s, and arrival of rats coincides with severe population declines in New Zealand's endemic bat species (as cited in Towns et al., 2006).

The greater short-tailed bat (*Mystacina robusta*) is a critically endangered ground forager belonging to the endemic family Mystacinidae (O'Donnell, 2008b). Fossil evidence indicates it was once widely distributed across the New Zealand archipelago and that numbers of bat and rat fossils are negatively correlated (as cited in Molloy, 1995). Coinciding with the introduction of ship rats on Big South Cape Island off Stewart Island, the greater short-tailed bat was extirpated around 1962 (Towns et al., 2006). There have been no live sightings since 1967, and a dead bat was last found in 1978 (Molloy, 1995), though the species might be on an offshore island or difficult to detect; mystacinid-like echolocation calls were detected in 1999 (O'Donnell, 2010).

The decline in numbers of New Zealand's vulnerable lesser short-tailed bat (*Mystacina tuberculata*) also coincides with rat introduction (O'Donnell, 2008c). Between 1975 and 1983, 40 bat skeletons with holes chewed in their skulls were retrieved from a bat nursery colony, though it is unknown whether rats killed the bats or merely scavenged their carcasses (Daniel and Williams, 1984). To establish an "insurance" population, the New Zealand Department of Conservation translocated 20 lesser short-tailed bats to Kapiti Island where exotic mammals are not present (Ruffell et al., 2007).

Rats might also threaten the long-tailed bat (*Chalinolobus tuberculatus*), as population declines are correlated with high rat numbers (Pryde et al., 2006). In addition, introduced little owls (*Athene noctula*) reportedly attempt to catch bats, which are common prey in the bird's native range, and possums (*Trichosurus vulpecula*) have been seen

attempting to reach maternity roosts (O'Donnell, 2001). New Zealand's bats are likely threatened by multiple invasive species, including stoats (*Mustela erminea*), though evidence of predation is lacking (O'Donnell, 2010).

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). Across its native range, the barn owl is a frequent predator of insectivorous bats (e.g., Ruprecht, 1978). The Seychelles sheath-tailed bat is functionally and morphologically similar to insectivorous bats in the native range of barn owls, and the bat roosts in caves at which barn owls likely ambush emerging bats. 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 likely 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 and 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 the Christmas Island flying fox (*Pteropus melanotus*) (Fritts, 1993) and the Christmas Island pipistrelle (*Pipistrellus murrayi*) (Lumsden et al., 2007). Remains of flying foxes were not found in examined snake guts (Walshe et al., 2012), but no pipistrelles were recorded at detector sites immediately adjacent to three locations with snakes (Lumsden et al., 2007).

In 1998, the endangered Marianas fruit bat (*Pteropus mariannus*) numbered fewer than 100 individuals and was limited to the Mariana and Caroline Islands (as cited in Fritts and Rodda, 1998). Illegal hunting is the primary threat to the species, but brown tree snake (*Boiga irregularis*) predation is likely significant (Wiles, 1987). Since its introduction to Guam in the 1940s, only one case of predation on a bat in 1982 has been documented, but the snake probably kills young bats at roosts while the mother is foraging (Wiles, 1987). Moreover, bats were extirpated from southern Guam by 1970s as snake numbers increased (Fritts and Rodda, 1998).

Owing to their abundance, the giant centipede (*Scolopendra morsitans*) might pose a significant risk to the Christmas Island pipistrelle (*Pipistrellus murrayi*) (Molinari et al.,

2005). Introduced during the 1980s, centipedes have become numerous in the canopy where bats roost, 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 (*Pteropus melanotus*) found immobilized by a centipede, but it is unknown if centipedes increase mortality or are simply a nuisance to roosting bats (Walshe et al., 2012).

Pathogens

Pathogens are disease-causing agents, 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 across the native ecological community (Hickling, 2011).

Much attention is afforded to zoonotic disease in bats, especially rabies virus, owing to its transmission to humans and domestic animals. Impacts of disease on bat communities, *per se*, are still largely unknown (Schountz, 2014), however, infectious disease ranks lowest as the cause of reported 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 likelihood of transmission. Moreover, some species can live very long: 34 years for *Myotis lucifugus*, 38 years for *M. myotis*, and 43 years for *M. 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 (Constantine, 2003).

The most pressing threat to cave-roosting bats in North America is white-nose syndrome. The disease is caused by the invasive fungus, *Pseudogymnoascus destructans*, that was transmitted to North America 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 US states and 5 Canadian provinces, infecting seven species

and killing an estimated six million bats (Anonymous, 2012). Disease-associated mortality has led to inclusion of the northern long-eared bat (*Myotis septentrionalis*) on the Endangered Species List as threatened, and conservation efforts focus on reducing “take” of the species (Anonymous, 2016). Causes and consequences of the disease are an increasing focus of research and are reviewed in Frick et al. (2015).

Large die-offs of bats without apparent causes have been attributed to an introduced disease epidemic. In 1987, high fatality in Solomons flying fox (*Pteropus rayneri*) occurred so suddenly in Bougainville and Buka populations that introduced disease was the presumed culprit (Flannery, 1989). Similarly on Manus and the Admiralty Islands, great flying foxes (*Pteropus neohibernicus*) were found dying from disease over several weeks, which resulted in the bats becoming rare. Invasive diseases might cause more mortality events in bats, however, the origin of the pathogen is not identified in the literature.

During a brief period in the 1900s, infectious disease was endorsed as a means of exterminating unwanted taxa (as cited in Spennemann and Wiles, 2002). A pest of fruit in plantations and villages on the Samoan Island of ‘Upolu, the since-extirpated Pacific flying fox (*Pteropus tonganus*) was the likely target of deliberate avian cholera introductions in the 1980s, but the Samoan flying fox (*Pteropus samoensis*) might have been killed as well (Spennemann and Wiles, 2002).

Competition

Invasive species are hypothesized to be so successful in novel environments because of their superior competitive ability (Dickman, 2011). Competition occurs when two species require the same resource, be it shelter, food, or space. Two types of competition are generally recognised: interference competition occurs when one species prevents another species from accessing a readily available, shared resource through aggression or chemical warfare; and exploitative competition occurs when one species consumes a shared and limited resource before the other species encounters it.

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 limited

disturbance (Kunz and Lumsden, 2003). Because maternity colonies must be protected from predators, selection is especially important for roosting females. Competition for limited, suitable roosting habitat forces bats to forage in poorer-quality habitat, which can be particularly burdensome for cavity roosters that require particular tree species, tree sizes, stand ages, or tree decay (Crampton and Barclay, 1998). Availability is also important when bats need to switch roosts seasonally or accommodate suitable microclimates (as cited in Crampton and Barclay, 1998), 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. There is at least one case of large-eared pied bats (*Chalinolobus dwyeri*) abandoning a roost after disturbance by ungulates (Anonymous, 2011). A top priority for conservation of this bat includes protecting roost sites with gates and a reduction of the goat population within bat foraging habitat.

For the long-tailed bat (*Chalinolobus tuberculatus*), suitable roosts have been found occupied by non-native starlings (*Sturnus vulgaris*), house sparrows (*Passer domesticus*), pigeons (*Columba livia*), wasps (*Vespula* sp.), and ship rats (O'Donnell, 2001). It is not known, however, if the sites were unoccupied or if bats were evicted by invasives. It would not be surprising if starlings competed with bats for roosts, because they do in their native range (as cited in O'Donnell, 2000).

The rose-ringed 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 bird nests in tree hollows formed by other animals (Ruczynski and Bogdanowicz, 2005). Competition between the invasive parakeets and bats could be common because the parakeet has been documented to evict native European red squirrels from cavities (Mori et al., 2013), and conflict for artificial cavities has been described in other native bat-invasive bird contexts (e.g., Meddings et al., 2011). A report from southern Tuscany described a lesser noctule bat (*Nyctalus leisleri*) being attacked and evicted from its tree hollow by a rose-ringed parakeet (Menchetti et al., 2014). The bat died minutes after falling to the ground with wounds to its head and abdomen.

Honeybees (*Apis mellifera*) often occupy tree hollows, excluding other potential roosting species for approximately three to seven years (Oldroyd et al., 1997). Honeybee

colonies were established in Australia in 1822, and the distribution and abundance of feral colonies have increased dramatically since the mid-1930s (Paton, 1996). Feral colonies might inhibit nesting by the native yellow-bellied sheath-tailed bat (*Saccolaimus flaviventris*) (McKenzie and Pennay, 2008), because bees have been found to occupy roosts suitable for bats. The negative impact of honeybees, however, likely depends on availability of tree hollows and frequency of honeybee occupation, which occurs in less than one percent of hollows in less than one percent of trees (Paton, 1996).

The little fire ant (*Wasmannia auropunctata*) was introduced to Choiseul, Solomon Islands, as a biocontrol for nut-fall bug (*Amblypelta* sp.) infestation of coconut and cocoa plantations (Fasi et al., 2012). The ant is considered the worst ant-threat in the Pacific region (Anonymous, 2017) because its sting can cause blindness (as cited in Fasi et al., 2012). The ants, which are cavity-nesters, have been observed attacking native cuscus (*Phalanger orientalis*) (Wetterer and Porter, 2003). Similarly, ants might displace the Solomon flying fox (*Pteropus rayneri*) from roosting trees (Bowen-Jones et al., 1997). According to locals interviewed in 1995, Solomon flying foxes were not present in previously occupied roosts within two to five years of the ant's 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 around 1915, but serious population impacts were not observed until the 1990s (O'Dowd et al., 1999). Evidence of ant threats to bats is limited, but ants have likely exacerbated ongoing reductions in bat numbers. Potential roost trees for the Christmas Island pipistrelle (*Pipistrellus murrayi*) have been infested by ants. Ant infestations likely alter invertebrate communities associated with some tree species (Schulz and Lumsden, 2004)—impacts that can scale-up to affect bat carrying capacity. There has been at least one documented death of a Christmas Island pipistrelle in relation to the ant (Lumsden et al., 2007). The Christmas Island flying fox (*Pteropus melanotus*) might abandon tree canopies owing to swarms of ants, and ant supercolonies probably reduce food resources for the frugivorous bat (Walshe et al., 2012). Adult bats are not likely killed by ants, but are injured by acid produced by ants defending the colony.

The diet of the only mammal endemic to the five Ogasawara (Bonin) Islands of southern Japan (Saitoh et al., 2015), the critically endangered Bonin flying fox (*Pteropus*

pselaphon), is nine endemic species and 44 alien plant species. Invasive rodents damage seeds of at least one endemic plant (*Elaeocarpus photiniifolius*) eaten by the Bonin flying fox (Hashimoto, 2009). Although its diet before plant invasion is unknown, alien plant consumption may signal a shortage of native species, which forces novel interactions (Inaba et al., 2004).

An introduced scarab beetle (*Protaetia orientalis*) likely consumes seeded breadfruit (*Artocarpus mariannensis*), a major food source of the Marianas fruit bat (*Pteropus mariannus*) (Wiles and Brooke, 2012). Moreover, an introduced cycad scale insect (*Aulacaspis yasumatsui*) and erythrina gall wasp (*Quadrastichus erythrinae*) attack fruit trees visited by the Marianas fruit bat, the Samoan (*Pteropus samoensis*) and Pacific flying foxes (*Pteropus tonganus*).

The coqui frog was introduced from its native Puerto Rico to Hawaii in the late 1980s. Frog density is as high as 20,000 individuals per hectare (Beard and Pitt, 2005), so frog dietary overlap may negatively affect the only terrestrial native Hawaiian mammal, the Hawaiian hoary bat (*Lasiurus cinereus semotus*). Beard and Pitt (2005) reported that most of what the frogs consumed were non-native, leaf litter invertebrates. However, a later analysis found nearly 40 percent of its diet was aerial insects and their larvae, including species in the Hawaiian hoary bat diet (Bernard, 2011). Moreover, the bats were shown to consume fewer beetle species when there were dense frog populations.

In New Zealand, the lesser short-tailed bat (*Mystacina tuberculata*) is the principal pollinator of the native, parasitic plant wood rose (*Dactylanthus taylorii*) (Lord, 1991). Invasive rats and wasps have been recorded visiting the plant but typically leave inflorescences intact (Ecroyd, 1996). However, brushtail possums (*Trichosurus vulpecula*), introduced from Australia and Tasmania to establish a fur industry (as cited in Ji and Clout, 2002), destroy the plant's flowers. Despite reductions in possum populations (Lloyd and McQueen, 2002), both the bat and plant are threatened across their ranges and co-occur in few areas (O'Donnell, 2010).

Indirect Interactions

Studies on how biological invasions affect bats have focused on direct interactions. Indirect effects of invasion occur when an invasive species alters the interaction between native

species (Strauss, 1991). Although many indirect effects have been hypothesized, causal mechanisms are difficult to detect, predict, and quantify (White et al., 2006). Because indirect effects can occur across trophic levels, invasive species can disrupt interactions of entire native communities (Wootton, 1994). In this section, we provide examples of indirect impacts of invasion on bats through modification of habitat structure and food availability.

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

Invasive burdock (*Arctium minus*) produce large, prickly flower heads with hooked bracts that trap bats and birds. In 2002, Hendricks et al., (2003) discovered two mummified western long-eared bats (*Myotis evotis*) entangled in clusters of live burdock flower heads, about one meter high. The authors offer past reports of bat fatality owing to burdock, including one eastern red bat (*Lasiurus borealis*), one big brown bat, and several little brown bats (*Myotis lucifugus*) (as cited in Hendrick et al., 2003). In Canada, two silver-haired bats (*Lasionycteris noctivagans*) were rescued from burdock, rehabilitated, and released (Norquay et al., 2010). Burdock might be a particular threat to bats gleaning insects from vegetation (Verts, 1988), where accidental ensnarement is likely, especially for clumsy juvenile bats (Norquay et al., 2010).

Invasive vegetation obstructs bat flight and conceal openings to roosts. The Ryukyu flying fox (*Pteropus dasymallus*) has reportedly become entangled in leaf fibres of two introduced palms (Wiles and Brooke, 2010). In 2004, only 32 and 18 individuals of the critically endangered Seychelles sheath-tailed bat (*Coleura seychellensis*) were counted on the islands of Silhouette and Mahé, respectively (Gerlach, 2009, Bambini et al., 2006). Caves

of roosting bats at both locations had invasive kudzu vines (*Pueraria phaesoloides*) overgrowing some entrances.

Anecdotal evidence suggests that habitat of the western yellow-bat (*Lasiurus xanthinus*) is threatened by invading tamarisk (*Tamarix ramosissima*), because it greatly reduces water availability for native vegetation (Barrows, 1993). The western yellow-bat is most active at riparian woodland habitat where it roosts in desert fan palms (*Washingtonia filifera*) (Williams et al., 2006). The occurrence of tamarisk was not an important predictor of bat activity according to a study conducted across palm oases of the Sonoran Desert (Ortiz and Barrows, 2014). However, the authors suggested that as tamarisk stands mature they might reduce water available to growing palms.

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 across a monoculture of invasive lantana (*Lantana camara*) than on native forests, likely in response to a lower abundance of nocturnal, volant insect prey (Welch et al., 2016). Similarly, habitat of the Seychelles sheath-tailed bat (*Coleura seychellensis*) has been invaded by the invasive plants *Cinnamomum serum* and *Tabebuia pallid*, which leads to reduced numbers of phytophagous insects relative to uninvaded areas, especially highly preferred beetles (Gerlach, 2009).

Heavy browsing by invasive ungulates can indirectly affect bats through 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 fruit bat (*Pteropus mariannus*) (Wiles and Brooke, 2010). In combination with typhoons and excessive hunting (Wiles et al., 1989), invasive ungulates exacerbate bat declines through habitat disturbance and facilitation of invasive flora (Anonymous, 2009).

Conclusion

Two main conclusions derive from these results. Firstly, the majority of cases of invasive species threatening bats occur on islands. Fittingly, impacts of invasive species on island

populations have been considered worse than those on mainland populations (Simberloff, 1995). Although less than five percent 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).

Secondly, conclusive evidence of invasive species threatening bat populations is lacking. For the majority of cases discussed here, negative interactions between invasive species and bats are presumed from circumstantial evidence. Outside of experimentation, however, it is difficult to measure the impacts of particular invasive species on biodiversity because pre-invasion assessments of biological communities are largely unavailable (Esler et al., 2010). Indirect effects of invasion are particularly difficult to measure, although the implications for native communities are numerous (Wootton, 1994). Given the diversity of roles bats play in ecosystems (reviewed in Kasso and Balakrishnan, 2013), impacts to a number of trophic pathways could conceivably end at negative consequences for bat species. Indeed, the greatest hindrance to bat conservation is lack of information (Hutson et al., 2001).

Reductions in population numbers are often the focus of invasion impact assessments (Parker et al., 1999), but for bats, other measures should be considered when deciding whether impacts of invasion are substantial. Aside from bat species that congregate in accessible caves, monitoring population trends of bats is difficult, as is evident by the fact that 55 percent of bat species have unknown population trends (Anonymous, 2015). In a tropical study, Meyer et al. (2010) showed that to detect greater than or equal to five percent annual change in population trends requires four surveys per site conducted biennially over 20 years, and the authors showed that temporal variation in abundance differs across species and monitoring locations. Given improvements in acoustic monitoring technology and camera traps, examining shifts in habitat use could be a useful surrogate for population abundance estimates in bats.

Although uncertainty surrounds the severity of invasive species impacts on bats, the absence of a "smoking gun" does not negate the likelihood that invasion has real effects on some bat species (Clavero and Garcia-Berthou, 2005). In most cases synergistic interactions of threatening agents will ultimately lead to bat species losses (Brook, 2008).

For example, some large-bodied bat species are hunted for human consumption (Mickleburgh et al., 2009) or culled when they are perceived as agricultural pests (Fujita and Tuttle, 1991). Because bats have “slow” life histories (Barclay and Harder, 2003), recovery from population-reducing processes is not guaranteed. In the wake of increasing ecosystem disruptions owing to climate change, distributions of hibernating (Humphries et al., 2002) and tropical bat species (Hughes et al., 2012) could be severely restrained.

In closing, we offer some general suggestions for addressing the impact of invasive species on bats. Conservation managers should establish records of high-activity bat locations and evaluate potential threats and habitat requirements so that deviations from baseline measurements can be observed. For island species, especially, research initiatives could assess the effects of particular invasive species by comparing bat behaviour and ecology on islands with and without invasion. Major roost sites should be monitored regularly, especially those of endangered bat species, and if potential invasive predators are encountered their stomach contents should be examined for signs of bats. Responses to biological invasion are rich for New Zealand, where introductions and associated extirpations received attention early (as cited in 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 Christmas Bird Counts (www.audubon.org/conservation/). 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 detrimental.

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Appendix

Table I.1. Bat species discussed in the review. The Red List Category abbreviations are as follows: LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR= Critically Endangered; PE = Possibly Extinct.

scientific name	family	common name	Red List category	threat type	invasive species
<i>Brachyphylla cavernarum</i>	Phyllostomidae	Antillean fruit-eating bat	LC	predation	cats
<i>Chalinolobus dwyeri</i>	Vespertilionidae	long-eared pied bat	NT	indirect effects	goats
<i>Chalinolobus tuberculatus</i>	Vespertilionidae	long-tailed bat	VU	predation competition	cats, rats, little owl, brush-tailed possum roost invaders
<i>Coleura seychellensis</i>	Emballonuridae	Seychelles sheath-tailed bat	CR	predation indirect effect	barn owl invasive vegetation
<i>Desmodus rotundus</i>	Phyllostomidae	common vampire bat	LC	predation	cats
<i>Emballonura semicaudata rotensis</i>	Emballonuridae	Pacific sheath-tailed bat	EN	indirect effects	lantana

Table I.1. Continued.

scientific name	family	common name	Red List category	threat type	invasive species
<i>Erophylla bombifrons</i>	Phyllostomidae	brown flower bat	LC	predation	cats
<i>Lasiurus borealis</i>	Vespertilionidae	eastern red bat	LC	indirect effects	burdock
<i>Lasiurus cinereus semotus</i>	Vespertilionidae	Hawaiian hoary bat	LC	competition	coqui frog
<i>Lasiurus xanthinus</i>	Vespertilionidae	western yellow-bat	LC	indirect effects	tamarisk
<i>Lasionycteris noctivagans</i>	Vespertilionidae	silver-haired bat	LC	indirect effects	burdock
<i>Monophyllus redmani</i>	Phyllostomidae	Leach's single-leaf bat	LC	predation	cats
<i>Mormoops blainvillei</i>	Mormoopidae	Antillean ghost-faced bat	LC	predation	cats

Table I.1. Continued.

scientific name	family	common name	Red List category	threat type	invasive species
<i>Myotis evotis</i>	Vespertilionidae	long-eared bat	LC	indirect effects	burdock
<i>Myotis lucifugus</i>	Vespertilionidae	big brown bat	LC	indirect effects	burdock
<i>Myotis septentrionalis</i>	Vespertilionidae	northern long-eared bat	LC	pathogen	<i>Pseudogemnoascus destructans</i>
<i>Myotis vivesi</i>	Vespertilionidae	fish-eating bat	VU	predation	cats, rats
<i>Mystacina robusta</i>	Mystacinidae	greater short-tailed bat	CR	predation	rats
<i>Mystacina tuberculata</i>	Mystacinidae	lesser short-tailed bat	VU	predation competition	cats, rats brush-tailed possum
<i>Nyctalus leisleri</i>	Vespertilionidae	lesser noctule bat	LC	competition	rose-ringed parakeet

Table I.1. Continued.

scientific name	family	common name	Red List category	threat type	invasive species
<i>Nyctophilus howensis</i>	Vespertilionidae	Lord Howe long-eared bat	CR (PE)	predation	rats
<i>Pipistrellus coromandra</i>	Vespertilionidae	Indian pipistrelle	LC	predation	cats
<i>Pipistrellus murrayi</i>	Vespertilionidae	Christmas Island pipistrelle	CR (PE)	predation indirect effects	common wolf snake, giant centipede yellow crazy ant
<i>Plecotus auritus</i>	Vespertilionidae	brown long-eared bat	LC	predation	cats
<i>Pteronotus parnellii</i>	Mormoopidae	common mustached bat	LC	predation	cats
<i>Pteronotus quadridens</i>	Mormoopidae	sooty mustached bat	LC	predation	cats
<i>Pteropus dasymallus</i>	Pteropodidae	Ryukyu flying fox	NT	indirect effects	plams

Table I.1. Continued.

scientific name	family	common name	Red List category	threat type	invasive species
<i>Pteropus mariannus</i>	Pteropodidae	Marianas fruit bat	EN	predation	brown tree snake
				competition	phytophagous insects
				indirect effects	ungulates
<i>Pteropus melanotus</i>	Pteropodidae	Christmas Island flying fox	VU	predation	cats, common wolf snake, giant centipede
				indirect effects	yellow crazy ants
<i>Pteropus neohibernicus</i>	Pteropodidae	great flying fox	LC	pathogen	unknown disease
<i>Pteropus pselaphon</i>	Pteropodidae	Bonin flying fox	CR	predation	rats
				competition	white-eye
<i>Pteropus rayneri</i>	Pteropodidae	Solomons flying-fox	NT	pathogen	unknown disease
				competition	little fire ant

Table I.1. Continued.

scientific name	family	common name	Red List category	threat type	invasive species
<i>Pteropus samoensis</i>	Pteropodidae	Samoan flying fox	NT	pathogen	avian cholera
				competition	phytophagous insects
<i>Pteropus tonganus</i>	Pteropodidae	Pacific flying fox	LC	pathogen	avian cholera
				competition	phytophagous insects
<i>Saccolaimus flaviventris</i>	Emballonuridae	yellow-bellied sheath-tailed bat	LC	competition	honeybees
<i>Syconycteris australis</i>	Pteropodidae	eastern blossom bat	LC	predation	cats

CHAPTER II

Indirect impacts of invaders: A case study of the Pacific sheath-tailed bat

(Emballonura semicaudata rotensis)

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JNW conducted the research, analyzed the data, wrote the first draft of the manuscript, and was the corresponding author on the publication. JAF contributed to the statistical methods. JAF and DSS contributed to manuscript revisions.

Abstract

Although many indirect consequences of biological invasions are plausible, few studies test hypotheses for management of threatened taxa. A case study of the endangered Pacific sheath-tailed bat (*Emballonura semicaudata rotensis*) illustrates the importance of investigating indirect effects of invasion on species of conservation concern. We hypothesized that two invaders, feral goats and *Lantana camara*, would indirectly affect the bat by decreasing availability of suitable resources. Specifically, that microclimate and bat prey abundances in lantana shrub differ from native forest habitat, and that preferential browsing by goats structures forests to be less suitable for bats. Our results suggest that bats avoid lantana shrub. However, we found no evidence that preferential goat browsing influenced bat activity. Our research implies that the impact of lantana on the persistence of the bat has been underestimated and that it is unclear how goats alter bat habitat aside from reducing understory vegetation. Future managers should prioritize efforts that restore native forest and reforest areas currently dominated by lantana. We urge conservation scientists to evaluate indirect effects of invasive species and publish findings that elucidate the consequences for native populations.

Introduction

Global conservation for bats is needed: fifteen percent of species are listed as extinct or threatened, 17 percent do not have a threat status owing to insufficient data, and over half have unknown population trends (IUCN, 2015). Moreover, bats are an oddity among mammals in that roughly a quarter of species are island endemics (Jones et al., 2009), making them important members of island communities. Given uncertainty regarding population viability and their significant contribution to island diversity, research on threats to bats is a priority for conservation (Mickleburgh et al., 2002).

Endangerment and extinction occur disproportionately on islands, in part owing to island systems vulnerability to invaders (Gimeno et al., 2006). Biological invasion can have profound ecological and socioeconomic impacts of isolated ecosystems (reviewed in Reaser et al., 2007). Studies on how biological invasions affect bats have focused on direct interactions, such as predation and epidemiology of introduced pathogens (e.g., Fritts and Rodda, 1993; Rodriquez-Duran et al., 2010). Few have evaluated indirect effects—how interactions between coexisting species are affected by another species (Strauss, 1991)—on bats.

The Pacific sheath-tailed bat (*Emballonura semicaudata*) is a small insectivore designated “endangered” because its geographic area is less than 5000 km² and highly fragmented (Bonaccorso and Allison, 2008). *Emballonura semicaudata rotensis* is a subspecies formerly distributed across limestone islands of Guam and the Commonwealth of the Northern Mariana Islands (CNMI) but now present only on the uninhabited island of Aguiguan (Wiles et al., 2011). The estimated 500 individuals of *E. s. rotensis* are commonly detected in forests and roost primarily in three caves (Wiles et al., 2011). Consequently, *E. s. rotensis* is highly vulnerable to stochastic demographic and environmental events.

Unconfirmed threats to *E. s. rotensis* include invasive species (Berger, 2005). Shrub covers at least 20 percent of Aguiguan (150 ha) and is dominated by lantana (*Lantana camara*) (Amidon, 2009), a “top 100” invasive species (IUCN, 2001). Many studies have shown that lantana can greatly alter native community structure (see review by Sharma et al., 2005), though its impacts on Aguiguan remain unstudied. Feral goats (*Capra hircus*) were introduced to Aguiguan during the mid-1800s (Butler, 1992), and their density has reached over 200 individuals per square kilometer (Esselstyn et al., 2002), earning

Aguiguan the nickname “Goat Island”. The detrimental effects of goats on Aguiguan’s native species are largely anecdotal.

Here, we consider the conservation of *E. s. rotensis* to illustrate indirect impacts of invasion (Figure II.1.). We hypothesized that goat browsing and lantana spread indirectly impact *E. s. rotensis* by altering habitat structure and prey abundances. To evaluate our hypotheses, we ask: (1) Do bats behave differently in lantana shrub than in native forest, and what factors account for this pattern? and (2) Does native understory cover indicate goat browsing, and is bat activity related to the structural complexity of native forest?

Methods

Study System

We conducted this study on Aguiguan, CNMI, (14°51’N, 145°33’E) from May 28 to June 14, 2013. The 7.09 km² island consists of three concentric limestone plateaus (Figure II.2.). Native limestone forest occurs primarily along the smaller terraces of the island and on steep slopes. The dominant native tree species are *Pisonia grandis*, *Cynometra ramiflora*, and *Guamia mariannae* (Esselstyn et al., 2002). Exotic grasses, *Jatropha gossypifolia*, and *Chromolaena odorata* seedlings are interspersed with lantana across portions of the shrub habitat (hereafter, lantana shrub). Before the 1930s Aguiguan was covered mostly in native forest, but lantana shrub is now extensive on the central plateau of the island where vegetation was cleared during Japanese occupation (Butler, 1992). We performed all statistical analyses in the R statistical computing environment (v3.0.3, R Development Core Team). Appendix B provides details of our study design.

Indirect Effects of Lantana

If lantana shrub provides an unfavorable microclimate for *E. s. rotensis*, lantana spread could indirectly affect bats as a consequence of it replacing native forest. Lantana shrub forms a dense monoculture with no canopy cover and little windbreak. Previous surveys on Aguiguan detected *E. s. rotensis* in forests (Esselstyn et al., 2004; Gorresen et al., 2009), where the microclimate is probably more suitable for a small bat (e.g., Rydell, 1991). Lantana shrub has likely limited the expansion of native forest on Aguiguan because lantana is allelopathic (Gentle and Duggin, 1997), has bird-dispersed seeds (Turner and

Downey, 2008), flourishes in disturbed environments (Duggin and Gentle, 1998), and ungulates avoid its unpalatable foliage (Sharma et al., 2005). Moreover, patches of *lantana* expand within native forest as it has invaded treefall gaps opportunistically (Amidon et al., 2014).

To test if bat activity differed between native forest and *lantana* shrub, we recorded bat calls using acoustic detectors at six pairs of sites—each pair consisting of a forest and shrub habitat. Sites were monitored for three consecutive nights. We determined bat activity using the acoustic activity index (Miller, 2001), a tally of the number of one-minute recording intervals per night containing two or more consecutive bat call pulses. We compared bat activity between native forest and *lantana* shrub using a hierarchical Bayesian model where the number of bat calls recorded in each habitat was modeled as being drawn from a binomial distribution described with parameter p . We assumed that the binomial parameters characterizing each pair of sites were drawn from a beta distribution that represented island-level activity between the two habitats (Fordyce et al., 2011). To determine which environmental factors correspond with bat habitat use, we recorded the elevation of each site and its distance to the nearest of three caves housing bats as well as nightly weather. We measured on-site temperature at thirty-minute intervals, and we retrieved hourly wind speed (knots) and sky conditions (METAR) for each sampling night from the Saipan International Airport Weather Station, the nearest weather station recording nightly conditions. We calculated Spearman's rank correlation coefficient to examine the relationship between these environmental factors and bat activity (R package "coin," Hothorn et al., 2008).

Irrespective of how appropriate *lantana* shrub microclimate is, *lantana* spread could also indirectly affect bats if the habitat does not support the bat's insect prey. Examination of *E. s. rotensis* fecal material showed that bats consume high volumes of wasps, moths, and beetles (Valdez et al., 2011). The interactions between *lantana* and Aguigan's native insects have not been examined, but *lantana* flowers might attract bat prey, especially moths (Sharma et al., 2005). Conversely, processed *lantana* has been used as a larvicide and insect repellent (Ogendo et al., 2006), so *lantana* shrub might not support every prey species.

To determine if abundances or composition of nocturnal, flying insects differed between native forests and *lantana* shrub, we sampled insects synchronically during bat

acoustic monitoring using a miniature blacklight trap and an aerial malaise trap with a bottom collector approximately 50 m from each of the acoustic detectors. We identified insects at least to order and calculated abundance and richness for each night. For each sampling night and site, we summed insect abundance by taxonomic order. We used distance-based redundancy analysis to determine if insect composition differed between native forest and lantana shrub (Legendre and Anderson, 1999). We used a hierarchical Bayesian model to compare the abundance of each insect order between native forest and lantana shrub, where insect abundance at each of the paired sites was modeled as being drawn from a binomial distribution with a beta prior (Fordyce et al., 2011). To determine how bat activity corresponds with insect abundance, we calculated Spearman's rank correlation coefficient for each pair of sites (R package "coin", Hothorn et al., 2008). To elucidate if intrinsic habitat factors or insect availability drives bat activity, we performed a redundancy analysis to relate bat behavior, as measured by call characteristics (Table A4), to habitat and insect abundance (R package "vegan", Oksanen et al., 2012).

Indirect Effects of Goats

Goats might indirectly affect bats by reducing native forest habitat, because goat browsing can impede regeneration of vegetation (Scowcroft and Hobdy, 1987). Goat numbers on Aguiguan are reportedly too high to allow seedling recruitment (e.g., Esselstyn et al., 2002; Amidon et al., 2014), although this conclusion is based on circumstantial evidence. To determine if goats are responsible for low understory recruitment on Aguiguan, we counted the number of seedlings <1 m tall within a random 2 m diameter circle at ten locations in Aguiguan forest. For comparison, we counted seedlings in native forests of Tinian, a populated island approximately 8 km NE of Aguiguan that shares a similar history of habitat degradation (Berger et al., 2005). In particular, we sampled in an area of native forest of approximately 0.5 km² that was historically browsed by goats and areas that had no history of goat browsing. We used a generalized linear model with a Poisson distribution to relate forest seedling counts to goat presence.

Goats might also indirectly affect bats through preferential browsing, which can affect habitat structure (Larkin et al., 2012). The proportional abundance of plant species can reflect their relative palatability to herbivores (Parsons et al., 1997), and changes in

habitat structure owing to browsers can influence vertebrate species presence (e.g., Piana and Marsden, 2014). On Aguiguan, species of seedlings that appear frequently have been presumed unpalatable to goats (Esselstyn et al., 2002), but measurements of forest structure beyond height and trunk diameter have not been reported. Habitat structure is relevant to managing *E. s. rotensis* because dense vegetation can hinder bat maneuverability (Muller et al., 2012) and prey detection (Arlettaz et al., 2001). *E. s. rotensis* wings are long and have above average aspect ratio and low wing loading, which suggests slow hawking in open spaces (Norberg and Rayner, 1987). Therefore, bats might avoid areas within forests where goat browsing has favored growth of plants that create high structural complexity (hereafter, clutter) (Brigham et al., 1997).

To determine relative preferences of tree vegetation for goats, we performed a cafeteria experiment (i.e., free-choice feeding) on 10 captive goats from the feral population on Aguiguan using leaves of three dominant native forest tree species, *P. grandis*, *C. ramiflora*, and *G. mariannae*. We chose these species because a previous vegetation survey (Esselstyn et al., 2002) suggested that *C. ramiflora* and *G. mariannae* dominate the small tree size classes because goats do not eat them and that other species (e.g., *P. grandis*) have low regeneration because goats eat them. We determined the percentage of each species of leaves remaining at the end of each trial, then coded the percentage as follows: 4=75-100%, 3=50-75%, 2=25-50%, 1=0-25%. We used a hierarchical Bayesian model to compare consumption of the three tree species by goats, where the percentage of each tree species leaves remaining after each trial was modeled as a multinomial distribution described with a theta prior (Fordyce et al., 2011).

To determine if habitat structure is related to bat activity, we recorded vegetation characteristics at each native forest site within 15 m of the acoustic detector. In particular, we used measurements of *P. grandis*, *C. ramiflora*, and *G. mariannae* (the three species used in the cafeteria experiment above) to estimate relative amounts of clutter at three-meter height intervals. Because these trees vary in densities and branching heights, we expected that bat activity would reflect clutter amount owing to preferential goat browsing. In particular, we predicted that bat activity would be low at locations with high amounts of *G. mariannae* because we have observed that this species creates high clutter in the forest understory relative to the other two tree species. We calculated Spearman's rank

correlation coefficient to determine the relationship between bat activity and habitat structure (Table A7) (R package “coin”, Hothorn et al., 2008).

Results and Discussion

Do bats behave differently in lantana shrub than in native forest, and what factors account for this pattern?

Bats were more active in native forest than lantana shrub (probability of recorded calls in native forest>lantana shrub=0.993; Table II.2.; Figure II.3.), though bats were not detected at every native forest site (Figure II.4.). Considerable differences in bat activity across native forest sites support the hypothesis that within-habitat structure is an important consideration for species management (Sharma et al., 2005). Bats were relatively inactive in lantana shrub when temperature was high ($\rho=-0.198$, $P=0.009$; Table II.3.) and wind was strong ($\rho=-0.199$, $P=0.006$). Strong winds likely inhibit bat navigation in lantana shrub, and inactivity during the high temperatures (relative to nightly averages) at dusk and dawn likely indicates retreat into the cover of forest. Given this interpretation, microclimate seems a reasonable explanation for low bat activity in lantana shrub. Contrarily to Gorresen et al. (2009), we found no strong correlation between bat activity and distance to known roosts ($\rho=-0.007$, $P=0.993$). Moreover, elevation was not related to activity ($\rho=-0.282$, $P=0.369$), which indicates bats are not limited in their distribution across Aguiguan.

Overall insect abundance was higher in native forest than lantana shrub ($P(\text{native forest} > \text{lantana shrub}) > 0.99$; Table II.2.; Figure II.5.), and habitat explained 29% of variation in insect community composition ($F_{1,16}=4.049$, $P=0.015$). Given their variety of insect prey (Valdez et al., 2011), we assume that *E. s. rotensis* will pursue flying insects that are the appropriate size for the bat to handle. Median body length of all insects captured was 4.5 mm (range 1-16 mm), likely the size of insects consumed by *E. s. rotensis* given its <7 g body weight (Wiles et al., 2011).

There were more dipterans, hymenopterans, microlepidopterans, and neuropterans in native forest (all $P(\text{native forest} > \text{lantana shrub}) > 0.900$, respectively; Table II.2.), but more isopterans in lantana shrub ($P(\text{native forest} < \text{lantana shrub}) = 0.933$). High abundances of hymenopterans and microlepidopterans in native forest, where bats are most active, concur with an earlier study showing that these insects make up a large

volume of the bat's diet (Valdez et al., 2011). Although only a small percentage of their diet consisted of dipterans, it is possible that bats eat a larger volume of these, but soft bodies are not easily located within the bats' feces (Dickman and Huang, 1988). There was no difference between habitats in beetle numbers though they were frequent in bat fecal pellets. Additional studies on the diet of bats, seasonal variation of insect abundances, and plant-insect interactions will elucidate possible indirect impacts of changes in forestation on bats via declines of tree species important to the bat's particular phytophagous prey.

We recorded 83 feeding buzzes (i.e., a rapid number of call pulses within a short period that indicates a bat encountering prey; Griffin et al., 1960), 92% of which were in native forest. We found a moderate positive correlation between bat activity and insect abundance ($\rho = -0.566$, $P < 0.001$). Forty-five percent of variation in bat calls was explained by habitat ($F_{1,16} = 15.269$, $P = 0.001$; Table II.4.; Figure II.6.) with call duration correlating positively with lantana shrub (Figure II.7.), but we failed to detect a relationship between call parameters and insect abundance ($R^2 = 0.08$, $F_{1,16} = 2.867$, $P = 0.093$). We interpret these results to suggest that habitat is a stronger driver of *E. s. rotensis* behavior than is insect abundance. Accordingly, the correlation between bat activity and insect abundance might reflect a corresponding reliance on native forest microclimate (Peng et al., 1992).

Does native understory cover indicate goat browsing, and is bat activity related to the structural complexity of native forest?

Our results show that the understory of Aguiguan has very few seedlings compared to both historically browsed and unbrowsed native forests on Tinian ($X^2 = 352.38$, $df = 1$, $P < 0.001$; Table II.5.), which suggests that goats limit regeneration of vegetation on Aguiguan. Although we did not confirm the species of seedlings, previous studies show that most seedlings in Aguiguan's native forest are *G. mariannae* and *C. ramiflora* (Esselstyn et al., 2002). Curiously, *G. mariannae* has very high and *P. grandis* has very low densities in native forest understory across Guam and the CNMI regardless of browsing history (Mueller-Dombois and Fosberg, 1998). Moreover, anecdote and aerial photographs suggest that the perimeter of native forest has not receded despite heavy understory browsing by goats.

Goats strongly preferred *P. grandis* and *C. ramiflora* foliage (low clutter tree species) over that of *G. mariannae* (high clutter tree species) ($P(P. grandis > G. mariannae) > 0.99$, $P(C.$

ramiflora>*G. mariannae*)=0.997, $P(P. grandis > C. ramiflora)$ =0.76; Table II.6.). Bat activity correlated negatively with total stem count ($\rho=-0.812$, $P=0.073$) and positively with average canopy height ($\rho=0.998$, $P=0.006$), but there was no relation to tree species except for one anomaly (*C. ramiflora* crown volume 3-6 m ($\rho=-0.841$, $P=0.043$); Table II.7.). This is consistent with our hypothesis that bats are more active in less cluttered forests (Gorresen et al., 2009), but not that they are affected by the clutter of particular tree species. The lack of an effect suggests that other processes are the main determinants of habitat structure on Aguiguan, or that there is a complicated interplay between goat browsing and natural disturbance on forest dynamics (e.g., Rojas-Sandoval et al., 2014). Nevertheless, because *E. s. rotensis* forages in spaces with low clutter, processes that reduce availability of open forest decrease the amount of suitable bat foraging habitat.

Conclusion

To improve management of endangered species, a first step is to identify and alleviate ongoing threats. Although indirect impacts of invasive species on native populations are plausible in many cases, most proposed consequences of invasion lack supporting research. Our results indicate that indirect impacts of lantana on the population of *E. s. rotensis* have been underestimated. Bats are largely inactive in lantana shrub, where the microclimate is harsh and prey are scarce, making remaining tracts of Aguiguan's native forest a vital resource. Although goats can be strong drivers of habitat change, it is unlikely that browsing alone will cause native forest to disappear. By contrast, if lantana impedes growth of native trees, the extent of forested habitat on Aguiguan might gradually recede, making lantana spread a concern beyond the context of *E. s. rotensis* conservation. Because the range of *E. s. rotensis* is currently limited to Aguiguan, declines of the population's carrying capacity owing to a lack of suitable resources might lead to demographic and genetic problems associated with small population size (e.g., Shaffer, 1981).

Conservation assessments for *E. s. rotensis* advise that goats should be eradicated in order to conserve bat habitat (Berger, 2005). Still, it is unclear how goats alter Aguiguan's native forest aside from reducing understory vegetation, because forested habitat remains despite high goat densities over the past 200 years. Aguiguan's jurisdictional authority strongly enforces regulations to preserve the goat population, making permanent removal

of goats unlikely without substantial evidence of harm to endangered fauna. No management strategies have been implemented for removing or managing lantana on Aguiguan, even though lantana is considered a serious pest in similar environments (Day et al., 2003). We support removal of goats, as this would undoubtedly lead to an increase in native vegetation (e.g., Kessler, 2011), but we insist that lantana should also be managed and subsequent reforestation should be attempted in order to restore *E. s. rotensis* habitat on Aguiguan.

Though the notion is untested, goats might negatively affect native vegetation and facilitate lantana spread because goats do not browse lantana (“indirect mutualism” in Wootton, 1994). In fact, a study on plant community succession found that lantana persisted longer in cleared plots with subsequent goat browsing than without (Larkin et al., 2012). We recommend long-term goat exclusion plots to characterize the regrowth of vegetation, and to examine if regeneration of native species is possible in lantana shrub if goats are absent. Additionally, wildlife managers should limit disturbances that might favor lantana spread. Multiple invaders within a community can affect the assemblage of native communities and alter interactions among native species (Kuebbing et al., 2013). Investigating interactions between common invasives species, like goats and lantana, will undoubtedly have broad relevance to invasion biology and conservation management.

We have found that indirect effects of an exotic plant and vertebrate herbivore might jeopardize long-term persistence of an endemic, endangered bat. The ubiquity of invasion by feral goats and *Lantana camara* makes our study relevant to conservation biology worldwide, and adds to the burgeoning topic of indirect effects. More generally, we contend that scientists should more frequently examine indirect effects of invasive species on threatened taxa.

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Appendix A: Figures

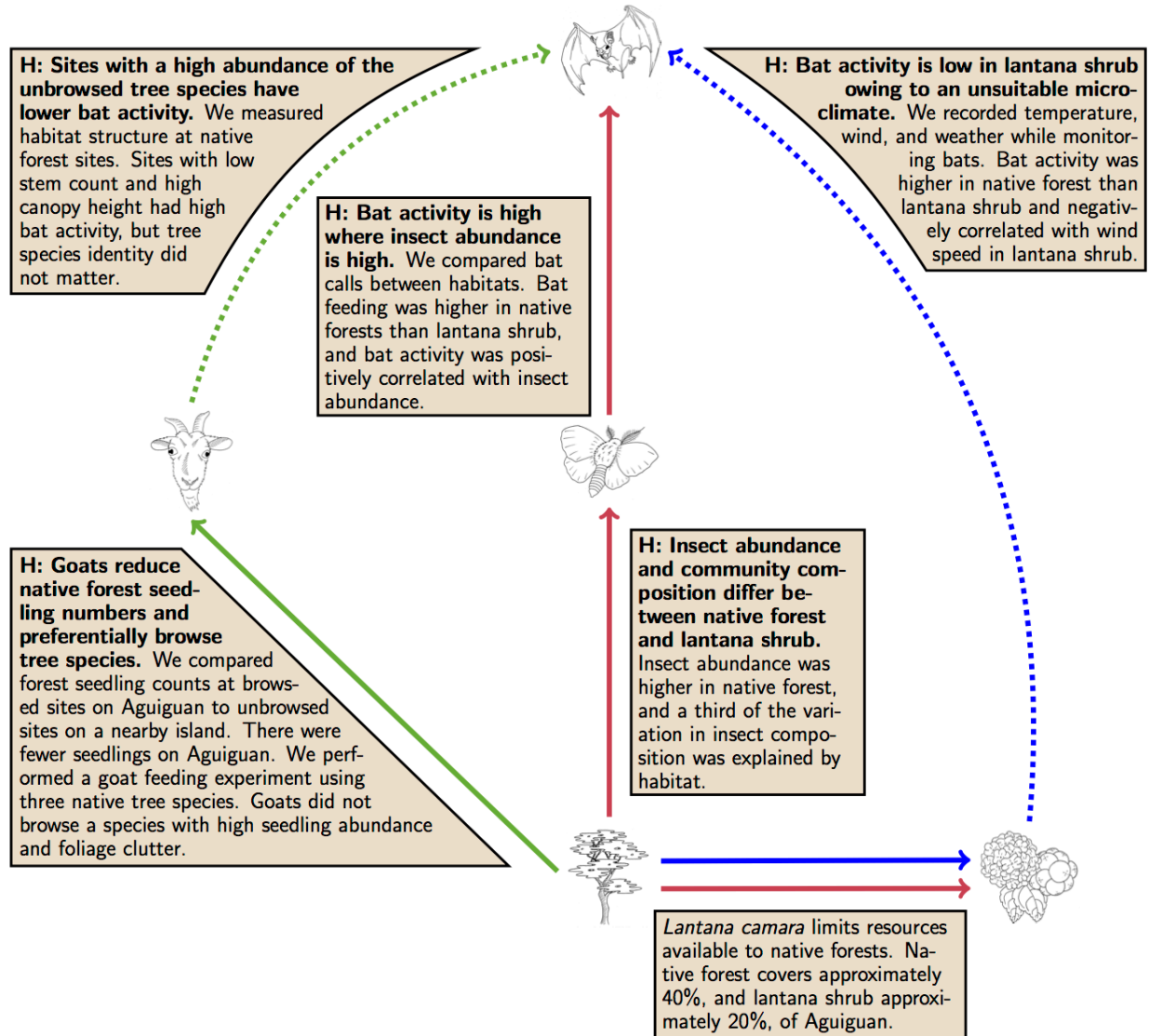


Figure II.1. Hypotheses for the indirect effects of invaders, feral goats and *Lantana camara*, on *Emballonura semicaudata rotensis*. Dashed lines signify indirect interactions and solid lines signify direct interactions. The arrow points to the resource user. The red path shows an interaction chain: lantana reduces native forest, which affects insect abundance and composition, which affects bat behavior. The blue path shows another interaction chain: lantana reduces native forest, which affects bat behavior. The green path shows exploitative competition: preferential browsing by goats change the structure of native forest, which affects bat activity.

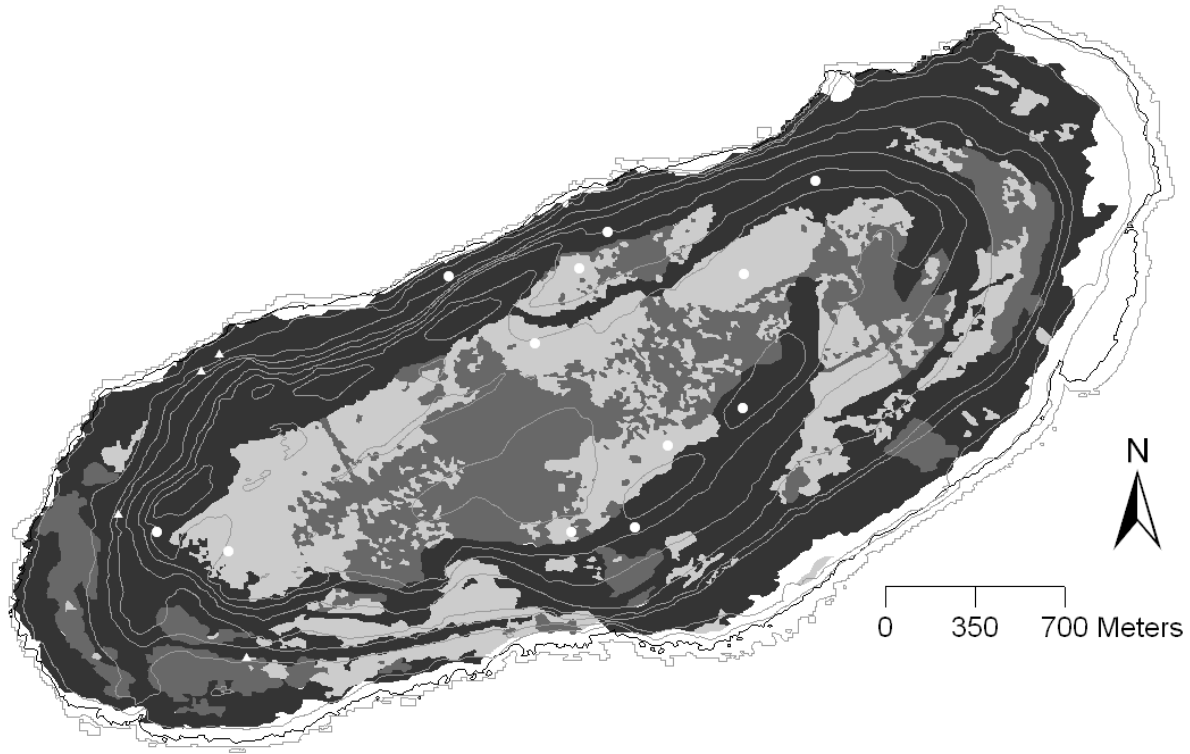


Figure II.2. A map of Aguiguan Island, CNMI (Amidon, 2009). We illustrate three habitats: native forest (dark shade), non-native forest (medium shade), lantana shrub (light shade). Thin, white lines show topographic contour. Three white triangles denote the most important caves for bat roosting. White circles signify acoustic stations and insect sampling sites.

Appendix B: Supplementary Methods

Acoustic Sampling

To measure bat activity we set up a SM2BAT+ acoustic detector (Wildlife Acoustics) and extended an omnidirectional microphone 3 m in the direction of the most contiguous patch of the habitat being sampled. In native forest, we directed the microphone towards closed-canopy flyways, and we cleared vegetation within 0.5 m of the microphone to decrease attenuation of recordings. Acoustic detector settings are listed in Table II.1. During analysis, we assumed each detection was an independent event correlated with habitat suitability and that the probability of detecting a bat, if one was present, was equal across sites.

We uploaded recordings to SonoBat Batch Scrubber v5.1 (Wildlife Acoustics) and discarded call files with less than “tolerant” quality or signals that were less than 20 kHz. We listened to each recording three times and averaged the number of audible call pulses (i.e., individual call pulses within a single bat pass). We discarded recordings with fewer than two call pulses and counted feeding buzzes (i.e., a rapid number of call pulses within a short period that indicates a bat encountering prey; Griffin et al., 1960) as one pulse. We quantified call parameters using SonoBat SonoBatch v3.05 (Wildlife Acoustics), and parameterized up to 10 calls with at least 0.8 quality per call file.

We used a hierarchical Bayesian model where the number of bat calls recorded in each habitat was modeled as being drawn from a binomial distribution described with parameter p . When it was applicable, we chose a Bayesian model over standard parametric and non-parametric methods in order to model response variables as a binomial or multinomial distribution with unique parameter values. The model estimated the parameters using 50,000 Markov chain Monte Carlo (MCMC) generations following a burn-in of 1,000 generations (Fordyce et al., 2011). We used the Deviance Information Criterion (DIC) to evaluate data fit to the models. Outputs of the models were examined for adequate mixing, and differences among models were considered negligible if DIC scores were within 2.0 points.

To elucidate if intrinsic habitat factors or insect availability drives bat activity, we performed a redundancy analysis (RDA) to relate bat behavior, as measured by call characteristics, to habitat and insect abundance (R package “vegan”, Oksanen et al., 2012).

We tested the relationship using standard bat call parameters (e.g., see Gannon et al., 2004): call duration, characteristic frequency, bandwidth, frequency at maximum power, and slope of the knee to the characteristic frequency. We also performed an ANOVA permutation test to determine the significance of the joint effect of constraints for the RDA (R package “vegan”, Oksanen et al., 2012).

Insect Sampling

We sampled insects during bat acoustic monitoring using a miniature blacklight trap (John W. Hock Co.) and an aerial malaise trap with a bottom collector (MegaView Science Co.) approximately 50 m from the acoustic detectors. We powered the blacklight trap and installed the plastic collectors in malaise traps at 17:30 and retrieved the catch at 06:30 the following morning. We identified insects at least to order and calculated abundance and richness for each night. We also measured body length of each insect to the nearest millimeter and calculated average body length.

We performed an ANOVA permutation test to determine the significance of the joint effect of constraints for the distance-based redundancy analysis (R package “vegan”, Oksanen et al., 2012). We used Spearman’s test of independence for the relationship between AI and insect abundance at each site pair to approximate a p-value using resampling (R package “coin,” Hothorn et al., 2008).

Site Characteristics

To measure environmental conditions at each site we installed an iButton Hygrochron Datalogger (Maxim Integrated) on the acoustic detector and recorded temperature and humidity every half hour during nightly sampling. We averaged temperature for each sampling hour at each site. Cloud cover was coded as follows: 0 = less than 1/8 coverage, 1 = 1/8 to 2/8 coverage; 2 = 3/8 to 4/8 coverage; 3 = 5/8 to 7/8 coverage; 4 = full coverage.

We calculated Spearman’s rank correlation coefficient to determine the relationship between bat activity per hour and temperature, wind speed, and cloud cover, and we used Spearman’s test of independence for each pair to approximate a p-value using resampling (R package “coin,” Hothorn et al., 2008). We tested weather correlations separately for the two different habitat types since conditions are likely to vary in their effect given the

structure of the two habitats. We used the Holm correction to adjust the p-values of results with multiple comparisons (R package “coin,” Hothorn et al., 2008).

We recorded vegetation characteristics of each site within 15 m of the acoustic detector. We measured average canopy cover using a densitometer at four cardinal directions along the circumference of each site. We measured diameter at 130 cm (DBH130) of all trees within the sampling area. We used ArcGIS (ESRI 2011) to calculate the elevation of each site and distance of each site to the nearest cave in which bats roost.

To investigate whether bat activity was related to habitat structure at forest sites, we performed several measurements to estimate complexity (Table II.7.). We chose *P. grandis*, *C. ramiflora*, and *G. mariannae* because a previous vegetation survey (Esselstyn et al., 2002) suggested that *C. ramiflora* and *G. mariannae* dominate the small tree size classes because goats do not eat them and that other species (e.g., *P. grandis*) have low regeneration because goats eat them. *G. mariannae* is an understory tree with horizontal branching beginning near the ground. *C. ramiflora* is both an understory and overstory tree that does not branch near the ground. *P. grandis* is an overstory tree. We selected an adult of each species in the understory and/or overstory within the sampling area and used a vertical clinometer (Suunto Tandem) to measure stem and canopy height, canopy diameter across perpendicular drip lines, and DBH130, and we used these measurements to represent the three species at that site. For each of the three tree species, we estimated canopy volume as a cylinder between 0-3 m, 3-6 m, 6-9 m, 9-12 m, and >12 m to account for clutter at multiple forest heights (see Avina et al., 2007; O’Keefe, 2009). We calculated minimum crown volume at each vertical height interval by combining each canopy volume estimate. We then calculated the proportion of the total minimum crown volume provided by each tree species at each height for each site. We used Spearman’s rank correlation coefficient to determine the strength of the relationships between AI and raw values of each predictor variable listed in Table II.7. that had measurements for at least three sites, and we used Spearman’s test of independence for each pair to approximate a p-value using resampling (R package “coin,” Hothorn et al., 2008).

Seedling Counts

Tinian is a populated island approximately 8 km NE of Aguiguan that shares a similar history of habitat degradation (Berger et al., 2005). During early 2005, approximately 0.4 km² of relatively undisturbed native forest on Tinian was designated a free-roaming animal enclosure. The area enclosed over 300 goats and a few deer, peacocks, turkeys, chickens and pheasants. Late in 2009, the sanctuary was closed and all animals were harvested. We considered this native forest to be historically browsed by goats and counted seedlings at 10 accessible locations. In addition, we counted seedlings at 10 sites within Tinian's native forest habitat that, according to locals, had no history of heavy goat browsing.

Goat Feeding Trial

We collected leaves from *P. grandis*, *C. ramiflora*, and *G. mariannae* in a similar environment just before the trial to ensure vegetation was fresh. The owner of the goats had not used these plant species as fodder for the goats, which were not provided fodder for six hours prior to the experiment. Because the leaves were different shapes and sizes, we used a flat, rectangular surface to measure equal amounts of leaves for each species. We randomly placed leaves of each species in a pile on the ground before each individually restrained goat. We monitored each goat for 25 minutes and noted which leaves were consumed. We estimated the proportion of leaves remaining at the end of the trial for each goat, then coded the percentage as follows: 4=75-100% remaining, 3=50-75% remaining, 2=25-50% remaining, 1=0-25% remaining.

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Appendix C: Supplementary Tables and Figures

Table II.1. SM2BAT+ acoustic detector settings.

option	setting
microphone filter	1000 kHz
microphone gain	+24.0 dB
sample rate	192,000 samples/second
digital high pass filter	fs/12 (filter <16,000 kHz)
trigger level	+6 dB
trigger window	2.0 seconds
recording duration	nightly from 18:00 to 06:00

Table II.2. Results from Bayesian analyses comparing bat activity and insect abundances between native forest and lantana shrub. The last column shows one post-burn-in probability for each pair in the models, where N=native forest, L=lantana shrub.

model description	n	unconstrain	constrain	median(95% highest density interval)
bat activity	6	18.11	22.26	
native forest				0.841(0.598,0.932)
lantana shrub				0.159(0.068,0.403)
insect abundance	6	47.09	50.49	
native forest				0.770(0.607,0.882)
lantana shrub				0.231(0.118,0.393)
dipterans	6	16.98	29.85	
native forest				0.932(0.823,0.970)
lantana shrub				0.068(0.030,0.177)
hymenopterans	6	20.55	25.00	
native forest				0.789(0.591,0.905)
lantana shrub				0.211(0.096,0.409)
isopterans	6	4.55	11.20	
native forest				0.285(0.083,0.558)
lantana shrub				0.715(0.442,0.917)
microlepidopterans	6	46.82	49.37	
native forest				0.714(0.530,0.840)
lantana shrub				0.286(0.160,0.470)
neuropterans	6	-40.35	4.39	
native forest				0.864(0.593,0.963)
lantana shrub				0.154(0.037,0.407)

Table II.3. Bat activity correlations with site location and site weather.

predictor variable	Z	ρ	p-value
elevation	-0.934	-0.282	0.369
distance to nearest known roost	-0.023	-0.007	0.993
hourly temperature			
native	2.166	0.148	0.063
lantana	-2.909	-0.198	0.009
hourly wind speed			
native	-1.613	-0.110	0.206
lantana	-2.914	-0.199	0.006
hourly weather			
native	-1.718	-0.117	0.158
lantana	-1.946	-0.133	0.106

Spearman permuted p-values are shown. P-values of multiple comparisons were corrected using the Holm method.

Table II.4. Detailed results from the RDA between bat call parameters and predictor variables. Values show the direction and magnitude of weightings. Numbers farther from zero, regardless of sign, indicate heavier loading for a given axis. The sign on the value indicates the direction of the relationship with an axis.

RDA Axes	RDA1	RDA2
Constrained predictor variables		
A. native vegetation	1.000	-0.009
B. insect abundance	0.352	-0.936
Correlation scaling to eigenvalues		
1. call duration	-1.328	-0.108
2. characteristic frequency	0.392	-0.660
3. bandwidth	0.451	0.075
4. frequency at maximum power	0.976	-0.396
5. slope of knee to characteristic frequency	1.082	0.432

Table II.5. Results from the generalized linear model comparing seedling counts at forest locations given the history of goat presence. AG=Aguiguan native forest, TB=Tinian Browsed native forest, TU=Tinian Unbrowsed native forest.

coefficients	estimate	standard error	p-value
AG (intercept)	0.588	0.236	0.013
TB	2.433	0.246	< 0.001
TU	2.930	0.242	< 0.001

Table II.6. Results from a Bayesian analysis comparing consumption of the three tree species by goats. The last column shows one post-burn-in probability for each pair in the models, where PG=*Pisonia grandis*, CR=*Cynometra ramiflora*, GM=*Guamia mariannae*.

model description	n	unconstrain	constrain	median(95% highest density interval)
leaf consumption	10	15.99	30.82	
<i>P. grandis</i>				0.458(0.346,0.584)
<i>C. ramiflora</i>				0.380(0.264,0.494)
<i>G. mariannae</i>				0.157(0.085,0.250)

Table II.7. Correlations between bat activity and site native forest characteristics.

predictor variable	Z	ρ	p-value
basal area	-0.454	-0.203	0.699
minimum tree richness	-0.267	-0.119	0.813
canopy closure	-0.895	-0.400	0.417
average canopy height	2.204	0.998	0.006
stem count	-1.815	-0.812	0.073
<i>P. grandis</i> stem count	0.000	0.000	1.000
<i>C. ramiflora</i> stem count	-1.621	-0.725	0.125
<i>G. mariannae</i> stem count	-0.259	-0.116	0.844
proportion <i>P. grandis</i> crown volume 3-6 m	1.685	0.754	0.104
proportion <i>P. grandis</i> crown volume 6-9 m	-0.259	-0.116	0.848
proportion <i>P. grandis</i> crown volume 9-12 m	-1.485	-0.664	0.166
proportion <i>C. ramiflora</i> crown volume 0-3 m	-1.513	-0.677	0.160
proportion <i>C. ramiflora</i> crown volume 3-6 m	-1.880	-0.841	0.043
proportion <i>C. ramiflora</i> crown volume 6-9 m	-0.592	-0.265	0.583
proportion <i>G. mariannae</i> crown volume 0-3 m	1.513	0.677	0.153
proportion <i>G. mariannae</i> crown volume 3-6 m	1.556	0.696	0.145

Spearman permuted p-values are shown. P-values of multiple comparisons were corrected using the Holm method.

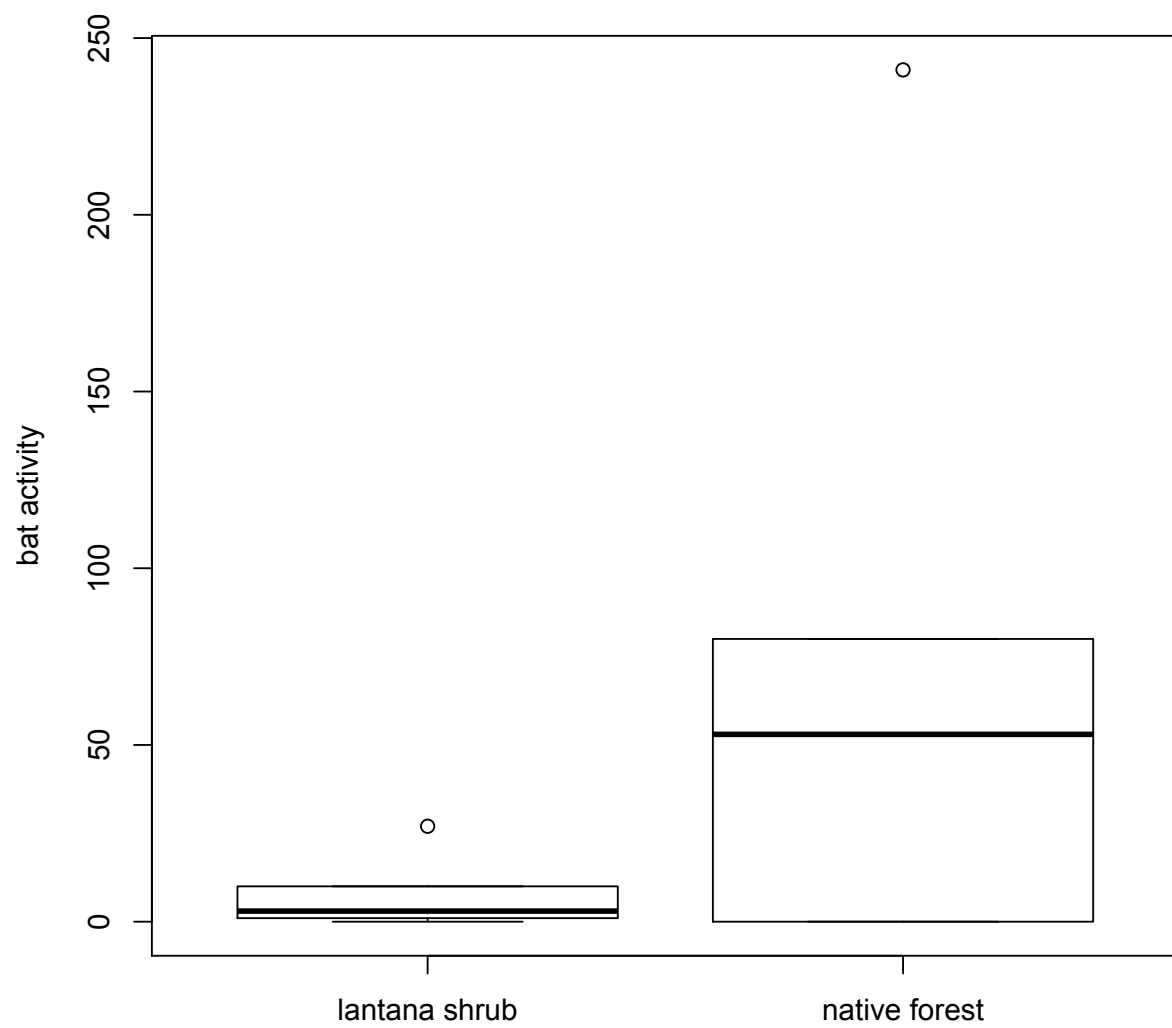


Figure II.3. Total bat activity at paired sites within two habitats.

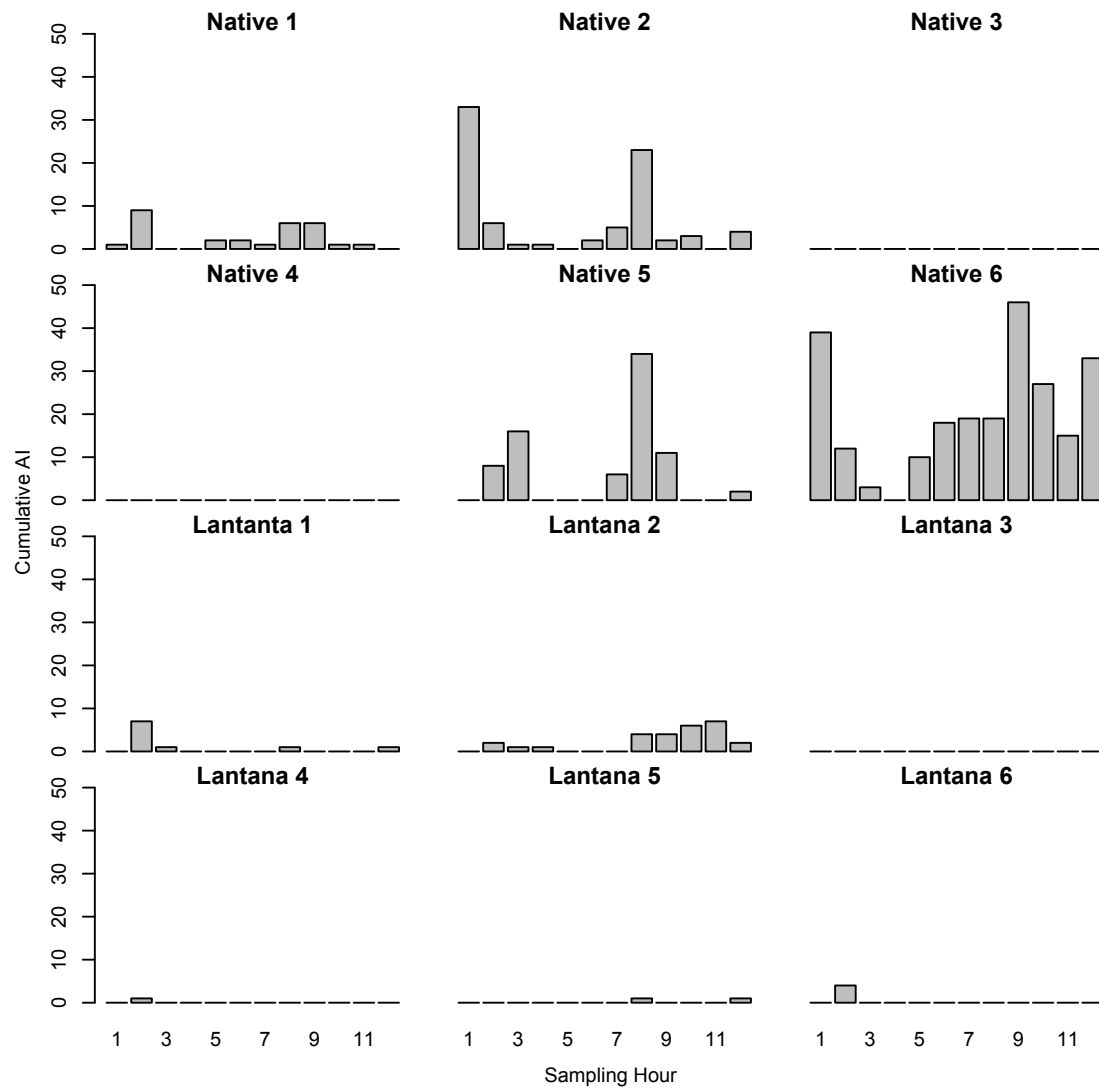


Figure II.4. Total bat activity at each site throughout the sampling period.

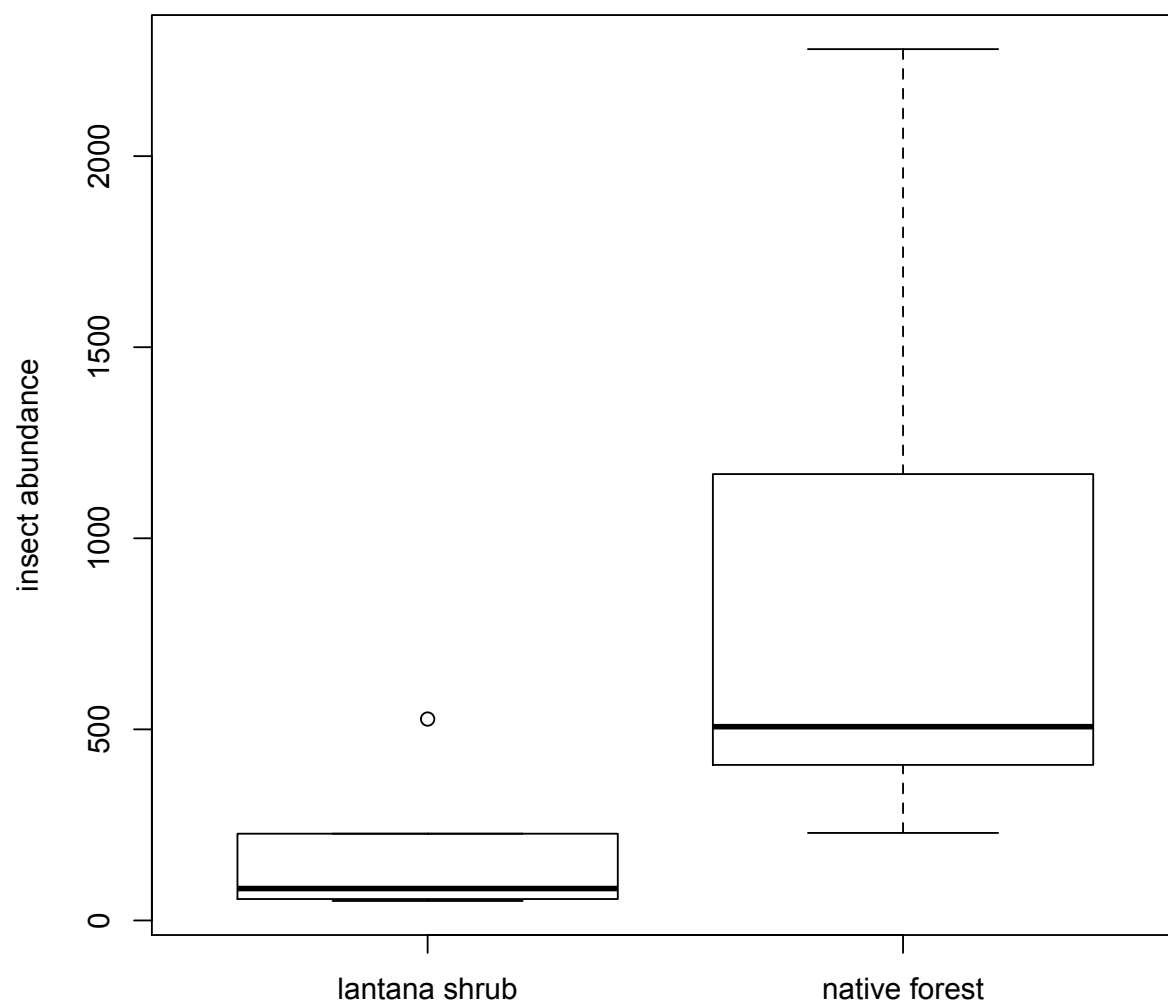


Figure II.5. Total insect abundance at paired sites within two habitats.

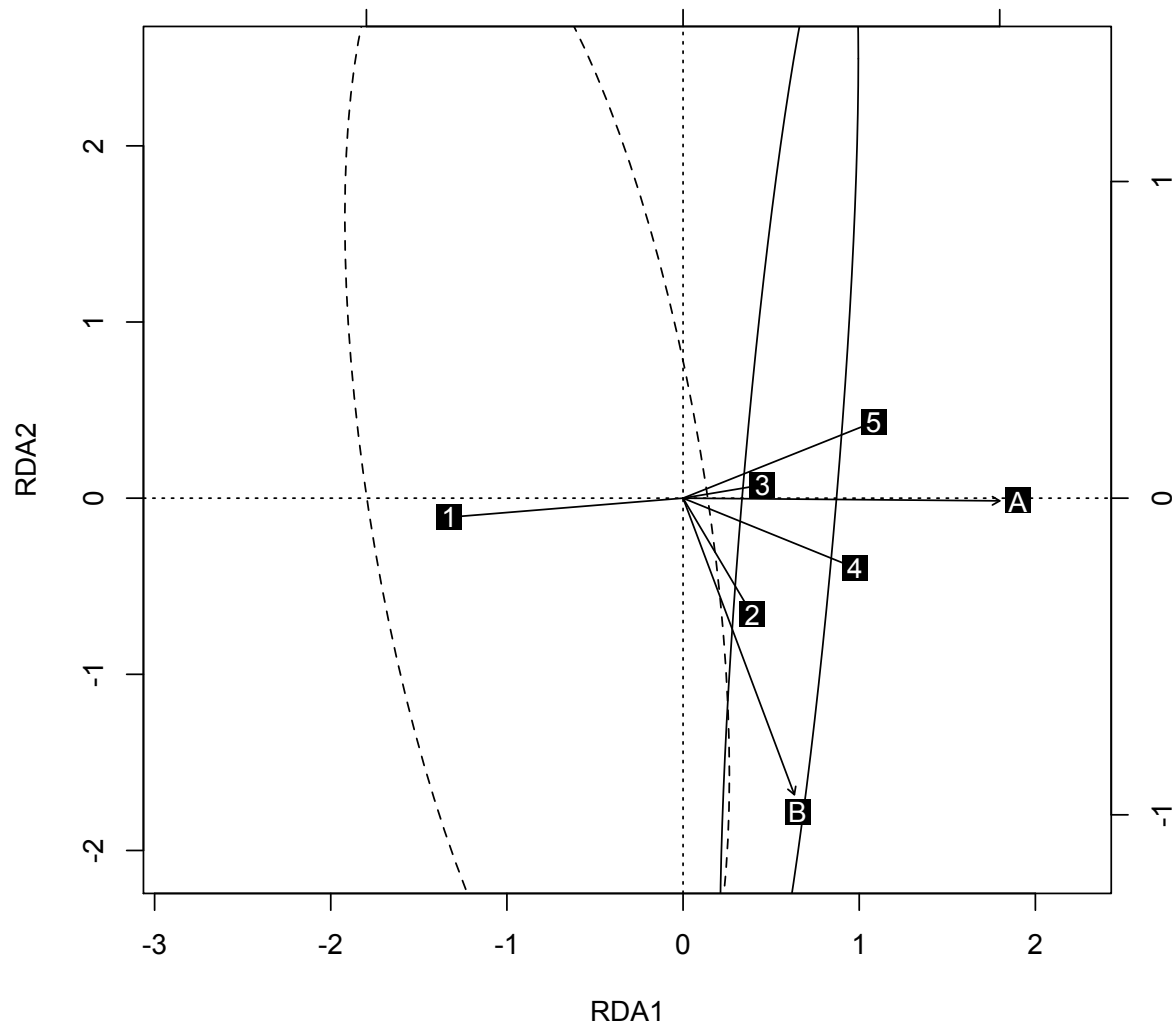
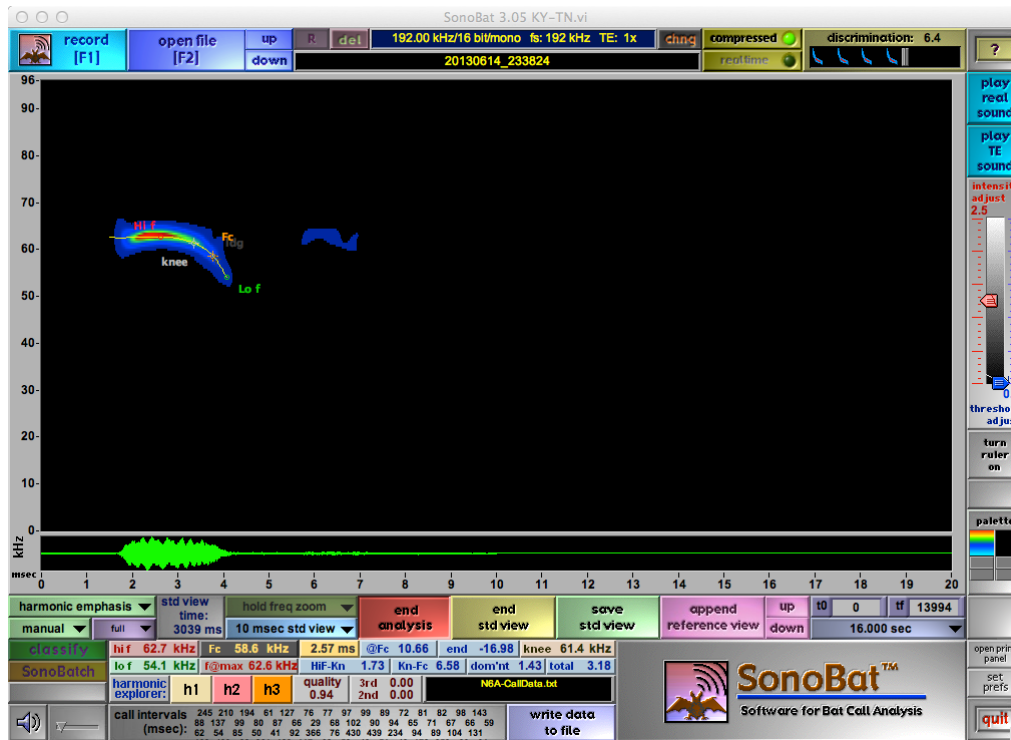


Figure II.6. The correlations between bat call parameters and predictor variables with two canonical axes. Ellipses show the 95% confidence intervals for bat calls recorded in native forest (solid) and lantana shrub (dashed). Response variables: 1. call duration, 2. characteristic frequency, 3. bandwidth, 4. slope of knee to characteristic frequency. Predictor variables: A. native habitat, B. insect abundance. The angles between response and predictor variables, and between response variables themselves or predictor variables themselves, reflect their correlations.

A.



B.

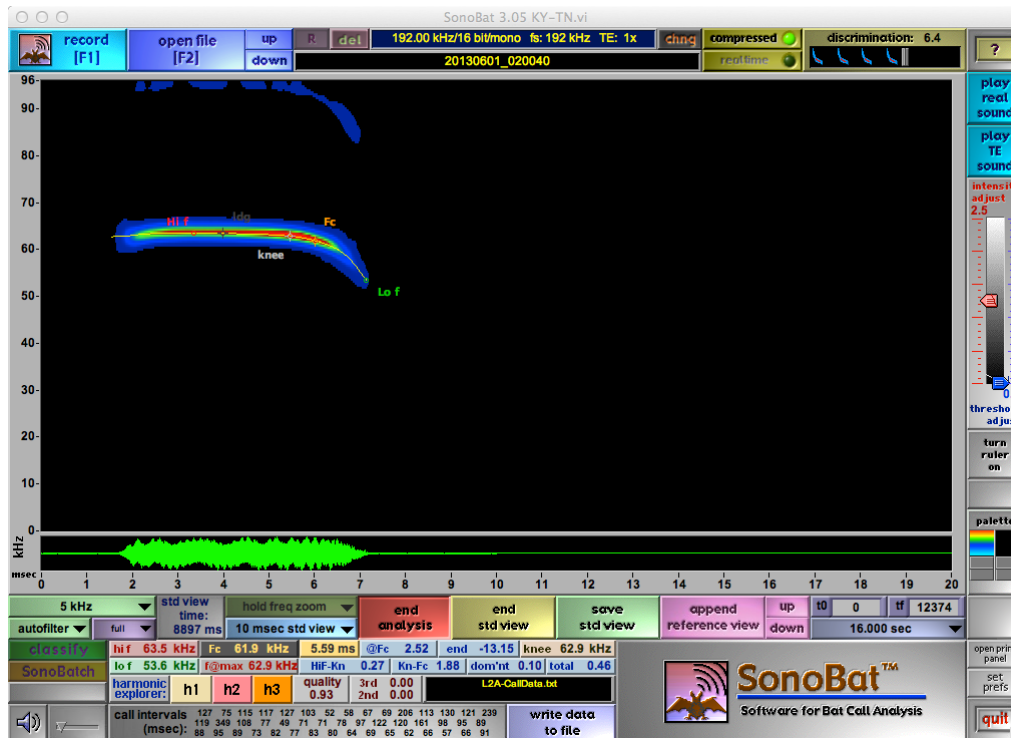


Figure II.7. Examples of bat call duration and bandwidth. **A.** Native forest. **B.** Lantana shrub.

CHAPTER III
Prioritizing bats for research effort

Abstract

Limited resources combined with growing species endangerment have motivated prioritization of conservation actions. Prioritization schemes that focus on species-level conservation generally agree that resources should be distributed according to vulnerability of extinction, but the irreplaceability of species' genetic value has become a prominent concern. According to the IUCN Red List of Threatened Species, 17 percent of bat species are data-deficient and 55 percent have unknown population trends, indicating a dearth of knowledge. In this study, I describe the state of academic literature ("research effort") for most of the bat clade and report publication intensity among broad research topics. I used phylogenetic linear regression and two phylogenetic models of evolution to uncover individual correlates of research effort, and I provide a ranking of bat species for research effort according to vulnerability and irreplaceability. My results can be incorporated into Biodiversity Action Plans to inform conservation biologists and funders of species with high research need.

Introduction

Biodiversity has been lost at an alarming rate over the past century (Regan et al., 2001), and human-induced global change is escalating species endangerment (Thomas et al., 2004). An inclusive understanding of all taxa would aid conservation, but the magnitude of the crisis (James et al., 2001) limits the resources available to invest in species research. Accordingly, biologists have begun to describe patterns of research effort by approximating the number of relevant peer-reviewed publications referenced in research databases (Lawler et al., 2006). Many studies document the mismatches between metrics of publication and areas of species conservation concern, including vulnerability and irreplaceability.

Research effort has not been distributed evenly among vulnerable taxa. In a strategy known as conservation triage (Arponen, 2012), the most endangered species should receive conservation resources first. But in carnivores, 62 percent of the most published species were globally non-threatened (Brooke et al., 2014). Trends like these are found even within smaller taxonomic units. A literature search to examine how research was allocated across Felidae found that the amount of research afforded to species was positively related to body size, not extinction risk (Brodie, 2009).

The incorporation of evolutionary history into conservation prioritization concedes the irreplaceability of species and the need to preserve the biological information they contain (Redding and Mooers, 2006). Measures of taxonomic distinctiveness (Barker, 2002, Isaac et al., 2007) quantify the amount of evolutionary history provided by a taxon of interest, where extinction of old, rare clades results in greater losses of unique evolutionary history (Purvis et al., 2000). Neither have taxa been researched equally across the tree of life. Most insect clades are understudied, except for charismatic groups like moths and butterflies (Clark and May, 2002). In a review of over 32,000 entries from 1979 to 1998, researchers found that mammals had ten times more published papers than amphibians, even though amphibian species outnumber mammalian species (Clark and May, 2002).

Furthermore, there are spatial biases in research effort. Biomes and areas with dense human populations have received high research effort (Trimble and van Aarde, 2012), while desert, tundra, and tropical systems remain understudied (Lawler et al.,

2006). Research on mammalian extinction risk is lacking particularly in Asia and the Caribbean (Verde Arregoitia, 2016), and the most biodiverse countries are relatively understudied (Wilson et al., 2016).

The discovery of echolocation has accelerated scientists' understanding of bats, but still, 17 percent of the approximately 1,200 species in Chiroptera have unknown extinction risk owing to insufficient information on the abundance or distribution of species (IUCN, 2013). Moreover, 55 percent of bat species have unknown population trends, compared to 8 percent of the 10,000 bird species. Of 125 bats considered threatened, 118 have decreasing or unknown population trends (IUCN, 2013). Many species belong to old clades with few members, which is affirmed by the EDGE (Evolutionary Distinct and Globally Endangered) of Existence program listing ten bat species among their top 100 mammals needing conservation action (EDGE, 2013).

Here I describe the state of academic literature for most of the bat clade. I indicate factors that are correlated with research effort and which topics are studied most. I finish by providing ranked prioritization for species research based upon vulnerability and irreplaceability. Identifying the distribution of research and revealing gaps in knowledge can inform future research allocation for bats.

Methods

I compiled the bat taxonomy using Wilson and Reeder's Mammal Species of the World v.2005 (MSW05, Simmons, 2005), a more recent species taxonomy based on MSW05 (Simmons and Cirranello, 2014, dataset), and the International Union for Conservation of Nature (IUCN) Red List of Threatened Species v3.1 (hereafter, Red List; IUCN, 2013). I matched species names from each taxonomy source to pair trait data with current genomic data and to prevent repeated analyses of synonymous bats. I refer to all bats using their GenBank taxonomic names (Benson et al., 2009), because only bats included on the phylogenetic tree are included in this paper. Details on the construction of the phylogenetic tree are provided in the Methods section of Chapter IV.

Trait data were assembled from the PanTHERIA database (Jones et al., 2009), Jones et al., (2003) supplementary dataset, and the Red List v3.1 (2013) (Table III.1.). I chose variables that provided coverage for at least 30 percent of taxa on our tree. All continuous

variables were log-base-10 transformed to correct left-skewed distributions, and all variables were scaled and centered so that beta coefficients were comparable despite different units of measurement. I organized bats into five geographic regions, but I included a bat species only once in each analysis involving region. I performed all analyses in R v.3.3.1 (R Core Team).

I used all databases available through Web of Science to locate articles pertinent to each bat species. I performed a topic search for the synonyms of each bat species by listing each binary or trinomial name within quotation marks and separating synonyms using commas. I exported article information to EndNote v.X7 (Clarivate Analytics) and organized articles according to bat species. I discarded articles in figures, gene depositories, periodic news bulletins, books, book sections, patents, and unknown titles or journals.

If an article contained at least one bat synonym in the citation name, keywords, or abstract, I attempted to retrieve the associated full-text article first using the retrieve tool in EndNote, then by Google Scholar bibliographic database (<http://scholar.google.com>) or through library exchange (only post-1990). I removed extraneous pages (i.e., cover pages, journal information, etc.), literature cited sections, and overlapping portions of other articles from the full-text article of interest.

I determined which of six broad categories best described each full-text article (Table III.6.). I began by listing keywords specific to each topic. Because keyword categorization is subjective, I took 10 random papers that I believed to belong to each topic, calculated the most used words, and added them to the keyword list. Using a programming script written in language Perl 5.18 (Perl Porters), I tallied the number of each keyword used in each full-text article. Keywords were searched as global and case insensitive and could occur within words or alone. I then determined the lead and secondary topics of each full-text article based upon the highest and second highest number of keywords per category. I discarded full-text articles that had more than a two-way tie for topic. For each lead topic I report the mean number of keywords and the mean number of bat species mentioned in the full-text article.

I used phylogenetic linear regression and compared results of two phylogenetic models of evolution to determine individual correlates of research effort. I performed the

regressions using the “*phylolm*” function in the *phylolm* package (Ho and Ane, 2014). For one model, I assumed a star phylogeny (STAR), that is, I assumed no phylogenetic relationship between traits by rescaling our tree with $\lambda=0$. For the other model I assumed that traits evolve by an Ornstein-Uhlenbeck (OU) process with a stationary distribution of the ancestral state at the root (i.e., “OUrandomRoot model option”). For the OU model, I did not adjust the upper or lower bounds for the optimization of the phylogenetic model parameter. I chose the best model for each regression using the Akaike information criterion (AIC), assuming that, if the STAR model had a lower AIC value the correlate does not have significant phylogenetic signal. I performed pairwise correlations using the Spearman method between all correlates.

I prioritized bat species for research effort according to number of articles weighted by evolutionary distinctiveness, and number of articles weighted by EDGE score (Isaac et al., 2004). I used Fair Proportion measures of species branch lengths (i.e., evolutionary time) provided by the “*evol.distinct*” function of package *picante* (Kembel et al., 2010) to calculate the evolutionary distinctiveness (hereafter, ED) of each species. Fair Proportion divides the sum of branch lengths by the number of subtending species leaves (Redding 2003). I divided the number of articles (plus one to avoid zero-errors) by the calculated ED. I then ranked the results treating ties by the standard competition ranking so that ties get joint ranking. I used the EDGE method to incorporate IUCN Red List threat category into our rankings. For the EDGE method I calculated the EDGE score for each bat (Isaac et al., 2004), divided the citation number by the calculated EDGE score, and then used standard competition ranking.

Results

I collected a total of 56,989 articles. Approximately 93 percent of articles pertained to species designated non-threatened by the IUCN Red List, 5 percent to threatened species, and 2 percent to species without a threat designation (Table III.2.). A comparison of observed proportions of articles to expected proportions given equal sampling effort for all species shows that all threat categories received less research effort than expected, except for Least Concern species, which received about 29 percent more research effort than expected.

Bats belonging to the families Megadermatidae, Mormoopidae, Mystacinidae, Noctilionidae, Rhinolophidae, Rhinopomatidae, and Vespertilionidae had higher research effort than expected (Table III.3.). All other families experienced less research effort than expected, with family Cistugidae having 92 percent less.

This highest proportion of articles concerned bats that inhabit Europe (Table III.4.), which is about 36 percent more than expected given the number of species that occur in that region. Africa and North America also had higher research effort than expected, and Asia-Pacific and Latin-Caribbean bats have less research effort than expected.

I collected 5,481 full-text articles (about 10 percent of articles) eligible for topic analysis. ‘Biology’ was the lead and secondary topic for the most full-text articles, followed by ‘habitat’ and ‘systematics’ (Table III.5.). Relative to other topics, ‘population’ was the lead topic for the smallest proportion of publications, and ‘disease’ was the secondary topic for the smallest proportion of publications. This pattern is not attributed to the number of keywords pertaining to a topic, as ‘population’ and ‘biology’ have the same number of keywords, but their associated mean number of keywords per publication was different by a factor of 6 (Table III.6.). About 9 percent of full-text articles had ties for lead and secondary topic. Most full-text articles were pertinent to more than one bat, with ‘population’ having the highest number of focal species and ‘biology’ the lowest. The number of full-text articles for all lead topics showed an increasing trend over time, especially after 1990 (Figure III.1.). Figure III.2. illustrates the proportion of topics given Red List designations, region, and families. Notably, a high proportion of full-text articles for species designated DD and NE are on systematics.

For the single predictor regressions, research effort is positively related to a bat’s listing on the Action Plan and ESA, carnivory, LC extinction risk, increasing population trend, number of occupied habitats, geographic range, known number of threats, and year of bat species description (Table III.7.; Table III.8.). Research effort is negatively related to island endemism and mean PET. Bat species with increasing population trend had the highest research effort—on average, bats with increasing population trends had 426 more articles than species with stable population trends. The OU model of evolution best described 35 percent of regressions, signifying that research effort is similar for species

that share correlates. Pairwise correlations are shown in Table III.9., and significant values of rho are less than or equal to a p-value of 0.05.

The top ten ranking of bats for research prioritization based on irreplaceability alone includes *Thoopterus nigrescens* and *Barbastella barbastellus* as first and second priority, respectively, reflecting that they have low numbers of articles and deep evolutionary histories (Table III.10.). Over half the top ten bats belong either to family Phyllostomidae in the Latin-Caribbean region or to Vespertilionidae in Europe. The EDGE method, which also incorporates vulnerability, includes four species identified by the ED method. Half the bats prioritized by this method belong to family Pteropodida in the Asia-Pacific region.

Discussion

Our results show clear biases in research effort for bats. Firstly, research effort has not been distributed relative to species vulnerability. Non-threatened bats had about 14 times more research effort than threatened and unevaluated bats combined. Moreover, 19 bat species designated as least concern had research effort higher than the highest number of articles for all other designations. Secondly, bats with ranges in Europe, North America, and Africa had higher research effort than expected. The Asia-Pacific region had the lowest research effort. Thirdly, research effort was distributed unevenly across the bat clade. The family Noctilionidae had research effort 140 percent higher than expected, and only two species were included in this study. Conversely, the family Cistugidae, also with two species, had 92 percent less research effort than expected.

Full-text articles with lead topics “biology” and “habitat” were published most, and lead topics “population” and “disease” were published least. The sample of full-text articles included only 10 percent of articles, and because I included only English-language, digitized articles, the sample was likely biased towards recent publications and common journals. Nevertheless, temporal trends in the proportion of topic keywords support the general trend that information concerning bat biology is published often and bat population information infrequently.

I did not evaluate full-text articles on their conservation value for particular species. The topic “population,” however, consists of keywords associated with conservation

measures to determine risk related to population size. This information might not be published as frequently as other topics because of the difficulty in measuring population changes in bats (Racey and Entwistle, 2005), or because most academic journals do not as often publish articles that focus primarily on this information (Fazey et al., 2005). New technology could make articles pertaining to bat habitat and ecology increasingly relevant for assessments of population size, as noninvasive approaches to estimating bat abundances and richness become more popular (Waits and Paetkau, 2005).

In general, the bats in need of research most are island endemics, have small ranges, occur in tropical latitudes, have unknown population trends, and are recently described. Owing to taxonomic “splitting” (Zachos, 2013), the number of articles pertaining to newly described species might be low because relevant publications do not use the relevant species name. There is a positive correlation between the year a bat was described and geographic range. I speculate that widespread bats were both discovered early and have high research effort because they are common. The OU model of evolution best described about a third of the single-predictor regressions for research effort, suggesting species that share certain traits also have similar research effort, and that trait regressions should account for evolutionary history to avoid erroneous estimates.

Conservation strategies commonly prioritize biodiversity according to vulnerability to extinction and more often by evolutionary irreplaceability. I used the Red List designations to prioritize species for research effort according to extinction risk. Although it is not intended for conservation prioritization, conservation planners regularly employ the Red List evaluation of extinction risk (Hoffmann et al., 2008). The measure of ED used here is the same used by the EDGE of Existence program, so I used the EDGE scoring method (EDGE, 2013) to prioritize species for research effort according to genetic distinctiveness of species (May, 1990). These two prioritization schemes can offer conservation organizations guidance on where to invest research funding.

Bat conservation is especially important because the diverse clade serves as pollinators, seed dispersers, predators, and prey in their natural habitats (Simmons and Conway, 2003) and might serve as bioindicators of environmental stressors (Jones et al., 2009c). Given the uncertain persistence of many bat species, appropriate scientific research must fill gaps in knowledge that could lead to effective conservation. However, a

review of Southeast Asian fruit bats showed that the majority of published research was focused on species considered non-threatened (Mildenstein, 2013), and studies conducted on threatened species lacked content relevant to species conservation. One suggestion to improve the conservation value of results presented here is to determine research effort particularly for at-risk bat populations, especially within protected areas where this is a higher probability of recovery.

This research contributes to recent efforts to direct attention towards understudied taxa and to identify neglected topics. My prioritization scheme for research effort can assist attempts to quickly apportion conservation resources towards species most in need and with high evolutionary value. Without research effort distributed across taxa, however, allocation of resources could neglect critical interests to our understanding of biodiversity.

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Appendix

Table III.1. Sources and descriptions of data used in this study.

source	variable	definition
PanTHERIA	geographic range area (km ²)	total extent of a species range from Sechrest 2003 ¹
	human population density mean (persons/km ²)	using the 1995 Gridded Population of the World ²
	potential evapotranspiration rate (PET) mean (mm)	monthly measures from 1920-1980 using Global Resource Information Database of UNEP ³
	trophic level	herbivore, omnivore, carnivore
Jones et al., 2003	aspect ratio	wingspan squared divided by wing area
IUCN Red List	actions	number of recognized conservation actions needed
	clade	Yinpterochiroptera, Yangochiroptera
	habitats	number of occupied habitat categories
	island endemism	observed only on islands, excluding Australia
	region	Asia-Pacific, Africa, Latin America-Caribbean, Europe, North America
	population trend	unknown, decreasing, stable, increasing
	threat category	critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), data deficient (DD), not evaluated (NE)
	threats	number of recognized threat categories
Simmons and Cirranello, 2014	Action Plan	recognized by the IUCN/SSC Bat Action Plan ^{4,5}
	CITES	listed on CITES ⁶
	ESA	listed on the Endangered Species Act ⁷
	years since described	year 2013 minus the year the bat species was first described

¹ Sechrest, 2003. Global diversity, endemism and conservation of mammals. University of Virginia, Charlottesville, Virginia, USA.

Table III.1. *Continued.*

² CIESIN, CIAT, 2005. Gridded Population of the World Version 3 (GPWv3): Population Grids. SEDAC, Columbia University, New York, New York, USA.

³ UNEP. 2009. The UNEP Environmental Data Explorer, as compiled from CSIRO Marine and Atmospheric Research . United Nations Environment Programme. <http://ede.grid.unep.ch>.

⁴ Mickleburgh, Hutson, Racey, 1992. Old World fruit bats: An action plan for their conservation. Gland, Switzerland.

⁵ Hutson, Mickleburgh, 2001. Microchiropteran bats: global status survey and conservation action plan. Gland, Switzerland.

⁶ U.S. CITES Appendices I, II, III. <https://cites.org/eng/app/appendices.php>

⁷ U.S. Congress, 1973. "Endangered Species Act." Washington D.C.

Table III.2. Proportion and number of species and articles for each Red List threat category. The fourth column shows the percent deviation between the observed and expected proportion of articles, assuming equal research effort for all species.

Red List threat category	species: proportion (number)	articles: proportion (number)	deviation from expected proportion
insufficient data	0.142 (112)	0.022 (1244)	85% less
NE	0.075 (59)	0.011 (614)	86% less
DD	0.067 (53)	0.011 (630)	84% less
not threatened	0.751 (593)	0.933 (53180)	24% more
LC	0.677 (535)	0.873 (49754)	29% more
NT	0.073 (58)	0.060 (3426)	18% less
threatened	0.108 (85)	0.045 (2565)	58% less
VU	0.068 (54)	0.029 (1645)	58% less
EN	0.027 (21)	0.014 (779)	49% less
CR	0.013 (10)	0.002 (141)	80% less

Table III.3. Proportion and number of species and articles for each family. The fourth column shows the percent deviation between the observed and expected proportion of articles, assuming equal research effort for all species.

clade	species: proportion (number)	articles: proportion (number)	deviation from expected proportion
Yinpterochiroptera	0.227 (179)	0.212 (12078)	6% less
Craseonycteridae	0.001 (1)	0.0006 (35)	51% less
Hipposideridae	0.063 (50)	0.029 (1625)	55% less
Megadermatidae	0.004 (3)	0.008 (459)	112% more
Pteropodidae	0.149 (118)	0.096 (5463)	36% less
Rhinolophidae	0.068 (54)	0.072 (4105)	5% more
Rhinopomatidae	0.004 (3)	0.007 (391)	81% more
Yangochiroptera	0.773 (611)	0.788 (44911)	2% more
Cistugidae	0.003 (2)	0.0002 (12)	92% less
Emballonuridae	0.053 (42)	0.023 (1338)	56% less
Furipteridae	0.001 (1)	0.0004 (25)	65% less
Miniopteridae	0.027 (21)	0.016 (925)	39% less
Molossidae	0.062 (49)	0.056 (3179)	10% less
Mormoopidae	0.010 (8)	0.0177 (1009)	75% more
Mystacinidae	0.001 (1)	0.002 (131)	82% more
Myzopodidae	0.003 (2)	0.0005 (28)	81% less
Natalidae	0.010 (8)	0.003 (199)	66% less
Noctilionidae	0.003 (2)	0.006 (319)	121% more
Nycteridae	0.009 (7)	0.005 (292)	42% less
Phyllostomidae	0.203 (160)	0.157 (8966)	22% less
Thyropteridae	0.004 (3)	0.002 (99)	54% less
Vespertilionidae	0.323 (255)	0.498 (28389)	54% more

Table III.4. Proportion and number of species and articles for each world region. The fourth column shows the percent deviation between the observed and expected proportion of articles, assuming equal research effort for all species. The sum of the number of species and articles are greater than 790 and 56,989, respectively, because 233 species occur in two or more regions.

region	species: proportion (number)	articles: proportion (number)	deviation from expected proportion
Africa	0.190 (195)	0.221 (21149)	17% more
Asia-Pacific	0.250 (257)	0.117 (11207)	53% less
Europe	0.179 (184)	0.244 (23325)	36% more
Latin-Caribbean	0.233 (240)	0.221 (21082)	6% less
North America	0.148 (152)	0.197 (18803)	33% more

Table III.5. Proportion and number of full-text articles for each primary and secondary topic. The last row reports the total number of ties between lead topics and secondary topics. The fourth column shows the mean proportion and number of keywords per topic for all full-text articles. The last column shows the mean number of bat species included in the full-text article topic, abstract, or keywords.

topic	lead topic: proportion (number)	secondary topic: proportion (number)	mean keywords: proportion (number)	mean focal bat species
biology	0.368 (2019)	0.271 (1451)	0.532 (49)	1.635
disease	0.096 (527)	0.033 (177)	0.020 (2)	1.795
ecology	0.105 (578)	0.115 (616)	0.148 (14)	1.822
habitat	0.194 (1066)	0.213 (1143)	0.300 (26)	2.027
population	0.050 (276)	0.076 (405)	0.083 (6)	2.490
systematics	0.163 (896)	0.225 (1209)	0.250 (20)	2.188
ties	0.022 (119)	0.067 (361)		

Table III.6. Keywords ascribed to each topic. Keywords were searched throughout each full-text article as global and case-insensitive and could occur within words or as their own words.

topic (count)	keywords
biology (32)	anatom, arous, auditor, biosonar, body mass, brain, breeding, cranium, dental, dermat, echolocat, energetic, frequenc, harmonic, heart, hibernat, hormone, immune, lactat, metabolism, morpho, muscle, ontogeny, organ, performance, physiolog, pineal, pregnan, reproduc, sperm, thermoreg, utero
disease (14)	buccal, disease, host, infect, parasit, pathol, rabid, rabies, spillover, viral, virodiversity, virus, white-nose, zoono
ecology (22)	alien, communit, compet, diet, ejecta, exotic, faecal, faeces, fecal, feces, feed, glean, hawking, interact, invasive species, non-native, nonnative, predat, prey, seed disperse, seed rain, trophic
habitat (17)	activity pattern, bat activity, behavio, agricult, buzz, clutter, environment, forag, habitat, hibernacul, landscape, occupanc, passes, pollut, roosting, roost site, roost habitat
population (32)	bat abund, carrying capacity, cluster size, colony size, conservation, decline of, direct count, emergence count, exit count, extinction risk, flyout count, first record, fossil, harem, new distribution, new record, new species, population dec, population densit, population estimate, population grow, population increase, population project, population rate, population reduc, population size, population status, population trend, roost count, roost population, survey, threaten
systematics (17)	12s, adapt, clade, cytb, evolve, genbank, gene, genom, karyotyp, lineage, mitochondr, nuclear, phylogen, sequence, speciat, subspecies, taxonom

Table III.7. Regressions for single predictors of *number of articles* using two models of evolution. The predictor estimate and p-value correspond to the model with the lowest AIC value. Significant p-values and respective models are bolded.

variable	n	AIC		predictor		p-value
		STAR	OU	est	intercept	
Action Plan	790	10526.881	10599.212	72.024	11.419	0.000
actions number	387	5324.020	5322.235	-14.094	105.002	0.260
aspect ratio	236	3391.130	3423.569	-17.634	183.932	0.394
CITES	790	10541.333	10614.183	-24.186	73.424	0.424
clade	790	10538.623	10612.165	27.313	52.742	0.068
ESA	790	10537.468	10610.548	128.488	70.512	0.034
geographic range	706	9301.037	9290.648	52.312	75.206	0.000
habitat number	728	9704.673	9774.460	43.951	-27.660	0.000
island endemic	738	9872.191	9942.442	-76.913	93.998	0.000
human population density	693	9194.914	9186.572	12.057	76.552	0.086
mean PET	627	8230.406	8228.550	-86.037	83.494	0.000
PD	790	10541.921	10614.677	-1.565	72.138	0.818
threat number	304	3798.575	3796.399	13.722	24.329	0.018
years since described	786	10345.138	10429.663	72.605	72.645	0.000

Table III.8. Details of regressions for single predictors that are factors. **A.** Population trend, **B.** Red List threat category, and **C.** trophic level. The predictor estimate and p-value correspond to the model with the lowest AIC value. Significant p-values and respective models are bolded.

A.

pop. trend	n	AIC		predictor	
		STAR	OU	est	p-value
unknown	731	9724.768	9804.480	41.678	0.000
decreasing				19.6	0.274
stable				102.402	0.000
increasing				528.179	0.000

B.

Red List	n	AIC		predictor	
		STAR	OU	est	p-value
NE	790	10529.231	10602.839	10.407	0.672
DD				1.480	0.967
LC				82.591	0.001
NT				48.662	0.163
VU				20.056	0.572
EN				26.689	0.578
CR				3.693	0.954

C.

trophic level	n	AIC		predictor	
		STAR	OU	est	p-value
herbivore	385	5363.800	5357.918	42.741	0.172
omnivore				73.997	0.114
carnivore				105.767	0.004

Table III.9. Pairwise correlations between variables used in single-predictor regressions. Significant correlations are bolded, and correlations greater than |0.500| are italicized.

	articles	Action Plan	actions numb.	aspect ratio	CITES	clade	ESA	geo. range	habitat numb.	island end.	human pop. dens.	mean PET	PD	pop. trend	Red List	threat numb.	trophic level
Action Plan	0.403																
actions numb.	-0.149	-0.075															
aspect ratio	0.079	0.038	0.091														
CITES	-0.055	0.102	0.356	0.116													
clade	0.054	-0.130	-0.347	0.146	-0.358												
ESA	0.118	0.018	0.176	-0.009	0.074	-0.027											
geo. range	0.598	0.189	-0.355	0.232	-0.266	0.269	-0.060										
habitat numb.	0.385	0.126	-0.048	0.132	-0.134	-0.086	-0.003	0.333									
island end.	-0.362	-0.041	0.267	0.009	0.333	-0.281	0.022	-0.587	-0.159								
human pop. dens.	0.125	-0.011	0.139	-0.081	-0.053	-0.158	-0.039	-0.211	0.031	0.080							
mean PET	-0.417	0.028	0.158	-0.066	0.138	-0.241	-0.067	-0.366	-0.222	0.440	-0.044						
PD	0.090	0.155	-0.029	-0.021	-0.249	-0.137	0.009	0.076	0.135	-0.080	0.033	0.048					
pop trend	0.286	0.094	0.158	-0.020	0.128	-0.073	0.085	0.034	0.123	0.009	-0.031	-0.070	0.001				
Red List	0.108	0.374	0.374	-0.154	0.260	-0.192	0.169	-0.263	-0.063	0.190	0.085	0.037	0.089	0.252			
threat numb.	0.149	0.021	0.275	-0.316	0.102	-0.209	0.138	-0.065	0.076	0.059	0.259	0.146	0.051	0.244	0.165		
trophic level	0.105	-0.004	-0.055	0.089	-0.293	0.066	-0.007	0.161	0.302	-0.079	0.191	-0.230	0.337	-0.112	-0.104	0.192	
year since described	0.651	0.407	-0.061	0.104	0.096	-0.036	-0.008	0.511	0.320	-0.097	0.125	-0.207	0.106	0.114	0.100	0.121	0.195

Table III.10. Top ten priority ranking for research effort across all regions. Lists are apportioned according to the incorporation of **A.** ED, or **B.** EDGE.

A.

ranking	species	family	region
1	<i>Thoopterus nigrescens</i>	Pteropodidae	Asia-Pacific
2	<i>Barbastella barbastellus</i>	Vespertilionidae	Africa, Europe
3	<i>Thyroptera lavalii</i>	Thyropteridae	Latin-Caribbean
4	<i>Hipposideros doriae</i>	Hipposideridae	Asia-Pacific
5	<i>Otonycteris leucophaea</i>	Vespertilionidae	Europe
6	<i>Chaerephon jobimena</i>	Molossidae	Africa
7	<i>Plecotus turkmenicus</i>	Vespertilionidae	Europe
8	<i>Emballonura tiavato</i>	Emballonuridae	Africa
9	<i>Platalina genovensium</i>	Phyllostomidae	Latin-Caribbean
10	<i>Carollia benkeithi</i>	Phyllostomidae	Latin-Caribbean

B.

ranking	species	family	region
1	<i>Pteropus temminckii</i>	Pteropodidae	Asia-Pacific
2	<i>Barbastella barbastellus</i>	Vespertilionidae	Africa, Europe
3	<i>Hipposideros doriae</i>	Hipposideridae	Asia-Pacific
4	<i>Pteropus ocularis</i>	Pteropodidae	Asia-Pacific
5	<i>Platalina genovensium</i>	Phyllostomidae	Latin-Caribbean
6	<i>Chiroderma improvisum</i>	Phyllostomidae	Latin-Caribbean
7	<i>Thoopterus nigrescens</i>	Pteropodidae	Asia-Pacific
8	<i>Pteropus tuberculatus</i>	Pteropodidae	Asia-Pacific
9	<i>Dermanura incomitata</i>	Phyllostomidae	North America
10	<i>Triaenops auritus</i>	Hipposideridae	Africa

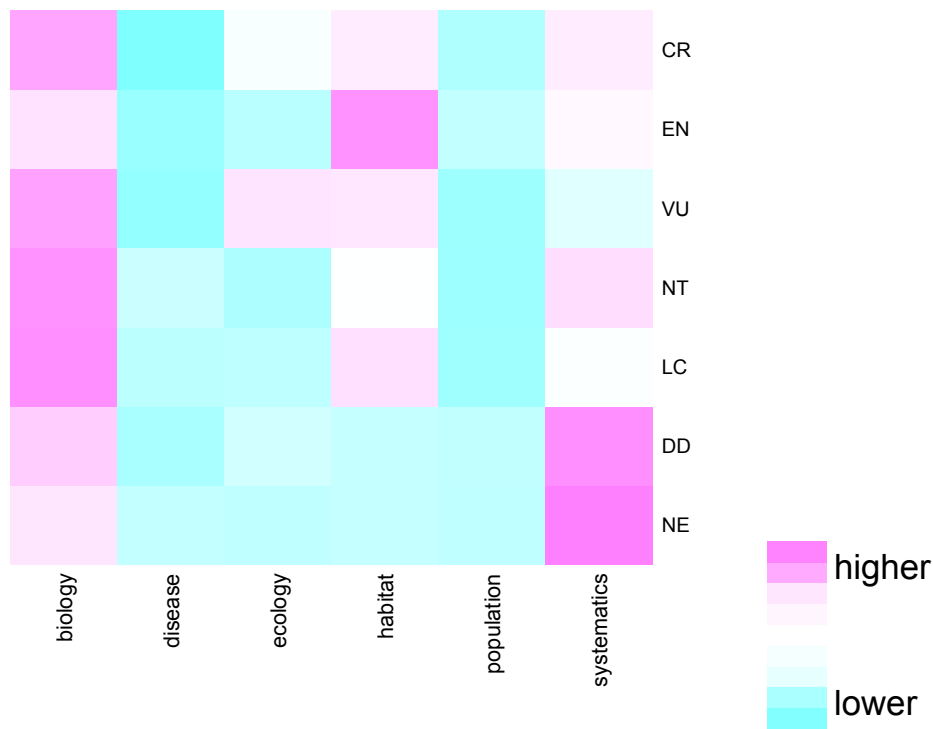


Figure III.1. Proportion of topic keywords for each full-text article by the year of publication.

Figure III.2. Number of topic keywords for full-text articles relative to row mean values. Values are apportioned by the following factors: **A.** Red List designations, **B.** regions, and **C.** families.

Figure III.2. Continued.

A.



B.

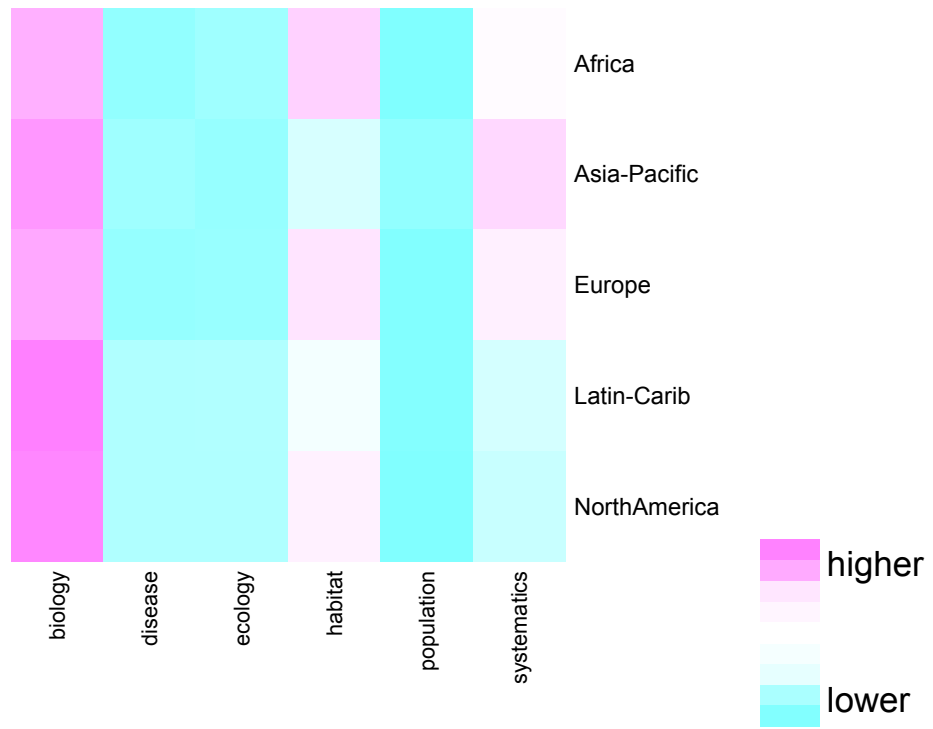
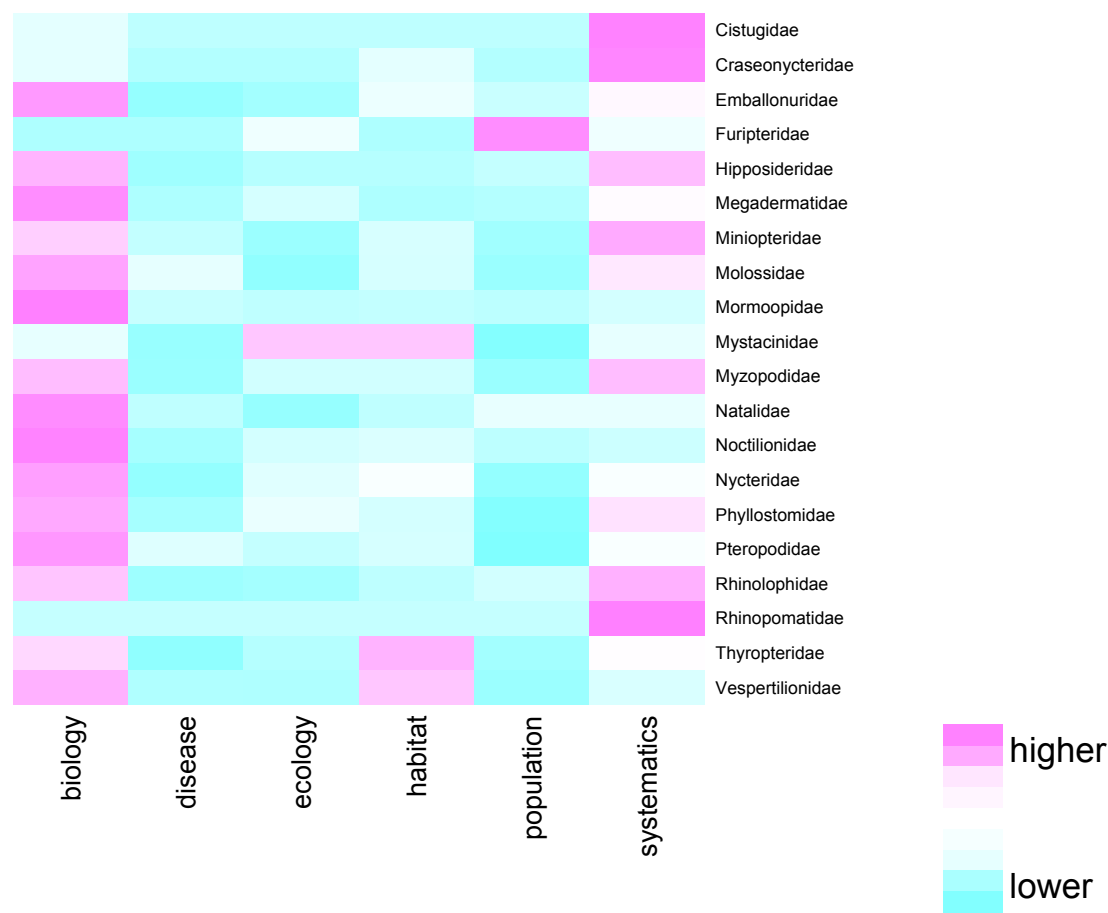


Figure III.2. Continued.

C.



CHAPTER IV

Predicting extinction risk for data-deficient bats

Abstract

Conservation biology aims to identify species most at risk of extinction and to understand factors that forecast species vulnerability. Of the approximately 1,150 recognized bat species (Chiroptera), nearly 17 percent are designated “data-deficient” by the International Union for Conservation of Nature (IUCN) Red List, denoting that a threat category has not been assigned due to insufficient knowledge. Here, we combine trait data with a comprehensive and well-resolved phylogenetic tree to determine the correlated of bat extinction risk, and then generate models to predict extinction risk in bats. We bypass traditional measures of model support by exploring the reliability of the models through a simulation approach, and we provide quantitative estimates of extinction risk for 59 species that have not been assigned a threat category on the Red List. We conclude that 31 data-deficient bat species should be considered threatened by extinction. In combination with expert knowledge, our results can be used as a quick, first-pass prioritization for conservation action.

Introduction

The central aim of conservation biology is to understand factors that forecast species vulnerability and identify species most at risk of extinction. The IUCN (International Union for Conservation of Nature) is a leading authority in documenting biodiversity peril, and its Red List of Threatened Species provides a systematic assessment of species extinction risk (IUCN, 2014). A number of quantitative criteria must be met for a species to be listed as threatened on the Red List. In particular, the risk of species extinction under prevailing circumstances is informed by population sizes, growth rates, and fluctuations. However, many taxa have not received extinction risk assessments owing to insufficient knowledge of relevant biology and threats.

Advances in phylogenetic methodology and access to large datasets of species traits have accelerated the use of comparative methods to address conservation questions. A phylogenetic comparative approach naturally tests an evolutionary hypothesis by estimating correlations between species traits while accounting for shared ancestry (Felsenstein, 1985). In conservation, comparative methods have been used to uncover trends in characteristics of invasive species, understand species susceptibility to harvesting, predict success for endangered species management, and identify correlates of extinction risk (reviewed in Fisher and Owens, 2004).

Many biological traits are strong predictors of extinction risk. Geographic range and body size are frequently tested as correlates of extinction risk (Fisher and Owens, 2004). Habitat specialization in primates, marsupials, birds, and insects is been related to some extinction risk indices, confirming the importance of habitat protection (Fisher and Owens, 2004). Because extinction risk is non-random across the phylogeny (Purvis et al., 2000a), one could conceivably predict extinction risk for a given species provided with the appropriate traits and degree of relatedness to a species with known risk (*sensu* Garland and Ives, 2000).

Of 1,150 species listed on the Red List, approximately 15 percent of bat species (Chiroptera) are extinct or threatened (IUCN, 2013). Using the first comprehensive phylogeny for bats, Jones et al. (2003) assessed the biological traits correlates of extinction risk. Extinction risk was non-randomly distributed among bat families, with family Pteropodidae having 36 percent of species considered threatened. Two biological traits,

geographic range and aspect ratio, explained 48 percent of the variation in bat extinction risk. A simulation using the minimum adequate model of extinction risk illustrated the under and overestimates of the model in relation to Red List designations.

Although the IUCN Red List was not intended for prioritization of species for conservation, extinction risk is certainly a top consideration for conservation practitioners (Mace et al., 2008). However, approximately 200 bat species are listed as data deficient on the Red List (IUCN, 2013). Jetz and Freckleton (2015) predicted extinction risk for data deficient mammals, including bats, using body mass and spatial distributions. These authors use the same phylogeny as Jones et al. (2013) and body mass as the predictor for extinction risk, although body mass was not a significant correlate according to Jones et al. (2013). They also used geographic range maps overlaid with anthropogenic encroachment.

Our research builds on previous studies by re-assessing correlates of bat extinction risk given a comprehensive, well-resolved phylogeny. We then develop two predictive models of extinction risk to illustrate trade-offs between model complexity and data availability. We use simulation to test the reliability of our models and to provide binary estimates of threat for species designated as data deficient or not evaluated on the Red List.

Methods

We compiled our bat taxonomy using Wilson and Reeder's Mammal Species of the World v2005 (MSW05, Simmons, 2005), a more recent species taxonomy based upon MSW05, (Simmons and Cirranello, 2014, dataset), and the Red List v3.1 (IUCN, 2013). We matched species names from each taxonomic source to pair trait data with current genomic data and to minimize repeated analyses of synonymous bats. We refer to all bats using their GenBank taxonomic names (Benson et al., 2009).

Data of extinction risk correlates were assembled from the PanTHERIA database (Jones et al., 2009), Jones et al. (2003) supplementary dataset, and the Red List v3.1 (IUCN, 2013) (Table IV.1.). We chose variables that were important for comparison to Jones et al. (2003) or that provided coverage for at least thirty percent of the taxa on our tree. All continuous variables were log transformed. We performed all analyses in R v.3.3.1 (R Core Team).

We used the large phylogeny construction pipeline outlined in Smith et al. (2009) and implemented in the program *PHLAWD*. The *PHLAWD* workflow first queries sequences from GenBank (Benson et al., 2009), compares the sequences to “known” gene segments of the taxa of interest, and aligns the sequences based on the degree of relatedness depending on the degree of sequence saturation. We used genes commonly sequenced for bats: *cytB*, *RAG2*, *Val*, *12S*, *16S* (e.g., Teeling et al., 2005, Almeida et al., 2011, Ruedi et al., 2013). We included *Equus*, *Diceros*, *Rhinoceros*, *Manis*, *Canis*, and *Rusa* as representative outgroups (e.g., Agnarsson et al., 2011). These genes were concatenated into a single matrix, and we used a by-gene partitioned maximum likelihood analysis in RAxML (Stamatakis, 2006).

Using our bat taxonomy, we trimmed the tree of synonymous species and subspecies so only one representative “per species” was included for analyses. Following the convention of Teeling et al. (2005), we refer to the two major clades of bats as Yinpterochiroptera (v. megabats, see Jones et al., 2003) and Yangochiroptera (v. microbats). The GenBank query returned 911 bats. Eighty-four bats did not have comprehensive trait data for analyses, but we retain them on illustrations of phylogeny to demonstrate missing data. Accordingly, our cumulative total of species used for analyses is 790 bats. Our maximum-likelihood tree included molecular branch lengths, which were smoothed to units of time in *treePL* (Smith and O'Meara, 2012) applying the same fossil calibration as in Shi and Rabosky (2015) and both minimum and maximum age constraints.

We used phylogenetic logistic regression (Ives and Garland, 2010) to determine individual correlates of extinction risk. We performed the regressions using the ‘*phyloglm*’ function in the package *phylolm* (Ho and Ane, 2014), which provides alpha coefficients that estimate the phylogenetic signal for each correlate – i.e., closely related species showing greater trait similarity than more distantly related species. We treated extinction risk as binary, where 1=threatened (i.e., Red List categories CR, EN, VU) and 0=not threatened (i.e., NT, LC). We chose to treat the response variable as binary instead of ordinal, as in Jones et al. (2003), because Red List categories are not truly additive. We attempted to determine whether there were any potential biases with our categorization scheme, by rerunning analyses where the “vulnerable” category was treated as not threatened. However, in doing so there were too few species remaining in the threatened category for any meaningful

analyses. For each correlate, we performed regressions for bats as a whole and separately for members of Yinpterochiroptera and Yangochiroptera.

For geographic range, we performed regressions including and excluded 39 bats that are categorized as threatened on the Red List due to “Criteria B” alone (i.e., small geographic range size). We did this to assess if parameter estimates for geographic range are inflated given circularity of the predictor variable and a Criteria B threat category (Purvis et al., 2000b).

We used the significant correlates of extinction risk to build our “predictor-rich” model, excluding correlates that are not reasonably considered biological traits. We also excluded adult forearm length because it was strongly correlated with adult body mass. We selected the best of 15 models based on the Akaike Information Criterion (AIC). Because nearly half of the bats on our tree have incomplete trait data, which excludes them from analysis using the predictor-rich model, we constructed a “taxon-rich” model using only the significant correlates available for a majority of taxa. We selected the best of 8 models according AIC. We assessed model fit when including and exclude the 39 bat species listed as threatened on the Red List due to Criteria B alone.

Using a jackknife approach, we generated a distribution of parameter estimates for the best predictor-rich and taxon-rich models using 75% of bat species, and then performed simulations of extinction risk across the entire bat phylogeny, including species that are considered data deficient (DD) or not evaluated (NE) on the Red List. We assessed differences in results depending on the inclusion of 39 bat species listed as threatened on the Red List due to Criteria B alone. We generated the predicted average, median, and upper and lower quantile estimates of extinction risk for each bat species. For each model, we ordered bats at risk of extinction based upon the median extinction risk prediction. Although the estimates are continuous, a species was considered threatened if its median estimate was great than or equal to 0.50.

Results

Correlates of extinction risk

For Chiroptera as a whole, significant single correlates of extinction risk included large body mass, large diet breadth, large forearm length, small geographic range, human

population density and rate change, island endemism, high PET, and trophic level (Table IV.2. and IV.3.). The strongest relationship was with geographic range ($R^2 = 0.474$ including Criteria B bats), followed by island endemism ($R^2 = 0.140$). It is worth noting that because island endemism and geographic range naturally covary (i.e., island endemics generally have small ranges), whether or not a species is an island endemic might not actually correlate well with extinction risk (see Jones et al., 2003). However, even when we control for geographic range, island endemism and the interaction between the two predictors are significant correlates of extinction risk in all bats (Table IV.2.C). Overall, extinction risk in bats is strongly conserved across the phylogeny for most traits as indicated by alpha values at or below 0.1, lending strong support that extinction risk is non-randomly distributed in bats, and that phylogeny is important to consider in these statistical analyses.

Examining relationships within Yinpterochiroptera and Yangochiroptera, the two major clades nested within Chiroptera, small geographic range and herbivory were significant predictors of extinction risk. For Yinpterochiroptera alone, variables associated with body size (i.e., body mass and forearm length) and life history (i.e., diet breadth and litter size) were also important predictors of their extinction risk. For species in Yangochiroptera, however, human population density was a significant predictor.

Results involving geographic range were different depending on the inclusion of species categorized as threatened due to Criteria B on the Red List. For all bats, geographic range is a much stronger predictor of extinction risk when “Criteria B species” are included. Excluding Criteria B species, the best predictor-rich and the best taxon-rich model adds variables. In particular, the best taxon-rich model includes the variables clade and endemism*clade as relevant variables. Clade differences are likely accentuated when Criteria B species are excluded because it removes about nine percent of Yinpterochiroptera bats from the dataset. For simplicity, the findings we report include species categorized as threatened due to Criteria B on the Red List.

The best-fit predictor-rich model, based on both AIC and w_i , is one in which geographic range, body mass, diet breadth, trophic level, and island endemism were all significant predictors of extinction risk. The model had an R^2 value of 0.518, which indicated that more than half of the variation in extinction risk is explained by just these

seven predictor variables. The alpha value ($\alpha = 0.026$) indicated that the predictor-rich model has a strong phylogenetic signal in extinction risk within bats.

Simulated extinction risk using the parameter estimates of the predictor-rich model generally agree with the Red List categories. Of 344 species, six (0.017) bats had overestimated extinction risk (i.e., species predicted to be threatened but are not designated as threatened on the Red List) and eleven (0.032) bats have underestimated extinction risk (i.e., species predicted not to be threatened but are designated threatened on the Red List). Half of the species that had overestimated risk were herbivores or had a wide diet breadth, whereas over half of the species that had underestimated risk were carnivores or had a narrow diet breadth.

We also tested a model where we reduced the number of predictors down to include only geographic range, island endemism, and clade identity as a means of maximizing the number of taxa in the tree. The best-fit “taxon-rich” model indicated that geographic range, island endemism, and an interaction term were all significant predictors of extinction risk (Table IV.5.). For island endemics, a 1 km² increase in geographic range resulted in a 2.30 decrease in the log odds of extinction risk, whereas 1 km² increase in geographic range for non-endemics resulted in a 1.37 decrease in the log odds of extinction risk. Keeping range constant, the odds of a species being threatened if it is endemic are two and a half-folds higher than if the species is not endemic.

The best taxon-rich model included only the predictors geographic range, island endemism, and their interaction, and explained only slightly less variation than the best predictor-rich model ($R^2=0.509$ v. $R^2=0.518$, respectively). The alpha value ($\alpha = 0.066$) indicated that the taxon-rich model had stronger phylogenetic signal in extinction risk than the predictor-rich model. Of the 647 species eligible for simulation using the parameter estimates provided by the taxon-rich model, eighteen (0.028) bats had overestimated extinction risk and 36 (0.056) had underestimated extinction risk relative to the corresponding Red List designations. Over half of the species that had overestimated risk were had geographic ranges less than 20,000 km² or were island endemic. For the species that had underestimated risk, all but four had ranges greater than 20,000 km² and most were not island endemics.

Predicting extinction risk

According to median estimates provided by the predictor-rich model simulation, ten of the most at risk bat species includes seven species listed as threatened on the Red List (Table IV.6.A.). Moreover, risk is especially high Pteropodids, with six of the species belonging to this family. However, four prediction intervals overlap 0.5 (i.e., delineation of threatened versus not threatened), demonstrating the uncertainty of extinction risk.

Ten of the most at risk bat species according to the predictions made by the species-rich model includes four species listed as threatened (Table IV.6.B.). The remaining six bat species are listed as data deficient on the Red List. Most of the species were of the family Vespertilionidae or Pteropodidae, but the single representative of Craseonycteridae was on each top ten list. None of the bat species had prediction intervals that overlap 0.5 demonstrating certainty of threatened status given the model.

Interestingly, the predicted extinction risk from the predictor-rich and taxon-rich models were highly congruent (Figure IV.1.). Of the 350 bat species that had extinction risk simulated by both the predictor-rich and taxon-rich models, we identified 3 percent (11 species) disagreement for predicted extinction risk. For seven of the species, the predictor-rich model concurred with the threat status given by the Red List, but the data-rich model did not.

For the 112 species without Red List designations, six bats without a Red List designation had enough trait data to simulate extinction risk under predictor-rich model, for which all were predicted to be not threatened. Fifty-nine species were analyzed using the taxon-rich model, for which about 31 percent (18 species) were predicted to be at risk of extinction (Figure IV.2.). Assuming the data-deficient and unevaluated bats our simulation predicted to be at risk (or ineligible for analysis) were to go extinct in addition to bats listed as critically endangered and endangered on the Red List, PD would be reduced by 8 percent.

Discussion

For all bats, geographic range was the most important predictor of extinction as it was for Jones et al. (2003) and many similar studies (reviewed in Fisher and Owens, 2004). After accounting for its interaction with geographic range, island endemism remained a

significant predictor for bats overall and for Yinpterochiroptera. Approximately 25% of bats are island endemics, and the family Pteropodidae (Yinpterochiroptera) has a higher proportion of island endemic species than other bat families (Jones et al., 2003). Contrary to Jones et al. (2003), we did not find aspect ratio or litters per year to be significant predictors of extinction risk in bats overall, and we found that large body mass was a significant predictor of extinction risk.

Predictors that have moderate phylogenetic signal indicate that extinction risk given that predictor is not conserved among closely related taxa. Diet breadth and trophic level are two significant predictors with moderate phylogenetic signal, meaning, for example, that herbivorous bats are at a higher risk of extinction, but that two herbivorous species chosen at random are not necessarily closely related. Both variables represent frugivory, which has evolved independently in family Phyllostomidae (New World, Yangochiroptera) and Pteropodidae (Old World, Yinpterochiroptera) (Dumont, 2003). Extinction within these bat families would have cascading effects across tropical ecosystems, as many species are seed dispersers and pollinators.

Given simulations of extinction risk using parameter estimates of the predictor-rich model, species that are carnivorous or have a narrow diet breadth were underestimated. For the taxon-rich model, non-endemic species and species with large ranges were underestimated. These results reflect the systematic nature of trait-based predictions and the absence of expert opinion. The bats that were underestimated, although they have biological traits of non-threatened species, are threatened due to reasons not necessarily reflected in their biology. For example, both our models underestimated extinction risk for *Myotis sodalis* because the bat is small, is insectivorous (i.e., carnivorous and a single diet item), and has a large, contiguous range on mainland. The Red List, however, has designated *M. sodalis* as endangered owing to habitat degradation and roost disturbance, which have reduced population sizes within the species' small area of occupancy.

The precautionary principle compels conservation biologists to treat all species with unknown risk as if they were threatened by extinction (Cooney, 2004). However, limited conservation resources necessitate approaches that can estimate extinction risk and uncertainty. For the 59 species without Red List designations that were eligible for analysis, most were predicted to have low risk of extinction given geographic range and

island endemism. We contend that species with prediction intervals above 0.5 (i.e., delineation of threatened versus not threatened) should be considered immediately for conservation, and species with median values of risk above 0.5 but have overlapping prediction intervals should be looked at more closely. Without expert opinion providing evidence otherwise, bats that have prediction intervals below 0.5 could be considered low priority for conservation resources.

We shared 28 data deficient species in common with Jetz and Freckleton (2015), for which 18 estimates of extinction risk were in agreement. Although the authors provided risk assessments for 126 species, 71 percent of which they predicted to be threatened, their representative trait was imputed body mass while we compare multiple models of trait information shown to be important for bats. They also used indices of human impact to inform simulations of risk, which are relevant to predict accelerated threat for a particular time span, but might erroneously predict extinction risk because to what extent high human impact over short time spans intensifies extinction risk across a species range is unknown.

Rapid conservation decision-making is crucial for bats, as “slow” life history limits population growth after perturbations (Racey and Entwistle, 2003). The IUCN Red List designates species threat based upon several quantitative measures (e.g., population sizes, number of mature individuals, etc.) that are difficult to collect for bat species (Racey and Entwistle, 2003). We have provided two models that reflect the trade-off between comprehensive trait data and applicability across taxa. Comparing simulations of risk between the predictor-rich and taxon-rich models, we identified only 3 percent (10 species) disagreement between estimates. Thus, the taxon-rich model, which requires only two trait variables, serves as an adequate surrogate for predicting extinction risk when quick assessments of risk are required. Still, the reliability of our model estimates is dependent upon data quality.

Here, we combined contemporary data and an evolutionary approach to identify species of conservation concern. Our modelling approach can be used as a quick, first-pass prioritization for conservation action. Such techniques are important to enhance Red List assessments when only expert knowledge is available, or, importantly, when funding resources are limited.

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Appendix

Table IV.1. Sources and descriptions of data used in this study.

source	variable	definition
PanTHERIA	adult body mass (g)	excluding pregnant females
	adult forearm length (mm)	total length from elbow to wrist
	diet breadth	number of dietary categories eaten
	geographic range area (km ²)	total extent of a species range from Sechrest 2003 ¹
	human population density mean (persons/km ²)	using the 1995 Gridded Population of the World ²
	litter size	number of offspring born per litter per female
	litters per year	number of litters
	potential evapotranspiration rate (PET) mean (mm)	monthly measures from 1920-1980 using Global Resource Information Database ³
Jones et al., 2003	trophic level	herbivore, omnivore, carnivore
	aspect ratio	wingspan squared divided by wing area
	wing loading	body mass times gravity acceleration divided by wing area
IUCN Red List	threat category	critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), data deficient (DD), not evaluated (NE)
	region	Asia-Pacific, Africa, Latin America-Caribbean, Europe, North America
	island endemism	observed only on islands, excluding Australia

¹ Sechrest, W. 2003. Global diversity, endemism and conservation of mammals. University of Virginia, Charlottesville, Virginia, USA.

² CIESIN, and CIAT. 2005. Gridded Population of the World Version 3 (GPWv3): Population Grids. SEDAC, Columbia University, New York, New York, USA.

Table IV.1. Continued.

³ UNEP (2009): The UNEP Environmental Data Explorer, as compiled from CSIRO Marine and Atmospheric Research. United Nations Environment Programme.
<http://ede.grid.unep.ch>.

Table IV.2. Results of single predictor phylogenetic logistic regressions predicting extinction risk in bats. The variable “geo range abbr.” excludes bats listed at threaten due to Criteria B alone. The parameter α represents the phylogenetic correlation parameter. An α near 0.1 indicates strong phylogenetic signal. Significant variables have bold p-values. **A.** Continuous and discrete variables. **B.** Details for the categorical variable trophic level. **C.** Details for the interaction between geographic range and island endemism.

A.

variables	all bats				Yinpterochiroptera				Yangochiroptera			
	α	est	p	R ²	α	est	p	R ²	α	est	p	R ²
aspect ratio	0.021	-8.315	0.078	0.058	0.057	-8.526	0.367	0.017	0.022	-8.007	0.154	0.051
body mass (g)	0.124	1.619	<0.001	0.069	0.961	1.506	<0.001	0.146	0.191	0.001	0.999	0.000
diet breadth	0.887	0.597	0.014	0.038	0.078	1.139	0.004	0.124	0.900	0.402	0.257	0.010
forearm length (mm)	0.101	3.976	<0.001	0.051	0.101	4.750	0.001	0.085	1.005	-2.316	0.219	0.005
geo range (km ²)	0.018	-1.524	<0.001	0.474	0.065	-1.373	<0.001	0.415	0.019	-1.768	<0.001	0.527
geo range abbr.	0.004	-0.646	<0.001	0.275	0.293	-0.957	<0.001	0.292	0.019	-1.264	0.002	0.261
human population density (n/km ²)	0.058	0.611	0.023	0.033	0.058	-0.497	0.158	0.051	0.367	1.378	0.001	0.067
island endemism	0.076	1.655	<0.001	0.140	0.070	1.048	0.007	0.071	0.140	1.961	<0.001	0.138
litter size	0.058	-23.788	0.131	0.049	0.103	-11.111	0.515	0.014	0.118	-12.715	0.230	0.052

Table IV.2. Continued.

variables	all bats				Yinpterochiroptera				Yangochiroptera			
	α	est	p	R ²	α	est	p	R ²	α	est	p	R ²
litters per year	0.063	-11.047	0.081	0.062	0.786	-11.074	0.054	0.141	0.183	-6.554	0.439	0.050
PET (mm)	0.006	2.002	0.006	0.000	0.019	5.397	0.100	-0.002	0.106	-0.496	0.776	0.001
wing loading	0.162	-0.482	0.708	0.001	0.068	-0.336	0.847	-0.003	0.213	-0.798	0.661	0.002

B.

variables	all bats				Yinpterochiroptera				Yangochiroptera			
	α	est	p	R ²	α	est	p	R ²	α	est	p	R ²
herbivore	0.294	-1.873	<0.001	0.140	0.047	-2.698	0.005	0.025	0.471	-2.342	<0.001	0.021
omivore		-1.672	0.064			0.723	0.691			-0.580	0.482	
carnivore		-1.204	0.007			0.830	0.433			-0.946	0.155	

C.

variables	all bats				Yinpterochiroptera				Yangochiroptera			
	α	est	p	R ²	α	est	p	R ²	α	est	p	R ²
intercept	0.021	10.727	<0.001	0.509	0.012	9.271	0.010	0.482	0.018	11.105	<0.001	0.537
range		-2.302	<0.001			-2.362	0.006			-2.323	<0.001	
endemism		-5.538	0.006			-7.160	0.046			-3.705	0.185	
range*endemism		0.931	0.018			1.174	0.131			0.545	0.318	

Table IV.3. Sample sizes for single predictor phylogenetic logistic regressions predicting extinction risk in bats.

sample size	all bats	Yinpterochiroptera	Yangochiroptera
aspect ratio	234	66	168
body mass (g)	526	177	349
diet breadth	372	124	248
forearm length (mm)	587	197	390
geo. range (km ²)	647	209	438
geo. range abbr.	608	190	418
human pop. density (n/km ²)	647	209	438
island endemism	678	210	468
litter size	381	114	267
litters per year	199	65	134
PET (mm)	585	168	417
trophic level	372	124	248
wing loading	228	66	162

Table IV.4. “Predictor-rich” model details. **A.** Ranks for 14 combinations of predictor variables included in phylogenetic logistic regression models predicting extinction risk in bats. The models are ranked based on the Akaike weights (w_i). **B.** Details of the best-fit model. We provide the odds ratio (OR) to compare the relative effect of each variable.

A.

rank	model ¹	α	R ²	AIC	w_i	lnLik
1	111110000000	0.026	0.518	101.224	0.312	-42.612
2	111110100000	0.024	0.527	101.848	0.228	-41.924
3	111111000000	0.024	0.520	102.942	0.132	-42.471
4	111111100000	0.029	0.531	103.164	0.118	-41.582
5	111110100100	0.023	0.526	103.959	0.079	-41.979
6	111111101000	0.023	0.531	105.291	0.041	-41.645
7	111111001100	0.019	0.523	106.487	0.022	-42.243
8	111111111111	0.189	0.570	106.995	0.017	-38.498
9	111111101010	0.020	0.532	107.002	0.017	-41.501
10	111111101100	0.022	0.531	107.176	0.016	-41.588
11	111111101110	0.019	0.533	108.972	0.006	-41.486
12	111111001000	0.002	0.490	109.687	0.005	-44.843
13	111011101000	0.022	0.476	109.813	0.004	-45.906
14	110011101000	0.020	0.433	114.390	0.000	-49.195
15	110111101000	0.021	0.457	114.646	0.000	-47.323

¹The variables are ordered as follows: (1) geo range, (2) body mass, (3) diet breadth, (4) trophic level, (5) island endemism, (6) clade, (7) geo range*island endemism, (8) geo range*clade, (9) body mass*island endemism, (10) body mass*clade, (11) diet*clade, (12) island endemic*clade.

Table IV.4. *Continued.*

B.			
variable	est	OR	p-value
intercept (trophic level-herbivore)	5.023	151.866	0.020
geo range	-1.946	0.143	<0.001
body mass	0.991	2.694	0.106
diet breadth	1.537	4.651	0.004
trophic level-omnivore	-1.363	0.256	0.266
trophic level-carnivore	1.303	3.68	0.186
island endemism	-1.589	0.204	0.038

Table IV.5. “Taxon-rich” model details. **A.** Ranks for 8 combinations of predictors included in phylogenetic logistic regression models predicting extinction risk in bats. The models are ranked based on the Akaike weights (w_i). **B.** Details of the best-fit model. We provide the odds ratio (OR) to compare the relative effect of each variable.

A.

rank	model ¹	α	R ²	AIC	w_i	lnLik
1	110100	0.066	0.509	276.215	0.627	-133.107
2	110000	0.057	0.499	278.538	0.196	-135.269
3	111000	0.050	0.500	279.993	0.095	-134.996
4	111101	0.020	0.504	282.274	0.030	-134.137
5	111110	0.019	0.504	282.561	0.026	-134.280
6	111111	0.024	0.507	282.905	0.022	-133.452
7	100000	0.018	0.474	287.654	0.002	-140.827
8	111011	0.022	0.487	290.043	0.001	-138.021

¹The variables are ordered as follows: geo range, island endemism, clade, geo range*island endemism, geo range*clade, island endemism*clade.

B.

variable	est	OR	p-value
intercept	10.727	45569.780	<0.001
geo range	-2.302	0.100	<0.001
island endemism	-5.538	0.004	0.006
geo range*island endemism	0.931	2.537	0.0184

Table IV.6. List of ten species at high risk of extinction according to two simulations. The median estimate is bold if it is above 0.5 (i.e., a threatened prediction), and bold and italic if the lower estimate is above 0.5. 95% prediction intervals are shown by lower and upper estimates. **A.** Predictor-rich model. **B.** Taxon-rich model.

A.

family	species	Red List	lower estimate	median Estimate	upper estimate
Pteropodidae	<i>Pteropus mariannus</i>	EN	0.942	0.992	1.000
Pteropodidae	<i>Pteropus rodricensis</i>	CR	0.857	0.961	0.996
Emballonuridae	<i>Coleura seychellensis</i>	CR	0.856	0.953	0.996
Craseonycteridae	<i>Craseonycteris thonglongyai</i>	VU	0.736	0.915	0.992
Pteropodidae	<i>Pteropus conspicillatus</i>	NT	0.565	0.802	0.969
Pteropodidae	<i>Aproteles bulmerae</i>	CR	0.550	0.791	0.946
Natalidae	<i>Chilonatalus tumidifrons</i>	LC	0.387	0.663	0.888
Pteropodidae	<i>Eidolon dupraenum</i>	VU	0.213	0.663	0.922
Pteropodidae	<i>Pteropus samoensis</i>	LC	0.348	0.640	0.818
Vespertilionidae	<i>Myotis vivesi</i>	VU	0.411	0.605	0.810

Table IV.6. Continued.

B.

family	species	Red List	lower estimate	median estimate	upper estimate
Vespertilionidae	<i>Eptesicus dimissus</i>	DD	0.996	1.000	1.000
Molossidae	<i>Otomops wroughtoni</i>	DD	0.994	1.000	1.000
Vespertilionidae	<i>Myotis annamiticus</i>	DD	0.990	0.998	1.000
Vespertilionidae	<i>Myotis anjouanensis</i>	DD	0.973	0.992	1.000
Phyllostomidae	<i>Dermanura incommitata</i>	CR	0.959	0.990	1.000
Pteropodidae	<i>Latidens salimalii</i>	EN	0.967	0.990	1.000
Craseonycteridae	<i>Craseonycteris thonglongyai</i>	VU	0.952	0.984	0.998
Phyllostomidae	<i>Micronycteris matses</i>	DD	0.946	0.984	0.998
Pteropodidae	<i>Pteropus voeltzkowi</i>	VU	0.951	0.984	0.998
Pteropodidae	<i>Styloctenium mindorensis</i>	DD	0.930	0.981	0.998

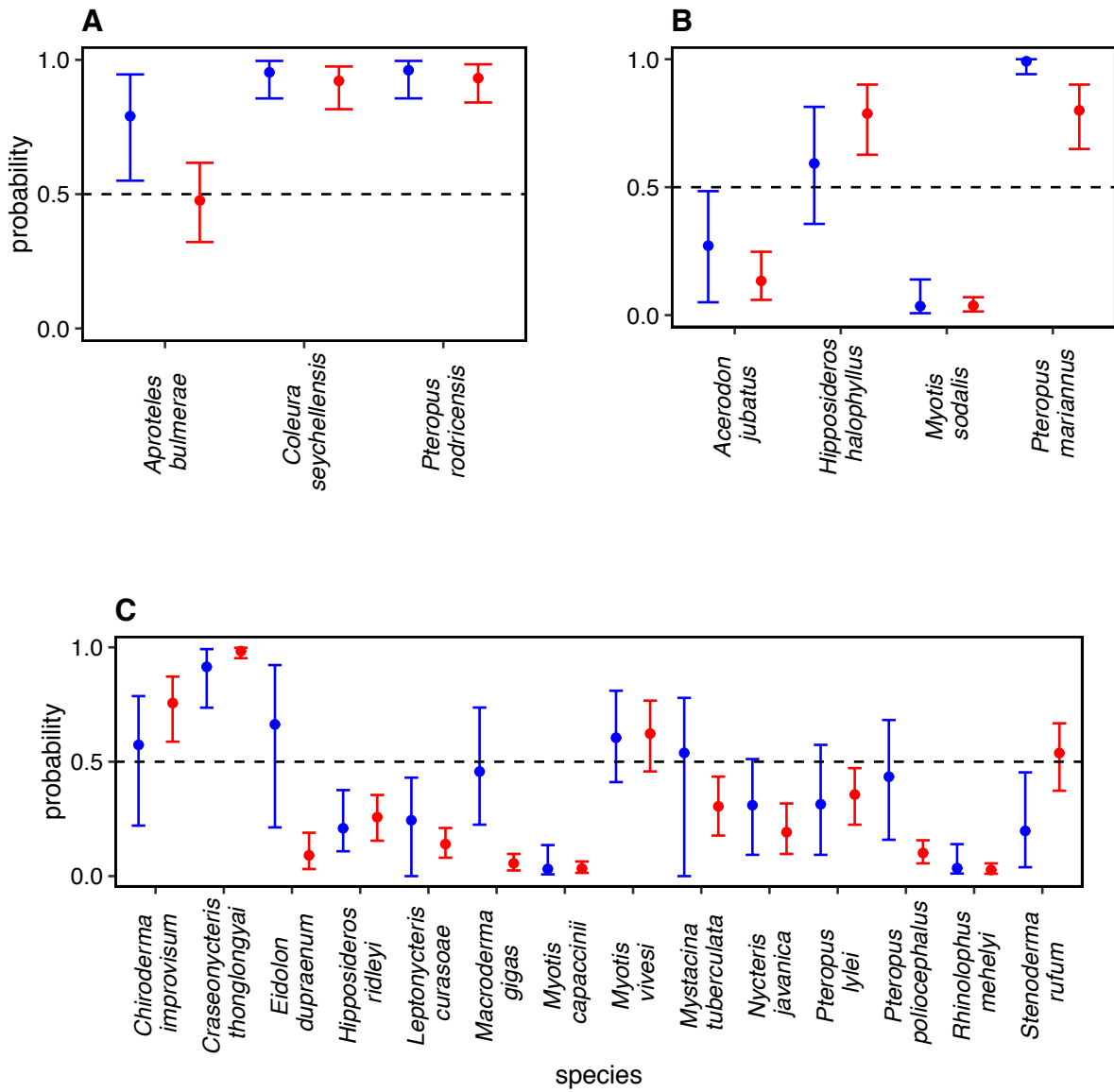


Figure IV.1. Comparison of prediction intervals between models. Estimated prediction median and intervals of predictor-rich model is illustrated in blue, and taxon-rich model in red. Red List designations as follows: **A.** Critically Endangered, **B.** Endangered, **C.** Vulnerable.

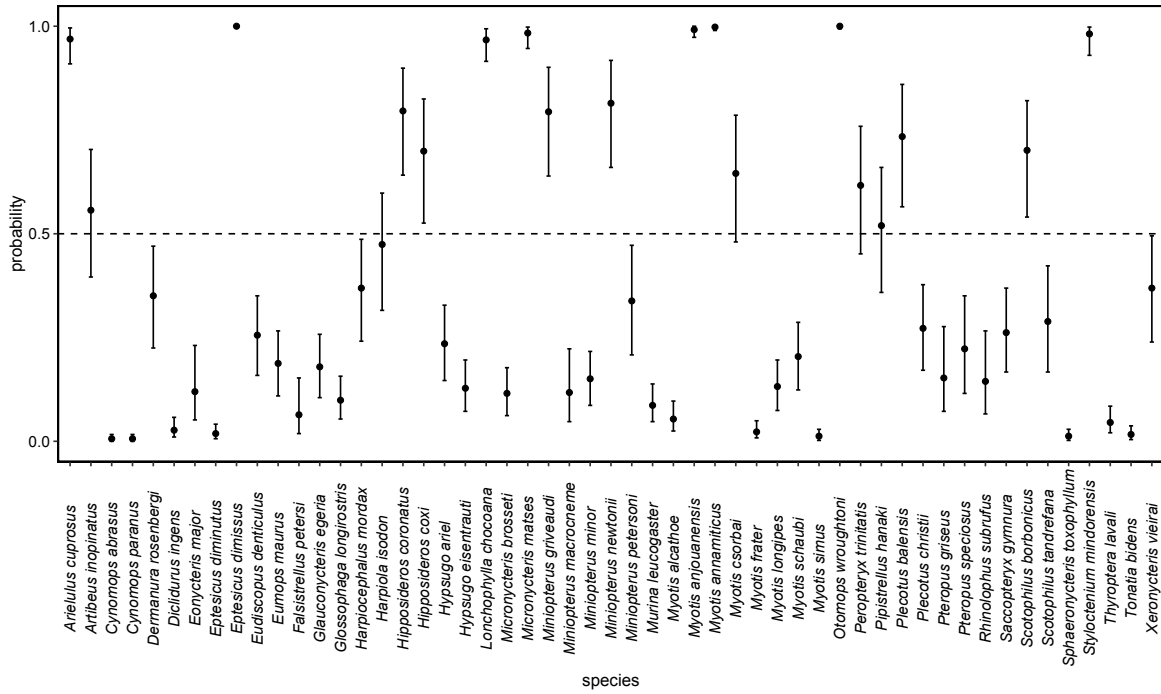


Figure IV.2. Estimated species threat for 59 species designated DD on the Red List according to the taxon-rich model parameter estimates. 95% prediction intervals are shown.

CONCLUSION

My dissertation used methods from both ecology and evolution to contribute to the study of bat conservation. My work in Chapters I and II used ecological knowledge and field observations to show that biological invasion is a conservation concern for many bat species, especially those on islands. Chapters III and IV incorporate an evolutionary perspective to estimate research needs across bat phylogeny, and to advise on species endangerment when knowledge is lacking. In closing, I provide the following summary and recommendations for future research.

In Chapter I, we showed that the majority of cases of invasive species threatening bats occur on islands, and that conclusive evidence of invasive species reducing bat abundance is lacking. Reductions in population numbers are often the focus of invasion impact assessments, but aside from species that congregate in accessible caves, monitoring population trends of bats is difficult. However, given advancements in acoustic monitoring technology and camera traps, we suggest that examining shifts in habitat use could be a surrogate for population abundance estimates in bats. Moreover, major roost sites that occur in areas where invasive species are present should be examined for mortality. Island bat species, especially, should be monitored regularly.

The results from Chapter II indicate that indirect, negative impacts of *Lantana camara* on the population of *Emballonura semicaudata rotensis* have been underestimated. Because both bats and bat prey are scarce in lantana shrub, likely owing to microclimate, the remaining tracts of Aguiguan's native forest is a vital resource. We insist that lantana should be managed and subsequent reforestation should be attempted in order to restore *E. s. rotensis* habitat. Although we support removal of feral goats, as this would undoubtedly lead to an increase in native vegetation, goat browsing is not the most substantial threat to *E. s. rotensis* without evidence that goats perpetuate lantana spread.

Chapter III shows that there are clear biases in research effort for bats. In general, bats in need of research most are those that are island endemics, have small ranges, occur in tropical latitudes, have unknown population trends, and are recently described. Additionally, topics associated with conservation measures to determine population sizes were published least. Our understanding of biodiversity at large will be enhanced if research effort is distributed more systematically. Therefore, we provided a ranked

prioritization of bats for research effort in the hopes that it will guide researchers and funding agencies on where to invest future resources.

In Chapter IV, we show that for all bats, geographic range was the most important predictor of extinction risk, as it was for similar studies on other taxa. We then combined trait data and an evolutionary approach to identify 31 bat species that should be considered immediately for conservation. Our modelling approach could be used as a quick, first-pass prioritization for conservation action, and can enhance conservation assessments when only expert knowledge is available, or, importantly, when funding resources are limited. Rapid conservation decision-making is crucial for bats, as “slow” life history limits population growth after perturbations.

VITA

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