Lee, Benjamin Paul Yi-Hann (2016) *The urban ecology of bats in Singapore: understanding the human-wildlife interface.* Doctor of Philosophy (PhD) thesis, University of Kent,.

The version of record is available from

https://doi.org/10.22024/UniKent/01.02.76177

This document version

UNSPECIFIED

DOI for this version

Title: The urban ecology of bats in Singapore: understanding the human-wildlife interface

Abstract: Urbanisation is a transformative land use change that has drastic ecological consequences worldwide, including biodiversity loss. There is more at stake in the tropics because these regions are global centres of biodiversity, yet very few studies of tropical wildlife in urban areas exist. Based in the urban tropics of Singapore, this thesis intends to fill a knowledge gap using acoustic approaches to sample biodiversity. I used acoustic recorders to quantify the impacts of major roads, the habitat value of green roofs, and the effects of large-scale transboundary smoke-haze pollution on biodiversity in Singapore. For the first two studies, bats were used as a focal taxon because of their ubiquity in the urban environment and their recommended roles as suitable indicators of the effects of urbanisation. Prior to these studies, acoustic guidelines for bat sampling were written and compiled. The third study involved soundscape recordings from a monitoring project, which coincided with one of the worst smoke-haze pollution events in Southeast Asia. The studies revealed that: i) Lighting on major roads had a negative impact on bat activity in both forest and urban habitats, and may present a barrier for forest-dependent bats, while some species utilised areas near to roads to some degree; ii) Green roofs supported substantial bat activity, especially on those that were newer, low, had higher shrub cover, higher night time temperature and a medium pruning regime, at the expense of pesticide use, and iii) Levels of acoustic activity dropped drastically during the peak of the pollution event and there was only partial recovery to pre-haze levels after 16 weeks. The outcomes from these three studies were informative for the design of mitigation and enhancement measures to support urban biodiversity, to identify future research directions using more process and mechanistic approaches to study the urban environment, and to explore avenues to involve citizens in biodiversity monitoring.

Word count / number of pages: 51912 words / 230 pages

Year of submission: 2016

Academic school: Durrell Institute of Conservation & Ecology, School of Anthropology & Conservation

The urban ecology of bats in Singapore: understanding the human-wildlife interface

Benjamin Paul Yi-Hann Lee

Durrell Institute of Conservation and Ecology (DICE)

School of Anthropology and Conservation

University of Kent, UK

November 2016

Thesis submitted for the degree of

Doctor of Philosophy in Biodiversity Management

Acknowledgements

This seemingly endless PhD quest would not have been possible without the help and support of many. First and foremost, my heartfelt thanks go to my dynamic duo of supervisors, Matt Struebig and Zoe Davies. They have been generous, insightful, and patient. They were not just interested in my research but also in my personal well-being. They constantly kept me on track despite a slow start and for that, I am forever grateful. At DICE and elsewhere at the University of Kent, I thank Bob Smith and Jake Bicknell for help with coding and database management; Simon Tollington and Eleni Matechou for discussions about modelling, and James Cugley for establishing a protocol to make soundscape processing less painful. The extremely helpful support staff at SAC are not forgotten, notably James Kloda, Chris Williams and Nicola Kerry-Yoxall.

My fellow PhD students — Alicia, Gail, Helena, Jamie, Rob, Simon, Tristan, Valeria and Vilma — were a constant source of encouragement, knowledge and fun in my last 10 months at DICE and made my journey more bearable, especially my "row mates", Aziz, Janna and Lydia.

This thesis was made possible by a National Parks Board (NParks) Overseas Scholarship and I would like to thank my employer, NParks, and the HR managers, Jason Soon and Chu Ai Buay, for dealing with all administrative matters related to my study. The grant from Wildlife Reserves Singapore Conservation Fund (WRSCF) was much appreciated and I thank Sonja Luz, John Sha, Paige Lee and Jessica Lee for taking an interest in my project. My other colleagues at NParks deserve a huge vote of thanks — Alex Yee for generously sharing his GIS and

vegetation map data, and all the staff of the Conservation Division, especially Sharon Chan for her kind support all these years, and for permission to access the Nature Reserves for research.

The preparatory work and permission for research on the green roofs was a mammoth task. It would not have been possible without the excellent team of James Wang, Poh Choon Hock, Chloe Tan, Vivien Lee, Ted Webb and the co-operation of most green roof managers. I thank the green roof team for allowing me to use the site data for each roof. I grateful to all my volunteers who accompanied me on my ‘road ecology’ bat surveys and kept me safe - Gregory Tan, Chung Yifei, Joey Gan, Robin Ngiam, Derek Yap, Lim Zong Xian, Joys, Natalia Huang and Paul Cheng.

For all discussions related to bat research and acoustics, I thank Tigga Kingston and the SEABRU members, Joe Huang, Arjan Boonman, Kyle Armstrong, Roger Coles, Neil Furey, and Jodi Sedlock. Gareth Jones was very kind to host me for a lab visit in Bristol. For statistical help and discussions on road and urban ecology, I thank Rodney van der Ree, James Wang, Chong Kwek Yan, Yong Ding Li and Ian Mendenhall. And Lisa Jones-Engel for checking in now and again.

Finally, I want to thank my parents for their unconditional love and for believing in me and the work that I do, although I may have caused them to worry at times. My dad was wonderful in helping me to solve challenges related to the power management and deployment of my bat detectors in urban areas. Emily, my long-suffering wife, was unstinting in her support for my PhD even though I had to be away from her. I wish to thank her by spending more time with her from now on.

Author’s declaration

All chapters in this thesis were written by Benjamin P. Y.-H. Lee and are formatted in the style of manuscripts for publication. Comments and editorial suggestions were made by M.G. Struebig and Z.G. Davies. Further contributions made by others are detailed on the cover pages or in the acknowledgements of this thesis.

Abstract

Urbanisation is a transformative land use change that has drastic ecological consequences worldwide, including biodiversity loss. There is more at stake in the tropics because these regions are global centres of biodiversity, yet very few studies of tropical wildlife in urban areas exist. Based in the urban tropics of Singapore, this thesis intends to fill a knowledge gap using acoustic approaches to sample biodiversity. I used acoustic recorders to quantify the impacts of major roads, the habitat value of green roofs, and the effects of large-scale transboundary smoke-haze pollution on biodiversity in Singapore. For the first two studies, bats were used as a focal taxon because of their ubiquity in the urban environment and their recommended roles as suitable indicators of the effects of urbanisation. Prior to these studies, acoustic guidelines for bat sampling were written and compiled. The third study involved soundscape recordings from a monitoring project, which coincided with one of the worst smoke-haze pollution events in Southeast Asia. The studies revealed that: i) Lighting on major roads had a negative impact on bat activity in both forest and urban habitats, and may present a barrier for forest-dependent bats, while some species utilised areas near to roads to some degree; ii) Green roofs supported substantial bat activity, especially on those that were newer, low, had higher shrub cover, higher night time temperature and a medium pruning regime, at the expense of pesticide use, and iii) Levels of acoustic activity dropped drastically during the peak of the pollution event and there was only partial recovery to pre-haze levels after 16 weeks. The outcomes from these three studies were informative for the design of mitigation and enhancement measures to support urban biodiversity, to identify future research directions using more process and mechanistic approaches to study the urban environment, and to explore avenues to involve citizens in biodiversity monitoring.

Contents

Figures

Tables

1. Introduction

With more than half of the world's population living in urban areas since 2008, urbanisation brings about considerable environmental impact, which can extend far beyond the boundaries of cities themselves (Grimm *et al.* 2015). One aspect of the global environmental change accompanying rapid urbanisation is biodiversity loss (McKinney 2002) as non-urban land is converted into urban and sub-urban areas, and natural, semi-natural, and the agricultural surroundings are replaced by buildings, roads and other associated grey infrastructure (McDonnell & Pickett 1990; Faeth *et al.* 2005). Biodiversity loss is especially acute in the rapidly urbanising tropics where high levels of species diversity is juxtaposed with high human population densities. It is in such places that research is urgently required to understand the impact of land-use change as a result of urbanisation on tropical biodiversity (Rompré, Robinson & Desrochers 2008).

1.1 Biodiversity in the urban environment

Urban environments are characterised by a large proportion of grey infrastructure (buildings and sealed surfaces), intermingled with managed greenery and few remnants of natural vegetation. This brings about physical changes that have a strong influence on the ability of native species to persist. Human population density, road density and air and soil pollution tend to be greatest at the interior, or core, of urban areas (Pickett *et al.* 2001). Such adverse conditions create changes to ambient temperature, rainfall, soil quality, and other abiotic indicators of environmental change (McKinney 2002). At the same time, heavily urbanised interiors typically lack native remnant vegetation, or even ruderal or managed vegetation, leaving few prospects as viable habitat for the majority of species (Whitney 1985).

1.1.1 Urban 'avoiders', 'adapters' and 'exploiters'

As can be expected in community ecology, animal and plant species respond in different ways to drastic land-use changes brought about by urbanisation from highly complex habitats in rural areas to highly simplified ones in cities. A convenient way to classify species along this rural to urban gradient is to use the urban responses of 'avoiders', 'adapters' or 'exploiters', a concept first coined by Blair (1996). These categories and their definitions (taken from McKinney 2002) are:

i. **Urban avoiders** are species that are sensitive to anthropogenic disturbance such as habitat loss, and are restricted to the interiors of large habitat patches;
ii. **Urban adapters** are species found in the matrix of suburban landscapes and typically depend on human-subsidised resources such as cultivated plants for food. They are often adapted to the forest edge and the surrounding open areas (Adams 1994).
iii. **Urban exploiters** are almost totally dependent on human resources and are well-suited to an intensely modified environment of open areas.

The three urban response guilds are distinguished by the extent to which they depend on human-subsidised resources to survive in an area (Johnston 2001). These terms have mostly been applied to birds (e.g. Leveau (2013); Ikin *et al.* (2013)), the most studied taxonomic group, but they are have also been adopted for butterflies, lizards and bats (Blair & Launer 1997; Germaine & Wakeling 2001; Jung & Kalko 2011). Although there have been some recent adaptations of Blair's framework and new categories proposed (e.g. Fischer *et al.* (2015)), classifying species as avoiders, adapters, or exploiters provides a useful starting point for conceptualising how ecological communities are shaped and supported in urban environments.

1.1.2 Geographic and taxonomic biases in urban wildlife studies

There has been increasing academic interest in urban wildlife research in the fields of animal behaviour, conservation, landscape ecology, and population ecology, although as of 2010 this still only represented <2% of publication volume (Magle *et al.* 2012). Most of these studies have been undertaken in North America, Europe and Australia, with only 10% of the urban wildlife literature originating from sites in Asia, South America or Africa. As these regions are arguably more biodiverse, there is a real risk that our understanding of how wildlife persists in the world's cities is oversimplified to fit the observations of predominantly temperate regions.

Taxonomically, the vast majority of urban wildlife studies have focused on responses of birds and mammals, and there are extensive reviews on the effects of urbanisation on the former (Marzluff 2001; Chace & Walsh 2006). However, avian responses do not always reflect those of other taxonomic groups (Gagné & Fahrig 2007). It is therefore important to extend this sampling bias to other taxa that may respond in idiosyncratic ways (Beninde, Veith & Hochkirch 2015; MacGregor-Fors *et al.* 2015) (Coleman & Barclay 2012), and which may thereby require specific management interventions. Of the urban mammal fauna studied, bats are underrepresented because they are cryptic, difficult to study and less charismatic compared to other mammals in urban areas (Gehrt & Chelsvig 2003). Insectivorous bats are known to exist in many urban areas worldwide (van der Ree & McCarthy 2005), which may have contributed to this lack of representation in the urban literature compared to more charismatic mammals.

1.2 Bats in the urban environment

Bats are the second most diverse order of mammals after rodents and there are more than 1100 extant species recorded (Simmons 2005) Approximately a quarter of the world's bat species are globally threatened (Mickleburgh, Hutson & Racey 2002), though this is likely to be an underestimate as an update on conservation status is long overdue. The underlying cause of global threat to bats is anthropogenic changes to the landscape resulting in loss of roosting and foraging habitats (Mickleburgh, Hutson & Racey 2002).

1.2.1 Land-use transition in tropical regions

A typical land use transition in tropical countries involves forests that are first logged, then fragmented and replaced with agriculture. As countries develop these agricultural lands have gradually been urbanised. The wildlife retained in urban areas is therefore a poorer subset of the original native flora and fauna, and has been influenced by land use change processes acting at various spatial and temporal scales long before the area became urban. It is now well established that logged forest can support a large proportion of the biodiversity found in old growth forest for many taxa (Gibson *et al.* 2011), including tropical bats (Bicknell *et al.* 2014). However, a comparison of studies from logged and unlogged forests show that there are differences in bat community structure and composition, and species loss is likely if forests do not recover from logging disturbance (Meyer, Struebig & Willig 2015). As forests become fragmented – reduced in size and more isolated – ecological communities undergo further changes in structure, with area and isolation-dependent declines in some species leading to local extinctions (Ewers & Didham 2006). In the Asian tropics, small forest fragments (ca. 100-350 ha) exhibit declines in bat abundance and richness, with the species composition of the smallest fragments dominated by common and generalist species (Struebig *et al.* 2008). Agricultural conversion presents a further reduction of biodiversity, as resulting habitats have simplified vegetation structure and offer comparatively fewer resources. The overall impact of agriculture on bat species diversity varies by land-use type and management system (Meyer, Struebig & Willig 2015), but in general, simple agroforestry systems (e.g. cacao under traditional shade regime; (Faria 2006)) can potentially support more species than intensively managed monocultures (e.g. industrial-scale oil palm, Fitzherbert *et al.* (2008); Fukuda *et al.* (2009))

1.2.2 Characteristics of urban bats

Bats often comprise a significant portion of the remaining mammalian fauna in urban environments (van der Ree & McCarthy 2005; Jung & Kalko 2011). From the studies available, bats are generally sensitive to urbanisation, although this is dependent on the scale of analysis, and responses are likely to be species-specific (Russo & Ancillotto 2015). Hence, chiropterans may serve as bio-indicators of environmental change and habitat quality in these rapidly developing areas (Jones *et al.* 2009).

Extrinsic factors such as habitat loss and degradation are responsible for the direct population declines of bat species, but it is intrinsic factors (i.e. biological traits) that determine how a species responds to such a decline, and the ability to recover and expand population to colonise new areas (Racey & Entwistle 2003). Insectivorous bat species are broadly classified into three groups based on differences in wing morphology and foraging ecology (McKenzie *et al.* 1995):

i) open space foragers;
ii) forest edge and gap foragers; and
iii) cluttered or narrow-space foragers.

Given the open nature of urban environments, most bats in the urban areas are expected to be open space foragers, which achieve fast flight at the cost of manoeuvrability due to their high aspect ratio and wing loading (Aldridge &

Rautenbach 1987; Norberg & Rayner 1987). However, several species of pipistrelles in Europe, such as the common pipistrelle (*Pipistrellus pipistrellus*), can thrive in urban areas despite being forest edge/gap foragers (Dietz *et al.* 2009). Conversely, the wings of narrow-spaced foragers have low aspect ratio and low loading and hence these species perform slow but highly manoeuvrable flight - typically in the forest understorey (Aldridge & Rautenbach 1987; Norberg & Rayner 1987). In Southeast Asia, narrow-space foragers in the families Rhinolophidae, Hipposideridae and some vespertilionids of the subfamilies Kerivoulinae and Murinae are speciose and they are expected to be very susceptible to habitat disturbance because they have energetically expensive flights coupled with specialised echolocation calls for prey detection in cluttered habitats such as forests (Kingston *et al.* 2003; Norberg & Rayner 1987). Although earlier studies demonstrated association between likelihood of extinction and wing morphology across bat species (Jones, Purvis & Gittleman 2003; Safi & Kerth 2004), Meyer *et al.* (2008) found limited support from his study of vulnerability to habitat fragmentation in neotropical bats.

1.2.3 Potential ecosystem services linked to urban bats

Bats have a rich variety of diets, feeding on both plant and animal matter. They support and sustain both natural and human dominated ecosystems by being primary, secondary and tertiary consumers, and hence, they are of value to ecosystems by performing arthropod suppression, seed dispersal and pollination (Kunz *et al.* 2011). However, only recently have we begun to investigate and understand these ecosystem services. For example, the ecosystem service of mango pollination provided by Indian flying foxes *Pteropus giganteus* in Pakistan (with sizeable populations in urban Lahore) has been valued at US$16.5 million in the fiscal year of 2007 (Mahmood-Ul-Hassan *et al.* 2010). Bats also play a role in arthropod suppression and are known to be important insect pest predators in agricultural habitats of Southeast Asia. For example, in cacao plantations in Indonesia, bats as well as birds, are responsible for increasing yield by decreasing the abundance of insect herbivores (Maas, Clough & Tscharntke 2013). Similarly, in Thailand, Wanger *et al.* (2014) found that wrinkle-lipped bats (*Tadarida plicata*) feed on the white-backed planthopper (*Sogathella furcifera*), a major rice pest in Asia, thereby protecting the rice crop, which is a critical source of food and income of local people. It is estimated that this bat species secures food for 26,200 people and protects almost 2,900 tons rice per year, worth more than USD 1.2 million annually (Wanger *et al.* 2014). These examples of the roles of hyper-abundant generalist bat species highlight the importance of ensuring conservation represents the needs of common but functionally important species as well as those that are rare and threatened. Many of the species retained in urban areas can be described as common and generalist.

1.2.4 Urban landscape ecology of bats

There has been an increasing number of landscape studies involving bats in urban areas (and other habitats) in recent years. Most of these studies have found that bat diversity is greatest in more natural areas but is reduced with increasing urbanisation

(Kurta & Teramino 1992; Gaisler *et al.* 1998; Lesinski, Fuszara & Kowalski 2000; Jung & Kalko 2010). In a meta-analysis of 23 studies collated globally on the urban landscape ecology of bats, Jung & Threlfall (2016) found that a high degree of urbanisation had a strong negative effect on habitat use compared to an intermediate degree of urbanisation. Hale *et al.* (2012) found that increasing density of landscape urbanisation has negative effects on the bat community. The bat species studied were sensitive to the composition and structure of the urban form at various spatial scales, and the authors argued that argued that planners and developers should specify development densities using information on ecological thresholds (Hale *et al.* 2012).

The impacts of land use and landscape changes on species behaviour remain a challenge for the conservation of species in urban areas. Luck *et al.* (2013) investigated the spatial variation in bat communities across 18 towns and cities in south-eastern Australia using a functional guild approach to find out if bat species with similar traits are affected by landscape change in a similar manner. They found that open space foragers (or the open-adapted guild) were not negatively affected by urbanisation compared to clutter-adapted species, which favoured native vegetation and appeared to be negatively affected by urbanisation (Luck *et al.* 2013). This observation seems to be supported by a study by (Threlfall *et al.* (2011) in Sydney, Australia, who reported that open-adapted bats were associated with more urban areas (higher housing density) compared to cluttered-adapted bats, which preferred areas with more bushland.

One consequence of urbanisation is the creation of habitat fragments within the urban matrix, which results in a heterogeneous landscape that benefits some urban-tolerant bats in terms of foraging opportunities(Jung & Kalko 2010). The urban matrix here is defined as a patchwork of various land use types such as industrial, low and high-density residential, green spaces, abandoned lots and transportation corridors (roads and railways) (Faeth, Saari & Bang 2012). In two counties in Chicago, Gehrt & Chelsvig (2004) studied the species-specific patterns of bat activity and found more bat species in habitat fragments within urban areas compared to habitat fragments in rural areas. They concluded that this relationship between urbanisation and bats depends on the context of a larger landscape scale and the quality of habitat patches within the urban matrix. Conversely, Coleman & Barclay (2011) found that habitat heterogeneity created by urbanisation in the prairies of North America favoured only the little brown bat *Myotis lucifugus* in terms of roosting sites but did not increase the individual fitness of these urban-adapted bats.

1.3 Singapore as a case study

Singapore is possibly the most modified country in the tropics in terms of development and urbanisation. This makes it an ideal case study to learn about the effects of extreme urbanisation, in order to inform the urbanisation of other countries as they continue to develop.

Singapore is an island city-state located near the equator (1°20’N, 103°50’E), south of the Malay Peninsula. The country comprises Singapore island and 58 smaller islands, all totalling 719.2 km^2 in land area (Department of Statistics Singapore 2016). Singapore is aseasonal and experiences an equatorial climate with daily temperatures ranging between 24 to 32 °C and a mean annual rainfall of more than 2000 mm that is uniformly distributed throughout the year, but with slightly more rain during the Northeast monsoons, which occurs between November to January (Meteorological Service Singapore 2016). There is very little variation in mean temperature between days and months.

When Sir Stanford Raffles founded Singapore in 1819, the island had a population of about 150 people (excluding the nomadic *Orang Laut* or 'sea-people' who lived in boats in the river system and estuaries) (Jackson 1965) and the island's natural habitats of rainforests, freshwater swamps, mangroves, mudflats and sandbars and corals reefs were largely intact (Tan *et al.* 2015). The transformation of Singapore from a small British trading outpost to a modern metropolis of economic success of today under two centuries came at a heavy price for its biodiversity. Singapore is considered by some to be an ecological "worst case scenario" in terms of economic and urban development in the tropics, and presents the rest of the Southeast Asian region with a glimpse of what intense habitat modification would entail for biodiversity conservation (Sodhi *et al.* 2004).

Two major landscape changes were responsible for the ecological transformation of Singapore and the extinction of native species - deforestation and urbanisation - (Corlett 1992) and these two changes occurred concurrently. While deforestation of the main island was largely completed by the end of 1900 as a result of the planting of cash crops such as gambier and rubber, urbanisation still occurs today with the urban portion of the country comprising 39% of total land area (Corlett 1992; Yee *et al.* 2011). The seaward reclamation of land since 1820 added 141 km^2 of land at the expense of coastal habitats such as mangroves and coral reefs (Hilton & Manning 1995). This represented an increase of 24% in land area to meet the housing and industrialisation needs of the land-scarce nation.

Land-use conversion and deforestation meant that biodiversity suffered a drastic loss in Singapore, extirpating 34-87% of the original butterfly, fish, bird and mammal species (Brook, Sodhi & Ng 2003). The current bat fauna of Singapore is modest, with just 25 species present compared to >100 species on the neighbouring Malay Peninsula (Simmons 2005). It is estimated that between 33-72% of the bat species have gone extinct since 1819, with forest dependent bats such as rhinolophid and hipposiderid bats faring the worst (Lane, Kingston & Lee 2006). This observation does not bode well for the forecast of extinction rates for bat species throughout the rest of Southeast Asia where species losses are expected to exceed 40%, with 23% of Southeast Asia’s bat fauna anticipated to be extinct by 2100, given the widespread deforestation and habitat loss in the region (Lane, Kingston & Lee 2006).

In a review of urban ecological studies in Singapore conducted between 1991-2012, Tan & Abdul Hamid (2014) found that majority of the studies dealt with biodiversity, with a main focus on pattern, which was to characterise the composition and spatial distribution of biodiversity. There were some studies dealing with process, which is the characterisation of interactions between species and aspects of the urban environment. But mechanistic studies (to investigate mechanisms that lead to species and ecosystem responses to urbanisation, and resulting in observed patterns and processes) were clearing lacking (Tan & Abdul Hamid 2014). They called for more mechanistic studies in urban ecology and argued that future urban ecological studies should be applied in nature and linked to urban sustainability, focusing more on the built component of the urban ecosystem (Tan & Abdul Hamid 2014). For instance, research should be directed at how vertical spaces can be made more biodiversity-friendly in a city environment.

1.3.1 Singapore’s environmental policy context

Since independence, it has been recognised by the founding Prime Minister of Singapore, Mr. Lee Kuan Yew, that greenery provision is important for the economy and pride of the country, and for the well-being of her people. He always believed that

"… a blighted urban landscape, a concrete jungle, destroys the human spirit. We need the greenery of nature to lift our spirits."

The greening objectives of Singapore are the responsibility of the National Parks Board (NParks), which seeks to transform the “Garden City” to a “City in a Garden”. NParks is the authority on urban greening and biodiversity conservation in Singapore, maintaining and managing 62 regional parks, 275 neighbourhood parks, 70 park connectors (multi-use paths connecting one park to another) that are 303 km in total length, in addition to 2676 ha of roadside greenery, 3347 ha of nature reserves, and other open green spaces (National Parks Board 2016). In addition, NParks also sets the standards for the provision of greenery buffers and planting strips, and administers the legislation for the protection of large and significant trees (National Parks Board 2011). In recent years, NParks has also devised a nature conservation masterplan to guide Singapore in creating a “biophilic city” — a city that is filled with biodiversity close to a large population, and getting the population to care for and co-exist with the biodiversity around them so as to bring about a more sustainable and liveable city (Beatley 2011; Er & Chan 2016).

In Southeast Asia where the bat fauna is highly diverse (at least 337 species reported, representing 25% of the World’s bats (Kingston 2013), the patterns of bat habitat use in most cities and towns have not yet been characterised, in part due to a lack of interest of urban bats in the scientific community. Research on bat ecology is still in its infancy in Southeast Asia and is very much focused on patterns (i.e. distribution of species), rather than processes (i.e. species performance) or mechanisms (e.g. predation). Within this geographic region Singapore represents an important case study from which much can be learned on urban ecology and the prospects for wildlife in developing Asian countries. Singapore is a highly urbanised city-state that has achieved great economic prosperity, but has also experienced a dramatic ecological transformation and lost much its biodiversity (Davison, Tan & Lee 2012). As one of the original ‘tiger’ economies the city island serves as an aspirational end point in the development of rural to urban economies in Southeast Asia.

1.4 Thesis aim and structure

In this thesis, I aim to use different acoustic methods to study the tropical urban environment of Singapore but with a focus on applied urban ecology of insectivorous bats. I investigate the processes determining bat activity and diversity in heavily urbanised Singapore in relation to major roads and green roof infrastructure.

Chapter 2 provides an overview of the bat acoustic equipment, survey approaches and considerations when planning and implementing an acoustic survey of bats. This forms part of a document written to provide a resource manual for the increasing number of bat researchers in Southeast Asia, and to encourage the uptake of acoustic methods in the ecological study of bats in a region of high bat diversity. These acoustic survey guidelines were subsequently used in the study designs of Chapter 3 and 4.

In Chapter 3, I examine the effects of major roads on bat activity and influence that different land covers surrounding the road can have on this. I examine the response of bats to roads by sampling activity at varying distances away from major highways in the middle of Singapore. I also identify key abiotic and land cover variables that predict bat activity near to roads, and recommend mitigation measures for forest-dependent bats that could be experiencing a road barrier effect.

In Chapter 4, I investigate the value of green roofs, more specifically intensive green roofs, and their role as habitat for bats. Hypotheses tested include those informed by island biogeography theory (more activity on larger roofs than smaller ones), vertical isolation (more bat activity on ‘low’ roofs compared to ‘high’ roofs), management regimes (more maintenance results in lower bat activity), and landscape factors (more bat activity on roofs surrounded by more urban greenery). I discuss the predictors of bat activity in relation to the building and operation of green roofs and how to make them more biodiversity-friendly in the future.

Chapter 5 is a study of applied soundscape ecology to elucidate the effects of transboundary smoke-haze pollution on biodiversity in the Southeast Asian region. Here I define bioacoustic activity more broadly at the level of a soundscape community before, during and after the haze (using four common indices of soundscape activity), and match these datasets to changes in the pollution standard index (PSI) over a period of a year. I discuss the implications of my findings and the role that soundscape ecology can play in large-scale environmental monitoring.

Finally, **Chapter 6** is a general discussion of the results, emphasizing the implications of my work and future research directions.

1.5 References

Adams, L.W. (1994) Urban Wildlife Habitats: A Landscape Perspective. *Wildlife Habitats*, **3**, 194.

Aldridge, H.D.J.N. & Rautenbach, I.L. (1987) Morphology, Echolocation and Resource Partitioning in Insectivorous Bats. *Journal of Animal Ecology*, **56**, 763–778.

Beatley, T. (2011) Biophilic Cities: What Are They ? *Biophilic Cities: Integrating Nature into Urban Design and Planning*, pp. 45–81.

Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, **18**, 581–592.

Bicknell, J.E., Struebig, M.J., Edwards, D.P. & Davies, Z.G. (2014) Improved timber harvest techniques maintain biodiversity in tropical forests. *Current Biology*, **24**, R1119–R1120.

Blair, R.B. (1996) Land use and avian species diversity along an urban gradient. *Ecological Applications*, **6**, 506–519.

Blair, R.B. & Launer, A.E. (1997) Butterfly diversity and human land use: Species assemblages along an urban gradient. *Biological Conservation*, **80**, 113–125.

Brook, B.W., Sodhi, N.S. & Ng, P.K.L. (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**, 420–426.

Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: A review. *Landscape and Urban Planning*, pp. 46–69.

Coleman, J.L. & Barclay, R.M.R. (2011) Influence of urbanization on demography of little brown bats (Myotis lucifugus) in the prairies of north america. *PLoS ONE*, **6**.

Coleman, J.L. & Barclay, R.M.R. (2012) Urbanization and the abundance and diversity of Prairie bats. *Urban Ecosystems*, **15**, 87–102.

Corlett, R. (1992) The ecological transformation of Singapore, 1819-1990. *Journal of Biogeography*, **19**, 411–420.

Davison, G., Tan, R. & Lee, B.P.Y.-H. (2012) *Wild Singapore*. John Beaufoy Publishing, United Kingdom.

Department of Statistics Singapore. (2016) Statistics Singapore - Population & Land Area, http://www.singstat.gov.sg/statistics/latest-data#16

Dietz, C., von Helversen, O. & Nill, D. (2009) *Bats of Britain, Europe & northwest Africa*. A & C Black Publishers Ltd., United Kingdom.

Er, K. & Chan, L. (2016) Networks for biodiversity. *Urban Solutions*.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Faeth, S.H., Saari, S. & Bang, C. (2012) Urban biodiversity: Patterns, processes and implications for conservation. *eLS*, 12.

Faeth, S.H., Warren, P.S., Shochat, E. & Marussich, W. (2005) Trophic Dynamics in Urban Communities. *BioScience*, **55**, 399.

Faria, D. (2006) Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest, Brazil. *Journal of Tropical Ecology*, **22**, 531–542.

Fischer, J.D., Schneider, S.C., Ahlers, A.A. & Miller, J.R. (2015) Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, **29**, 1246–1248.

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F. & Phalan, B. (2008) How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution*, **23**, 538–545.

Fukuda, D., Tisen, O.B., Momose, K. & Sakai, S. (2009) Bat diversity in the vegetation mosaic around a lowland dipterocarp forest of Borneo. *Raffles Bulletin of Zoology*, **57**, 213–221.

Gagné, S.A. & Fahrig, L. (2007) Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. *Landscape Ecology*, **22**, 205–215.

Gaisler, J., Zukal, J., Rehak, Z. & Homolka, M. (1998) Habitat preference and flight activity of bats in a city. *Journal of Zoology*, **244**, 439–445.

Gehrt, S.D. & Chelsvig, J.E. (2003) Bat activity in an urban landscape: Patterns at the landscape and microhabitat scale. *Ecological Applications*, **13**, 939–950.

Gehrt, S.D. & Chelsvig, J.E. (2004) Species-specific patterns of bat activity in an urban landscape. *Ecological Applications*, **14**, 625–635.

Germaine, S.S. & Wakeling, B.F. (2001) Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biological Conservation*, **97**, 229–237.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, **478**, 378–381.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bal, X. & Briggs, J.M. (2015) Global Change and the Ecology of Cities Global Change and the Ecology of Cities. *Science (New York, N.Y.)*, **319**, 756–760.

Hale, J.D., Fairbrass, A.J., Matthews, T.J. & Sadler, J.P. (2012) Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large UK conurbation. *PLoS ONE*, **7**.

Hilton, M.J. & Manning, S.S. (1995) Conversion of Coastal Habitats in Singapore: Indications of Unsustainable Development. *Environmental Conservation*, **22**, 307–322.

Ikin, K., Knight, E., Lindenmayer, D.B., Fischer, J. & Manning, A.D. (2013) The influence of native versus exotic streetscape vegetation on the spatial distribution of birds in suburbs and reserves. *Diversity and Distributions*, **19**, 294–306.

Jackson, J.C. (1965) Chinese agricultural pioneering in Singapore and Johore, 1800-1917. *Journal of the Malayan Branch of the Royal Asiatic Society*, **38**, 77–105.

Johnston, R.F. (2001) Synanthropic birds of North America. *Avian ecology and conservation in an urbanizing world*, p. 585.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93–115.

Jones, K.E., Purvis, A. & Gittleman, J.L. (2003) Biological correlates of extinction risk in bats. *The American naturalist*, **161**, 601–614.

Jung, K. & Kalko, E.K. V. (2010) Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *Journal of Mammalogy*, **91**, 144–153.

Jung, K. & Kalko, E.K. V. (2011) Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Diversity and Distributions*, **17**, 262–274.

Jung, K. & Threlfall, C.G. (2016) Urbanisation and its effects on bats - A global meta-analysis. *Bats in the Anthropocene: Conservation of Bats in a Changing World*, pp. 13–33.

Kingston, T., Francis, C.M., Akbar, Z. & Kunz, T.H. (2003) Species richness in an insectivorous bat assemblage from Malaysia. *Journal of Tropical Ecology*, **19**, 67–79.

Kunz, T.H., de Torrez, E., Bauer, D., Lobova, T. & Fleming, T.H. (2011) Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, **1223**, 1–38.

Kurta, A. & Teramino, J.A. (1992) Bat community structure in an urban park. *Ecography*, **15**, 257–261.

Lane, D.J.W., Kingston, T. & Lee, B.P.Y.H. (2006) Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. *Biological Conservation*, **131**, 584–593.

Lesinski, G., Fuszara, E. & Kowalski, M. (2000) Foraging areas and relative density of bats (Chiroptera) in differently human transformed landscapes. *Zeitschrift für Säugetierkunde*, **65**, 129–137.

Leveau, L. (2013) Bird traits in urban-rural gradients: how many functional groups are there? *Journal of Ornithology*, **154**, 655–662.

Luck, G.W., Smallbone, L., Threlfall, C. & Law, B. (2013) Patterns in bat functional guilds across multiple urban centres in south-eastern Australia. *Landscape Ecology*, **28**, 455–469.

Maas, B., Clough, Y. & Tscharntke, T. (2013) Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters*, **16**, 1480–1487.

MacGregor-Fors, I., Avendaño-Reyes, S., Bandala, V.M., Chacón-Zapata, S., Díaz-Toribio, M.H., González-García, F., Lorea-Hernández, F., Martínez-Gómez, J., Montes de Oca, E., Montoya, L., Pineda, E., Ramírez-Restrepo, L., Rivera-García, E., Utrera-Barrillas, E. & Escobar, F. (2015) Multi-taxonomic diversity patterns in a neotropical green city: a rapid biological assessment. *Urban Ecosystems*, **18**, 633–647.

Magle, S.B., Hunt, V.M., Vernon, M. & Crooks, K.R. (2012) Urban wildlife research: Past, present, and future. *Biological Conservation*, **155**, 23–32.

Mahmood-Ul-Hassan, M., Gulraiz, T.L., Rana, S.A. & Javid, A. (2010) The diet of Indian Flying-Foxes (*Pteropus giganteus*) in urban habitats of Pakistan. *Acta Chiropterologica*, **12**, 341–347.

Marzluff, J. (2001) Worldwide urbanization and its effects on birds. *Avian ecology and conservation in an urbanizing world*, 19–47.

McDonnell, M.J. & Pickett, S.T.A. (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*, **71**, 1232–1237.

McKenzie, N.L., Gunnell, A.C., Yani, M. & Williams, M.R. (1995) Correspondence between flight morphology and foraging ecology in some paleotropical bats. *Australian Journal of Zoology*, **43**, 241–257.

McKinney, M.L. (2002) Urbanization, Biodiversity, and Conservation. *BioScience*,

52, 883.

Meteorological Service Singapore. (2016) Climate of Singapore, http://www.weather.gov.sg/climate-climate-of-singapore/

Meyer, C.F.J., Fründ, J., Lizano, W.P. & Kalko, E.K. V. (2008) Ecological correlates of vulnerability to fragmentation in Neotropical bats. *Journal of Applied Ecology*, **45**, 381–391.

Meyer, C.F.J., Struebig, M.J. & Willig, M.R. (2015) Responses of tropical bats to habitat fragmentation, logging, and deforestation. *Bats in the Anthropocene: Conservation of Bats in a Changing World*, pp. 63–103.

Mickleburgh, S.P., Hutson, A.M. & Racey, P.A. (2002) A review of the global conservation status of bats. *Oryx*, **36**, 18–34.

National Parks Board. (2011) *Handbook on Tree Conservation & Tree Planting Provision for Development Projects*.

National Parks Board. (2016) *Green Matters - NParks Annual Report 2016/2017*.

Norberg, U.M. & Rayner, J.M. V. (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **316**, 335–427.

Pickett, S.. T.A., Cadenasso, M.. L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.. C. & Costanza, R. (2001) Urban Ecological Sysytems : Linking Terrestrial Ecological , Physical , and Socioeconomic of Metropolitan Areas. *Annual Review of Ecology and Systematics*, **32**, 127–157.

Racey, P. & Entwistle, A. (2003) Conservation Ecology of Bats. *Bat Ecology* (eds T. Kunz & M. Fenton), pp. 680–743. The University of Chicago Press.

van der Ree, R. & McCarthy, M. a. (2005) Inferring persistence of indigenous mammals in response to urbanisation. *Animal Conservation*, **8**, 309–319.

Rompré, G., Robinson, W.D. & Desrochers, A. (2008) Causes of habitat loss in a Neotropical landscape: The Panama Canal corridor. *Landscape and Urban Planning*, **87**, 129–139.

Russo, D. & Ancillotto, L. (2015) Sensitivity of bats to urbanization: A review. *Mammalian Biology*, **80**, 205–212.

Safi, K. & Kerth, G. (2004) A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology*, **18**, 1293–1303.

Simmons, N. (2005) Order Chiroptera. *Mammal species of the world* (eds D. Wilson & D. Reeder), pp. 312–529.

Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K.L. (2004) Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*, **19**, 654–660.

Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A. & Rossiter, S.J. (2008) Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation*, **141**, 2112–2126.

Tan, P.Y. & Abdul Hamid, A.R. bin. (2014) Urban ecological research in Singapore and its relevance to the advancement of urban ecology and sustainability. *Landscape and Urban Planning*, **125**, 271–289.

Tan, C.K.W., O’Dempsey, T., Macdonald, D.W. & Linkie, M. (2015) Managing present day large-carnivores in ‘island habitats’: lessons in memoriam learned from human-tiger interactions in Singapore. *Biodiversity and Conservation*, **24**, 3109–3124.

Threlfall, C., Law, B., Penman, T. & Banks, P.B. (2011) Ecological processes in urban landscapes: Mechanisms influencing the distribution and activity of insectivorous bats. *Ecography*, **34**, 814–826.

Wanger, T.C., Darras, K., Bumrungsri, S., Tscharntke, T. & Klein, A.M. (2014) Bat pest control contributes to food security in Thailand. *Biological Conservation*, **171**, 220–223.

Whitney, G.G. (1985) A quantitative analysis of the flora and plant communities of a representative midwestern U.S. town. *Urban Ecology*, **9**, 143–160.

Yee, A.T.K., Corlett, R.T., Liew, S.C. & Tan, H.T.W. (2011) The vegetation of Singapore — an updated map. *Gardens' Bulletin Singapore*, **63**, 205–212.

2. Acoustic sampling guidelines for surveys of Southeast Asian bats

This chapter formed part of an acoustic guidelines document commissioned by the Southeast Asian Bat Conservation Research Unit (SEABCRU) in 2015 - http://www.seabcru.org/. The document received additional review by Joe Huang and Tigga Kingston of Texas Technical University, and the writing was simplified to help target to ecologists of Southeast Asian countries (i.e. non-specialist on acoustic methods with English as a second language). The final version included an additional section on reference call library development by Joe Huang and will be published electronically in 2018.

2.1 Abstract

The use of acoustic monitoring for bat research offers several advantages over capture-based methods, including being non-invasive, able to detect species that avoid capture, easier to sample in difficult terrain, and able to be left unattended for extended periods in the field. Acoustic sampling therefore promises greater sampling efficiency, thereby saving research resources. However, the uptake of acoustic methods to conduct ecological studies of bats in Southeast Asia has been slow due to a combination of prohibitive cost of equipment, lack of expertise and scarcity of information. Recently, bat detectors have become more affordable, and capacity building in expertise is underway in some countries and sectors. However, an incomplete knowledge of bat echolocation calls is still an important research barrier. For bat calls to be useful in ecological research, one needs to understand the variation of echolocation call characteristics within and between taxa over a large part of a species distribution range. Here, I present part of a resource manual specially written for the bat researchers of Southeast Asia that gives an overview of the different types of bat detecting equipment available, and considerations to take when designing, managing and implementing acoustic bat surveys. It is envisaged that these guidelines will promote best practices and standardized information sharing for more collaborative work on bat ecology using acoustic surveys in Southeast Asia. In addition, a partial list of bat calls from Singapore are presented, which forms the basis of bat species identification for research in the proceeding chapters. *Rhinolophus stheno* is recorded for the first time in Singapore based on acoustic sampling.

2.2 Introduction

The nocturnal and cryptic nature of bats makes survey and monitoring using capture methods difficult relative to other animal groups. This is particularly an issue in tropical regions, which are characterized by high biodiversity, poorly resolved taxonomy, and challenging working environments (Harrison *et al.* 2012). Acoustic techniques (i.e. those that sample bats from the ultrasonic sounds they produce) offer a potential alternative to capture techniques for sampling echolocating bats. However, the effective application of these techniques, requires an understanding of the ecology of bat species, and both the levels of inter- and intra-species variation in echolocation calls in order to identify a bat species from its echolocation call (Russ 2012). If used appropriately, acoustic methods offer some clear advantages over capture methods for studying bats. For example:

1. *Non-invasive sampling*: animal handling is avoided. This has clear ethical benefits, and is particularly useful for sampling highly sensitive populations, while also helping minimize cross-contamination between individuals.
2. *Detecting species that can avoid capture:* this is particularly useful for species that forage in edges and more open areas and are known to detect and avoid mist nets (e.g. Pipistrelles). High-flying aerial insectivorous species are also potentially more easily sampled by acoustic methods, whereas they are near-impossible to capture unless at roost.
3. *Detecting species that are logistically difficult to sample*: acoustic detectors can be set in a variety of habitats and terrain types in closed and

open areas, in places where it is logistically unfeasible to capture bats. This means that sampling can often be more standardized and systematic.

4. *Can be left unattended for long periods*: several acoustic monitoring products are capable of recording continuously for long periods regardless of weather and environmental conditions, which offers opportunities for long-term monitoring of sites.
5. *Higher sampling efficiency:* acoustic sampling can involve considerable savings in field time compared to capture techniques, as the main costs concern equipment. However, acoustic sampling involves a lot more time spent processing recordings.

Acoustic methods are now therefore routinely used by bat researchers in many European countries, as well as North America, and Australia, where most bat species are quite well known, and their echolocation calls are well characterized. The use of acoustic methods is also gaining ground in the Neotropics with the development of bat call classifiers (see http://www.wildlifeacoustics.com/products/kaleidoscope-software-ultrasonic/classifiers.) However, the uptake of acoustic methods has been relatively slow elsewhere in the tropics, and this is particularly true of Southeast Asia. Here, several research groups currently use acoustic methods to characterize the echolocation calls of certain bat species for identification purposes, but few people use detectors to survey and monitor bats.

To date, the main barriers to implementing acoustic monitoring studies in Southeast Asia have been cost, expertise, and the scarcity of information available for the region's bat fauna. However, costs are reducing, and expertise is improving rapidly.

Therefore, our main barrier remains lack of information, and specifically, knowledge of the echolocation calls that these bats produce (Harrison *et al.* 2012). We need to know which species produce which calls, but we also need to better understand the variation of echolocation characteristics within and between taxa over large geographic parts of the region. Collectively, bat researchers in Southeast Asia are beginning to tackle these problems, and explore the use of acoustic methods to survey and monitor some bats in certain circumstances.

Here we present an overview of acoustic survey approaches, and outline the main factors that bat researchers should consider when planning and implementing an acoustic survey. We first **review the types of equipment available** and their potential advantages and disadvantages from a technical, financial and ecological perspective. We then **review the ways in which acoustic surveys can be designed, managed and implemented**, and suggest ways to archive and share information on new records and discoveries for the first time.

These guidelines are not intended to be prescriptive, and review the technologies available in 2015. The science and technologies involved in bioacoustics are constantly changing, and many designs and procedures have not yet been well tested in Southeast Asia. However, based on the experiences of a few bat researchers trialing acoustic survey approaches in the region, we hope that following common best-practices and standardized information sharing will help us collectively overcome some of the barriers that currently hinder our abilities to use acoustic surveys as widely as we would like.

2.3 What detector? Choosing and using acoustic recording devices

Understanding the science behind bat bioacoustics, surveys and monitoring can be quite a steep learning process. Although one of the main considerations of detector selection decisions is often cost, the most important thing for users to consider is the objective of their research (Adams *et al.* 2012). This influences the selection of equipment and how it will be used. Fundamentally, using inappropriate equipment for your research objective has serious implications for results. Therefore, users need to think very carefully about what questions their research is designed to address, before they choose equipment.

Here we distinguish between the two primary uses of acoustic equipment - collecting voucher calls for bat echolocation libraries, and implementing field surveys/monitoring. Although some devices can be used interchangeably for these purposes, the design features for field surveys tend to be a trade off against requirements for detailed sound recording.

2.3.1 Key specifications to consider in acoustic recorders

Key considerations for all acoustic research include **microphone sensitivity** and the **sampling rate**. These features are particularly important for collecting high quality echolocation calls for reference libraries, but are also useful to consider for designing a survey. The key criteria here are that microphones need to be sufficiently sensitive, and the sampling rate appropriate to record the species, or set of species under study

– many of which may be calling at very high frequencies. See Table 2.1 for examples of recording devices that fulfill these criteria for Southeast Asian bats.

The **sampling rate** is the number of times a signal is “sampled” over a period of time (Russ 2012). This affects the maximum recordable frequency in any detector, and the Nyquist criterion dictates that the maximum recordable frequency is approximately half of the sampling frequency (Parson & Szewczak 2009). For example, the minimum sampling rate of a full-spectrum detector should be at least 300 kHz to record a vocalization with a high frequency of 150 kHz. However, further constraints are imposed by the recording equipment, so the highest frequency obtained might actually be lower than this. Therefore, users need to check the specifications of the equipment used. Most manufacturers will advise on these features.

Frequency range / recording bandwidth is the range of frequencies over which the detector can record effectively (has a flat response). This is a property of the microphone and the common cut-off is 120 kHz. Recordings can be made at higher frequencies but quality and sensitivity to these frequencies might be compromised.

Bit resolution relates to the signal-to-noise ratio, which in turn determines the detail and clarity of the bat calls displayed as sonograms. A detector with a high bit resolution has better signal-to-noise ratio, which gives detailed recordings of bat calls. The downside of a high bit resolution is that it creates large files, thus taking up storage space quickly. A bit resolution of 16 would generally suffice for recording bat calls (Russ 2012).

Field research in the tropics is much more challenging than it is in temperate regions where recording devices have been developed. Key factors that also influence detector selection decisions for fieldwork include ruggedness of terrain and weather-proofing, versatility (e.g. storage and power capacity, different recording systems), as well as cost. See Table 2.2 for a comparison of bat recorders that have been designed primarily for field use and have been trialed by SEABCRU researchers in Southeast Asia.

Equipment decisions should also consider the type of sound processing utilized in detectors. Bats tend to produce ultrasonic calls that can be very high in frequency (16 to >220 kHz). Most calls cannot be heard by humans, as the majority of people have a hearing range of 1-15 kHz. Detector microphones need to be sensitive to these high frequencies and the electronic capabilities of bat detectors need to transform the high-frequency sounds into outputs that are audible and/or digitally visible to people. In the past, acoustic research required equipment to first detect sound, a processor to convert the sound to a useable format, and a recorder to store the processed sound in an appropriate format. Most modern acoustic equipment is now able to undertake these three processes into a single device.

2.3.2 Call transformation techniques

There are four main call transformation techniques that are used by bat detectors to transform ultrasonic information: **heterodyne, frequency division (including zero crossing), full spectrum time expansion, and full spectrum direct recording**. An understanding of the concepts behind these different techniques helps us select the most appropriate detector for recording bats for a given situation.

Heterodyning is used in inexpensive bat detectors to convert ultrasound to the audible range for people, and is great for detecting incoming signals in real time (i.e. when the bat is being observed and can be heard from the transformed call at the same time). This has uses for demonstrating bat echolocation to non-specialists, or for surveys of bats with clearly recognized calls such as *Rhinolophus* bats. The trade-off is that heterodyne detectors are usually only capable of monitoring a narrow range of frequencies at any given time (typically c. 10 kHz), so detectors need to be tuned to the target frequency. In addition, because the output signal does not contain any information about call structure, heterodyne systems are unsuitable for bioacoustic analysis, or the monitoring of multiple bat species. Hence, heterodyning will not be discussed further but the reader is encouraged to read a concise account of bat call detecting, recording and analyzing by Parson and Szewczak (2009).

Frequency division (FD) decreases the frequency of a signal by permitting only the *n*th cycle to pass through to an output file to a recording device. This saves on the sampling rate, processing time and storage requirements of the recording, so the system can also operate in real time. Historically, this was necessary to achieve long recording times, because of limitations with memory capacity and cost. It also has clear advantages for active recording where the bat's flight style and behavior can be associated with the incoming signal which can be visualized. Information about bat activity and identification of some species can be reliably performed using an analysis of the frequency-divided signals known as zero crossing. However, although overall call structure is preserved in FD recording, much of the detail of the call is missing because the sound is divided by a factor of *n*. The full spectrum of call information cannot be resolved under this system, and so recordings often lack important information for tropical bat identification, such as harmonics and amplitude. Zero crossing is also unable to resolve separate frequencies if they are received at the same time – i.e. from multiple bats calling in the same recording, or from multiple harmonics from a single call. An example of such a detector is the Anabat SD2 by Titley Electronics. Because this system was widely used before the arrival of full spectrum technologies, several recent detectors can optionally convert back to this file system.

Full spectrum - time expansion (TE) systems work on the principle that if the duration of a sound is increased while leaving the number of sound waves unchanged, then the frequency of the signal will be decreased. For example, if a sound of one-second duration is expanded 10-fold, it will take 10 seconds to produce an output to the detector. Nothing else can be recorded during this time and bats calls may be missed. This technique of sound transformation preserves all the information from the original call (sometimes also referred to as full spectrum time expansion) and hence it is suitable for species identification, and other studies of bat bioacoustics requiring many call parameters, but may be less suitable for long-term monitoring work. The Pettersson D240x is an example of a time expansion bat detector.

Full spectrum - direct recording retains the information on all or most of the echolocation signals without experiencing a lag time in recording. This has been made possible with relatively recent advances in electronics and the advent of capable (and affordable) sound cards that are able to sample sound at much higher rates (250-500 kHz). Examples of equipment using full spectrum direct recording devices include Wildlife Acoustic's Echometer and Songmeter platforms, and the Petersen D1000X.

Table 2.1 Specifications of bat detectors designed for high quality call recordings, and hence highly appropriate for voucher call collection. Adapted from Adams *et al.* (2012) with additional information from product specification sheets of each individual detector. Restricted to those recorders tested by the SEABCRU.

System manufacturer / specifications	**D240X** *Pettersson Elektronic*	**D1000** *Pettersson Elektronik AB*	**Batbox** *Griffin*	**M500** *Pettersson Elektronik AB*
Recording technology	Heterodyne, full spectrum	Heterodyne, frequency division, time expansion, direct recording	Heterodyne, frequency division, time expansion	Direct recording
Frequency range (kHz)	10-120	5 - 235	16-190	Up to 500
Sampling rate (kHz)	307	32-768	705.6	500
Sound file type	.wav	.wav	.wav	.wav
Storage type / max. capacity	1 x SDHC (32 GB)	1 x CF (32GB)	1 x CF (32 GB)	Requires a Windows PC/tablet
Battery	1 x IEC 6LF22 (9 V)	5 x AA	4 x AA	USB bus powered
Microphone type	Advanced electret, built in	High capacitance	Electret (1.5v)	Advanced electret
Microphone directionality	Directional	Omni-directional?	-	Directional / Omni-directional
Recording schedule	Yes (via digital recorder)	-	Yes	No
Proprietary software	BatSound (Pro)	No	No	Batsound (Pro)
Weatherproofing	No	No	No	No
Weatherproof microphone	No	No	No	No
GPS	No	Yes	No	No
Temperature sensor	No	No	Yes	No
Price (USD) for functioning unit	1178 (recorder not included)	4375	1222	393

Table 2.2 Specifications of bat detectors suitable for ecological survey and monitoring of tropical bats that have been field tested by the SEABCRU. Adapted from (Adams *et al.* 2012) with additional information from product specification sheets of each individual detector. Note that detectors outlined in Table 2.1 may also be used for survey and monitoring, but will require substantial weather-proofing.

System manufacturer / specifications	**Batlogger** *Elekon AG*	**Echometer, EM3+*** *Wildlife Acoustics*	**D240X** *Pettersson Elektronic*	**Anabat SD2 *** *Titley Electronics*	**Songmeter SM2+BAT/ SM3BAT** *Wildlife Acoustics*	**D500x *** *Pettersson Elektronic*
Primary use in acoustic survey	Mobile	Mobile	Mobile and stationary	Mobile and stationary	Stationary	Stationary
Recording technology	16-bit full spectrum	16-bit full spectrum, heterodyne and ZC mode	Heterodyne, full spectrum time expansion	Zero-crossing frequency division	16-bit full spectrum and ZC mode	16-bit full spectrum
Frequency range (kHz)	10-150	Up to 192	10-120	5-200	Up to 192	15 – 190
Sampling rate (kHz)	312.5	256 and 384	307	N/A	192 and 384	44.1, 300 and 500
Sound file type	.wav and .xml	.wav and .wac	.wav	Anabat	.wav and .wac	.wav
Storage type / max. capacity	1 x SDHC (32 GB)	1 x SDHC (32 GB)	1 x SDHC (32 GB)	1 x CF (128GB)	4 x SDHC (128GB)	4 x CF (512 GB)
Battery	LIB 3.7V, 4600 mHa, rechargeable	4x AA (rechargeable within the unit)	1 x IEC 6LF22 (9 V)	4 x AA	4 x D cell	4x AA
Typical run time (with Alkaline batteries)	34 hours	12 hours	15 hours	24 hours	50-60 hours	Unknown
Microphone type	Electret, built in	Electret, built in (plus SM2 option)	Advanced electret, built in	Condenser, built in	Electret, optional cable	Advanced electret, built in
Microphone	Omni	Omni	Directional	Directional *	Omni	Omni

System manufacturer / specifications	**Batlogger** *Elekon AG*	**Echometer, EM3+*** *Wildlife Acoustics*	**D240X** *Pettersson Elektronic*	**Anabat SD2 *** *Titley Electronics*	**Songmeter SM2+BAT/ SM3BAT** *Wildlife Acoustics*	**D500x *** *Pettersson Elektronic*
directionality						
Recording schedule	Yes	Yes	Yes (via digital recorder)	Yes via CF reader	Yes	Yes
Proprietary software	BatExplore	Kaleidoscope Pro	BatSound (Pro)	Analook	Kaleidoscope Pro	BatSound (Pro)
Channels	1	1	1	1	2	1
Weatherproofing	Requires housing	Resistant	No	No	Yes	Yes
Weatherproof microphone	No	No	No	No	Yes	Yes
GPS	Yes	External	No	External	Optional	No
Temperature sensor	External temperature	No	No	Internal temperature	Internal and external	No
Price (USD) for functioning unit	2035	1099	1227 (recorder not included)	2200	SM2+BAT: 1248 SM3BAT: 1498	2222
Additional costs to consider	-	GPS	-	-	GPS, cables, microphones	GPS

2.4 Designing, managing and implementing a bat acoustic survey

This section contains information that will be useful when designing an acoustic survey or monitoring study, and should be read in conjunction with the first section. This is because the limitations of the recording equipment will to a large degree influence what can and cannot be done in an acoustic study. This is a good opportunity to reiterate that it is therefore good practice to determine what is required of the acoustic survey before choosing bat detectors! It is assumed that the reader has a good understanding of ecological survey design, particularly the need for replication and appropriate sample sizes for biodiversity studies.

Acoustic monitoring is inherently 'passive' - the recorder samples sound for a set time period, which can include the calls from various individuals and species. Recordings can be continuous, timed or defined by triggers of the microphone. By contrast, in some research situations 'active' recordings may be more appropriate – for example, following a hand-released bat, or targeting recordings to specific individuals or species. Here we are just concerned with passive recording for acoustic monitoring.

We begin by describing the benefits and problems associated with **mobile versus stationary sampling** with bat detectors. We then review the key considerations for **deployment of bat detectors**, including settings, microphone set-up and schedules. We then describe the **key outputs of acoustic sampling** and define ways by which bat researchers determine and monitor sampling effort. Finally, we **review some**

proprietary software packages available for processing sound files, and suggest ways that **bat recordings can be organized and processed** so that meaningful data can be produced from acoustic surveys.

2.4.1 Stationary versus mobile sampling

Bat acoustic surveys typically utilize either point-based stationary recorders or mobile sampling over line transects, or a combination of both. No single approach is perfect, and each has its own advantages. The key issue is to consider what would be the appropriate way to sample bats systematically across all sites of interest. Since few people have attempted acoustic sampling in Southeast Asia, a pilot study to test the effectiveness of possible designs is recommended.

Point-based stationary detectors are particularly ideal for repeated surveys of key sites of interest, and have the clear advantage that the researcher does not need to be present. This decision is strongly influenced by security and trust in the weather resistance of equipment, but in principle, modern detectors can be programmed and left unattended for substantial periods of time. For example, it has historically been common to customize Anabat units with weather-proofing and leave unattended overnight to be collected the following morning. More recently, the weather-resistant Songmeters and Pettersson D500x detectors have a clear advantage in this regard as they have been designed specifically with this use in mind, and a set of full batteries can last several consecutive nights of full spectrum recording at forest localities (Table 2.1).

In terms of bat detection, the overarching assumption of a point-based (stationary) sampling approach is that bat activity recorded is representative of the study area of interest. If the objective of the study is to compare bat activity between sites, repeated sampling with equal effort at all sites would reduce the variability of bat activity. Therefore, researchers need to think carefully about the number of nights and number of points needed to appropriately sample a bat assemblage under investigation, but also whether to treat points as replicates of a larger area or pool data across points. For these reasons, stationary surveys are often used in situations when the same sites of interest will be monitored (i.e. have repeated surveys over time). The benefits and limitations of each approach are summarized in Table 2.3.

Transect-based mobile surveys, in contrast, can potentially cover larger areas (albeit for shorter time periods), but will usually require a researcher to be present and a constant travelling speed to be decided. Such examples include walking transects along paths and vehicle transects along roads or rivers in which the detector is secured on top of the car or manned by people in a boat.

Studies from other parts of the world can give us some insight into the relative benefits of stationary and mobile surveys. Whitby *et al.* (2014) evaluated both mobile and stationary methods in detecting bats by carrying out simultaneous bat acoustic surveys on a boat and car simultaneously along transects in Shawnee Forest Reserve in Illinois, USA. Two stationary points were also chosen along these transects to place stationary bat detectors. While they found that there was no significant difference in species density between the two designs, the stationary method accumulated species faster than both mobile methods.

In Germany, Stahlschmidt and Brühl (2012) compared transect surveys and stationary detectors for surveying bat activity in an agricultural landscape comprising of cereal fields, and found that stationary detectors deployed in the landscape were more precise in assessing spatial bat activity in a standardized manner. They also concluded that (in Europe at least) using stationary detectors was more cost-effective than mobile approaches because this approach was less laborious and time-consuming, and did not require specialist knowledge to interpret acoustic equipment in the field. Both mobile and static approaches to sampling bat activity have their advantages and disadvantages, and deciding on which method to use is determined by the aim of the study and the resources that are available.

To our knowledge these approaches have not been thoroughly tested in Southeast Asia. Having a researcher present usually means that the sample time during the evening is limited - often to just the evening emergence - which may be appropriate if most activity of interest is concentrated during that period and the same period is sampled across all transects. However, true transects, whereby sound is recorded continuously along the whole transect length, are much more difficult to implement in tropical regions, especially in forest environments where walking with sensitive recording equipment at night risks damage from trips and falls, and unintentional noises can interfere with recordings.

'Mobile-point-transect' surveys are a possible compromise between the two designs. Here, the survey involves a transect of timed stops (e.g. 10-minute recordings, stop, then walk to next point), and possibly additional longer-term stationary recording at selected sites. This approach is sometimes referred to as transect sampling (e.g. Wordley *et al.* 2014) but strictly speaking, it is a hybrid of a mobile and stationary recording, especially if the recordings are still being collected when moving between points. In a study in North America, Ellison *et al.* (2005) surveyed four different vegetation zones (lower elevation riparian and canyon bottom vegetation, La Mesa fire, piñon-juniper, and mixed coniferous forest) using transects of fixed lengths (2.25km) with 10 points that were 250m apart, and sampled for 5-minutes each. This hybrid design produced sufficient acoustic data to reliably discriminate between the different vegetation zones in terms of bat species richness and community structure, while also being cost-effective with a single detector and limited field crew.

When proposing recommendations for designing effective habitat studies that involve bats, Fischer *et al.* (2009) noted that if coarse differences are of interest, such as bat activity in various land use types, then a single detector operating on a single night would suffice at times. However, this is very much contingent on the amount of data collected and how well the bat community has been sampled. Bat researchers need to think carefully about increasing the number of localities recorded a single time, versus repeated recordings at the same locality.

Table 2.3 Benefits and limitations of using stationary- versus transect-based sampling designs for acoustic studies.

Design	**Benefits**	**Limitations**	**Examples**
Point based, stationary survey	Detects species more consistently and evenly than mobile acoustic and transect methods (Whitby *et al.* 2014). Ideal for presence/absence surveys. Good for very small areas.	Bat activity and species may be missed in large landscapes if insufficient replication. Likely to detect the same individual multiple times and so some correction to the measure of bat activity is warranted.	Phommexay *et al.* 2011; Pearce and Walters, 2012; Furey, Mackie & Racey 2009; Sedlock, 2001; Lee 2016, chapter 4, this thesis.
Transect-based, mobile survey	Car-based mobile surveys; most economical in terms of human resources (Whitby *et al.* 2014). Can cover a larger area. Less training required and can be undertaken by volunteers (Whitby *et al.* 2014). Less likely that the same individuals are detected multiple times so bat activity is a closer indicator of bat abundance.	Walking transects in homogenous habitat may not account for spatial variation. Vehicle-based transect surveys may have an influence on bat activity or presence/absence. May be biased to particular habitats (e.g. roadside edges for cars; riparian vegetation for boats).	Stahlschmidt and Brühl, 2012; Whitby *et al.* 2014.
Walking-point-transect, (points along a transect)	Addresses bias in spatial variation by covering a wider landscape. A compromise for detecting the same individual multiple times (only likely at single points for short sampling periods).	Temporal turnover in bat activity needs to be taken into account along the transect.	Wordley *et al.* 2014; Berthinussen and Altringham, 2012; Lee 2016, chapter 3, this thesis.

2.4.2 Detection zones

An effective acoustic monitoring research programme needs careful consideration of factors that might influence the detection of bats around an acoustic microphone, and the discrimination of echolocation calls from other sounds. The detection zone refers to the volume of space around a microphone within which a bat call can be reliably detected. Crucially the detection zone is dependent on microphone design (Section 2.1), and it is important to appreciate what can and cannot be detected by any given microphone. Historically, and for some detectors currently on the market, the detection zone has been uni-directional or cone-like. For example, the Anabat SD2 uses a directional microphone with the most receptive zone being a 90-degree cone in front of the microphone. Other detectors such as the Echometer and Songmeter from Wildlife Acoustics are omnidirectional, meaning that bat calls can be detected in a near 360° space around the microphone. Even with these microphones, however, sensitivity can vary within the detection zone, and some loss in sensitivity can be expected over time. Researchers should handle microphones and cables with great care to avoid damage. Testing kits are available to check sensitivity for some devices.

Microphone orientation and direction can strongly affect the detection capabilities of recording equipment and consequently the number of bat calls recorded. Horizontal placement is least effective while vertical and 45° is most desirable (Britzke *et al.* 2010; Weller and Zabel, 2002). Although the detection range of a recorder is initially dictated by the microphone design, it is important to understand that true detection is also confounded by the properties of the echolocation calls under study, local weather conditions (especially humidity, which exacerbates attenuation of sound), and the degree of clutter near the microphone.

It is important to minimize the amount of clutter within the detection zone of the microphone (Weller & Zabel 2002) and maximize the amount of time bats spend in the detection zone (Britzke, Gillam & Murray 2013). Researchers should therefore select suitable sites in which bats are present in the detection zone for the longest period of time (i.e. placing units parallel to expected flight paths), while minimizing the amount of vegetation present (thereby decreasing the amount of clutter).

As far as possible bat researchers should undertake acoustic sampling on calm, mild and dry nights, and avoid unfavorable weather such as high winds and rain. Rain and high winds will compromise the ability of the microphone to detect ultrasonic sound, and the foam protectors used on some microphones will be compromised for substantial time after the rain has stopped – at least until the foam dries. Ultimately, these issues will add extra variability between recordings and affect estimates of bat activity from the sampling (Fischer *et al.* 2009).

The height at which a microphone is deployed also has implications for data collection because ultrasound signals can be distorted by surface echoes, thermal layering or near-ground convection currents (Frick 2013). This consideration is more important when deploying full spectrum recorders than using frequency division. Frick (2013) recommended that microphones should be placed 1-2 m above ground, and preferably at 2 m or above because most bats are not expected to fly below that height apart from trawling species (e.g. some *Myotis* spp.) or understory forest bats restricted by low-hanging vegetation. Poles or tripods can be used to raise the microphones of detectors above the surrounding vegetation to reduce noise and improve call quality.

For omni-directional microphones set in open areas, placing the microphone high above the ground (> 5.5 m) effectively increases the sample volume. Typically, at sites in Southeast Asia where acoustic recorders have been trialed a microphone height of 2-3 m is sufficient to reduce interference from unwanted insect noise. However, researchers should trial their own deployment heights in their own pilot study.

Researchers may wish to further protect their recording equipment from adverse weather by using additional weatherproofing measures (e.g. plastic sheeting, umbrellas, plastic cones), but it is important to consider whether these interventions could also affect acoustic detection. This may be considered an acceptable trade-off if the protective measures are deployed consistently across recorder sites, and biases reported appropriately. Alternatively, replacement of more effective detectors or microphones damaged by the weather may be acceptable to those with large budgets.

2.4.3 Recording schedules

The start and end times of acoustic surveys vary greatly in the published literature, and there is no definitive ideal period that can be recommended. In transect surveys, Ellison *et al.* (2005) began a transect when the first bat was detected or 30 minutes after sunset (whichever occurred earlier), whereas (Skalak, Sherwin & Brigham 2012) adopted a system of stationary detectors which were automatically switched on at 90 min before sunset and ended 90 min after sunrise the next day. Regardless of subtle differences in the start and end times, acoustic sampling covering the entire night is valuable to elucidate the patterns of bat activity in areas not surveyed previously, and also for recording less frequently detected species (Skalak, Sherwin & Brigham 2012). Such a deployment will of course produce more data which later needs to be processed, but it would at least indicate when the most appropriate times to limit the recording could be.

Nowadays, acoustic surveys are more limited by data processing time than they are by technological capability, and so researchers need to decide on what comprises sufficient data and a sufficient sampling period. This is a difficult decision to make and is often left to local logistical constraints to dictate (e.g. people only available to walk transects during evening emergence). A conservative approach, if time, power and storage capacity are not limiting, would be to record all night and later sub-sample to particular time periods if need be. Otherwise, it is imperative to keep recording schedules consistent across sites to make acoustic data comparable across a study. Researchers should always communicate clearly their deployment schedules for this reason.

2.4.4 Recording settings

Ensuring all sound is recorded and of sufficient quality

Recall from Section 2.2 that the sampling rate, bit resolution and the frequency range detectable by the equipment are key considerations when choosing acoustic equipment. Equipment capabilities also place important constraints on the types of bat that can be reliably detected in acoustic surveys – i.e. species detection.

These constraints are additional to the general biases of acoustic surveys: that species with short-range calls (e.g. *Kerivoula, Murina, Coelops*) can very rarely be detected, regardless of how common they are, simply because they would need to fly right next to the microphone, and this rarely happens. This issue is rarely considered by bat researchers new to sampling tropical bats, but leaves a fundamental bias in the results of acoustic surveys in terms of species diversity and activity.

For acoustic surveys in Southeast Asia, to detect the high frequencies used by many echolocating bats, the ideal settings for recording from a full-spectrum bat detector are 500 kHz sampling rate and 16-bit resolution. In principle, a detector set in this way could detect species >200 kHz (such as *Hipposideros doriae*, Huang *et al*. unpublished). However, few detectors can sample at this rate, and many are unaffordable to the average field scientist in the region. More importantly, the frequency range is also limited by the microphone (Section 2.2.1). Put simply, there is little point recording at 500 kHz sampling rate (i.e. >200 kHz frequencies) if the microphone is limited to 120 kHz!

The decision on which sampling rate to use very much depends on the objective of the study. In many situations, acoustic studies recording at a sampling rate of 384 kHz and 16-bit resolution suffice, but are limited to sampling at 192 kHz even with a perfect microphone. This means that researchers will need to accept and report that some high frequency species will not be detected. Also recall that even under perfect acoustic recording circumstances, the chances of detecting species with high frequencies is very low because high frequency calls operate over very short distances. Of course, this may not actually be a problem if such species are not known from the study region, or are not the focus of the study.

Continuous (automated) versus triggered recordings

Continuous recordings typically take up a lot of processing power and storage space, and the resulting large files can be difficult to work with unless they are split into smaller units. Continuous recordings might also result in more noise being recorded than the bat calls of interest, and hence more data processing is required before analysis.

To save on wasted recording time, power and storage capacity, many bat detectors can be programmed to trigger mode, in which the unit records only when a sound passes a threshold of intensity via the microphone. An individual trigger event can be defined by a minimum and maximum recording time, which can also be useful for arbitrarily defining a bat pass, which reflects bat activity. Triggered recordings can save greatly on space, but can miss some bat species if the trigger thresholds are not appropriate for the recording circumstances.

We are unaware of studies that have explicitly compared the effectiveness of continuous versus triggered recordings in full spectrum recordings. However, Matos *et al.* (2013) compared a time-expansion detector used in two different triggered modes – automatic (using an arbitrary intensity threshold) versus manual mode in which the user started recordings when a bat was thought to pass. They sampled bat activity in five different habitats in a forest-farmland mosaic in Portugal with two bat detectors operating simultaneously, but used in either the manual or automatic mode.

The study showed significant differences in total bat activity as well as species richness between the two modes of trigger, with more bat activity and species detected with the manual mode. They therefore cautioned against the use of automatically triggered bat detectors due to the probable loss of data, thus affecting monitoring and underestimating bat community composition in ecological studies. Overall, the decision about whether to use triggers very much depends on the type of data required by the study, and in many situations some loss of data may well be acceptable if data can be processed easier.

Time expansion detectors also present a way of automating sampling, which was unavoidable in the past before full-spectrum recorders became available. These detectors can be set to record “continuously”, but the nature of time expansion means there will be an interval in which nothing is recorded. For example, a three-second recording followed by a 30 second download. The three-second recording can be used as a standardised unit of bat activity.

Frequency-division versus full spectrum

As mentioned previously, frequency-divided signals analyzed using the zero-crossing method are fast to process and take up little memory, but result in lower resolution recordings. Sound files recorded via full spectrum equipment present a high data burden, but are arguably much better for acoustic identification purposes.

If battery consumption and memory capacity of a full spectrum detector is not an issue, as is increasingly the case with modern detectors (Table 2.1), then it is best to record calls in full spectrum to retain the full information of the calls. Increasingly, acoustic processing software (e.g. Kaleidoscope), provide the option to convert full spectrum .wav files into zero-crossing equivalents (ZC), hence giving flexibility to the bat researcher for downstream analyses, and for better matching recordings from different devices.

Defining and standardizing sampling effort

In traditional biodiversity inventories survey or sampling effort is defined by the sampling method and unit time. For bat capture studies, units of sampling effort include the harp trap night and mist net hour (Kingston 2009). For acoustic surveys, hours or nights are a useful basic unit of record effort if this is standardized across replicates.

Acoustic surveys should be conducted over multiple nights and across multiple sampling locations to maximize the detection of large numbers of species. To quantify sources of variability in bat activity in habitat study design, Fischer *et al.* (2009) reported that nightly variability in a forest-agriculture area of Australia accounted for 20% of the overall variability in bat activity levels, and recommended multi-night surveys to reduce within-site variability.

The number of nights required to effectively sample bat activity is an open question and will vary by region and bat fauna. More research is needed in Southeast Asia before recommendations can be given for this region. In Australian forest-agriculture mosaics, Fischer *et al.* (2009) noted that a reasonable level of precision was reached after four suitable nights using stationary detectors. In North America, (Hayes 1997) recommended 6-8 nights to estimate overall bat activity, while in Europe, Skalak, Sherwin & Brigham (2012) reported that 2-5 nights was sufficient for stationary detectors to detect common bat species. However, much longer periods (>45 nights) were required to detect rare species.

The fact that the onset and duration of night-time varies geographically, and in some places, seasonally, makes it difficult to reliably compare bat activity data across sites or studies. Therefore, it is advisable to keep effort consistent within a study by normalizing recording times to the number of hours past sunset for each date surveyed. This also makes it easier to pool and compare data across a single study season and identify any peaks in bat activity that may indicate any particular threats to bats (Kunz *et al.* 2007). There are online resources to calculate sunset and sunrise times for any point in the world, such as that provided by the National Oceanic and Atmospheric Administration in the USA (www.esrl.noaa.gov/gmd/grad/solcalc/), and some detectors (e.g. the Songmeter series) have a built-in function to do this using latitude and longitude information, making normalizing recordings over long term monitoring period much easier.

2.4.5 Defining the ‘bat pass’ as the basic sampling unit

In most biodiversity studies the basic unit of sampling is the number of individuals to give estimates of abundance or relative abundance (Magurran 2003). However, acoustic surveys present difficulties in estimating abundance, since individuals cannot be discriminated from recordings and variation in echolocation properties amongst species means that different taxa can have quite different detection probabilities. This presents a problem because various echolocation calls may represent multiple individuals near the microphone, or a single individual passing the microphone multiple times.

Therefore, in bat acoustic sampling studies the basic unit of reporting is usually **'bat activity'**, which is broadly defined as the number of bat passes of (and being detected by) a microphone. By convention most acoustic studies report bat activity as the average passes per detector-hour or detector-night per site or some variation of this theme. This makes the 'bat pass' a very important unit to define in an acoustic sampling study.

Two criteria are typically used to define a bat pass: **the number of pulses**, and the **inter-pass interval** (Box 1). There is no single definition that fits all studies, and so researchers must define a bat pass early in their planning, use this definition consistently, and clearly communicate this definition in their reporting.

Bat passes can sometimes lead to large volumes of data for certain species or certain periods of the night, and then no data for other times. Therefore, information on bat passes is sometimes aggregated into an **activity index (or acoustic activity index)**. One objective of such an index is to reduce the large volume of calls from dominant species which can have unintended consequences for downstream analyses. Several examples are given in Box 1.

An alternative index was proposed by Miller (2001) which removes the need to define, identify and count bat passes altogether. This method is based on the **presence/absence of a species occurrence in a one-minute interval** and it has been shown to be an effective measure of bat activity for comparisons across sites, times and species. More recently, (Britzke, Gillam & Murray 2013) has suggested that with recent improvements in call analysis, bat activity patterns can be quantified directly by counting pulses, or indirectly by measuring the size of the recorded files (Britzke and Murray, 2000; Broders, 2003), although special care needs to be taken to distinguish between true bat calls and unwanted noise files, which is a significant problem in the tropics due to large numbers of noisy insects (see Section 2.3.2).

For some bat genera, and particularly vespertilionids, foraging activity can be visually distinguished in the spectrogram by the **'feeding buzz'**. A feeding or terminal buzz is defined as a sequence of calls becoming shorter in duration and, in FM bats, broader in bandwidth, and is emitted by foraging bats in the air closing in on a prey item (Russ 2012). This is unique to bat acoustics and has been used as a proxy for the value of foraging habitats for bats in some studies (e.g. Vaughan, Jones & Harris 1997). Full spectrum detectors are a much better choice in detecting feeding buzzes compared to zero-crossing detectors because the faint calls do not activate the zero-crossing period meter (Fenton *et al.* 2001).

Box 1. What is a bat pass and how does this relate to bat activity?

Bat calls are impossible to attribute to individuals and so bat passes are typically used as an index of bat abundance or activity. A bat pass refers to an individual bat passing (and being recorded by) the acoustic microphone, but can be defined in many ways. Examples include:

Comparison of detectors in Germany (Stahlschmidt & Brühl 2012)	"*A sequence of calls that end five or more seconds before the next sequence begins*."
Impacts of a road on UK bats (Berthinussen & Altringham 2012)	"*One or more clearly recognizable echolocation calls from a single species, separated from the next pass by a gap of at least 1s*"
Bats in rubber plantations, Thailand (Phommexay *et al.* 2011)	"*an echolocation call with at least two consecutive pulses*."
Bats using rooftop gardens, Singapore (Lee 2016, chapter 4, this thesis)	"*at least 3 consecutive pulses before the next sequence is triggered again, or after a trigger interval of 1 second*."

Aggregating bat passes into a simple index is a useful way of quantifying and communicating bat activity. Again, there is no standard bat activity index, but simple examples include:

1. The **acoustic activity index (AI)**, devised by Miller (2001) to quantify bat activity without having to define, identify and count bat passes. If bats can be reliably identified through their recorded calls, date-time information is known, and sampling periods are defined, we can quantify bat activity as well as relative activity of species present within a site or between different sites. The formula is:

$$AI = \sum_{1}^{n} P$$

where the number of one-minute time blocks for which the species was detected (n) as being present (P) is summed and divided by the unit effort (which can be **time** data for a fixed site survey or stationary detector, or a specified **distance** for a transect survey) (Miller 2001).

2. **Mean bat passes per detector-hour**, which is the current standard for bat monitoring studies near wind farm projects (Kunz *et al.* 2007)

Online resources:

https://www.bu.edu/cecb/files/2009/12/kunzbats-wind07.pdf

http://ir.lib.uwo.ca/cgi/viewcontent.cgi?article=2679&context=etd

2.4.6 Managing and processing bat acoustic data

Given the substantial resources allocated to bat monitoring research, ideally, bat detectors should be checked a day after their deployment to ensure that the equipment is working as intended, and that calls have been recorded the night before.

Location data (and GPS-tagging for some bat detectors) are vital to identify the call files recorded and designate them to locations. Remember that acoustic projects will generate large amounts of data, and so planning a file management system in the early days of the research is vital. Some detectors allow for specific prefixes to be added to file names to help organize files by location later. This can be cumbersome, but very useful if managing several detectors at the same time.

Calls should be downloaded and stored in named folders for each sampling location. Before analyzing and classifying the calls, many bat researchers filter their files using a process known as “scrubbing”. This is used to remove unwanted noise files, such as false triggers from insect sounds, anthropogenic noise, wind, and rain, but also call fragments that are unusable for analysis. The noise files should be kept in a separate folder and retained in case they are needed for a subsequent search for calls that were misclassified as noise later. Remember, the definition of a noise file is arbitrary, and no algorithm will be 100% accurate!

Decades of acoustic research in Europe, North America and Australia have resulted in classification schemes for echolocating bats and proprietary algorithms, known as classifiers, to objectively classify calls to a bat species identity (Adams *et al.* 2010; Agranat 2012). However, European bats of the genera *Myotis* and *Plecotus* are still challenging to differentiate based on call structure alone (Russ 2012; Barataud 2015). In contrast, bat acoustic research has lagged in most of Asia. It will be some time before classifiers are available for Asian countries, although there are the beginnings of a classification system for India (Wordley *et al.* 2014) and Thailand (Hughes *et al.* 2011). For most of the Southeast Asia region, processing still needs to be done manually and can be very time consuming. Acoustic software packages are available to help with this (Table 2.4).

A first step for countries without a bat call library, or an incomplete inventory, is to make a list of all echolocating bats known, or thought to occur, in the country and seek out literature on acoustic studies published elsewhere in the region on those listed species. The manual call classification process begins by deriving call parameters using dedicated software (Table 2.4), and sorting sounds into groups based on call morphology. These parameters are then compared to published information (or other reliable unpublished information such as personal call libraries or databases – for example, http://www.batecho.eu/) to guide the process of call classification and analysis. Most calls can be broadly classified into several acoustic categories, or phonic types (see Table 2.5 for examples). Using the same sorting and naming process recommended for call library development will help the Southeast Asian bat research community develop acoustic research effectively. So, in the event that a call cannot be reliably classified and assigned to a species, provisional call identification with a unique alpha-numeric code can be given. For example, FM42.5 where FM refers to a broadband frequency modulated call with a FMAXE of 42.5 kHz (see example in Furey, Mackie & Racey 2009)

Bat acoustic software packages facilitate this process by allowing users to ‘tag’ their files with names and other useful information. The tag information is typically stored in the metadata associated with the sound file, and can be outputted into tabulated format, where it can be edited in any standard spreadsheet or database programme.

Over time, and by sorting many, many files in this way, researchers will soon produce some certain species identities, many tentative ones, and few unknowns. This can feel very daunting, but it is important to realize that this is to be expected. By naming the phonic-types as we have suggested above it is possible to more easily communicate and share these recordings with other acoustic researchers across the region. Over time, many of those tentative identities will be confirmed. It is still important to realize that there will still probably be many unknown calls in the dataset. How many ‘unknowns’ is acceptable in acoustic studies is difficult to answer, but a more important issue to report is the proportion of useable and unusable files in the dataset.

Table 2.4 Comparison of software for viewing and processing bat calls. The prices stated are of August 2015, and for the basic version (i.e. without call classifiers, which have no use in Southeast Asia).

Software/ parameter	**Analook**	**Bat Call Identification (BCID)**	**Batsound**	**Kaleidoscope Pro**	**SCAN'R**	**Sonobat**
Parent company / developer	Chris Corben	Bat Call Identification	Pettersson Elektronik AB	Wildlife Acoustic, Inc.	Binary Acoustic Technology	Joe Szewczak
File format	.zca	.zca	.wav, mp3, .wma	.zca, .wav, .wac	.zca and .wav	.wav
File conversion	No	Converts .wav to .zca	No	Converts full spectrum (.wac or .wav) to .zca	Unsure?	No
Automated measurement	No	Yes	No	Yes	Yes	Yes
Batch processing	Yes	Yes	No	Yes	Yes	Yes
Noise scrubbing	No?	No?	No	Yes	Yes	Yes
Processing speed	Fast	Fast	Not applicable	Fast	Fast	Fast
Tagging	Yes	Yes	No	Yes	Yes	Yes
Capacity for automated ID	Yes (with creation of filters)	Yes	No	Yes	Yes	Yes
Price (single license)	Free, open access	$979	$465	$399 (for viewer) (As of 4 Oct 2016, the viewer is free!)	$195	$320 (base version) - $680 (batch processing and automated call parameter extraction).

2.5 Towards a regional bat call database for Southeast Asia

The growing interest in using acoustic techniques amongst Southeast Asian bat researchers has highlighted the need to develop standard protocols for recording and analysing bat calls. For call data to be of use to the wider Southeast Asian bat community it is important to systematically record information associated with bat recordings and include this information within databases.

Ideally, the regional database should reside with an organization that has the necessary resources to support and update the database indefinitely. The main objective of such a database is to encourage both basic and applied research on bats and their conservation. Although there have been ambitious calls for a global bat-signal database (Karine & Kalko 2001), it is perhaps much more feasible to develop several such databases at the regional scale. The European database described by Walters *et al.* (2012) sets a great example.

2.5.1 Metadata required for the SEABCRU bat call library

Ideally, researchers would contribute large amounts of associated information as ‘metadata’ to the bat call database. However, in practice submitting sound files and metadata can be quite time consuming. Therefore, to encourage researchers to contribute to the database we highlight four key features of bat recordings that are essential to include. These include 1) **general description** (or information to attribute the call to a location, field recorder, bat species, etc.), 2) **recording environment**, 3) **recording equipment and method** used, and finally, 4) **basic call parameters**.

We have adapted our database from the proposed global database recommended by Karine and Kalko (2001), which is more detailed. The study of bats using acoustic techniques is still in its infancy in Southeast Asia compared to Europe and North America, and we have deliberately made the metadata fields simple to encourage bat research workers to participate in building the database. We believe the stated fields in the proposed database are the minimum needed to build a useful regional bat call database, and revisions will be made in the future with user feedback. The various fields of the database are explained and presented in Table 2.5.

Table 2.5. Metadata required for the SEABCRU Southeast Asia Bat Call Library. Fields highlighted in yellow are essential and must be filled in. The rest of the fields are optional.

I. GENERAL DESCRIPTION	
Recorder	This is the person that made the recording. **Full name, institution affiliation and email required**
Species ID	Common name / scientific name / species code **E.g. Whiskered Myotis/*Myotis muricola*/MYMU**
Locality	Location name where the call was recorded. **E.g. Krau Wildlife Reserve**
Country	Name of country / territorial waters in which the call was obtained. Country codes for Southeast Asia are: **BN**: Brunei; **ID**: Indonesia; **KH**: Cambodia; **LA**: Laos; **MM**: Myanmar; **MY**: Malaysia; **PH**: Philippines; **SG**: Singapore; **TH**: Thailand; **TL**: Timor-Leste; **VN**: Vietnam
GPS location	Latitude and longitude of the record to be shown in decimals and the geodetic datum used should be WGS84 (World Geodetic System 1984) e.g. 4.07, 114.93 for Mulu, Sarawak.
Recording date	Date that record was made – YYYY-MM-DD. **e.g. 2010-01-17**
Recording time (24h)	Time that record was made – HH:MM. **e.g. 21:35**
RECORDING ENVIRONMENT	
Degree of clutter	Amount of clutter in the recording environment. There are 3 options for this field: 1. **Cluttered** – Surrounded by closed forest and undergrowth 2. **Semi-cluttered** – some overhanging vegetation and short ground cover 3. **Non-cluttered** – open areas and large waterways without overhanging vegetation
RECORDING EQUIPMENT AND METHOD *Only accepted from a full-spectrum bat detector / microphone system*	
Brand / Model	This is the brand name of the detector used for the recording and the model number as well. **E.g. Wildlife Acoustics / SM2+BAT**
Method	The method adopted to record the bat call – Table 2.4. There are 4 options for this field: **Stationary** – Recording performed when bat is resting **Enclosure** – Recording performed when bat is flying within an enclosure **Free flight** – Recording performed during free flight of bat **Tethered flight** – Recording performed when bat is linked to a string
CALL PARAMETERS	
Call type	This is a broad classification of the call recorded of each bat species, and defined in Table 2.2. There are 5 options for this

	field: **Constant Frequency,** *CF bats* **Quasi-CF, multi-harmonic,** *QCF bats* **Frequency Modulating, broad-band,** *FMb bats* **Frequency Modulating, multi-harmonic,** *FMH bats* **Frequency Modulating – Quasi Constant Frequency,** *FM-QCF bats*
FMAXE	Frequency with the highest energy level
PI	Time between start points of two consecutive pulses in a call sequence
D	Length of a single pulse
Others	

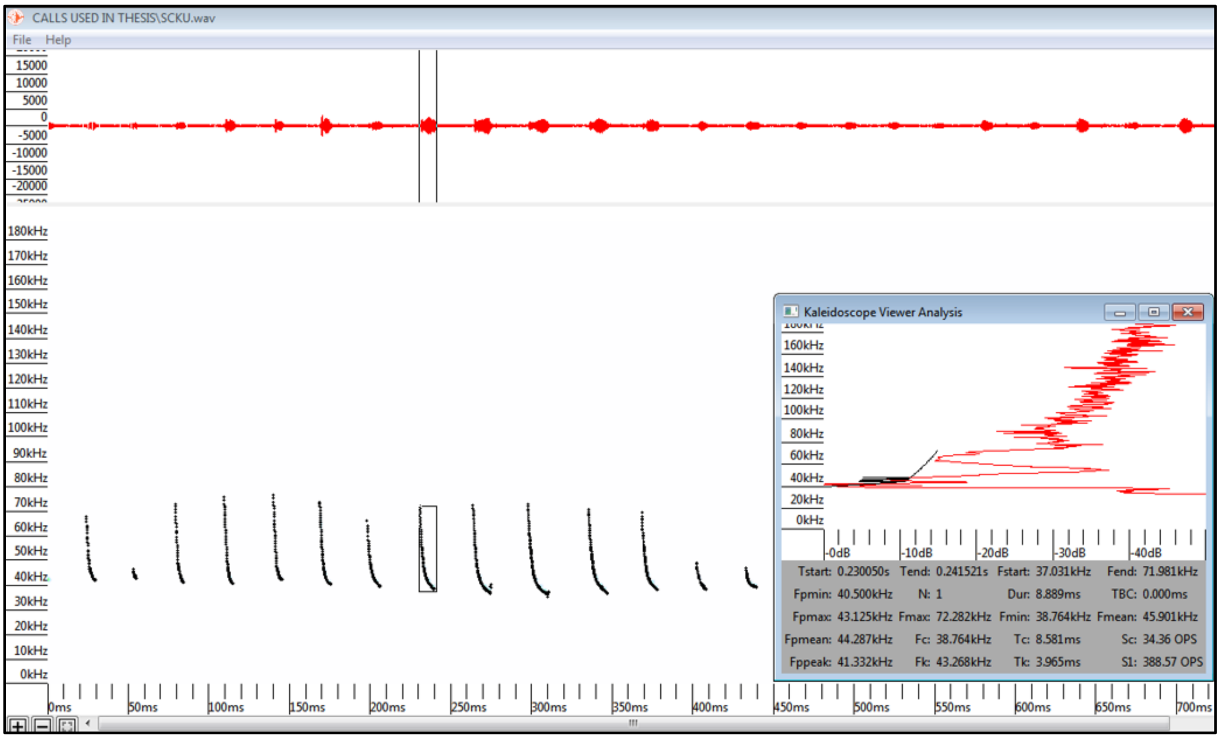
2.6 Bat calls from Singapore

This section collates the bat calls collected during my study in Singapore and forms the basis of bat species identification of the calls recorded in all transects originating from the major roads and from the green roofs (Figures 2.1 – 2.7). In places with a high bat diversity, acoustic identification of free-flying bats can be challenging due to the overlap in call parameters (Parsons & Jones 2000) and very similar looking calls. However, given the limited number of bat species in Singapore it is possible to identify the majority of calls following the parameters in Pottie *et al.* (2005). For each of the bat calls in Figures 2.1 – 2.7, there are three parts which represents the call. The echolocation pulses are represented by an oscillogram in the top section, which corresponds to a sonogram in the bottom section. The inset shows the characteristics of the selected echolocation pulse(s). The start position (**Tstart**) and end position (**Tend**) in time and frequency (**Fstart** and **Fend**) of the selection is shown on the first line of the inset. For full spectrum recordings, subsequent fields on the left of the inset refer to an estimate of the minimum (**Fpmin**) and maximum (**Fpmax**) frequency containing energy from the selection, as well as the power-weighted mean frequency of the spectrum (**Fpmean**), and the frequency of the peak power (**Fppeak**), which is equivalent to the commonly used FmaxE. The inset window also displays the number of selected pulses (**N**) and the duration of the selected pulses (**Dur**). The rest of the fields pertain to zero-crossing recordings which was not used in my study.

The call parameters of six species encountered in the field in Chapters 3 and 4 are shown in Table 2.6 and these are taken from Pottie *et al.* (2005). Each bat pass was visually inspected, measured and assigned to a species in Kaleidoscope Viewer (Wildlife Acoustics, Inc.). No bat classifiers were used in bat call identification because none have been developed for Singapore and the wider Southeast Asian region. FmaxE in the figure legends below stands for frequency containing maximum energy. Identification of bat species is usually done by looking at the echolocation call shape and measuring the FmaxE.

Table 2.6. Characteristics of search phase calls (mean ± SE) for six species of bats encountered during acoustic surveys in Singapore. (Taken from Pottie *et al.* 2005.)

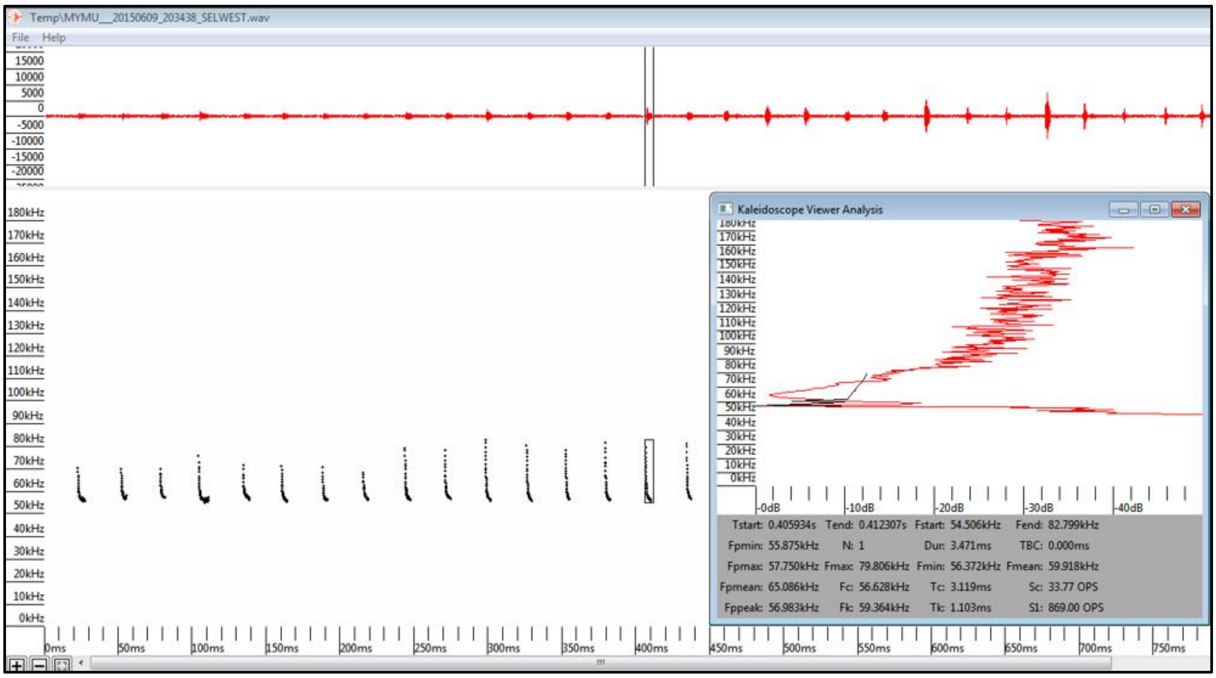
Species			**Frequency (kHz)**		**FmaxE (kHz)**	**Search call duration (ms)**
	Bats	**Calls**	**Maximum**	**Minimum**		
Scotophilus kuhlii	27	270	84.9 ± 22.5	36.6 ± 0.46	43.3 ± 0.16	4.01 ± 0.03
Myotis muricola	18	180	79.9 ± 1.02	53.7 ± 0.48	57.2 ± 0.01	4.98 ± 0.07
Saccolaimus saccolaimus	23	198	23.5 ± 1.32	21.8 ±1.42	22.6 ± 0.42	12.20 ± 0.08
Taphozous melanopogon	6	60	28.7 ± 1.24	25.2 ± 0.82	27.9 ± 0.56	10.43 ± 0.06
Rhinolophus lepidus	24	240	-	-	97.8 ± 0.07	28.30 ± 1.36
Rhinolophus trifoliatus	4	40	-	-	53.1 ± 0.03	44.50 ± 2.15



Tstart: 0.230050s Tend: 0.241521s Fstart: 37.031kHz Fend: 71.981kHz
Fpmin: 40.500kHz N: 1 Dur: 8.889ms TBC: 0.000ms
Fpmax: 43.125kHz Fmax: 72.282kHz Fmin: 38.764kHz Fmean: 45.901kHz
Fpmean: 44.287kHz Fc: 38.764kHz Tc: 8.581ms Sc: 34.36 OPS
Fppeak: 41.332kHz Fk: 43.268kHz Tk: 3.965ms S1: 388.57 OPS

Figure 2.1 Search calls of the Lesser Asiatic Yellow House Bat *Scotophilus kuhlii* (SCKU)

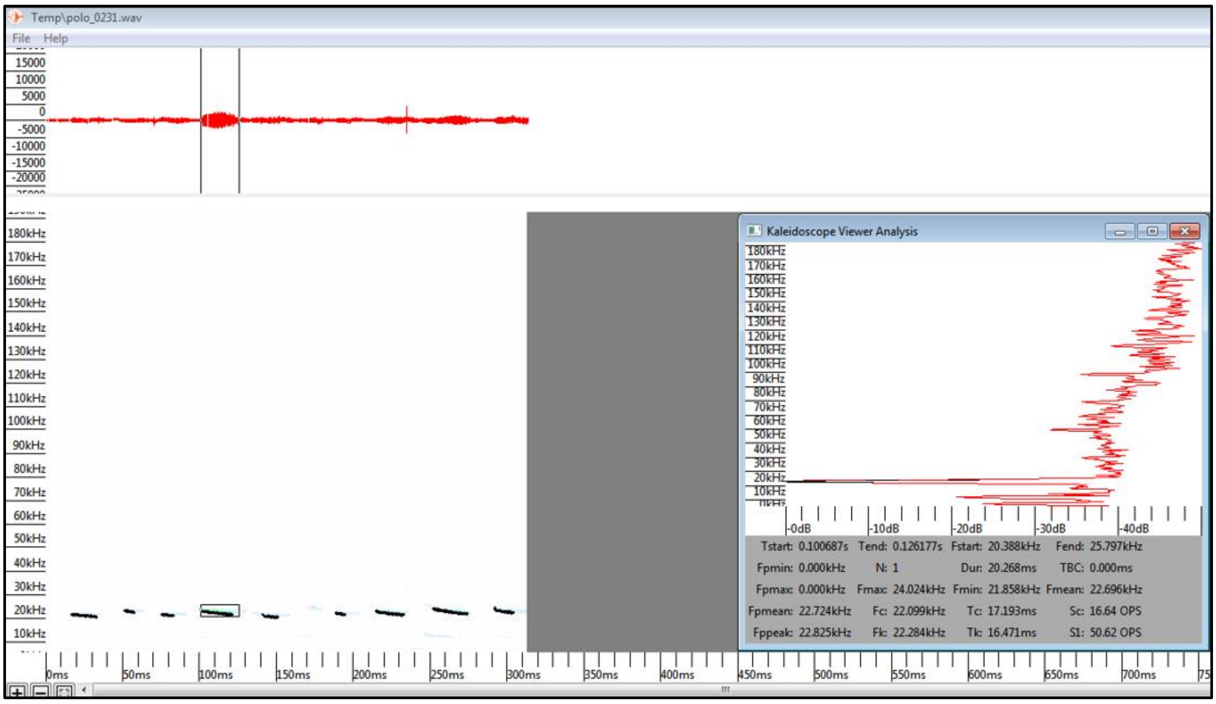
FmaxE: 41.3 kHz



Tstart: 0.405934s Tend: 0.412307s Fstart: 54.506kHz Fend: 82.799kHz
Fpmin: 55.875kHz N: 1 Dur: 3.471ms TBC: 0.000ms
Fpmax: 57.750kHz Fmax: 79.806kHz Fmin: 56.372kHz Fmean: 59.918kHz
Fpmean: 65.086kHz Fc: 56.628kHz Tc: 3.119ms Sc: 33.77 OPS
Fppeak: 56.983kHz Fk: 59.364kHz Tk: 1.103ms S1: 869.00 OPS

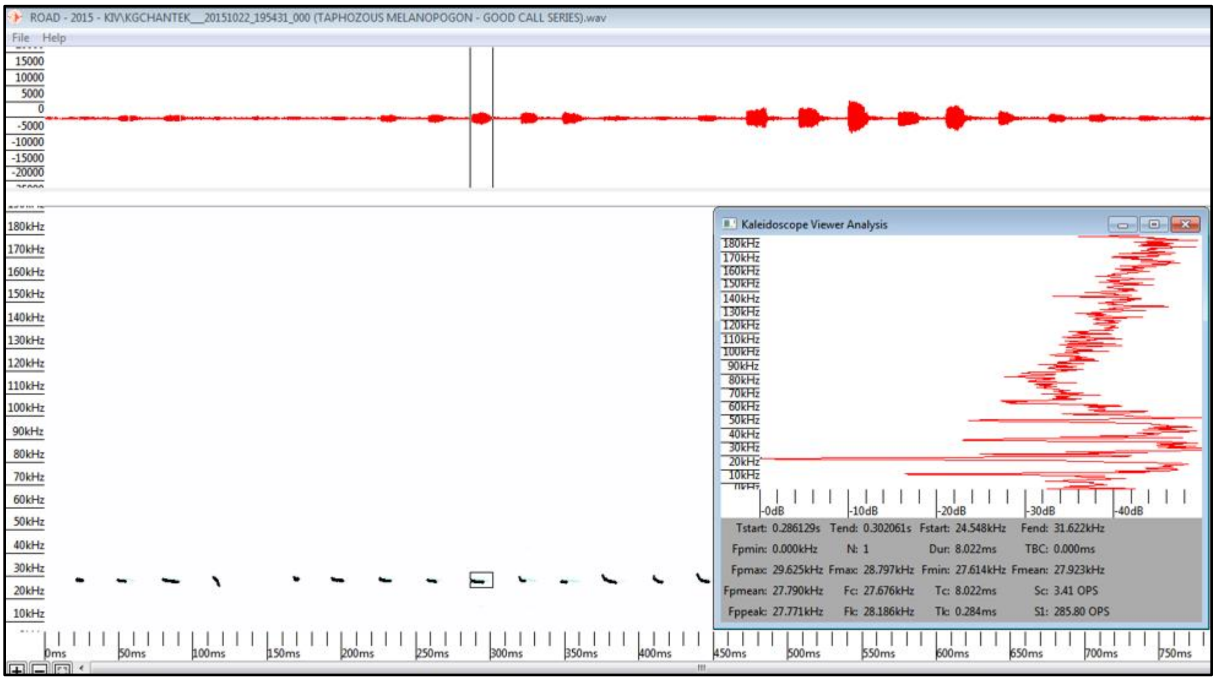
Figure 2.2 Search calls of the Whiskered Myotis *Myotis muricola* (MYMU)

FmaxE: 57.0 kHz



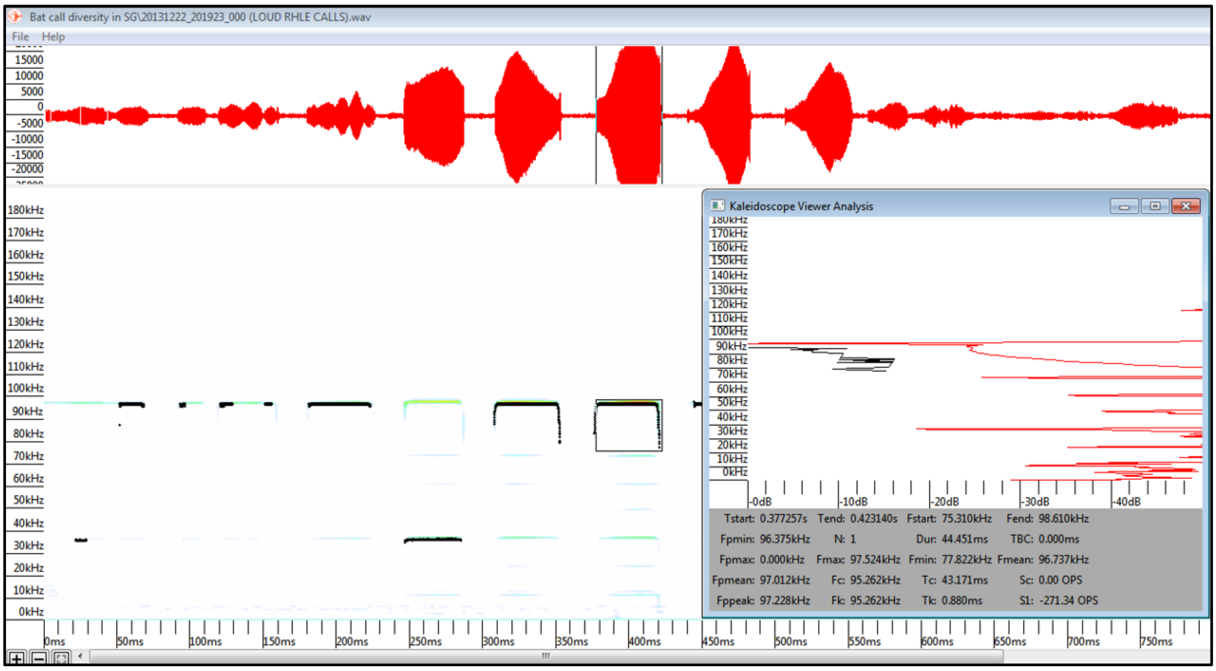
Tstart: 0.100687s Tend: 0.126177s Fstart: 20.388kHz Fend: 25.797kHz
Fpmin: 0.000kHz N: 1 Dur: 20.268ms TBC: 0.000ms
Fpmax: 0.000kHz Fmax: 24.024kHz Fmin: 21.858kHz Fmean: 22.696kHz
Fpmean: 22.724kHz Fc: 22.099kHz Tc: 17.193ms Sc: 16.64 OPS
Fppeak: 22.825kHz Fk: 22.284kHz Tk: 16.471ms S1: 50.62 OPS

Figure 2.3 Search calls of the Pouched Tomb Bat *Saccolaimus saccolaimus* (SASA), FmaxE: 22.8 kHz



Tstart: 0.286129s Tend: 0.302061s Fstart: 24.548kHz Fend: 31.622kHz
Fpmin: 0.000kHz N: 1 Dur: 8.022ms TBC: 0.000ms
Fpmax: 29.625kHz Fmax: 28.797kHz Fmin: 27.614kHz Fmean: 27.923kHz
Fpmean: 27.790kHz Fc: 27.676kHz Tc: 8.022ms Sc: 3.41 OPS
Fppeak: 27.771kHz Fk: 28.186kHz Tk: 0.284ms S1: 285.80 OPS

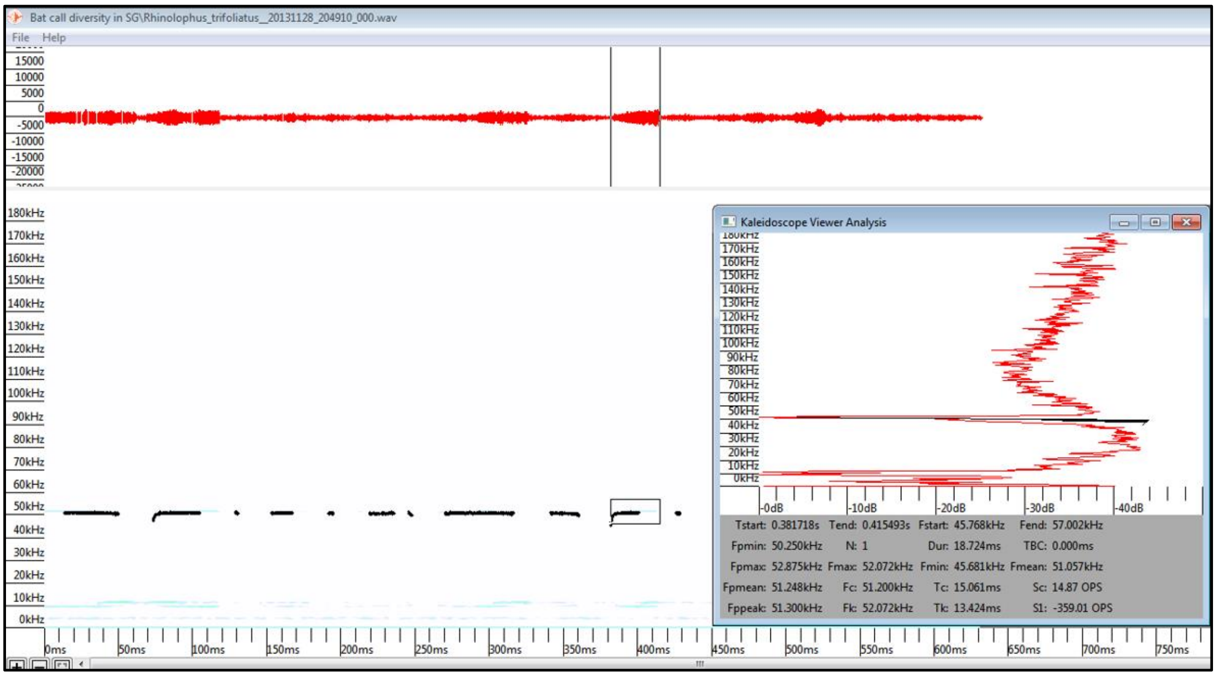
Figure 2.4 Search calls of the Black-bearded Tomb Bat *Taphozous melanopogon* (TAME), FmaxE: 27.8 kHz



Tstart: 0.377257s Tend: 0.423140s Fstart: 75.310kHz Fend: 98.610kHz
Fpmin: 96.375kHz N: 1 Dur: 44.451ms TBC: 0.000ms
Fpmax: 0.000kHz Fmax: 97.524kHz Fmin: 77.822kHz Fmean: 96.737kHz
Fpmean: 97.012kHz Fc: 95.262kHz Tc: 43.171ms Sc: 0.00 OPS
Fppeak: 97.228kHz Fk: 95.262kHz Tk: 0.880ms S1: -271.34 OPS

Figure 2.5. Search calls of the Blyth's Horseshoe Bat *Rhinolophus lepidus(RHLE)*

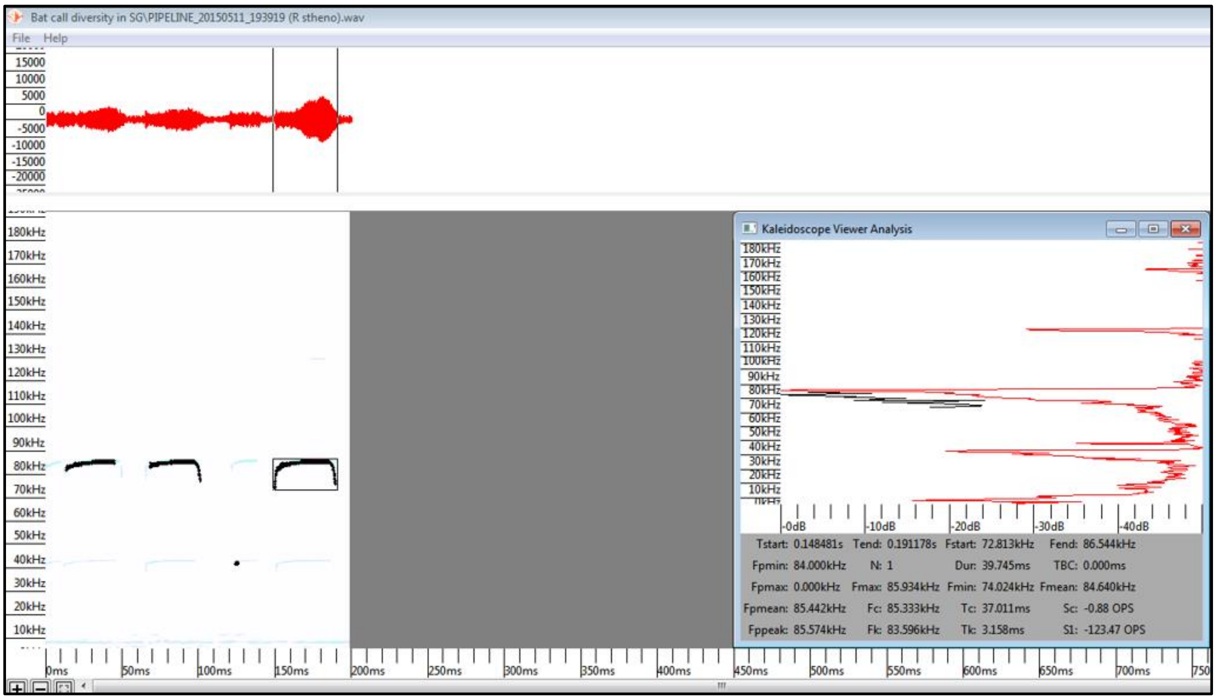
FmaxE: 97.2 kHz



Tstart: 0.381718s Tend: 0.415493s Fstart: 45.768kHz Fend: 57.002kHz
Fpmin: 50.250kHz N: 1 Dur: 18.724ms TBC: 0.000ms
Fpmax: 52.875kHz Fmax: 52.072kHz Fmin: 45.681kHz Fmean: 51.057kHz
Fpmean: 51.248kHz Fc: 51.200kHz Tc: 15.061ms Sc: 14.87 OPS
Fppeak: 51.300kHz Fk: 52.072kHz Tk: 13.424ms S1: -359.01 OPS

Figure 2.6. Search calls of the Trefoil's Horseshoe Bat *Rhinolophus trifoliatus (RHTR)*

FmaxE: 51.3 kHz



```
  Tstart: 0.148481s   Tend: 0.191178s  Fstart: 72.813kHz    Fend: 86.544kHz
  Fpmin: 84.000kHz       N: 1             Dur: 39.745ms      TBC: 0.000ms
  Fpmax: 0.000kHz     Fmax: 85.934kHz    Fmin: 74.024kHz   Fmean: 84.640kHz
Fpmean: 85.442kHz       Fc: 85.333kHz      Tc: 37.011ms       Sc: -0.88 OPS
 Fppeak: 85.574kHz      Fk: 83.596kHz      Tk: 3.158ms        S1: -123.47 OPS
```

Figure 2.7. Search calls of the Lesser Brown Horseshoe Bat *Rhinolophus stheno* (RHST)

FmaxE: 85.6 kHz

NOTE: This is a **new bat record** for Singapore as there have been doubts if this species did actually exist in Singapore based on anecdotal accounts and not museum specimens. The call was recorded during a pilot study to find out bat activity throughout the night to guide the design of transect surveys. Further monitoring using physical capture techniques would be needed to confirm its presence.

2.7 References

Adams, A.M., Jantzen, M.K., Hamilton, R.M. & Fenton, M.B. (2012) Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution*, **3**, 992–998.

Adams, M.D., Law, B.S. & Gibson, M.S. (2010) Reliable automation of bat call identification for eastern New South Wales, Australia, using classification trees and Anascheme software. *Acta Chiropterologica*, **12**, 231-245.

Agranat, I. (2012) *Bat species identification from zero crossing and full spectrum echolocation calls using HMMs, Fisher scores, unsupervised clustering and balanced Winnow pairwise classifiers*. Wildlife Acoustics, Inc.

Barataud, M. (2015) *Acoustic ecology of European bats - species identification, study of their habitats and foraging behaviour*. Biotope, Mèze; Muséum national d'Histoire naturelle, Paris.

Berthinussen, A. & Altringham, J. (2012) The effect of a major road on bat activity and diversity. *Journal of Applied Ecology*, **49**, 82–89.

Britzke, E.R., Gillam, E.H. & Murray, K.L. (2013) Current state of understanding of ultrasonic detectors for the study of bat ecology. *Acta Theriologica*, **58**, 109–117.

Britzke, E.R. & Murray, K.L. (2000) A quantitative method for selection of identifiable search-phase calls using the Anabat system. *Bat Research News*, **41**, 33–36.

Britzke, E.R., Slack, B.A., Armstrong, M.P. & Loeb, S.C. (2010) Effects of Orientation and Weatherproofing on the Detection of Bat Echolocation Calls.

Journal of Fish and Wildlife Management, **1**, 136–141.

Broders, H.G. (2003) Another quantitative measure of bat species activity and sampling intensity considerations for the design of ultrasonic monitoring studies. *Acta Chiropterologica*, **5**, 235–241.

Ellison, L.E., Everette, A.L., Bogan, M.A. & Edwards, C.W. (2005) Examining patterns of bat activity in Bandelier National Monument, New Mexico, by using walking point transects. *The Southwestern Naturalist*, **50**, 197–208.

Fenton, M.B., Bouchard, S., Vonhof, M.J. & Zigouris, J. (2001) Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. *Journal of mammalogy*, **82**, 721–727.

Fischer, J., Stott, J., Law, B.S., Adams, M.D. & Forrester, R.I. (2009) Designing effective habitat studies: quantifying multiple sources of variability in bat activity. *Acta Chiropterologica*, **11**, 127–137.

Frick, W.F. (2013) Acoustic monitoring of bats, considerations of options for long-term monitoring. *Therya*, **4**, 69–78.

Furey, N.M., Mackie, I.J. & Racey, P.A. (2009) The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. *Current Zoology*, **55**, 327–341.

Harrison, M.E., Boonman, A., Cheyne, S.M., Husson, S.J., Marchant, N.C., Struebig, M.J. & Matthew, J. (2012) Biodiversity monitoring protocols for REDD+: Can a one-size-fits-all approach really work? *Tropical Conservation Science*, **5**, 1–11.

Hayes, J.P. (1997) Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of mammalogy*, **78**, 514–524.

Hughes, A.C., Satasook, C., Bates, P.J.J., Soisook, P., Sritongchuay, T., Jones, G. & Bumrungsri, S. (2011) Using echolocation calls to identify Thai bat species: Vespertilionidae, Emballonuridae, Nycteridae and Megadermatidae. *Acta Chiropterologica*, **13**, 447–455.

Karine, C. & Kalko, E.K. V. (2001) Toward a global bat-signal database. *Engineering in Medicine and Biology Magazine, IEEE*, **20**, 81–85.

Kingston, T. (2009) Analysis of species diversity of bat assemblages. *Ecological and behavioural methods for the study of bats*, 2nd ed (eds T. Kunz & S. Parsons), pp. 195–215. The John Hopkins University Press.

Kunz, T.H., Arnett, E.B., Cooper, B.M., Erickson, W.P., Larkin, R.P., Mabee, T., Morrison, M.L., Strickland, M.D. & Szewczak, J.M. (2007) Assessing Impacts of Wind-Energy Development on Nocturnally Active Birds and Bats: A Guidance Document. *The Journal of Wildlife Management*, **71**, 2449–2486.

Magurran, A. (2003) *Measuring Biological Diversity*. Wiley-Blackwell.

Matos, M., Pinto, N.L., Pereira, M.J.R. & Fonseca, C. (2013) Triggering bat detectors: Automatic vs. manual mode. *Mammalia*, **77**, 461–466.

Miller, B.W. (2001) A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, **3**, 93–105.

Parson, S. & Szewczak, J. (2009) Detecting, recording and analysing the vocalisations of bats. *Ecological and behavioral methods for the study of bats* , 2nd ed (eds T. Kunz & S. Parson), pp. 91–111. John Hopkins University Press.

Pearce, H. & Walters, C.L. (2012) Do green roofs provide habitat for bats in urban areas? *Acta Chiropterologica*, **14**, 469–478.

Phommexay, P., Satasook, C., Bates, P., Pearch, M. & Bumrungsri, S. (2011) The impact of rubber plantations on the diversity and activity of understorey insectivorous bats in southern Thailand. *Biodiversity and Conservation*, **20**, 1441–1456.

Russ, J. (2012) *British Bat Calls: A Guide to Species Identification*. Pelagic Publishing.

Sedlock, J.L. (2001) Inventory of insectivorous bats on Mount Makiling, Philippines using echolocation call signatures and a new tunnel trap. *Acta Chiropterologica*, **3**, 163–178.

Skalak, S.L., Sherwin, R.E. & Brigham, R.M. (2012) Sampling period, size and duration influence measures of bat species richness from acoustic surveys. *Methods in Ecology and Evolution*, **3**, 490–502.

Stahlschmidt, P. & Brühl, C.A. (2012) Bats as bioindicators–the need of a standardized method for acoustic bat activity surveys. *Methods in Ecology and Evolution*, **3**, 503–508.

Vaughan, N., Jones, G. & Harris, S. (1997) Habitat Use by Bats (Chiroptera) Assessed by Means of a Broad-Band Acoustic Method. *Source Journal of Applied Ecology Journal of Applied Ecology Journal of Applied Ecology*, **34**, 716–730.

Walters, C.L., Freeman, R., Collen, A., Dietz, C., Fenton, M.B., Jones, G., Obrist, M.K., Puechmaille, S.J., Sattler, T. & Siemers, B.M. (2012) A continental-scale tool for acoustic identification of European bats. *Journal of Applied Ecology*, **49**, 1064–1074.

Weller, T.J. & Zabel, C.J. (2002) Variation in bat detections due to detector orientation in a forest. *Wildlife Society Bulletin*, 922–930.

Whitby, M.D., Carter, T.C., Britzke, E.R. & Bergeson, S.M. (2014) Evaluation of mobile acoustic techniques for bat population monitoring. *Acta Chiropterologica*, **16**, 223–230.

Wordley, C.F.R., Foui, E.K., Mudappa, D., Sankaran, M. & Altringham, J.D. (2014) Acoustic identification of bats in the southern Western Ghats, India. *Acta Chiropterologica*, **16**, 213–222.

3. Impact of major roads on insectivorous bats in Singapore

3.1 Abstract

The tropics hold much of the world's biodiversity, and face increasing pressures from expanding road networks, yet there are very few studies on the biodiversity impacts of roads in these regions. The ecological effects of roads may also be greater in urban areas compared to rural ones due to the dense road networks and heavier traffic typical of cities. I investigated the effects of roads on insectivorous bat activity by using 20 walked transects perpendicular from roads in either forest or urban habitat. Activity was quantified via a full-spectrum bat detector, and four repeated surveys were implemented over two field seasons. The extent to which potential explanatory variables, such as noise, light, distance from road and land cover metrics, could predict bat activity was determined via generalised linear mixed models (GLMMs). I found proximity to major roads predicted low levels of bat activity in forest habitats, but no distance effect was evident in urban areas. Bat activity increased more than two-fold between the road and recordings collected 800 m away into forest, and overall bat activity was 1.5 times higher in the forests compared to urban areas. High levels of tree, scrub and cultivated vegetation cover had a positive influence on bat activity in both forest and urban habitats. Forest-dependent bats such as *Rhinolophus lepidus* may be experiencing a barrier effect, but other species are also detected near the road, albeit in low numbers. This study is the first in the tropics to show that roads have negative effects on bats and it agrees with previous work on bats and road effects conducted in the northern hemisphere. The study is also a first to examine the effects of roads on forest and urban bat communities.

3.2 Introduction

Roads constitute one of the most pervasive human impacts globally, and road development is one of leading causes of habitat loss, fragmentation and degradation (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Fahrig and Rytwinski, 2009; Laurance, Goosem & Laurance 2009). With the human population increasing worldwide because of urbanisation, the area of natural landscapes being replaced by roads is set to grow. By 2050, an additional 25 million lane-kilometre of paved roads are expected to be built, of which 90% will be in non-Organisation for Economic Co-operation and Development (OECD) countries (Dulac 2013). These countries include tropical and subtropical regions that hold most of the world's biodiversity (Olson & Dinerstein 2002), and so impacts of future road development are expected to be especially severe (Laurance *et al.* 2014).

Roads affects wildlife in several ways. Road construction will inherently involve habitat destruction as well as habitat fragmentation in formerly contiguous, or near contiguous, landscapes. In the Brazilian Amazon, for example, roads and highways are known to be strong predictors of deforestation in remote regions subjected to development and major land-use change (Laurance *et al.* 2002). The resulting habitat fragmentation can severely limit animal movements for some species, thereby restricting dispersal. For example, it was found that roads and the edge-affected habitat beside roads inhibited the movement of forest-dependent insectivorous birds in Brazil between forest patches (Laurance, Stouffer & Laurance 2004). Elsewhere, the presence of light sources such as street lamps and vehicle lights, as well as traffic noise and chemical pollution, can further degrade habitats surrounding roads.

Improved road access also entails visitor impacts, resource extraction (including illegal harvest of wildlife and plants) (e.g. Amur tigers in Russia, Kerley *et al.* 2002; African elephants in Congo, Blake *et al.* 2007; timber in Gabon, Laurance *et al.* 2006a), and the possible introduction of invasive species (e.g. spread of fire ants *Wasmannia auropunctata* using logging roads in Africa, Walsh, Henschel & Abernethy 2004). Finally, roads can result in direct mortality of wildlife through vehicle collisions, which also sometimes result in the loss of human lives. For example, there are about 2 million wildlife-vehicle collisions (WVC) involving large mammals in the United States of America yearly, resulting in 29,000 people injured and the deaths of 200 more (Conover *et al.* 1995). In a global review of 79 studies, Fahrig and Rytwinski (2009) found that the negative impacts of roads far outweigh the positive effects for wildlife. One example of a positive effect of roads would be the provision of road-killed carcasses for scavengers apt at vehicle avoidance such as vultures, which increases their abundance (Fahrig and Rytwinski 2009).

There is an apparent geographic and taxonomic bias among studies that investigated the effects of roads on wildlife. From 1998 – 2008, about 75% of 244 studies published in English on road ecology and wildlife were conducted in North America and Europe, with a strong focus on mammals (Taylor & Goldingay 2010). In contrast, there is a paucity of research undertaken in tropical countries, despite these regions supporting higher levels of biodiversity while being subject to rapidly expanding human populations and habitat loss. Tropical road impact studies also tend to focus on mammals (e.g. Goosem 2001; Austin *et al.* 2007; Clements *et al.* 2014), but also in relation to other conservation challenges such as hunting and rapid land conversion (Laurance *et al.* 2006b; Clements *et al.* 2014). Despite a recent ‘call to arms' to undertake more road-impact research in the tropics (Laurance *et al.* 2014), these studies have been slow to materialise.

The road impact literature on bats lags that of other taxa, although it is growing in countries where there are protected species and mitigation requirements to minimise damage or abandonment of roosts. For example, in Europe, bat species are of high conservation priority, are protected under European Union (EU) law (CMS 1994), and are listed in Annex 4 of the Habitats Directive. Some bat species (e.g. *Barbastella barbastellus*) have designated protected areas because they are listed in Annex 2 of the Habitats Directive (Council Directive 92/43/EEC). Hence, any infrastructure development, including roads, that is likely to affect bat populations are subjected to environmental impact assessments and the implementation of mitigation measures. As well as exhibiting great potential as bio-indicators of environmental change (Jones *et al.* 2009), bats are an ideal group for investigating the impacts of roads because they are often the most speciose mammal group remaining in highly urbanised areas (van der Ree and McCarthy, 2005; Jung and Kalko, 2011). Moreover, bats can be sampled remotely via acoustic methods so there is no need for physical capture, which can be difficult in urban areas for security and public safety reasons (Scanlon 2007). The biology and life history of bats are crucial considerations when assessing the impacts of roads on bats (Altringham & Kerth 2016). Bats are long-lived, have low reproductive rates and have relatively large home ranges compared to many small mammals (Altringham 2011). In general, these biological attributes predispose bats to a slow recovery if subjected to environmental disturbances (Jones *et al.* 2009).

Roads and their development may affect bats in several ways including:

i) creating a barrier effect through the severing of flight routes (Kerth & Melber 2009);

ii) reducing foraging and roosting areas (Altringham & Kerth 2016); and,

iii) direct mortality by collision with a vehicle (Lesinski, 2007; Russell et al., 2009; Medinas et al., 2013).

Moreover, there are secondary effects of roads, such as increased lighting and noise, which may also adversely influence bat populations. Lighting has been shown to be associated with a reduction in density or absence of slow-flying and woodland-adapted *Rhinolophus*, *Myotis* and *Plecotus* bat species (Rydell 1992; Blake *et al.* 1994; Stone, Jones & Harris 2009; Stone, Harris & Jones 2015) while noise (in the form of recorded highway traffic) has been shown to reduce foraging efficiency of bats by acting as an aversive stimulus (Luo, Siemers & Koselj 2015). From the studies undertaken to date in the northern hemisphere, proximity to roads is an important factor predicting bat activity and diversity. For example, bat activity was found to increase two- -fold away from a UK motorway, and in the USA a three-fold increase in activity was detected between 300 m and 1600 m away from a major highway (Berthinussen and Altringham, 2012; Kitzes and Merenlender, 2014). In the former example, bat diversity was positively correlated with distance from the road (Berthinussen & Altringham 2012).

Landscape characteristics may also explain impacts of roads on bats. For example, in southern Portugal, roads traversing or adjacent to good quality habitats consisting of thick woodland, riparian vegetation or waterbodies, resulted in significantly more bat road kills (Medinas, Marques & Mira 2013). Nevertheless, despite these important insights, our understanding of road impacts on bats is limited, and more studies from the tropics are needed to overcome a clear bias towards temperate regions (Altringham & Kerth 2016). It is also recognised that the impacts of roads in urban areas warrant further investigation because the ecological effects of roads are likely to be more intense in urban areas, given that there are concentrated road networks and high traffic density (Jones, Bekker & van der Ree 2015). Therefore, a challenge for urban ecology is to disentangle the effects of urbanisation (as a land-use) and that of roads and traffic (van der Ree 2009).

Most research in road ecology to date has been conducted in relatively pristine or rural landscapes, and impacts are seldom compared to road effects in different habitats or taxa (van der Ree 2009). An exception to this is a study done in Singapore by Chong *et al.* (2014) who investigated the effects of different urban greenery components as well as vehicular traffic (quantified as road lane density) on bird and butterfly diversity. They found that butterfly and bird species richness declined with increasing road lane density, and there was an interaction between road lane density and cultivated tree cover on bird species richness (Chong *et al.* 2014).

The 719 km^2 tropical island city-state of Singapore provides the ideal study system to investigate road ecology given its dense road network associated with intense urbanisation. There are 3496 km of roads across the island, of which 164 km are expressways carrying the majority of daily traffic, especially during the morning and evening peak periods (Land Transport Authority 2015). Here I investigate the effects of roads on Singapore’s bats, and the influence of land cover types surrounding the road on bat activity. Based on previous research conducted in temperate regions, I expected bat activity to be lowest next to the road and to increase with increasing distance away from the road. To test this hypothesis, I undertook acoustic sampling of bats at varying distances from major roads. Since the presence of grey infrastructure could confound the effect of roads on bats my sampling was stratified between transects in forest habitat and urban, grey infrastructure areas. I sought to identify key variables associated with high or low bat activity in order to give recommendations for urban greening to the state of Singapore.

3.3 Methods

3.3.1 Study system

Fieldwork was undertaken in the centre of Singapore (1°22”N, 103°48”E) where forest remnants and suburban areas are intersected by three major roads: the Bukit Timah (BKE), Pan-Island (PIE) and Seletar (SLE) Expressways (Figure 1). Together, these expressways span the length and width of the island. All are dual carriageways with grade-separated access, and typically have three to four lanes excluding the hard shoulders. Planted vegetation in the form of low trees, shrubs and turf is found in the centre reservation and on the sides of the expressways. The speed limit on all three expressways is between 80-90 km/h and the average speed during peak hours drops to 64.1 km/h (Land Transport Authority 2015). The PIE is the oldest and longest expressway, at 42.8 km in length. The 10-km long BKE was built in 1983, bisecting a lowland rainforest reserve into the Bukit Timah and Central Catchment Nature Reserves. The most recently built expressway, SLE, was completed in 1995 and is 10.8 km in length. Singapore has an equatorial climate with high rainfall (more than 2000 mm annually), humidity and temperature year-round. There is no significant month-to-month variation for climate variables such as temperature and humidity (MSS 2016).

3.3.2 Data collection

I conducted acoustic surveys of bats along 20 point-transects (see Chapter 2) that ran perpendicular to one of the three major roads (Figure 3.1), with ten of these transects in forested habitats (‘Forest’), and the other ten extending into urban habitats (‘Urban’). Transects were selected using Google Earth imagery and on-the-ground-validation using the following criteria:

i) Each transect needed to be at least 800 m in length starting from one of the roads;

ii) Transects needed to be a minimum of 500 m apart so that they could be treated as independent samples;

iii) Transects needed to be accessible with permissions granted by the land owner/manager.

Along each transect I established nine sampling points starting from the edge of the road (0 m) and, subsequently, at 100 m intervals until 800 m. An extra sampling point was added at 50 m to maximise data collection near to the road, thus totalling 10 sample points per transect. The co-ordinates of each sampling point were marked and recorded using a handheld GPS device (Garmin GPS 64s) to an accuracy of at least 3 m prior to sampling. Transects were walked and sampled for bats in a random order four times in total between 2013 and 2015. However, to account for variation

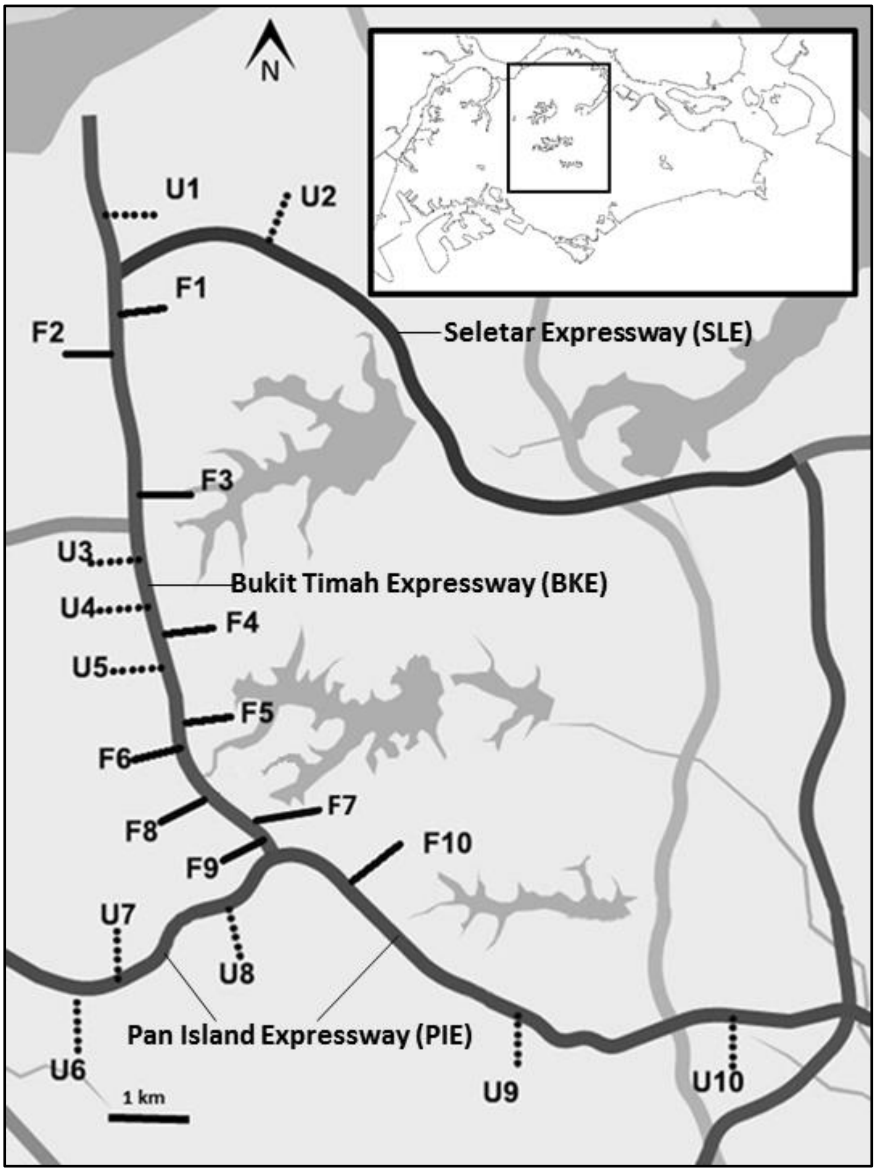


Figure 3.1 Bat acoustic sampling transects running perpendicular to major expressways in Singapore in either forest (F) or urban (U) habitat. Transects U6-10 and F10 begin from the Pan-Island Expressway, transect U2 begins from the Seletar Expressway, and the remaining transects are on both sides of the Bukit Timah Expressway. The inset indicates the location of the study area and positions of transects on a map of Singapore. Dark grey areas in the main map indicate waterbodies.

in bat activity over the course of an evening, all transects were walked twice in a night - once starting at the road (i.e. travelling between the sampling point at 0 to 800 m), and then travelling towards the road (800 to 0 m). The direction of the walk was reversed on the next sample night. Two samples were undertaken in the first field season (September 2013 – February 2014), and an additional two samples were collected between July and December 2015. Time between transect walks ranged from 7 to 30 days within field season and 400 to 450 days between seasons. Here, I aimed for a balanced transect design but, in 2013 sampling was terminated in one of the forest transects due to access restrictions. 2013 data from this transect are therefore not used in analyses. A replacement forest transect was established in 2015, giving a total of 20 transects in forested and urban habitats.

Bat surveys along each transect were initiated at sunset and lasted 3 h 15 mins. This duration was determined following a pilot study using three stationary SM2+BAT Songmeter recorders (192 kHz sample rate – Wildlife Acoustics Inc., Concorde, MA, USA), which confirmed that most bat activity was concentrated in the three hours post-sunset, as it is elsewhere in the Southeast Asian tropics (Phommexay et al. 2011). All transects were sampled in fair weather conditions with no rain or strong winds; the three-night period of a full-moon was avoided as these conditions are known to reduce bat activity (Weinbeer, Meyer and Kalko 2006). For each of the four samples per transect, there were 10 mins of bat recordings per point, recorded in two five-minute sessions taken at different times in the 3 hr 15-minute period. For analytical purposes, we use the 10-minute pooled sample per point per transect walk, of which there are four per point over the sampling period. The total number of data points for all transects in the two habitat types is 200.

The number of bat calls was used as a proxy of bat activity. Calls were recorded as .wav files at each sampling point using a handheld Echometer EM3+ integrated full-spectrum bat detector (192 kHz sampling rate - Wildlife Acoustics Inc., Concorde, MA, USA). This bat detector was chosen because it was highly portable and allows direct storage of the recorded calls onto a memory card without the need for a separate device (Chapter 2). Moreover, it was programmable and enabled easy documentation of calls for analysis, as well as the location of each recorded call via an attached GPS.

3.3.3 Acoustic surveys

I applied a systematic protocol to record bats at each sample point using the trigger function on the detector (i.e. the detector automatically records sound when thresholds are reached, thereby putting the equipment in a power saving mode when there is no bat activity). Trigger amplitude and frequency thresholds were set at 18 dB and 18 kHz respectively. The trigger setting of 18Db is recommended by the manufacturer and worked well during a pilot phase, while 18 kHz was set as the frequency threshold to eliminate the recording of excessive unwanted insect noise, but to respond to the expected lowest frequency of bat call known in the study area (an emballonurid calling at ca. 21 kHz peak frequency, Chapter 2). The interval window between subsequent triggers was set at 1 s and the maximum duration of each triggered recording was limited to 10 ms. Thus, bat activity was recorded as the number of independent bat calls recorded at each point along the length of the transect.

3.3.4 Environmental and land cover variables

The potential effects of roads on bat activity could be confounded by other characteristics of the study environment, such as abiotic variables and land cover. I therefore sought to account for these confounding variables as much as possible in the study design.

Noise and light have been shown to affect the foraging behaviour of bats (Siemers and Schaub 2011; Stone, Jones and Harris 2009) (Table 3.1). As such, these two explanatory variables were recorded at each point using a multi-function environment meter CEM DT-8820 (Shenzhen Ever Best Machinery Co. Ltd.) at the start of each 5-minute sampling period. Land cover in both rural and urban areas is also known to affect bat activity and species richness (Heim *et al.* 2015; de Araújo & Bernard 2016). Therefore, I investigated the potential effect of land cover type on bat activity using percentage areal extent estimates from within a circular buffer around each georeferenced sampling point. These data were extracted from the most recent and detailed 10 x 10 m resolution land cover map available for Singapore (Yee et al. 2011). The map was derived from two SPOT 5 satellite images, with land cover types delineated via a supervised classification technique, using the maximum likelihood method found in the software package ENVI version 4.4 (ITT Visual Information Solution 2007). Five land cover types were classified by the authors: *Trees, Scrub, Cultivated greenery, Water and Sealed surface* (see Table 3.1 for a full description). The data were extracted for various buffer radii (25 m, 50 m, 100 m, 1000 m) using QGIS (QGIS Development Team 2016) and R version 3.2.4 (R Core Team 2016).

Table 3.1 Abiotic and land cover variables used to predict bat activity in Singapore. The abiotic variables were quantified in this study and the five land cover types were derived from an updated land cover map (Yee et al. 2011). The proportion of each land cover type within a buffer of 50 m of the point polygon boundaries is expressed as %.

Variables	**Description**	**Unit**
Abiotic		
Light	Light level at each transect check point	lux
Noise	Noise level at each transect check point	dB
Distance	Distance of transect check point from road	m
Land cover type		
Trees	Tall woody plants forming a closed canopy, including young and old secondary forests, as well as primary lowland dipterocarp forest	%
Scrub	Long grass (e.g. *Imperata cylindrica*), shrubs (e.g. *Mimosa* spp.) and ferns (e.g. *Dicranopteris* spp.)	%
Cultivated greenery	Cultivated greenery such as short grass (including lawns), street trees and shrubs	%
Water	Water bodies	%
Sealed surface	Land covered by buildings, impervious surface or bare soil	%

3.3.5 Acoustic analysis

I used the number of bat passes as a proxy of bat activity at each sampling point, with a single bat pass defined as at least three consecutive pulses before the next call sequence, or after the 1 s trigger interval. Call identification from sound recordings was done manually using Kaleidoscope Pro software (Wildlife Acoustics Inc., Concorde, MA, USA) to view sonograms and power spectra, and measure key call characteristics (see Chapter 2 for summary of full-spectrum recordings of study species). Published bat call measurements from Singapore and the Southeast Asian region (Heller 1989; Pottie et al. 2005; Kingston, Lim and Akbar 2006) were also used to assist in the identification of each recorded bat call. Any files that could not be identified were labelled as ‘unknown’. Additionally, feeding ‘buzzes’ at each sampling point were used as an indicator of bat foraging activity and habitat use. These calls were differentiated from search phase calls by the presence of steep linear calls in rapid succession.

3.3.6 Statistical analyses

All analyses were performed in R version 3.2.4 (R Core Team 2016) in the packages *arm*, *MuMIn* or *lme4*. Prior to conducting an analysis, all non-categorical explanatory variables were scaled and centred so that their effect sizes were comparable and to improve model fit. Variance inflation factors (VIFs), pair plots and Spearman’s rank correlation coefficients were then computed to help identify possible multi-collinearity between the variable set. Following statistical recommendations in the literature, variables were excluded if Spearman’s rank correlation coefficients were more than 0.5 (Booth, Niccolucci & Schuster 1994), or if VIFs were greater than 3.0 (Zuur *et al.* 2009). If there were two highly correlated variables, the variable that was most ecologically meaningful was retained. The 50 m buffer for the land cover variables was chosen as the most appropriate (i.e. least correlated), and represents the likely maximum detection zone around the detector microphone in open areas.

A general linear mixed model (GLMM) with binomial error terms was used to first explore which explanatory variables characterised forest and urban transects (Model 1). *Habitat* was a binary response variable coded as 1 (Forest) or 0 (Urban). *Site* (transect name) and *Point ID* (sampling point) were included in the model as random effects to account for spatial and temporal pseudo-replication associated with repeated samples at each point. The following covariates were entered as fixed effects in the model: *Noise*, *Light*, *Cultivated Vegetation* and *Scrub*. The variables *Trees* and *Sealed Surface* were excluded from this model due to high collinearity. However, Model 1 failed to converge.

Bat activity was then modelled as a response using GLMMs with Poisson error terms (Bolker et al. 2009) (see Model 2). *Habitat, Light* and *Distance* were entered as fixed effects, and *Site* was entered as a random effect. An observation-level random effect (OLRE) dummy variable unique to each data row (visit_ID) and coded as a factor was added to lower the dispersion parameter to 1 for the model (Harrison 2014). In addition, a “bobyqa” optimiser (with a default of 10,000 iterations) was specified explicitly in the model to overcome issues of non-convergence.

An information theoretic approach was used in model selection. This approach estimates parameters based on multi-model inference because it is acknowledged that the collected data could support many competing models and hypotheses (Burnham & Anderson 2002). Model selection was based on AIC_c, a variant of AIC (Akaike Information Criterion) corrected for potential bias due to small samples (Burnham & Anderson 2002). Many models with different variable combinations were run and the best model emerged as the one with the smallest AIC_c value.

Models with ΔAIC_c <2 were used to estimate model average parameters. The relative plausibility of each model was quantified by calculating the Akaike weight, *w*. The final model was obtained by calculating the model average, with the weight of each model used to rank importance.

3.4 Results

3.4.1 The urban versus forest environment

Although *Trees* and *Sealed surface* land covers dominated forest and urban habitats respectively, an average of 1.9 % of *Sealed surface* land cover was found in forest transects and 6.2 % of *Trees* land cover was found in urban transects. Cultivated greenery in urban habitats made up about 32.6% of the land cover (Table 3.2). At the transect level, noise and light levels were significantly greater in urban habitats compared to forest habitats (*Noise*: t= -5.2959, p < 0.001; *Light*: t= -8.3221, p < 0.001).

3.4.2 Patterns of bat activity and diversity

A total of 3612 bat passes from at least seven species were recorded across 80 detector nights of sampling (Table 3.3). Although 1.5 as many bat passes were detected along forest transects compared to the urban counterparts (Table 3.3; 'Forest' n = 2292; 'Urban' n = 1320), this trend was not significant. The commonest species recorded across the study was *Scotophilus kuhlii* (41 % and 73 % of all bat passes recorded on the 'Forest' and 'Urban' habitats respectively) followed by *Myotis muricola* (29 % and 18 %). *Rhinolophus lepidus* recordings were restricted to 'Forest' sampling points, with the species represented at all but two transects. *Rhinolophus trifoliatus* was recorded in only two forest transects (BP and MA) and an unidentified *Myotis* species was only recorded in one urban transect (ZH). Bat passes that could not be reliably identified made up 0.008% of the total bat passes in all transects.

3.4.3 Patterns of bat foraging activity

Feeding buzzes made up 3% of all bat passes. There were twice as many feeding buzzes in forest habitats (80) compared to urban habitats (40) and these were detected mainly in two forest transects. The feeding buzzes were mainly detected from *Scotophilus kuhlii* followed by *Myotis muricola*. Thirteen out of the total 20 transects in both habitats had less than five bat passes. Due to the zero-inflated nature of the counts of the feeding buzzes, it was not possible to model foraging data under the GLMM framework implemented.

Table 3.2 Characteristics of the 20 transects sampled for bat activity near major roads in Singapore. The bat species detected are as follows: *Myotis muricola* (MYMU), Unidentified *Myotis* (MYUI), *Rhinolophus lepidus* (RHLE), *Rhinolophus trifoliatus* (RHTR), *Saccolaimus saccolaimus* (SASA), *Scotophilus kuhlii* (SCKU), *Taphozous melanopogon* (TAME). A 50m buffer radius was applied to obtain the land cover of each transect.

		Abiotic variables		**Mean ± SD land cover (%)**					**Number of bat passes**									
Transect		**Noise (dB)**	**Light (lux)**	**Water**	**Sealed surface**	**Cultivated greenery**	**Scrub**	**Trees**	**MYMU**	**MYUI**	**RHLE**	**RHTR**	**SASA**	**SCKU**	**TAME**	**Unknown**	**Total**	**Species**
Forest																		
F1	Asrama	58.11 ± 2.07	8.92 ± 3.86	0.00 ± 0.00	1.10 ± 1.10	3.20 ± 2.60	26.50 ± 5.92	46.90 ± 5.86	206	0	0	0	8	200	1	1	416	5
F2	Mandai	60.88 ± 1.66	8.81 ± 3.56	0.00 ± 0.00	5.20 ± 4.29	2.10 ± 1.99	28.60 ± 6.57	41.9 ± 7.47	228	0	0	0	7	371	1	11	618	5
F3	Seletar West	57.88 ± 1.87	3.24 ± 1.61	0.00 ± 0.00	0.90 ± 0.80	11.20 ± 2.30	1.60 ± 0.88	64.30 ± 2.49	94	0	90	0	27	184	12	0	407	5
F4	Bukit Panjang	60.21 ± 1.90	4.77 ± 4.08	0.00 ± 0.00	0.70 ± 0.70	0.30 ± 0.30	5.80 ± 3.87	70.00 ± 3.84	14	0	25	3	0	12	0	0	54	4
F5	Dairy Farm	53.75 ± 2.35	8.23 ± 5.34	11.80 ± 5.73	2.50 ± 2.50	1.60 ± 1.60	0.00 ± 0.00	61.70 ± 6.53	0	0	66	0	4	40	0	0	110	3
F6	Bukit Timah	58.85 ± 1.90	2.11 ± 1.07	0.00 ± 0.00	0.80 ± 0.61	6.60 ± 3.79	2.90 ± 1.39	67.70 ± 4.34	47	0	78	0	0	80	0	0	205	3
F7	Rifle Range	26.60 ± 4.53	2.92 ± 1.31	0.00 ± 0.00	3.00 ± 2.57	11.90 ± 4.55	0.00 ± 0.00	61.50 ± 6.30	20	0	21	0	0	9	6	1	57	5
F8	Ecolink	54.22 ± 1.59	5.30 ± 3.89	0.00 ± 0.00	0.30 ± 0.30	5.50 ± 3.51	0.00 ± 0.00	71.70 ± 5.73	9	0	134	0	0	11	0	0	154	3
F9	Kampong Chantek	56.50 ± 1.84	6.36 ± 4.53	0.00 ± 0.00	3.00 ± 1.40	16.40 ± 5.67	0.10 ± 0.10	57.50 ± 6.66	21	0	19	0	41	25	68	3	177	6
F10	MacRitchie	58.50 ± 1.92	3.39 ± 1.54	0.00 ± 0.00	1.90 ± 1.90	13.60 ± 5.02	0.10 ± 0.10	61.00 ± 5.47	36	0	35	1	0	15	1	0	88	5
Urban																		
U1	Woodlands	61.42 ± 1.56	9.41 ± 2.75	0.00 ± 0.00	24.60 ± 5.02	32.80 ± 6.09	3.20 ± 2.15	16.50 ± 8.43	63	0	0	0	1	26	0	1	91	4
U2	Sports School	62.82 ± 1.47	15.45 ± 3.19	0.00 ± 0.00	30.10 ± 8.53	47.30 ± 8.47	0.00 ± 0.00	0.10 ± 0.10	0	0	0	0	3	32	0	1	36	3
U3	Zhenghua 3	65.28 ± 1.36	12.02 ± 2.04	0.10 ± 0.10	36.00 ± 9.39	37.60 ± 8.58	0.00 ± 0.00	3.50 ± 3.50	13	0	0	0	4	104	0	1	122	4
U4	Zhenghua 2	58.65 ± 2.24	39.58 ± 0.74	0.00 ± 0.00	29.10 ± 8.20	42.20 ± 6.64	0.00 ± 0.00	6.50 ± 3.59	4	0	0	0	12	74	0	2	92	4
U5	Zhenghua 1	60.98 ± 1.68	5.00 ± 0.87	0.00 ± 0.00	31.70 ± 8.67	27.40 ± 4.95	0.00 ± 0.00	18.40 ± 8.80	0	2	0	0	3	109	0	2	116	4
U6	Clementi	55.07 ± 2.16	11.68 ± 2.73	0.00 ± 0.00	20.50 ± 5.27	44.50 ± 6.16	0.00 ± 0.00	11.90 ± 7.20	39	0	0	0	29	96	2	0	166	4
U7	Cheng Soon	59.00 ± 1.83	25.91 ± 3.66	0.00 ± 0.00	38.30 ± 6.48	39.20 ± 6.55	0.00 ± 0.00	0.00 ± 0.00	27	0	0	0	1	95	0	1	124	4
U8	Sian Tuan Ave	55.75 ± 2.21	20.59 ± 4.31	0.00 ± 0.00	35.50 ± 5.31	41.90 ± 5.38	0.00 ± 0.00	0.00 ± 0.00	57	0	0	0	24	109	0	2	192	4
U9	Kheam Hock	57.34 ± 2.15	12.45 ± 3.05	0.00 ± 0.00	29.90 ± 3.93	42.20 ± 4.17	0.00 ± 0.00	5.30 ± 2.52	40	0	0	0	15	200	1	3	259	5
U10	Balestier	64.89 ± 1.33	25.22 ± 3.26	0.00 ± 0.00	50.60 ± 6.09	26.20 ± 6.08	0.00 ± 0.00	0.00 ± 0.00	0	0	0	0	5	117	0	0	122	2

Table 3.3 Bat species present in forest and urban landscapes. A bat pass is defined as at least three consecutive pulses before the nest sequence, or after a trigger interval of one second.

Species	**Number of bat passes**	
	Forest	**Urban**
Scotophilus kuhlii	947	962
Myotis muricola	675	243
Myotis spp.	0	2
Saccolaimus saccolaimus	87	97
Taphozous melanopogon	89	3
Rhinolophus lepidus	474	0
Rhinolophus trifoliatus	4	0
Passes from unidentified bat species	16	13
Total number of bat passes	2292 (63.5%)	1320 (36.5%)

Table 3.4 Model-averaged coefficients of abiotic variables in a GLMM fitted (Model 2) with Poisson errors to predict bat activity in both forest and urban habitats in Singapore. The model averages were computed from 3 models with ΔAICc < 2. Significant explanatory parameters, where confidence do not cross zero, are highlighted in bold.

Response variable	**Predictor**	**B**	**SE**	**CI 2.5 %**	**CI 97.5%**
Bat passes	Intercept	0.165	0.187	-0.201	0.531
N = 3612	Habitat	0.604	0.360	-0.103	1.310
	Distance	0.067	0.135	-0.198	0.332
	Light	**-0.603**	**0.163**	**-0.923**	**-0.283**

3.4.4 Effects of distance from roads, habitats and light on bat activity

No relationship was found between levels of bat activity and distance to roads as a single predictor in Model 2 (Table 3.4). Although more bat passes were detected in forest transects compared to urban transects, *Habitat* (i.e. ‘Forest’ or ‘Urban’) was not found to be a predictor of bat activity in the model. However, model-averaged parameters of the GLMM analysis confirmed increasing bat activity with decreasing light levels (Table 3.4).

3.5 Discussion

I present the first study of responses to roads by tropical bats in a highly urbanised tropical environment. In Singapore, a moderate reduction in bat activity is evident in forest areas that are next to (i.e. 0 m) major roads compared to localities further away. This trend is not evident in urban areas, where only scrub and cultivated vegetation were found to be more important predictors of bat activity. These impacts are still evident despite three decades having passed since construction of one of the major roads in the study system.

3.5.1 Road effects and study design

Due to the intensity of urbanisation in Singapore, I stratified the study design between forested and urban areas to minimise the potential for presence of grey infrastructure to confound road effects. These results demonstrate that bat activity increased by as much as twice from the roads in forest transects. In a study of bat activity in relation to a motorway in the United Kingdom, Berthinussen & Altringham (2012) implemented acoustic surveys over transects that were twice the length of those used in this study and they reported a threefold increase in bat activity between 0-1600 m from the road. However, in the San Francisco Bay area of North America, road effects were detected over a much shorter distance, finding a doubling of bat passes between 0 and 300 m from the road (Kitzes & Merenlender 2014). While I sought to maximise transect length, this was ultimately limited to 800 m by the availability of continuous habitat and access in the highly heterogeneous landscape of Singapore. Nevertheless, despite the different transect lengths employed in these road-effect studies, it is clear that road development, and the habitat degradation and segregation that this implies, significantly impacts bat populations. It is notable, however, that adoption of short transects may lead to an underestimation of bat activity near to roads compared to interior habitat (Kitzes & Merenlender 2014), and that where possible road ecologists should seek transect lengths longer than 300 m in wildlife studies.

3.5.2 Light as a predictor of bat activity

The negative relationship between bat activity and light in all transects originating from major roads is expected as artificial lighting is one of the most important factors in shaping how bats use and orientate within the urban landscape (Fensome and Mathews 2016). Artificial light sources have been found to affect bats by interfering with their foraging and commuting routes, delaying their emergence times, and disturbing their hibernation (Stone *et al.* 2015). Even for a common bat in UK cities such as *Pipistrellus pipistrellus*, it has been found that this species is selective in its choice of gap crossings between tree cover in the city, which is determined by crossing distance and lighting level (Hale *et al.* 2015). Bats crossed gaps between tree cover by using darker parts of the gaps, but as the crossing distance increased between tree cover, light levels required to create a barrier effect was reduced (Hale *et al.* 2015). Street lighting is likely to have a species-specific effect and while fast-flying urban-adapted bats like *P. pipistrellus* uses some lit roads for commuting and foraging, artificial light sources are thought to deter slow-flying species (Stone *et al.* 2009). For the design of safer roads for bats in the future, a better understanding of the different road widths, traffic densities and lighting source, as well as the role of the surrounding topography and habitat are needed (Fensome and Mathews 2016).

3.5.3 Species-level effects

The effects of roads on Singapore’s bat fauna is likely to be species-specific, with response determined by ecological traits such as wing morphology and foraging style (Fensome & Mathews 2016). The most ubiquitous species detected in forested and urban landscapes in this road study was *Scotophilus kuhlii*, with a combined total of 1909 bat passes. This is a fast-flying species with a high wing loading and a moderate aspect ratio, traits associated with foraging in open areas (Kingston *et al*. 2006). *S. kuhlii* is also the most common vespertilionid in Singapore, being regularly detected in mangroves, primary forest, secondary forest, rural, suburban, city and around waterbodies (Pottie *et al.* 2005). The next most common species detected, *Myotis muricola* (675 passes in forest, 243 in urban) is characterised by a low wing loading and a moderately high aspect ratio, and is known to forage in edges and forest gaps, as well as around street lighting (Pottie *et al.* 2005). Elsewhere in the palaeotropics, this species aerial feeds and gleans in partly cluttered environments (McKenzie *et al.* 1995).

By contrast, *Rhinolophus lepidus*, a species considered to be forest dependent (Kingston *et al.* 2003), comprised ca. 20% of bat activity in the forest transects and was never detected from urban habitats. This is somewhat surprising given that population genetic analyses from a habitat mosaic in peninsular Malaysia indicate that the species is capable of traversing large distances between forest patches in agricultural areas (Struebig *et al.* 2011). It is likely that the ability of this species to traverse non-forest habitats is dependent on the composition of the landscape matrix. In Singapore, the heavily urbanised matrix impedes the movement of forest-dependent bat species more than agricultural landscapes do in nearby territories. A study by Rodríguez-San Pedro & Simonetti (2015) supports this hypothesis. These researchers investigated how forest quantity and fragmentation influenced bat activity in landscapes dominated by agricultural landscapes (high-contrast system) and forestry plantation-dominated landscapes (low-contrast matrix) in central Chile, and found that fragmented landscapes with native forest remnants surrounded by a low-contrast matrix supported a higher activity of insectivorous bats. Struebig *et al.* (2011) conducted their study in a landscape matrix that comprised of lowland dipterocarp rainforest fragments and both oil palm and rubber plantations. This would be deemed a low-contrast matrix *sensu* Rodríguez-San Pedro & Simonetti (2015) compared to my study in Singapore where the little remaining forest remnants are surrounded by an intense urban matrix. A landscape matrix with plantations would offer a more hospitable matrix due to the presence of stands of trees (with some clutter) for forest-dependent bat species, as shown by Phommexay *et al.* (2011) in southern Thailand. They detected 10 bat species (including forest-dependent species such as *R. lepidus*) in rubber plantations compared to 19 bat species in the adjacent rainforests of protected areas (Phommexay *et al.* 2011).

Although I did not detect *R. lepidus*, as expected, in urban areas, I have detected this species from a largely unlit park with remnant vegetation (Zhenghua Park) adjacent to the Bukit Timah Expressway outside my study period (unpublished data). This suggests that wooded parks may act as a ‘soft matrix’ (Fischer *et al.* 2005) to provide habitat for forest bats that would not otherwise forage outside the nature reserves.

Thus, the negative effects of roads on tropical bats is likely associated with the severing of foraging grounds as is indicated by studies in temperate regions. For example, in a study of two threatened woodland bats in Germany, Kerth & Melber (2009) found that the severing of habitat by a busy motorway had a much stronger effect on the forest-adapted and less mobile species, Bechstein's bat (*Myotis bechsteinii*). In Singapore, I observed very few bats crossing the major roads during this study. On three occasions, I observed road crossing at the 0 m sampling point: two *M. muricola*, and one *Saccolaimus saccolaimus*.

3.5.4 Mitigating the impacts of roads on tropical bat fauna

My study confirms that major roads acts as a barrier for the two species of bats from the family Rhinolophidae. A meta-analysis conducted by Jung & Threlfall (2016) confirmed the negative response of Rhinolophidae to urbanisation as a land-use change across the Old World. One possible mitigation option would be to establish underpasses, but these would need to be monitored regularly to ensure that they are effective in helping bats to cross the road safely (Abbott *et al.* 2015). Kerth & Melber (2009) found that *M. bechsteinii* rarely used underpasses despite the provision of three underpasses specifically targeted to this species. Another mitigation option would a vegetated wildlife overpass, which shows great potential as bat crossings. Monitoring is already underway at the EcoLink@BKE — a wildlife overpass in Singapore, which serves to connect two rainforest reserves that were fragmented about three decades ago by a major road (Lee 2016). *R. lepidus* has been detected to use the overpass a year after its construction and bat passes increased with the growing vegetation (personal observation, unpublished data).

3.6 References

Abbott, I.M., Berthinussen, A., Stone, E., Boonman, M., Melber, M. & Altringham, J.D. (2015) Bats and roads. *Handbook of Road Ecology*, 1st ed (eds R. van der Ree, D. Smith, & C. Grilo), pp. 290–299. John Wiley and Sons, Ltd.

Altringham, J.D. (2011) *Bats: From Evolution to Conservation*. book, Oxford University Press.

Altringham, J. & Kerth, G. (2016) Bats and roads. *Bats in the Anthropocene: Conservation of Bats in a Changing World* Bats in the Anthropocene: Conservation of Bats in a Changing World. (eds C.C. Voigt & T. Kingston), pp. 35–62. inbook, Springer.

de Araújo, M.L.V.S. & Bernard, E. (2016) Green remnants are hotspots for bat activity in a large Brazilian urban area. *Urban Ecosystems*, **19**, 287–296.

Austin, S.C., Tewis, M.E., Grassman, L.I. & Silvy, N.J. (2007) Road ecology of the leopard cat in khao yai national park thailand. *Acta Zoologica Sinica*, **53**, 373–377.

Bennet-Clark, H.C. (1999) Resonators in insect sound production: how insects produce loud pure-tone songs. *The Journal of Experimental Biology*, **202**, 3347–3357.

Berthinussen, A. & Altringham, J. (2012) The effect of a major road on bat activity and diversity. *Journal of Applied Ecology*, **49**, 82–89.

Blake, D., Hutson, A.M., Racey, P.A., Rydell, J. & Speakman, J.R. (1994) Use of lamplit roads by foraging bats in southern England. *Journal of Zoology*, **234**, 453–462.

Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossmann, F., Bene-Bene, L., De Semboli, B., Mbenzo, V., S'hwa, D., Bayogo, R., Williamson, L., Fay, M., Hart, J. & Maisels, F. (2007) Forest elephant crisis in the Congo Basin. *PLoS Biology*, **5**, 945–953.

Booth, G.D., Niccolucci, M.J. & Schuster, E.G. (1994) Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. *Research paper INT (USA)*.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*.

Chong, K.Y., Teo, S., Kurukulasuriya, B., Chung, Y.F., Rajathurai, S. & Tan, H.T.W. (2014) Not all green is as good: Different effects of the natural and cultivated components of urban vegetation on bird and butterfly diversity. *Biological Conservation*, **171**, 299–309.

Clements, G.R., Lynam, A.J., Gaveau, D., Yap, W.L., Lhota, S., Goosem, M., Laurance, S. & Laurance, W.F. (2014) Where and how are roads endangering mammals in Southeast Asia's forests? *PLoS ONE*, **9**.

CMS. (1994) Agreement on the conservation of populations of European Bats. , **2016**.

Conover, M., Pitt, W.C., Kessler, K.K., DuBow, T.J. & Sanborn, W. a. (1995) Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin*, **23**, 407–414.

Dulac, J. (2013) Global land transport infrastructure requirements. *International Energy Agency, Paris*.

Fahrig, L. & Rytwinski, T. (2009) Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society*, **14**, 21.

Fensome, A.G. & Mathews, F. (2016) Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review*, **46**, 311–323.

Fischer, J., Fazey, I., Briese, R. & Lindenmayer, D. (2005) Making the matrix matter: challenges in Australian grazing landscapes. *Biodiversity and Conservation*, **14**, 561–578.

Forman, R.T.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 207-C2.

Goosem, M. (2001) Effects of tropical rainforest roads on small mammals: Inhibition of crossing movements. *Wildlife Research*, **28**, 351–364.

Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G. & Sadler, J.P. (2015) The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Global Change Biology* **21**, 2467–2478.

Harrison, X. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2**, e616.

Heim, O., Treitler, J.T., Tschapka, M., Knoernschild, M. & Jung, K. (2015) The Importance of Landscape Elements for Bat Activity and Species Richness in Agricultural Areas. *Plos One*, **10**, e0134443.

Jones, D., Bekker, H. & van der Ree, R. (2015) Road Ecology in an Urbanising World. *Handbook of Road Ecology*, pp. 391–396.

Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009) Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, **8**, 93–115.

Jung, K. & Kalko, E.K. V. (2011) Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Diversity and*

Distributions, **17**, 262–274.

Jung, K. & Threlfall, C.G. (2016) Urbanisation and its effects on bats - A global meta-analysis. *Bats in the Anthropocene: Conservation of Bats in a Changing World*, pp. 13–33.

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B. & Hornocker, M.G. (2002) Effects of roads and human disturbance on Amur tigers. *Conservation Biology*, **16**, 97–108.

Kerth, G. & Melber, M. (2009) Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation*, **142**, 270–279.

Kingston, T., Francis, C.M., Akbar, Z. & Kunz, T.H. (2003) Species richness in an insectivorous bat assemblage from Malaysia. *Journal of Tropical Ecology*, **19**, 67–79.

Kingston, T., Lim, B.L. & Akbar, Z. (2006) *Bats of Krau Wildlife Reserve*. book, Penerbit Universiti Kebangsaan Malaysia.

Kitzes, J. & Merenlender, A. (2014) Large Roads Reduce Bat Activity across Multiple Species. *Plos One*, **9**, e96341.

Land Transport Authority. (2015) *Singapore Land Transport Statistics in Brief 2015*. Singapore.

Laurance, W.F., Albernaz, A.K.M., Schroth, G., Fearnside, P.M., Bergen, S., Venticinque, E.M. & Da Costa, C. (2002) *Predictors of Deforestation in the Brazilian Amazon*. *Journal of Biogeography*, **29**, 737–748.

Laurance, W.F., Alonso, A., Lee, M. & Campbell, P. (2006a) Challenges for forest conservation in Gabon, Central Africa. *Futures*, **38**, 454–470.

Laurance, W.F., Clements, G.R., Sloan, S., O’Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B. & Balmford, A. (2014) A global strategy for road building. *Nature*, **513**, 229–232.

Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P. & Ondzeano, C. (2006b) Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, **20**, 1251–1261.

Laurance, W.F., Goosem, M. & Laurance, S.G.W. (2009) Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, **24**, 659–669.

Laurance, S.G.W., Stouffer, P.C. & Laurance, W.F. (2004) Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology*, **18**, 1099–1109.

Lee, B.P.Y.-H. (2016) Road impacts on tropical bats. *Student Conference on Conservation Science, Cambridge - Talk and poster abstracts*, p. 30.

Lesinski, G. (2007) Bat road casualties and factors determining their number. *Mammalia*, **71**, 138–142.

Luo, J., Siemers, B.M. & Koselj, K. (2015) How anthropogenic noise affects foraging. *Global Change Biology*, **21**, 3278–3289.

McKenzie, N.L., Gunnell, A.C., Yani, M. & Williams, M.R. (1995) Correspondence Between Plight Morphology and Foraging Ecology in Some Palaeotropical Bats. *Australian Journal of Zoology*, **43**, 241–257.

Medinas, D., Marques, J.T. & Mira, A. (2013) Assessing road effects on bats: the role of landscape, road features, and bat activity on road-kills. *Ecological Research*, **28**, 227–237.

MSS. (2016) Climate of Singapore.

Olson, D.M. & Dinerstein, E. (2002) The Global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden*, **89**, 199–224.

Phommexay, P., Satasook, C., Bates, P., Pearch, M. & Bumrungsri, S. (2011) The impact of rubber plantations on the diversity and activity of understorey insectivorous bats in southern Thailand. *Biodiversity and Conservation*, **20**, 1441–1456.

Pottie, S.A., Lane, D.J.W., Kingston, T. & Lee, B.P.Y.-H. (2005) The microchiropteran bat fauna of Singapore. *Acta Chiropterologica*, **7**, 237–247.

van der Ree, R. (2009) The ecology of roads in urban and urbanising landscapes. *Ecology of cities and towns: a comparative approach* (eds M.K. McDonnell, A.K. Hahs, & J.H. Breuste), pp. 185–196. Cambridge University Press.

van der Ree, R. & McCarthy, M.A. (2005) Inferring persistence of indigenous mammals in response to urbanisation. *Animal Conservation*, **8**, 309–319.

Rodríguez-San Pedro, A. & Simonetti, J.A. (2015) The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? *Landscape Ecology*, **30**, 1561–1572.

Russell, A.L., Butchkoski, C.M., Saidak, L. & McCracken, G.F. (2009) Road-killed bats, highway design, and the commuting ecology of bats. *Endangered Species Research*, **8**, 49–60.

Rydell, J. (1992) Exploitation of Insects Around Streetlamps by Bats in Sweden. *Functional Ecology*, **6**, 744–750.

Scanlon, A. (2007) Difficulties associated with urban bat research. *Xanthopus*, **25**, 8.

Siemers, B.M. & Schaub, A. (2011) Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 1646–1652.

Stone, E.L., Harris, S. & Jones, G. (2015) Impacts of artificial lighting on bats: a review of challenges and solutions. *Mammalian Biology*, **80**, 213–219.

Stone, E.L., Jones, G. & Harris, S. (2009) Street Lighting Disturbs Commuting Bats. *Current Biology*, **19**, 1123–1127.

Struebig, M.J., Kingston, T., Petit, E.J., Le Comber, S.C., Zubaid, A., Mohd-Adnan, A. & Rossiter, S.J. (2011) Parallel declines in species and genetic diversity in tropical forest fragments. *Ecology Letters*, **14**, 582–590.

Taylor, B.D. & Goldingay, R.L. (2010) Roads and wildlife: Impacts, mitigation and implications for wildlife management in Australia. *Wildlife Research*, **37**, 320–331.

Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.

Walsh, P.D., Henschel, P. & Abernethy, K. (2004) Logging speeds little red fire ant invasion of Africa. *Biotropica*, **36**, 637–641.

Yee, A., Corlett, R., Liew, S. & Tan, H. (2011) The vegetation of Singapore - an updated map. *Gardens' Bulletin Singapore*, **63**, 205–12.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) Mixed effects models and extensions in ecology with R; Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. *New York, NY: Spring Science and Business Media*.

4. The habitat value of green roofs for bats in a tropical urban environment

4.1 Abstract

In adopting a land-sharing approach to urban development, it is possible for development to co-exist with biodiversity conservation in urban areas through the use of green infrastructure. Green roofs, defined as building rooftops with growing substrate and vegetation, offer some potential in urban biodiversity conservation as a co-benefit of providing other ecosystem services such as reduction in storm-water runoff. Here, I investigated the habitat value of intensive green roofs for bats in highly urbanised Singapore using acoustic sampling. Bat activity was monitored using stationary bat detectors for seven nights each over 27 green roofs. Roof characteristics, management regimes and surrounding land cover metrics were investigated as possible predictors of bat activity using generalised linear mixed models (GLMMs). Four bat species (*Scotophilus kuhlii*, *Saccolaimus saccolaimus*, *Taphozous melanopogon* and *Myotis muricola*) were recorded on or around the green roofs sampled. The mean number of bat passes recorded per night was 30.6, pooled across all four species, and the most common species, *S. kuhlii*, accounted for 80.3% of all bat passes. Planted roof area was not a predictor of bat activity, but the age of the roof and building height had a strong negative influence. Bats responded positively to roofs with higher nigh time temperature. Green roof maintenance operations such as pruning at medium levels, and pesticide application had positive and negative effects on bat activity respectively. Maximising vegetation cover, particularly shrubs on the roof, while minimising pesticide use are two key recommendations to improve the value of Singapore's green roofs for bats.

4.2 Introduction

In 2014, 54% of the world's population resided in urban areas, and by 2050 this proportion is expected to increase to 66 % (United Nations 2014). As an extreme form of land use alteration (Shochat *et al.* 2006), urbanisation drives environmental change at local to global scales (Grimm *et al.* 2008). One of the most significant changes is the loss of habitats and biodiversity as natural vegetation is replaced by built infrastructure. In response, Dearborn & Kark (2009) outlined several motivations for conserving urban biodiversity. Apart from preserving threatened species or populations found in urban areas (Ives *et al.* 2016), conservation of urban biodiversity is important because it:

i. Provides ecosystem services such as climate regulation by trees (Bolund & Hunhammar 1999);
ii. Keeps residents engaged with the natural environment who may engender future conservation action (Miller 2005); and
iii. Contributes to the health and well-being of residents through the facilitation and promotion of psychological relaxation, stress alleviation and increased physical activity (WHO 2016) via greenspaces (although the evidence is unclear on the specific role of biodiversity in generating these benefits (Dallimer *et al.* 2012; Lovell *et al.* 2014))

It is possible for development to co-exist with biodiversity conservation in urban areas through reconciliation ecology. This is an alternative biodiversity conservation approach to preservation and restoration, which seeks to modify and diversify man-made habitats in order to accommodate greater species richness without compromising the original intent of the land-use (Rosenzweig 2003). In densely urbanised areas, in which tall buildings are ubiquitous, rooftops may occupy up to 32% of the horizontal built-up area, yet are often under-utilised (Frazer 2005). The principles of reconciliation ecology therefore have great potential to be applied on roofs through ecological engineering and greening (i.e. addition of soil and plants) of these surfaces, which would otherwise remain bare. This is emphasized in a review of reconciliation approaches by Lundholm & Richardson (2010), who state that the recognition of habitat analogues and ecosystems on rooftops help could boost biodiversity conservation and ecosystem functioning in urban areas.

Green roofs are defined as roofs with a vegetated surface and substrate (Oberndorfer *et al.* 2007; Francis & Lorimer 2011), and are broadly classified as ‘extensive’ or ‘intensive’ types. The benefits of having greens roofs are primarily to improve the thermal properties of buildings and to reduce storm-water run-off at a local level. Collectively, many green roofs may function to reduce the urban heat island effect (heat generated by cities due to human activities) and to a lesser extent, for carbon storage (Getter *et al.* 2009). When built as an intensive roof, these structures also provide an increased living space for people via provision of greenery and other park facilities, and may also function as habitats for plant and animal communities. Extensive roofs typically have a shallow substrate depth, a low-growing plant community and require little maintenance. In contrast, intensive roofs differ by having a deep substrate, a plant community of diverse forms and heights, and requires more maintenance. A summary of these differences is presented in Table 4.1.

To date, most of the investigations of biodiversity on green roofs have involved invertebrate groups such as ants, bees, beetles, flies, leafhoppers, spiders (Brenneisen 2006; Coffman & Davis 2005), and more recently, butterflies (Tan *et al.* 2015). The conservation importance of green roofs as urban habitats is further emphasized when rare invertebrates are found on them (Kadas 2006). Studies on green roof systems in Europe have also documented the importance of these structures for breeding of rare birds, such as the black redstart (*Phoenicurus ochruros*) in the UK and the northern lapwing (*Vanellus vanellus*) and little-ringed plover (*Charadrius dubius*) in Switzerland (Baumann 2006).

Table 4.1 A comparison of extensive and intensive green roofs (Adapted from Oberndorfer *et al.* 2007).

Characteristic	**Extensive roof**	**Intensive roof**
Purpose	Functional; storm-water management, thermal insulation, fireproofing	Functional and aesthetic; increased living space
Structural requirements	Typically with standard roof weight-bearing parameters; additional 70 to 170 kg per m^2 (Dunnett & Kingsbury 2008)	Planning required in design phase or structural improvements necessary; additional 290 to 970 kg per m^2
Substrate type	Lightweight; high porosity, low organic matter	Lightweight to heavy; high porosity, low organic matter
Average substrate depth	2 to 20 cm	> 20 cm
Plant communities	Low-growing communities of plants and mosses selected for stress-tolerance qualities (e.g., *Sedum* spp.)	No restrictions other than those imposed by substrate depth, climate, building height and exposure, and irrigation facilities
Irrigation	Most require little or no irrigation	Requires irrigation
Maintenance	Little or no maintenance required; some weeding or mowing as necessary	Maintenance similar to garden at ground level
Accessibility	Generally functional rather than accessible; accessibility needed for maintenance	Typically accessible; bylaw considerations

Green roof habitats are of particular interest to ecologists because they represent “green islands” in an adverse urban matrix (Blaustein, Kadas & Gurevitch 2016). Therefore, our understanding and expectations of how biodiversity might utilize green roof space can be informed by the extensive ecological literature on island biogeography, and to some extent habitat fragmentation (although note that strictly speaking green roofs are not habitat remnants or fragments since they are man-made and did not form part of the original vegetation cover).

The theory of island biogeography predicts that more species are supported on larger islands/habitats/green roofs, and that richness also decreases with increasing distance from a colonising source (MacArthur & Wilson 1967). The principles of habitat fragmentation inform us that colonisation and dispersal between fragments is also mediated by the quality of habitat in the intervening matrix (i.e. urban environment) (Ewers & Didham 2006). However, rooftop ecological communities are potentially also constrained by vertical isolation from ground habitats as well as horizontal isolation from other communities. Rooftops are therefore quite unique habitats because they are isolated from ground habitats and each other, and present substantial challenges for plants and animals to colonise, in particular those with limited dispersal ability. In the only study to date investigating green roofs and habitat connectivity, Braaker *et al.* (2014) compared four arthropod groups with contrasting mobility on green roofs and ground habitats in Zurich, Switzerland. They found that the communities of highly mobile groups such as bees and weevils were influenced by horizontal habitat connectivity, whereas abundance and diversity of low-mobility communities, such as beetles and spiders, were determined by local conditions such a proportion of forbs and bare ground on the roofs. This study demonstrated that while there is interaction and movement of high-mobility arthropods between green roof habitats, the arthropods characterised by as poor dispersers were restricted between ground and roof habitats (Braaker *et al.* 2014). Hence, both the horizontal distance between roofs and vertical height of a green roof is an important factor in dictating the structure of rooftop communities.

Research on green roofs has risen dramatically, being represented by one country in 1993 to 24 countries in 2012, including eight from Asia (Blank *et al.* 2013). This impetus in green roof research is driven by the need to provide sound scientific knowledge to guide sustainable urban design and development (Blank *et al.* 2013). Most of the studies to date have been conducted in the United States of America and Europe, and there is limited research from the urban tropics where the interest in green roofs is growing (Blank *et al.* 2013).

At present, Singapore has more than 72 ha of rooftop greenery throughout the country and this is projected to increase to about 200 ha by 2030 (National Parks Board 2016). The proliferation of green roofs in Singapore follows the country’s goal in striving to be a “City in a Garden”, in which planning authorities are strongly encouraged to incorporate greenery into built infrastructure for better building performance, aesthetics and other urban ecosystem services. Policies to encourage the implementation of green roofs include the Skyrise Greenery Incentive Scheme (SGIS) and the Landscaping for Urban Spaces and High-Rises Programme (LUSH), introduced by the National Parks Board and the Urban Redevelopment Authority respectively (Urban Redevelopment Authority, 2015; National Parks Board, 2016). The SGIS was started in 2009 and further refined in 2015. This scheme funds up to

50% of the installation costs of rooftop and vertical greenery, and there have been 163 projects to date (National Parks Board 2016)**.** The LUSH programme further sets out guidelines for greenery replacement for green areas lost to building development, and gross floor area (GFA) exemptions for greenery implementation within the development, which includes green roofs.

In Singapore, roof biodiversity studies have so far focused on plants and animals colonising on an experimental wild roof garden (Hwang, 2014; Hwang & Yue, 2015), patterns of bee, bird and butterfly communities on various green roofs throughout the island (Roscoe, 2015; Tan *et al.* 2015). In contrast, there is a global paucity of studies investigating the value of green roof infrastructure for mammals, except for bats. Bats are an ideal mammal group to investigate in urban areas because of their mobility, and simplified community of a few dominant species that are "urban adapters" (*sensu* McKinney, 2002). To date, there are only two studies investigating the use of green roofs by bats using acoustic approaches and both of them were conducted in temperate cities. The first study was undertaken in London by Pearce and Walters (2012). They compared three roof types – conventional (no planting), sedum and biodiverse. It was found that bat activity was significantly higher over biodiverse roofs than conventional roofs, whereas there was no difference between conventional and sedum roofs. There was a negative influence on bat activity with increased roof height. The other green roof involving bats was based in New York City where Parkins and Clark (2015) used a paired design consisting of a conventional roof and a green roof to control for location, height, and local variability in surrounding habitat and bat species diversity. This study used four pairs of roofs and had a larger dataset as it was conducted over an entire season but over fewer roofs as compared to Pearce and Walters (2012). Parkins and Clark (2015) also found that the levels of bat activity were higher over green roofs than over conventional roofs.

Here, I investigate insectivorous bat activity on intensive green roofs (roof gardens) throughout Singapore with a diverse range of heights (12-189 m) and much larger rooftop areas (235-7027 m^2) than investigated in the previous two studies (Figure 4.1). My approach attempts to account for the characteristics and management regimes of each roof as well as the landscape context surrounding roof sites. Insectivorous bats in the urban areas interact with vegetation and water bodies while foraging, and arthropods are known to be influenced by many aspects of urban vegetation (e.g. tree cover, vegetation structure and herb density) and management regimes (Beninde, Veith & Hochkirch 2015; Threlfall *et al.* 2016). I first hypothesized that bat activity would be greater on larger roof gardens than smaller ones as expected under an island biogeography framework. Second, there would be lower bat activity on high roofs compared to low ones due to vertical isolation of the high roofs from ground habitats. Third, I expected that heavily managed and maintained green roofs would also be characterised by low bat activity than those with minimal maintenance. At a landscape scale, I hypothesized that there will be more bat activity on roofs surrounded by more urban greenery.

Figure 4.1 A. Locations of green roofs in Singapore used in this study with selected roofs sites: **B.** AscentiaSky (AS) **C.** Solaris (SL) **D.** National Library (NL) **E.** Marina Bay Sands (MB) – highest green roof in this study at 189 m (arrowed) with a green roof in the foreground for comparison **F.** Khoo Teck Puat Hospital (KT) **G.** Subaru MotorImage (SB) **H.** Village Residences (private apartment with swimming pool) (HG) **I.** Sengkang 437 (SK) (green roof built above a multi-storey car park adjacent to public housing).

Table 4.2. Characteristics (shaded green) and explanatory variables of the 27 green roofs surveyed for bats. Age refers to the number of years since the garden was constructed, using the start of 2014 as a reference point. Water, maintenance and pesticide are categorical variables. P125: Proportion of non-vegetated land within buffer of 125 m of the site polygon boundaries, P1000T: Proportion of tree-covered land within buffer 1000m of the site polygon boundaries.

Roof_ID	Area (m^2)	Height (m)	Age (years)	Temp (°C)	Water	Shrub (m^2)	Tree height (m)	Tree height diversity (m)	Maintenance	Pesticide	P125	P1000T
CK	1401	12	3	22.3	1	360.99	4.07	1,21	2	1	0.98	0.41
SK	2925	15	6	22.9	1	324.49	2.57	1.86	2	1	1.00	0.21
ES	1206	16	10	22.6	2	363.80	3.26	2.79	2	1	0.67	0.18
DV	3333	28	1	22.1	1	868.40	2.29	1.73	3	1	0.74	0.35
SC	1220	24	11	23.3	3	86.83	8.10	1.28	2	1	0.65	0.29
SE	4813	14	4	23.1	3	1186.23	2.50	1.93	3	2	0.43	0.31
KT	2464	14	4	22.1	3	1529.87	2.73	1.91	3	1	0.74	0.10
PG	5736	12	22	23.0	1	2428.97	3.16	2.07	2	4	0.81	0.05
PU	4583	13	13	22.8	1	872.36	2.25	2.52	3	4	0.86	0.10
SA	7027	50	5	22.6	1	1517.24	4.44	1.83	3	4	0.88	0.44
WK	544	40	6	26.0	1	139.00	6.25	0.45	2	3	0.95	0.22
NO	714	51	2	22.8	2	426.50	5.96	4.00	3	2	1.00	0.22
SO	1525	21	6	22.6	2	367.73	5.81	1.89	3	1	0.80	0.19
EU	3204	16	7	23.3	1	1047.27	5.90	2.51	3	2	0.75	0.05
QT	4840	15	18	23.1	1	1362.89	5.53	2.21	1	1	0.71	0.34
GR	668	48	3	23.0	2	210.76	2.01	2.13	3	3	0.43	0.25
HG	2913	15	0.5	23.6	2	1080.43	1.85	1.56	3	4	1.00	0.11
SB	1169	26	9	22.4	3	290.79	2.87	1.37	2	4	0.63	0.22
SH	1747	30	21	22.5	1	961.89	2.04	2.00	3	1	0.85	0.55
JH	2045	14	19	23.3	2	592.09	3.65	2.70	3	2	0.71	0.52
CL	459	77	6	25.7	1	232.77	2.26	2.09	3	4	0.99	0.11
SL	2405	70	4	22.3	1	1082.08	2.27	2.00	2	3	0.84	0.32
OC	2171	61	5	22.3	3	772.38	2.60	2.25	3	3	0.82	0.49
PP	1334	16	28	22.3	3	554.87	1.51	0.78	3	4	1.00	0.17
NL	235	51	9	22.3	1	131.45	3.48	0.51	3	4	0.94	0.15
AS	236	141	1	22.4	1	102.63	2.32	1.46	3	3	0.73	0.32
MB	5997	189	4	22.1	2	94.34	3.20	2.54	2	2	0.82	0.08

Water: No water = 1, Chlorinated pool = 2, Fish pond = 3. **Maintenance:** low = 1, medium = 2, high = 3. **Pesticide (application frequency):** none = 1, ad-hoc = 2, monthly = 3, fortnightly = 4.

4.3 Methods

4.3.1 Study system

Fieldwork was undertaken on green roofs in the heavily urbanised areas of Singapore (1°22”N, 103°48”E). Since the 1960s, Singapore has embarked on an urban greening campaign which has resulted in 27.5% of the country being covered by managed vegetation in the form of public parks, roadside greenery and other green spaces, while 39% of the land is non-vegetated and taken up by buildings, roads and other urban infrastructure (Yee *et al.* 2011; Tan, Wang & Sia 2013). This study focussed on greenery on rooftop gardens.

4.3.2 Green roof selection

The green roofs sampled for bats in this study were part of a broader investigation of biodiversity and habitat use across different taxonomic groups (Tan *et al.* 2015). The selection of green roof sites consisted of three steps.

First, a comprehensive list of roof gardens was compiled using information from three government agencies (the National Parks Board (NParks), the Housing Development Board (HDB) and the Urban Redevelopment Authority (URA)) coupled with an internet search for hotels, hospitals, shopping malls, and office buildings that has a roof garden. Based on this list, only roofs gardens with the following features were selected:

i) The garden was accessible to building occupants or the public;

ii) The garden was accessible to volant animals (i.e. not enclosed by skylights or netting); and
iii) Vegetation in the garden was grown in permanent planting pits and not in containers.

This yielded 259 green roofs that met the above criteria.

Second, through telephone interviews with roof site managers and, using online map resources, the 259 roofs were subjected the following criteria:

i) At least four storeys above ground level;
ii) A minimum vegetated area of at least 300 m^2 for the garden;
iii) Not completely enclosed by walls; and
iv) No active management to exclude wildlife (e.g. cutting of flowers).

The height criterion of four storeys in the selection was based on the typical height of the roof gardens built by the HDB; this height was also typically above the street tree canopy, and therefore separates ground-level gardens. After this filter was applied, 76 roof garden sites remained. This was finally reduced to 32 available sites for bird and butterfly surveys, considering a reasonable range of heights. However, bat activity could only be assessed at 29 of these 32 sites because the managers of three roof gardens refused to allow bat detectors to be placed on the roof as they believed the microphone pole could be prone to lightning strikes.

4.3.3 Green roof variables – surrounding land cover, roof characteristics and management regimes

Land cover variables were derived from SPOT-5 imagery produced for the urban area by Joanneum Research, Graz, Austria (https://www.joanneum.at/) as part of a carbon accounting study in April 2013 (Schmitt & Hirschmugl 2016). The land cover map derived from the remote sensed data defined four land cover classes (tree cover, non-tree vegetation cover, water and non-vegetated land) at a minimum resolution of 0.25 ha, and had an overall accuracy of 87% as assessed from ArcGIS World Imagery (ESRI) (Scale Range: 1:591,657,528 down to 1:1,128) (Schmitt & Hirschmugl 2016). Cover of trees, non-tree vegetation and non-vegetated land was quantified within buffer areas of 125 m, 250 m, 500 m and 1000 m from the perimeters of the roof garden boundaries in ArcGIS 10.2 (ESRI).

The height of each green roof was measured using a LTI TruPulse 200 Rangefinder (+/- 0.1 m). Green roofs were also separated into two exposure classes based on whether plants experienced natural light directly overhead (1) or were covered by a ceiling (0). Site area, shrub cover (including planter pits for trees), lawn cover, shrub cover, water area, were measured on-site using a measuring wheel. Ambient temperatures were logged at 15-minute intervals at each roof using a Tinytag Plus 2 TGP-4500 temperature data-logger (-25 to 85°C) (Germini Data Loggers Ltd) between September 2014 and January 2015. Each data-logger was placed in an inconspicuous and shaded location in the roof garden at an approximate height of 1.5 m and out of direct sunlight. The presence of water bodies was recorded at each site and roofs classified into three levels (no water = 1, chlorinated pool = 2 and fish pond = 3). Maintenance categories were assigned that accounted for both frequency and intensity of vegetation pruning, based on monthly photographic records at each site (low = 1, medium = 2, high = 3). Information on frequency of pesticide application (none = 1, *ad hoc* = 2, monthly = 3, fortnightly = 4) and site age (years) were obtained either from the site managers or gardeners. Heights of all plants taller than 2 m (palms/trees) were estimated to the nearest metre by visual reference to a 1 m pole placed against each trunk; these excluded plants maintained as hedges whose stems were clumped or otherwise inaccessible.

4.3.4 Bat activity data collection

I collected data from 29 roofs but two roofs had to be excluded due to equipment malfunction, which sampled bat calls for less than 7 evenings each. Hence, 27 roofs were used for the final analysis.

Bat activity (in the form of bat passes) was recorded using SongMeter SM2BAT+ (Wildlife Acoustics, Concord, MA) full spectrum ultrasonic recording units from 29 September 2014 to 28 January 2015. One detector was deployed in the centre of each roof garden and left for between seven to nine consecutive nights, with data collected on rainy nights excluded. Seven nights of recordings were available for each roof to allow for comparisons at a standard sample size. Sites were sampled in a random order, with up to three detectors operating simultaneously on different roofs. Each detector was connected to a SMX-US omni-directional microphone attached to the top of a 1.8 m pole to minimize echolocation bounce off hard surfaces and to maximize the number of calls and improve the quality of the calls recorded. Microphones were calibrated before each deployment (Parson & Szewczak 2009) using an ultrasonic calibrator (Wildlife Acoustics, Concord, MA) with a 40 kHz pulse.

I applied a systematic protocol to record bats at each roof using the trigger function on the detector (i.e. the detector automatically records sound when thresholds are reached, thereby putting the equipment in a power saving mode when there is no bat activity). Detectors were set to record calls continuously from sunset to 7 am each day. The equatorial position of Singapore means that the daytime period (and night) is fixed at 12 hours throughout the year; therefore, sunrise and sunset times did not change significantly during the sampling period. Detectors were set with a 384 kHz sample rate, fs/24 digital high pass filter, 18 dB trigger level, microphone bias off, and 36 dB gain. A 2.0 s trigger window minimum was set, and calls were recorded in .wav format onto SD data cards and copied to hard drives for storage and subsequent analysis.

4.3.5 Processing of sound recordings

Recordings from all roof gardens were processed using Kaleidoscope Pro 3.0 (Wildlife Acoustics, Concord, MA) with an initial filter using signal parameters to remove files that did not contain bat passes: any signal between 20-120 kHz and lasting between 2-500 ms was retained for further inspection. For the purposes of analyses a bat pass is defined as a recording with at least three consecutive sound pulses, and with each pass separated by one or more seconds. The call files in the output folder were visually inspected to identify the associated bat species, and to remove any non-bat files that may have not been eliminated in the initial processing steps.

4.3.6 Bat foraging activity

The foraging activity of bats is often indicated by the detection of 'feeding buzzes' or 'terminal buzzes', which are produced as a rapid sequence of calls when individuals attempt to capture prey (Griffin, Webster & Michael 1960; Russ, 2012). For the acoustic monitoring of green roofs as well as ground habitats, the detection of these unique call sequences is a useful proxy for actual habitat use because search phase calls may just indicate that bats are commuting over a particular habitat. Bat passes were examined for the characteristic high inter-pulse repetition rate, steep pulse slope, and short pulse duration of a feeding buzz. The number of feeding buzzes were tallied for each green roofs and a 'buzz ratio' or ratio of feeding buzzes to bat passes was calculated (Vaughan, Jones & Harris 1997). Feeding buzzes were pooled for each roof and overall bat foraging activity was quantified for each roof. I adopted the method used by Fukui *et al.* (2006) and Park, Mochar & Fuentes-Montemayor (2012) of using bat passes as an indicator of foraging activity, because these studies found bat passes to be highly correlated with feeding buzzes. To do this I assessed correlation between the number of feeding buzzes and number of bat passes using a Spearman rank correlation test.

4.3.7 Statistical analyses

Prior to conducting analyses, all non-categorical explanatory variables were scaled and centred so that their effect sizes were comparable and to improve model fit. These variables were then visualised and explored to identify levels of multi-collinearity using variance inflation factors (VIFs), pair plots and Spearman's rank correlation coefficients. Variables were excluded if Spearman rank correlation coefficients were more than 0.5 (Booth, Niccolucci & Schuster 1994), or if VIFs were greater than 3.0 (Zuur *et al.* 2009). If there were two highly correlated variables, the variable that was most ecologically meaningful was retained. See Table 4.3 for a description of all 12 predictor (explanatory) variables.

I undertook two sets of models to predict bat activity around green roof gardens. First, I assessed the relative influence of height, age, planted roof area and two landscape variables (P125 and P1000T) on bat activity using a general linear mixed model (GLMM) with Poisson error terms. This model (Model 1) sought to identify landscape-level covariates of influence in the dataset prior to a broader exploration of habitat quality variables on the roofs themselves:

Bat passes ~ (Age + Height + Planted area + P125 + P1000T) + (1| Site_ID) + (1|Roof_row)

where P125 = Proportion of non-vegetated land within buffer of 125 m of the site polygon boundaries, and

P1000T = Proportion of tree-covered land within buffer 1000m of the site polygon boundaries.

I then used a separate GLMM with Poisson error terms to quantify the influence of green roof characteristics and roof management activities on bat activity (Model 2).

Bat passes ~ (Water + Shrub + Temp + TreeHt + TreeHtD + Main + Pest) + (1| Site_ID) + (1|Roof_row)

The co-variates or predictors of bat activity in Models 1 and 2 are fully explained in Table 4.3. For each model, total bat passes per night was used as the response variable. Models were repeated for species level bat activity, but none of the models converged, and so only results from total bat passes are reported. Roof site (Site_ID) was included in the both models as a random effect to account for pseudo-replication associated with seven repeated samples in each garden. To address over-dispersion in both models, an observation-level random effect (OLRE) dummy variable unique to each data row (Roof_row) was coded as a factor and added to lower the dispersion parameter to 1 (Harrison 2014). A "bobyqa" optimizer with 20,000 iterations was specified explicitly in both models to overcome issues of non-convergence. All analyses were performed in R version 3.3.1 (R Core Team 2016) using the packages *arm*, *MuMIn*, *lme4*, and *blmeco*.

An information theoretic approach was used in model selection. This approach estimates parameters based on multi-model inference because it is acknowledged that the collected data could support many competing models and hypotheses (Burnham & Anderson 2002). Model selection was based on AIC_c, a variant of AIC (Akaike Information Criterion) corrected for potential bias due to small samples (Burnham & Anderson 2002). Many models with different variable combinations were run and the best model emerged as the one with the smallest AIC_c value. Models with ΔAIC_c <2 were used to estimate model average parameters. The relative plausibility of each model was quantified through calculating the Akaike weight, *w*. The final model was obtained by calculating the model average, with the weight of each model in the set considered.

Table 4.3 List of 12 covariates investigated in relation to bat activity on green roofs in Singapore. The short form of the co-variate is in parentheses and is used in the equation of the GLMMs.

Co-variates	Description	Unit
Site height (Height)	Relative height of green roof above ground level	m
Site age (Age)	Number of years since the green roof was constructed, since 2014	years
Planted area (Parea)	Total area of lawn, shrubs, climbers, ferns and other non-tree vegetation	m^2
Temperature (Temp)	Minimum ambient temperature recorded at each site	°C
Water (Water)	Presence of water: 1 = no water; 2 = chlorinated water; 3 = pond	factor
Shrub cover (Shrub)	Total area of shrubs, climbers, ferns and other non-tree vegetation	m^2
Tree height (TreeHt)	Average height of all trees and palms on the green roof	m
Tree height diversity (TreehtD)	Standard deviation of the heights of all trees and palms in the garden	m
Maintenance (Main)	Frequency/intensity of vegetation pruning: 1 = low; 2 = medium; 3 = high	ordinal
Pesticide application (Pest)	Frequency of application: 1 = none; 2 = as and when needed; 3 = monthly; 4 = fortnightly	factor
P1000T (P1000T)	Proportion of tree-covered land within buffer 1000m of the site polygon boundaries	%
P125 (P125)	Proportion of non-vegetated land within buffer of 125 m of the site polygon boundaries	%

4.4 Results

4.4.1 Overall bat diversity and activity

A total of 7670 bat passes were recorded over all 27 green roofs (189 nights) and the mean number of bat passes recorded per night was 40.6 (range: 0.43 – 159.43 passes) (Table 4.2). Four bat species (*Scotophilus kuhlii*, *Saccolaimus saccolaimus*, *Taphozous melanopogon* and *Myotis muricola*) were recorded. The most common species was *S. kuhlii*, which accounted for 84.7 % of all bat passes, with *T. melanopogon* and *S. saccolaimus* representing 13.6% and 1.9% respectively. *M. muricola* was recorded just four times (0.0005% of all bat passes). For bat diversity, one roof (SE) had all four bat species recorded, and another had only one species (PU). Roofs with two and three bat species recorded comprised 26% and 67% of those sampled respectively. Recordings containing feeding buzzes constituted only 1.7% of all bat passes, and the number of passes containing feeding buzzes was moderately, and significantly, correlated with total bat passes at each site (Spearman Rho = 0.57, p-value = 0.004).

4.4.2 Response of bat activity to green roof characteristics, management regime and land cover

Model average parameters of Model 1 revealed the age and height of green roofs to be important predictors of bat activity and any response to planted area as well tree- and non-vegetated cover around the roof to be low and non-significant (Table 4.4). In other words, low bat activity was found on older or taller roof gardens (Figures 4.2 & 4.3). In this model, height was deemed a more important predictor than age, with the estimated response in bat activity being twice greater to the former (Table 4.4).

In Model 2, the most important variables significantly associated with bat activity were pruning at medium frequency and monthly application of pesticides, which had a positive and a negative response in bat activity respectively (Table 4.5). Temperature and shrub cover were found to be positive predictors of bat activity, implying that higher night temperature and green cover of medium height is important for bats. The application of pesticide (whether *ad hoc*, monthly or fortnightly) was negatively associated with bat activity. The presence of water bodies had no effect on bat activity (Table 4.5).

Table 4.4 Model-averaged coefficients of GLMM Model 1 to predict bat activity on Singapore roofs: roof height, age, total planted area and land-cover variables fitted with Poisson errors. Model averages were computed from four models with ΔAICc < 2. Significant explanatory parameters, where CIs do not cross zero, are highlighted in bold.

Response variable	**Explanatory variable**	**Estimate**	**CI 2.5%**	**CI 97.5%**
Bat passes N = 7670	Intercept	2.913	2.625	3.201
	Height	**-2.577**	**-3.283**	**-1.871**
	Age	**-1.114**	**-1.731**	**-0.497**
	Tree-covered land (P1000T)	0.204	-0.372	0.780
	Planted area (Parea)	0.175	-0.456	0.807
	Non-vegetated land (P125)	-	-	-

Table 4.5 Model-averaged coefficients of GLMM Model 2 to predict bat activity on Singapore roofs: presence of water, shrub cover, temperature, tree height and height diversity together with management variables, fitted with Poisson errors. Model averages were computed from four models with ΔAICc < 2. Significant explanatory parameters, where CIs do not cross zero, are highlighted in bold.

Response variable	**Explanatory variable**	**Estimate**	**CI 2.5%**	**CI 97.5%**
Bat passes N = 7670	Intercept	3.421	1.322	5.519
	Pruning: (medium)	**2.186**	**0.208**	**4.164**
	(high)	1.712	-0.269	3.693
	Pesticide: (*ad hoc*)	**-1.810**	**-2.978**	**-0.643**
	(monthly)	**-2.104**	**-3.215**	**-0.993**
	(fortnight)	**-1.779**	**-2.801**	**-0.756**
	Shrub cover	**0.815**	**0.017**	**1.613**
	Temperature	**0.830**	**0.056**	**1.604**
	Tree height diversity	0.464	-0.448	1.375
	Tree height	0.308	-0.517	1.134

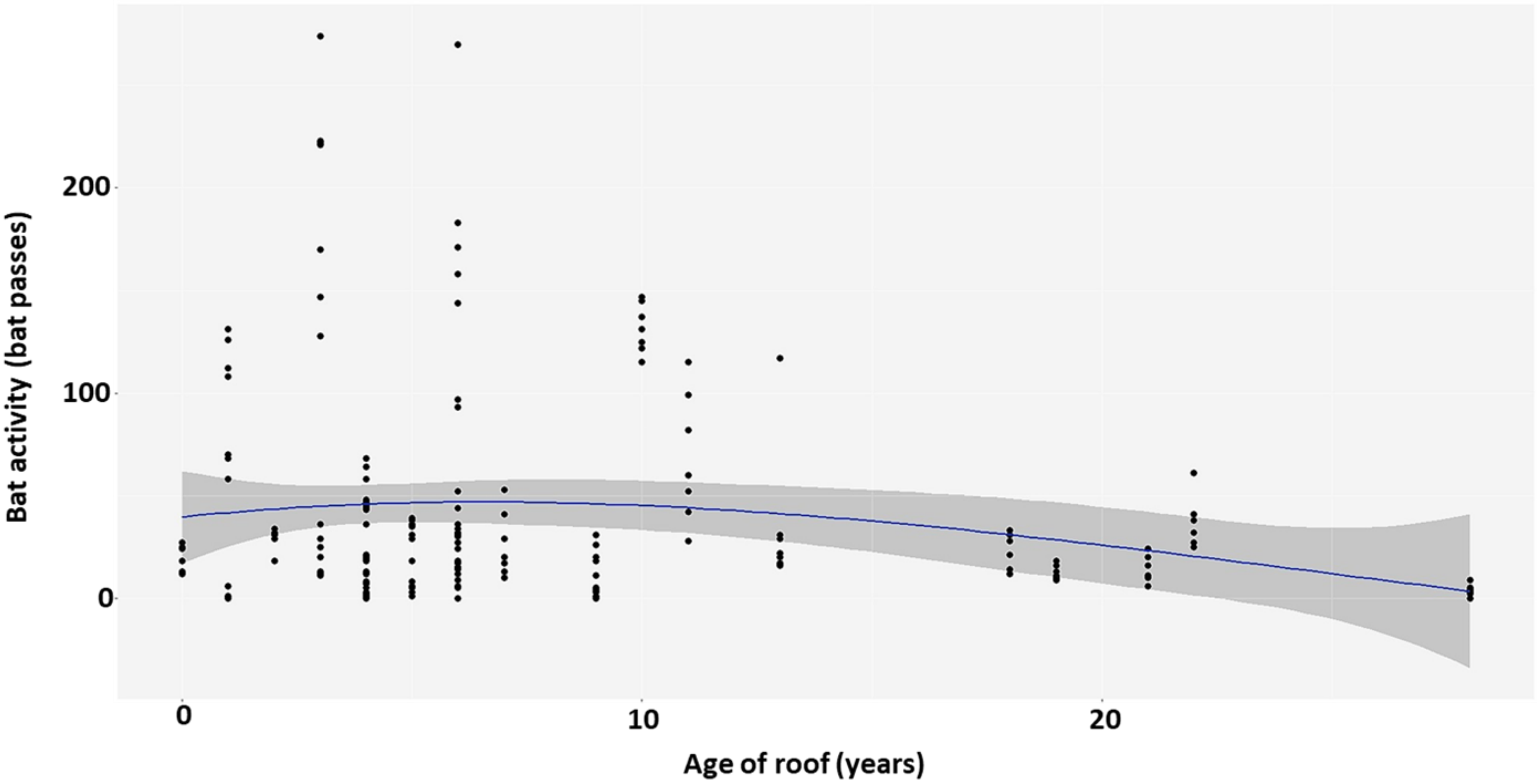


Figure 4.2. GLMM prediction showing the relationship between bat activity (bat passes) and the age of green roof (years). The confidence interval for the fitted line is represented as the shaded area.

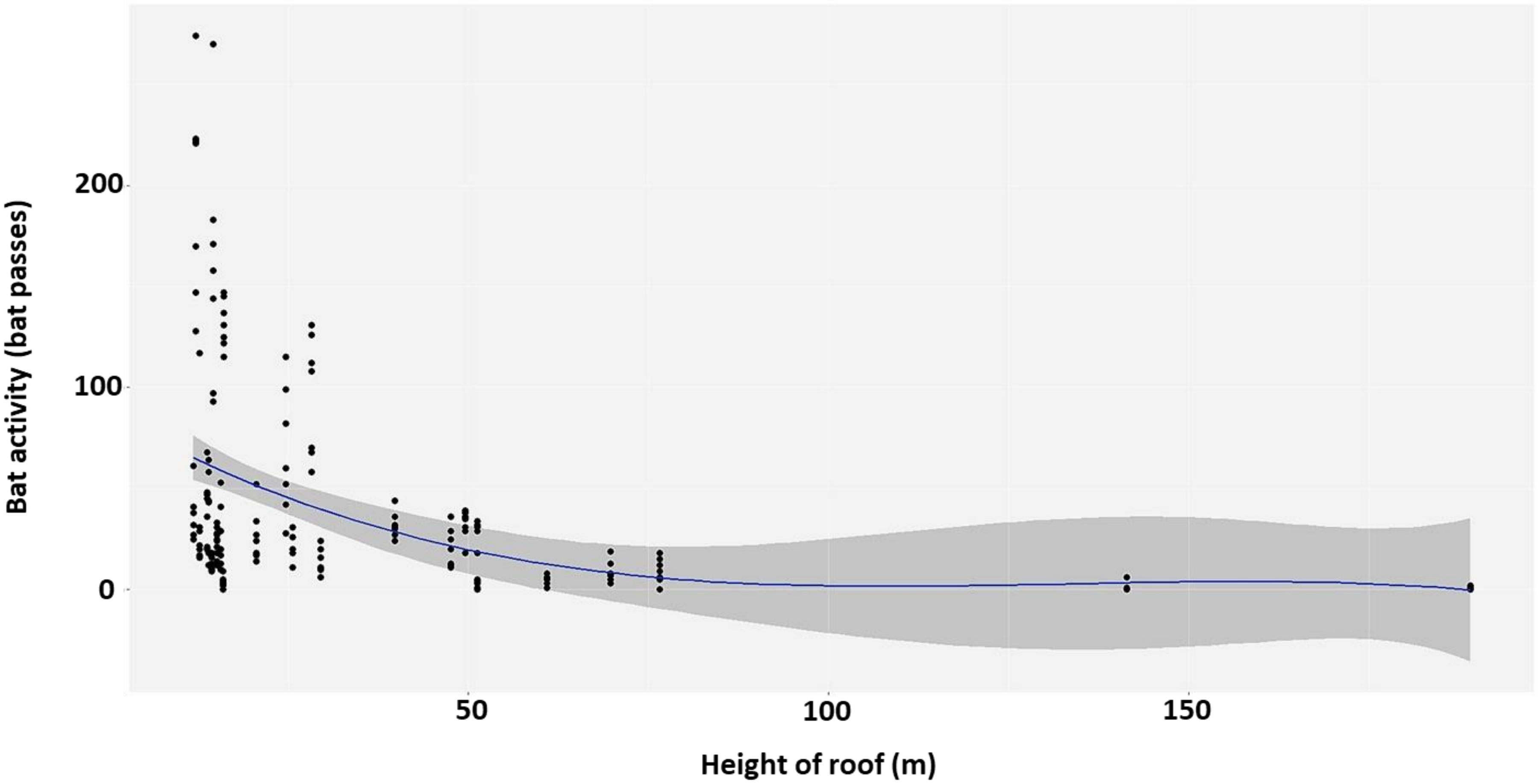


Figure 4.3. GLMM prediction showing the relationship between bat activity (bat passes) and the height of green roof (m). The confidence interval for the fitted line is represented as the shaded area.

4.5 Discussion

Results from this study demonstrate that some bat species use intensive green roofs as a foraging habitat in Singapore’s urban environment, despite the bat fauna being impoverished overall. The age and the height of green roofs have a strong influence on the bat activity a roof can support. There were more bats on newer roofs, and low roofs (≤ 24 m) had greater bat activity than high ones. Warmer nights were found to have a positive effect on bat activity. In terms of vegetation on the green roofs, only shrub cover had a positive influence on bat activity, but neither tree height nor tree height diversity had a demonstrable effect. The use of pesticides and pruning at medium frequency had negative and positive effects on bat activity respectively.

4.5.1 Influence of roof area and land-cover co-variates

From an extensive literature on island biogeography theory and fragmentation, we would expect bat activity to be strongly influenced by the area of the green roof. For example, in a study of 27 forest fragments in a disturbed rainforest landscape in peninsular Malaysia, Struebig *et al.* (2008) found greater abundance and species richness of insectivorous bats in larger forest fragments. However, this pattern was not found on the green roofs in Singapore. Some plausible explanations for this are that green roofs or gardens are created habitats at a height and not remnants of original vegetation, and they have relatively little to offer in terms of natural roosting resources. The other possible reason is that there was only small sample of roofs (n=27) in my study and there was a limited variation in the size of the green roofs. In a study of bat assemblages in heavily disturbed forest in Borneo, Struebig *et al.* (2013) demonstrated that more bats utilised sites with greater number of tree cavities for example. Moreover, green roofs are generally very small in size compared to remnant ground habitats, and the area of vegetation planted within green roofs is limited. In a meta-analysis on intra-urban biodiversity variation across a range of taxonomic groups (birds, herptiles, insects, plants and fungi), Beninde, Veith & Hochkirch (2015) found that there was a rapid decline in species richness in habitat patches at an average of ca. 27 ha. In order to conserve urban-adapter species, an area threshold of at least 4.4 ha for a habitat patch is needed (Germaine *et al.* 1998; Drinnan 2005). While these area thresholds may not necessarily apply to bats and other taxa not mentioned in the meta-analysis, it is notable that the green roofs in my study are typically below a hectare in size and hence its habitat value may be limited for most taxa.

I did not find both landscape variabes - proportion of non-vegetated land in a 125 m buffer, and tree-covered land in a 1000 m buffer - to have any effect on bat activity. This differed from the work of Pearce & Walters (2012) in urban London. They mapped the percentage cover of vegetation and water habitats within a 100 m radius of the centre of each roof, and found that the area of suitable habitat in that buffer had a positive influence on bat activity. They attributed their observation to higher insect biomass with the presence of vegetation and water bodies in the surrounding area coupled with linear features such as tree lines and canals acting as connectors to the green roofs. On the other hand, the study by Parkins and Clark (2015) in New York found the surrounding vegetation in a 1000 m buffer around each roof to have a strong effect and positive effect on bat activity. They postulated that the availability of nearby habitat for three tree roosting bat species in their study (*Lasiurus borealis*, *L. noctivagans* and *L. cinereus*) increased the habitat value of green roofs as foraging sites. While bat diversity and habitat use of bats generally decreases in urban areas compared to more natural areas, the response of bats to local and landscape scale factors in urban environments are rather specific and equivocal (Jung & Threlfall 2016). Fundamentally, it is the behavioural and/or morphological traits of individual species that determines whether they can adapt and survive in the urban environment rather than only the availability of suitable habitat (Jung & Threlfall 2016).

4.5.2 Species-specific responses

Mobility is one of the most important ecological traits influencing the persistence of bat species in urban areas, and this is usually associated with species-specific morphological traits such as differing wing shape and body mass (Norberg & Rayner, 1987; Jung & Kalko, 2011). Although the nature of data collected precluded species-specific analyses within the modelling framework used, it is clear from my study that rooftop bat activity in urban Singapore is dominated by a single species *Scotphillus kuhlii* (80.3% of all bat passes). This is not surprising as *S. kuhlii* is one of the most commonly recorded microchiropteran bat species in Singapore (Chapter 3; Pottie *et al.* 2005) This aerial insectivore has adapted well in urban areas by roosting in buildings, and its high wing loading and moderately high aspect ratio makes it capable of fast open-air flight (Pottie *et al.* 2005), making green roofs an ideal habitat for foraging. However, my data suggest that this species tends to be more associated with ‘low’ roofs (<25 m) than ‘high’ roofs (>25m). Both *T. melanopogon* and *S. saccolaimus* are aerial insectivores in the same family (Emballonuridae), but are characterised by higher wing loading and aspect ratios than *S. kuhlii*, which are traits associated with fast flight performance and hawking of insects from the air (Norberg & Rayner 1987). Conversely, *M. muricola* was rarely recorded on green roofs. This species is characterised by low wing loading and moderately high aspect ratio (Pottie *et al.* 2005), and is known to be strongly associated with edge and semi-cluttered habitats. It is notable that *M. muricola* was only recorded on two 'low' roofs (JH and SE), both of which were found to contain banana plants, either on the roof or in the immediate surrounding area, which are known to be a preferred roost for this species (Payne & Francis 2007). While *M. muricola* may be detected on green roofs, it is likely that it is using a plant resource on the roof for roosting and foraging in other habitats, as demonstrated by the limited number of bat passes (0.07% of total bat passes recorded) recorded for this species.

4.5.3 Do bats use green roofs or are they merely passing through?

The mean number of 30.6 bat passes per night per roof demonstrated substantial levels of bat activity over green rooftop infrastructure and this is comparable to the mean number of bat passes per night (33) detected in urban (ground) habitats in **Chapter 3**. However, it remains difficult to determine whether bats are utilising green roofs for foraging or simply commuting to other urban locations. Feeding buzzes are a useful proxy of foraging activity, but they were rarely recorded in my rooftop study, comprising only 1.7% (87 bat passes) of total bat passes. In **Chapter 3,** feeding buzzes made up 3% (40 bat passes) of total bat passes in the urban habitats surveyed. In comparison, Pearce & Walters (2012) found that 16% (217) of passes were foraging events in their London green roof study, whereas Parkins & Clark (2015) found only 2% (20) of all calls consisted of feeding buzzes in New York. However, McCracken *et al.* (2008) warned that feeding buzzes are more difficult to detect and record with automated acoustic equipment than search phase calls, due to the rapid degradation of the feeding buzz signal over short distances. Moreover, the recording of feeding buzzes in urban areas is hampered by the constant high frequency noise in the environment (Parkins & Clark 2015), possibly caused by vehicles and other anthropogenic noises. Hence, I adopted the method of using bat passes as an indicator of foraging activity as proposed by Fukui *et al.* (2006) and Park, Mochar & Fuentes-Montemayor (2012). I found a moderately strong correlation of total bat passes with feeding buzzes at each site (Spearman's Rho = 0.57, p-value = 0.004) and given the highly urbanised landscape where the study was conducted, some feeding buzzes may not have been detected in a noisy environment. Therefore, although the overall number of feeding buzzes detected was low, it is likely that bats are utilizing the green rooftop space for foraging as well as commuting, and that roof top gardens provide some role as habitat for Singapore's microchiropteran species. Future monitoring through visual observation or remote image recording could be used to verify bat foraging behaviour on the green roofs.

4.5.4 Influence of roof characteristics and other variables

High green roofs were found to be associated with lower levels of bat activity. This is in agreement with the study by Pearce & Walters (2012) in the UK, even though the roof heights and height range in my study is substantially greater (ranging from 3-15 m in the UK versus 12-189 m in Singapore). Pearce & Walters (2012) found that the mean number of calls from *Pipistrellus* spp. and *Nyctalus/Eptesicus* spp. per night decreased as roof height increased, and that the reduction was sharp between two to three storeys. The roofs in my study had a greater range of heights, and only three bat passes (and no feeding buzzes) were detected on the highest green roof (189 m) over seven nights of recording. In a study of wind farm sites in eastern

England, Collins & Jones (2009) found fewer bat calls at 30 m height compared to near-ground level, and also observed that the proportion of bat passes by *Pipistrellus* spp. and *Nyctalus/Eptesicus* spp. changed between the two heights, with more of the former species recorded at ground level, and *vice versa* for the latter.

Green roof studies from temperate regions have reported invertebrates to be negatively affected by increasing green roof height (Madre *et al.* 2013; MacIvor, 2015). Increasing green roof height decreased the use of trap nests by bees and wasps in Toronto (MacIvor 2015), and negatively affected the richness and abundance of spiders and the community structure of true bugs and beetles as found in northern France (Madre *et al.* 2013). In general, these observations suggest that green roofs may provide poor habitat for some species despite traits associated with high mobility, possibly due to the increasing energetic cost of overcoming the urban wind velocity associated with tall buildings (Pelliccioni, Monti & Leuzzi 2016).

High levels of bat activity were related to high levels of shrub cover. This is likely due to structural complexity of the vegetation promoting arthropod abundance and diversity. On 115 green roofs studied by Madre *et al.* (2013), arthropod species richness and abundance were found to be significantly higher on green roofs that had more vegetation complexity consisting of 3 layers — moss/sedum, meadow and shrub — compared to those that had fewer layers. Additional supporting evidence comes from a study by Kalcounis *et al.* (1999), who showed that bats respond more strongly to differences in vegetation structure due to their foraging ecology rather than composition in their study of bat activity in the boreal forests of Canada.

Hence, green roofs should always have a naturalistic and diverse planting and landscaping plan to introduce vegetation complexity to this man-made ecosystem.

Contrary to the study by Pearce and Walters (2012), higher ambient temperature on green roofs was found to positively influence bat activity. Other studies elsewhere (e.g. Vaughan, Jones & Harris, 1997; Gaisler *et al*., 1998; Erickson & West, 2002) have also found that bat activity is positively correlated with ambient temperature and one possible explanation could be due to the increase in insect abundance at higher temperatures (Williams, 1961; Rydell, 1989).

The availability of water features such as chlorinated pools and ponds on green roofs did not have an effect on bat activity. This seems surprising given that water bodies in most landscapes, especially arid environments, are known to serve as drinking points or foraging places for bats (Korine *et al.* 2016; Salvarina, 2016). (Park, Mochar & Fuentes-Montemayor 2012) found bat activity was three times greater in urban parks in Scotland adjacent to water bodies compared to a park not beside a water body. The use of swimming pools by bats for drinking has been reported by Nickerson (2013) and Russo & Ancillotto (2015) in the USA and small Mediterranean islands respectively, hence it is clear that chlorinated pools do not discourage drinking by bats. In Singaporean green roofs, water bodies are substantial in size compared to the planted area but offer little in the way of insect prey due to their chlorine treatment. The other possible explanation for the unexpected result is that water bodies were found in less than half (48%) of the 27 roofs surveyed, and this represents a small sample size, with a reduction in statistical power in detecting whether the presence of water affected bats.

4.5.5 Influence of greenery management practices

Management interventions on the green roofs affected bat activity. Plant pruning at medium frequency had a positive influence on bat activity. Two possible explanations prevail. First, pruning reduces vegetation clutter, and it is well documented that the three dominant bat species all exhibit high wing loading and moderate to high aspect ratios that are adaptations associated with fast flight in open spaces (Pottie *et al.* 2005). Another reason for the positive association between pruning and bat passes could be due to the increase in insects brought about through pruning. For example, Cloyd (2000) reported that plants undergo stress when subject to injury, and pruning at medium frequency may bring about plant injury and accompanying stress, thereby attracting wood-boring insects, particularly beetles. It is possible, therefore, that the greater bat activity on green roofs with pruned vegetation could be attributed to this sudden increase in insect pests.

Pesticide application at all three frequencies (*ad hoc,* monthly, and fortnightly) was associated with low levels of bat activity on green roofs. This is expected given that pesticides target arthropods, and that these are often potential prey items for bats on the green roofs. Shwartz *et al.* (2013) found that the use of pesticides negatively affected birds but not insect pollinators in a survey of 36 small private gardens in Paris, France. In another study focused on the impacts of pesticides on insects in private gardens in France using citizen science data, Muratet & Fontaine (2015) showed that heavy pesticide use decreased the abundance of butterflies and bumblebees, and the negative effect of pesticides was more pronounced in highly urban areas compared to those that were less urbanised. In Singapore, the application of pesticides to treat or prevent outbreaks on the vegetation on green roofs is sometimes supplemented with insecticidal fogging to keep disease-carrying mosquitoes in check. This has a detrimental effect on other insects in addition to the target mosquitoes because the insecticidal fog used is non-selective (Devine & Furlong 2007). My study evaluated the relative influence of pesticide application on bat activity in green roof spaces, but further studies on insect diversity and prey availability on green roofs would provide a better understanding of the direct and indirect effects of pesticides on urban biodiversity.

4.5.6 Improvements to green roofs for tropical bats

To promote the habitat use of green roofs by bats or other species in Singapore, intervention is necessary. This could include the construction of vertical green walls or mid-tier planted balconies or boxes to provide some shelter and connection to reach the green roof (Wang *et al.*, 2016, unpublished manuscript). The placement of bat boxes with different configurations could be trialled on green roofs of various heights, because all three bat species detected in my study are known to use man-made structures as roosts. For example, *S. saccolaimus* and *T melanopogon* can be encouraged to roost by retrofitting of some smooth vertical walls to provide a textured surface in a hidden corner of the green roof instead of bat boxes (Leong & Chan 2011). With artificial roosts occupied by bats at different heights, could result in reduced distances for commuting and foraging between near-ground habitats and green roofs, and between green roofs. As a consequence, bats could possibly utilise more green roof spaces during foraging flights as they are added to the urban landscape.

My study examined the management of the green roofs to understand how human intervention affects bat activity, as previous studies have demonstrated that management variables were more crucial than landscape effects in maintaining biodiversity in urban landscapes (Evans, Newson & Gaston 2009; Shwartz *et al.* 2013). The negative effects of pesticides and the unexpected consequences of pruning underscores the importance of human factors in the management of urban green spaces, and the need to improve management practices to take biodiversity conservation into account. Although it is shown that land cover variables, management regimes and roof characteristics are important for supporting bat habitat use, it must be cautioned that green roofs should not be viewed as isolated green spaces in the urban environment for biodiversity conservation, and neither should they be replacements for natural habitats, but rather complement them (Parkins & Clark 2015). The intensive green roofs in my study have many similarities with domestic gardens. They are both small green spaces that should be considered as part of a wider landscape. Ideally, these small typologies of greenery could function as corridors or “stepping stones” to connect to other larger green spaces in the urban matrix, thereby operating at multiple spatial scales (Goddard, Dougill & Benton 2010) and achieving multi-species conservation in an urbanizing world.

4.6 References

Baumann, N. (2006) Ground nesting birds on green roofs in Switzerland: preliminary observations. *Urban Habitats*, **4**, 11.

Beninde, J., Veith, M. & Hochkirch, A. (2015) Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, **18**, 581–592.

Blank, L., Vasl, A., Levy, S., Grant, G., Kadas, G., Dafni, A. & Blaustein, L. (2013) Directions in green roof research: A bibliometric study. *Building and Environment*, **66**, 23–28.

Blaustein, L., Kadas, G.J. & Gurevitch, J. (2016) Integrating ecology into green roof research. *Israel Journal of Ecology and Evolution*, **62**, 1–6.

Bolund, P. & Hunhammar, S. (1999) Ecosystem services in urban areas. *Ecological Economics*, **29**, 293–301.

Booth, G.D., Niccolucci, M.J. & Schuster, E.G. (1994) Identifying proxy sets in multiple linear-regression - an aid to better coefficient interpretation. *USDA Forest Service Intermountain Research Station Research Paper*, 1–13.

Braaker, S., Ghazoul, J., Obrist, M.K. & Moretti, M. (2014) Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology*, **95**, 1010–1021.

Brenneisen, S. (2006) Space for urban wildlife: Designing green roofs as habitats in Switzerland. *Urban Habitats*, **4**, 27–36.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*.

Caryl, F.M., Lumsden, L.F., van der Ree, R. & Wintle, B.A. (2016) Functional responses of insectivorous bats to increasing housing density support 'landsparing' rather than 'land-sharing' urban growth strategies. *Journal of Applied Ecology*, **53**, 191–201.

Cloyd, R. (2000) Plant stress favors pests in urban landscapes. *Grounds maintenance*.

Coffman, R.R. & Davis, G. (2005) Insect and Avian Fauna on the Ford Assembly Plant Ecoroof. *Greening Rooftops for Sustainable Communities*, p. 12.

Collins, J. & Jones, G. (2009) Differences in Bat Activity in Relation to Bat Detector Height: Implications for Bat Surveys at Proposed Windfarm Sites. *Acta Chiropterologica*, **11**, 343–350.

Dallimer, M., Irvine, K.N., Skinner, A.M.J., Davies, Z.G., Rouquette, J.R., Maltby, L.L., Warren, P.H., Armsworth, P.R. & Gaston, K.J. (2012) Biodiversity and the feel-good factor: Understanding associations between self-reported human well-being and species richness. *BioScience*, **62**, 47–55.

Dearborn, D.C. & Kark, S. (2009) Motivations for conserving urban Biodiversity. *Conservation Biology*, **24**, 432–440.

Devine, G.J. & Furlong, M.J. (2007) Insecticide use: Contexts and ecological consequences. *Agriculture and Human Values*, **24**, 281–306.

Drinnan, I.N. (2005) The search for fragmentation thresholds in a Southern Sydney Suburb. *Biological Conservation*, **124**, 339–349.

Dunnett, N. & Kingsbury, N. (2008) *Planting Green Roofs and Living Walls*. Timber Press.

Erickson, J. L. & West, S. D. (2002) The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. *Acta Chiropterologica*, **4**, 17–24.

Evans, K.L., Newson, S.E. & Gaston, K.J. (2009) Habitat influences on urban avian assemblages. *Ibis*, **151**, 19–39.

Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Francis, R.A. & Lorimer, J. (2011) Urban reconciliation ecology: The potential of living roofs and walls. *Journal of Environmental Management*, **92**, 1429–1437.

Frazer, L. (2005) Paving paradise: The peril of impervious surfaces. *Environmental Health Perspectives*, **113**.

Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006) Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, **75**, 1252–1258.

Gaisler, J., Zukal, J., Rehak, Z. & Homolka, M. (1998) Habitat preference and flight activity of bats in a city. *Journal of Zoology*, **244**, 439–445.

Germaine, S.S., Rosenstock, S.S., Schweinsburg, R.E. & Richardson, W.S. (1998) Relationships among breeding birds, habitat, and residential development in greater Tucson, Arizona. *Ecological Applications*, **8**, 680–691.

Getter, K.L., Rowe, D.B., Robertson, G.P., Cregg, B.M. & Andresen, J.A. (2009) Carbon sequestration potential of extensive green roofs. *Environmental Science and Technology*, **43**, 7564–7570.

Goddard, M.A., Dougill, A.J. & Benton, T.G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, **25**, 90–98.

Griffin, D.R., Webster, F. & Michael, C.R. (1960) The echolocation of flying insects by bats. *Animal Behaviour*, **8**, 141–154.

Grimm, N.B., Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. & Briggs, J.M. (2008) Global change and the ecology of cities. *Science (New York, N.Y.)*, **319**, 756–760.

Harrison, X. a. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2**, e616.

Hwang, Y.H. (2014) Green roofs as local habitats in Singapore. *Proceedings of the IFLA Asia Pacific Congress*, pp. 1–13. Kuching.

Hwang, Y.H. & Yue, J.Z.E. (2015) Observation of biodiversity on minimally managed green roofs in a tropical city. *Journal of Living Architecture*, **2**, 9–26.

Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrard, G.E., Bekessy, S.A., Fuller, R.A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L.E. & Kendal, D. (2016) Cities are hotspots for threatened species. *Global Ecology and Biogeography*, **25**, 117–126.

Jung, K. & Kalko, E.K. V. (2011) Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Diversity and Distributions*, **17**, 262–274.

Jung, K. & Threlfall, C.G. (2016) Urbanisation and its effects on bats - A global meta-analysis. *Bats in the Anthropocene: Conservation of Bats in a Changing World*, pp. 13–33.

Kadas, G. (2006) Rare Invertebrates Colonizing Green Roofs in London. *Urban Habitats*, **4**, 66–86.

Kalcounis, M.C., Hobson, K.A., Brigham, R.M. & Hecker, K.R. (1999) Bat Activity in the Boreal Forest: Importance of Stand Type and Vertical Strata. *Journal of Mammalogy*, **80**, 637–682.

Korine, C., Adams, R., Russo, D., Fisher-Phelps, M. & Jacobs, D. (2016) Bats and Water: Anthropogenic Alterations Threaten Global Bat Populations. *Bats in the*

Anthropocene: Conservation of Bats in a Changing World, pp. 215–241. Springer International Publishing, Cham.

Leong, T.M. & Chan, K.W. (2011) Bats in Singapore - ecological roles and conservation needs. *Proceedings of Nature Society, Singapore's Conference on 'Nature Conservation for a Sustainable Singapore'*, pp. 41–64. Nature Society (Singapore), Singapore.

Lovell, R., Wheeler, B.W., Higgins, S.L., Irvine, K.N. & Depledge, M.H. (2014) A systematic review of the health and well-being benefits of biodiverse environments. *Journal of Toxicology & Environmental Health B*, **17**, 1–20.

Lundholm, J.T. & Richardson, P.J. (2010) Habitat analogues for reconciliation ecology in urban and industrial environments. *Journal of Applied Ecology*, **47**, 966–975.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*.

MacIvor, J.S. (2015) Building height matters: nesting activity of bees and wasps on vegetated roofs. *Israel Journal of Ecology & Evolution*, 1–9.

Madre, F., Vergnes, A., Machon, N. & Clergeau, P. (2013) A comparison of 3 types of green roof as habitats for arthropods. *Ecological Engineering*, **57**, 109–117.

McCracken, G.F., Gillam, E.H., Westbrook, J.K., Lee, Y.F., Jensen, M.L. & Balsley, B.B. (2008) Brazilian free-tailed bats (Tadarida brasiliensis: Molossidae, Chiroptera) at high altitude: Links to migratory insect populations. *Integrative and Comparative Biology*, **48**, 107–118.

McKinney, M.L. (2002) Urbanization, Biodiversity, and Conservation. *BioScience*, **52**, 883.

Miller, J.R. (2005) Biodiversity conservation and the extinction of experience. *Trends in Ecology and Evolution*, **20**, 430–434.

Muratet, A. & Fontaine, B. (2015) Contrasting impacts of pesticides on butterflies and bumblebees in private gardens in France. *Biological Conservation*, **182**, 148–154.

National Parks Board. (2016) Skyrise Greenery Incentive Scheme 2.0, https://www.nparks.gov.sg/skyrisegreenery/incentive-scheme

Nickerson, Z. (2013) Bats and Pools Survey | Assessing how bats use pools across North America, https://batsandpools.wordpress.com/

Norberg, U.M. & Rayner, J.M. V. (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **316**, 335–427.

Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y. & Rowe, B. (2007) Green Roofs as Urban Ecosystems: Ecological Structures, Functions, and Services. *BioScience*, **57**, 823.

Park, K.J., Mochar, F. & Fuentes-Montemayor, E. (2012) Urban Biodiversity: Successes and Challenges: Bat activity in urban green space. *Glasgow Naturalist*, **25**, 42–50.

Parkins, K.L. & Clark, J.A. (2015) Green roofs provide habitat for urban bats. *Global Ecology and Conservation*, **4**, 349–357.

Parson, S. & Szewczak, J. (2009) Detecting, recording and analysing the vocalisations of bats. *Ecological and behavioral methods for the study of bats* , 2nd ed (eds T. Kunz & S. Parson), pp. 91–111. John Hopkins University Press.

Payne, J. & Francis, C.M. (2007) *A Field Guide to Mammals of Borneo*. Sabah Society, Malaysia.

Pearce, H. & Walters, C.L. (2012) Do green roofs provide habitat for bats in urban areas? *Acta Chiropterologica*, **14**, 469–478.

Pelliccioni, A., Monti, P. & Leuzzi, G. (2016) Wind-Speed Profile and Roughness Sublayer Depth Modelling in Urban Boundary Layers. *Boundary-Layer Meteorology*, 1–24.

Pottie, S.A., Lane, D.J.W., Kingston, T. & Lee, B.P.Y.-H.Y.-H. (2005) The microchiropteran bat fauna of Singapore. *Acta Chiropterologica*, **7**, 237–247.

Roscoe, C. (2015) *Supporting Pollinator Communities and Supported by Stakeholders? Measuring Ecological and Social Values of Green Roofs in Singapore*.

Rosenzweig, M.L. (2003) Reconciliation ecology and the future of species diversity. *Oryx*, **37**, 194–205.

Russ, J. (2012) *British Bat Calls: A Guide to Species Identification*. Pelagic Publishing.

Russo, D. & Ancillotto, L. (2015) Sensitivity of bats to urbanization: A review. *Mammalian Biology*, **80**, 205–212.

Rydell, J. (1989) Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. *Oecologia*, **80**, 562–565.

Salvarina, I. (2016) Bats and aquatic habitats: A review of habitat use and anthropogenic impacts. *Mammal Review*, **46**, 131–143.

Schmitt, U. & Hirschmugl, M. (2016) *Singapore Carbon Accounting - Activity Data (Land Use Mapping)*. Johanneum Research, Graz.

Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E. & Hope, D. (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology and Evolution*, **21**, 186–191.

Shwartz, A., Muratet, A., Simon, L. & Julliard, R. (2013) Local and management variables outweigh landscape effects in enhancing the diversity of different taxa in a big metropolis. *Biological Conservation*, **157**, 285–292.

Struebig, M.J., Kingston, T., Zubaid, A., Mohd-Adnan, A. & Rossiter, S.J. (2008) Conservation value of forest fragments to Palaeotropical bats. *Biological Conservation*, **141**, 2112–2126.

Struebig, M.J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H. & Bell, D. (2013) Quantifying the Biodiversity Value of Repeatedly Logged Rainforests. Gradient and Comparative Approaches from Borneo. *Advances in Ecological Research*, **48**, 183–224.

Tan, C., Lee, V., Webb, E. & Bramley-Alves, J. (2015) A Study of 32 Roof Gardens in Singapore | citygreen | Publications. *Citygreen*, 114–119.

Tan, P.Y., Wang, J. & Sia, A. (2013) Perspectives on five decades of the urban greening of Singapore. *Cities*, **32**, 24–32.

Threlfall, C.G., Williams, N.S.G., Hahs, A.K. & Livesley, S.J. (2016) Approaches to urban vegetation management and the impacts on urban bird and bat assemblages. *Landscape and Urban Planning*, **153**, 28–39.

United Nations. (2014) *World Urbanization Prospects: The 2014 Revision, Highlights*. New York.

Urban Redevelopment Authority. (2015) *An Overview of the LUSH Programme*. Singapore.

Vaughan, N., Jones, G. & Harris, S. (1997) Habitat Use by Bats (Chiroptera) Assessed by Means of a Broad-Band Acoustic Method. *Journal of Applied Ecology*, **34**, 716–730.

Wang, J.W., Poh, C.H., Tan, C.Y.T., Lee, V.N., Jain, A. & Webb, E.L. (2016)

Building Biodiversity: Drivers of Bird and Butterfly Diversity O Tropical Urban Roof Gardens.

WHO. (2016) *Urban Green Spaces and Health*. Copenhagen.

Williams, C.B. (1961) Studies in the effect of weather conditions on the activity and abundance of insect populations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **244**, 331–378.

Yee, A., Corlett, R., Liew, S. & Tan, H. (2011) The vegetation of Singapore - an updated map. *Gardens' Bulletin Singapore*, **63**, 205–12.

Zuur, A.F., Mira, A., Carvalho, F., Ieno, E.N., Saveliev, A.A., Smith, G.M. & Walker, N.J. (2009) Negative Binomial GAM and GAMM to Analyse Amphibian Roadkills. *Mixed effects models and extensions in ecology with R* , pp. 1–15.

5. Smoke pollution disrupts bioacoustics activity during the 2015 El Niño forest fires

This chapter was published on 20 September 2017 as: Lee, B.P.Y-H., Davies, Z.G. & Struebig, M.J. (2017) Smoke pollution disrupted biodiversity during the 2015 El Niño fires in Southeast Asia. *Environemntal Research Letters*, 12, 094022, https://doi.org/10.1088/1748-9326/aa87ed

5.1 Abstract

The use of soundscapes to study ecological communities, landscapes and environmental change is an emerging field in ecological monitoring and can help document spatio-temporal responses of acoustic signals to environmental change. The forest fires in Southeast Asia during the 2015 El Niño drought provided an opportune environmental crisis to test the efficacy of soundscape monitoring in Singapore. The fires were amongst the worst on record, and contributed over 227 Tg of carbon emissions, with the associated smoke-induced haze causing an air pollution crisis that affected millions of people. I present the first evidence of smoke pollution impacts on the region's biodiversity. Using daily acoustic recordings in Singapore, I monitored bioacoustic activity before, during and after the haze event. I demonstrate that levels of bioacoustic activity dropped dramatically during the haze, and that this decline was significantly associated with unhealthy levels of air pollution. Acoustic disruption was apparent across four common indices of soundscape activity (acoustic complexity, acoustic diversity, bioacoustic and normalised difference soundscape), with only a partial recovery to pre-haze levels observed four months after the smoke had dissipated. These biodiversity impacts were likely to be even more severe closer to the forest fires, where air pollution levels were 15-fold greater than those recorded in Singapore. The acoustic signature results indicate that large-scale atmospheric pollution events may have hitherto underestimated and far-reaching impacts on biodiversity. I demonstrated that the use of acoustic methods in environmental monitoring is a safe and useful approach to investigation large-scale environmental change.

5.2 Introduction

5.2.1 A primer of soundscape ecology

The inter-connectedness of sounds to the state of the environment is well known and is epitomised by *Silent Spring* (Carson 1962) in which the detrimental effects of the indiscriminate use of pesticides on the environment, and in particular to birds, were documented. Human activities have both direct and indirect effects on acoustic activity. For example, it has been shown that European robins (*Erithacus rubecula*) sing during the night instead of daytime in an urban environment with constant traffic noise in order to minimise acoustic interference (Fuller, Warren & Gaston 2007). Sounds are therefore an inherent and ever-changing feature of landscapes, and are a key focus of the emerging field of soundscape ecology, which is broadly defined as the study of sounds originating from a given landscape to create signature acoustical patterns at various spatial and temporal scales (Pijanowski *et al.* 2011). Soundscape ecologists are primarily focused on macro or community acoustics, and typically categorise sounds into three main components originating via biological, geophysical and anthropogenic activities: the biophony, geophony and anthrophony respectively (Pijanowski *et al.* 2011). These three components collectively form the soundscape of an area. Soundscape ecology has many commonalities with the practice of landscape ecology (Farina 2008) and these include the categorisation of soundscape to a geographic context, the attention to interactions between anthropogenic and biological factors, and the development of tools to quantify patterns (Pijanowski *et al.* 2011).

Soundscape ecology can be seen as a progression from the field of bioacoustics - the study of the emission, propagation and reception of sounds produced by animal species (Sueur *et al.* 2014). Bioacoustics as a discipline arose from the paradigm of Shannon and Weaver (1949) who considered communication as an emitter-receiver duo sharing signal(s) encoded with information. Shannon and Weaver's premise was that the reception of acoustic signals may alter the behaviour or the physiology of the receiver, but while this discrete and linear chain of events (emission, propagation, reception) is useful for understanding the emitter-receiver paradigm, it is a rather restrictive view of how animal communication actually works (Sueur *et al.* 2014). In reality, animal communication in the wild occurs as a community network rather than a closed system where information is shared between two individuals, as shown in frog choruses (Grafe 2005). Hence, bioacoustic research investigates sounds mostly at infra-specific and specific levels, rather than considering sounds collectively by the community, ecosystem or landscape (Sueur *et al.* 2014). When bioacoustics is scaled up to account for sounds produced by communities or all sounds from a landscape, it becomes soundscape ecology (Pijanowski *et al.* 2011)

There are several advantages of using acoustic measurements to study the landscape or faunal community in an area. Firstly, sampling acoustic metrics passively is relatively easier and cheaper to deploy in the field, and can be undertaken by non-expert personnel trained only in acoustic equipment set-up and deployment (Michener *et al.* 2001; Thompson *et al.* 2001; West *et al.* 2001; Pijanowski *et al.* 2011). Sampling actual biological diversity often requires substantial fieldwork effort to acquire enough species to quantify diversity metrics reliably, requires trained staff and is labour-intensive. Secondly, with the assignment of stationary sites for continuous recording, spatio-temporal patterns can be documented, which is not possible from many traditional sampling designs involving repeated site visits with time intervals between visits. The acoustic information obtained from continuous recording at a site can reveal changes in ecosystems at multiple temporal scales, for example, diurnal, weekly, seasonal and annual (Truax 2001). Thirdly, the ability of a network of acoustic recorders to monitor in different locations simultaneously denotes that variances in acoustics can be compared in a heterogeneous environment or landscape structure (Michener *et al.* 2001; Thompson *et al.* 2001; West *et al.* 2001; Pijanowski *et al.* 2011). Fourthly, unlike unidirectional detections from diurnal observational field surveys, microphones can record sounds from all directions, and in darkness unless the sound source is obstructed (Kasten *et al.* 2012), or very faint. Lastly, the passive nature of acoustic measurements means that there is no recording bias with regard to human interference (West *et al.* 2001), very much like a camera-trap. The chief drawback of using acoustic measurements is that quiet or less vocal species may not be detected in a community and hence do not always contribute to the diversity of the soundscape.

With the advent of affordable digital autonomous audio recorders, weatherproof microphones, large file storage capability in a compact manner and renewable power sources, it is now possible to collect acoustic data over a wide range of environments and landscapes to address questions pertaining to ecology, conservation and large-scale environmental changes. However, these massive acoustic datasets need to be managed and processed with dedicated acoustic tools (e.g. processing of bat calls in Chapters 2-4). The need for such tools has led to the development of acoustic indices to analyse soundscape recordings. The development of acoustic indices draws from the experience of traditional ecological research that uses indices to describe ecological complexity with a single value at both community and landscape scales (Sutherland 2006).

5.2.2 Fire and haze crises in Southeast Asia

Throughout the tropics, the use of fire is a common and relatively inexpensive method for the clearing of forest stands and disposing crop residues for land development, and for preparation of agriculture land on both small and commercial scales (Ketterings *et al.* 1999; Siegert *et al.* 2001) However, fires often become uncontrollable during times of drought, and can spread over vast areas. Across the tropics uncontrolled forest fires are becoming more frequent and severe due to rapid expansion of commercial agricultural land and climate change events (Cochrane 2003). However, global attention has focussed very much on Southeast Asia in recent years, where forest fires have become a major environmental problem, contributing more than 100 Mt of carbon emissions annually in Indonesia alone (van der Werf *et al.* 2008). Fire intensity and severity is known to be exacerbated by the El Niño–Southern Oscillation (ENSO) interacting with the Indian Ocean Dipole, which results in prolonged drought (Tacconi 2016). These unusually warm and dry conditions, coupled with a peak in burning activities during the dry inter-monsoon season of July to October, allow fires to advance unchecked in disturbed tropical forests and degraded peatlands, which are normally fire-resistant in their pristine state (Uhl, Kauffman & Cummings 1988; Whitmore 1984). Most of the uncontrolled forest fires in Southeast Asia happen in Indonesia on an annual basis, and the large-scale plumes of airborne pollution cause by these fires are known as “smoke-haze” (Velasco & Rastan 2015), which is a by-product that contributes to serious transboundary air pollution and affects neighbouring countries, particularly Malaysia and Singapore (Lee *et al.* 2016). Henceforth, I will refer to “smoke-haze” as haze or the haze event in describing the phenomenon air pollution as a result of the ENSO-induced fires.

Southeast Asia’s forest and peat fires result in human mortality, property destruction, habitat and biodiversity loss, lowered work productivity, as well as significant emission of hazardous greenhouse gases and aerosols (Kinnaird & O’Brien 1998; Cochrane 2003; Reddington *et al.* 2014; Tacconi 2016). In years with extensive fires and smoke the number of premature deaths as a result of particulate emissions is estimated to be about 10,800 across the region (Marlier *et al.* 2013). However, during the 1997-98 El Niño event, fires affected around 25,000 km^2 of Indonesia’s peatland, contributing to the largest ever recorded annual increase in global atmospheric CO_2 (Page *et al.* 2002). The resulting smoke and haze caused an air pollution crisis across Southeast Asia, which was implicated in around 20 million cases of respiratory problems among Indonesians and up to 48,000 premature mortalities in that country alone (Heil 2007).

Despite public attention, most fire research has focussed on emissions and consequences to people and society, and there have been few studies on impacts on wildlife. The limited research available to date is limited to biodiversity remaining after a burning event. For example post-fire research in burned forest land in Sumatra and Borneo demonstrated a range of impacts on vertebrate ecology and diversity. O’Brien *et al.* (2003) showed that gibbons inhabiting burnt forests in Sumatra are smaller in group size, had lower infant and juvenile survival, and had less access to food resources than those groups in unburned forests in. In a study of lowland tropical rainforest birds, Adeney *et al.* (2006) found that the severity of original burns affected the composition of Sumatran bird communities at the genus and family levels, and although richness and abundance of birds increased in burned areas, understory insectivores declined, which corresponded to a gradient of fire severity. This has implications for the conservation of understorey birds because they have specific habitat requirements (Canaday 1996) and may not adapt well to widespread changes in forest structure (Thiollay 1997) as a result of fire. Butterflies in Borneo responded similarly to ENSO-induced fires where there was a steep species decline from 211 to 39 species after the fire event, followed by the community dominance of a generalist species (Cleary & Grill 2004). Moreover, Cleary *et al.* (2006) revealed that in addition to reduced butterfly diversity in the burnt forest habitats in Borneo, the species in remnant unburnt forests were genetically depauperate and were unlikely to survive future environmental degradation. To date, the only published research on wildlife responding to a burn event in real time was undertaken on gibbons in Central Kalimantan, Borneo. Cheyne (2008) followed gibbons for 47 days during a haze event (or “smoke” months in her study), and found that individuals vocalised less frequently daily, and had shorter singing bouts in months with haze compared with the earlier haze-free months.

5.2.3 The 2015 Southeast Asian fire and haze crisis

During my PhD research in September and October 2015, forest fires recurred and covered many parts of Southeast Asia with haze. In this season the severity of fires was greatly exacerbated by prolonged drought brought about by a strong ENSO event, which greatly suppressed precipitation in the region (Huijnen *et al.* 2016). Indeed 2015 saw the worst burning episode since the major ENSO event in 1997/1998. An average of 11.3 Tg CO_2 was emitted each day during September and October (Huijnen *et al.* 2016), a figure that exceeded the fossil fuel CO_2 emissions of the European Union (8.9 Tg CO_2 per day). The transboundary haze event was so serious that it forced airport operations and school activities to cease in parts of the region when the air pollution was at its peak (Anonymous 2015; Anwar 2015; Chan 2015; Ghazali 2015; Seow & Hio 2015). The estimated economic cost of the fire and haze event in 2015 is US$16.124 billion to Indonesia alone (The World Bank 2015).

One of the soundscape research themes recommended by Pijanowski *et al.* (2011) was to improve our understanding of how important environmental covariates, such as air pollution, influence soundscape dynamics. I therefore took opportunity of the transboundary haze event to investigate whether the high levels of air pollution that drifted into Singapore had a detectible influence on the soundscape. During 2015 and 2016 I was able to amass a dataset of daytime (morning) acoustic recordings at a monitoring site in central Singapore. Since birds and other animals are known to be affected by pollution and are also major contributors to soundscapes, I hypothesized that acoustic indices would respond negatively to an increase in haze levels, and would potentially recover once the air quality improves.

5.3 Methods

5.3.1 Study system

Soundscape data were collected as part of a wildlife monitoring programme on the "EcoLink" wildlife overpass (1.357°N, 103.784°E) in Singapore. Two-hour morning recordings began daily in January 2015 before the haze, and continued until March 2016, after the haze had passed. The wildlife overpass serves to reconnect two tropical lowland rainforest reserves, Bukit Timah Nature Reserve (163 ha) and Central Catchment Nature Reserve (c. 2000 ha), that have been separated by the Bukit Timah Expressway (BKE) for 30 years. The overpass measures 62 m in length and 50 m in width, and the construction was completed in October 2013 followed by a planting phase which was completed in December 2013. The densely planted native vegetation on the overpass consist of a ground cover of herbs and grasses, shrubs, epiphytes and small trees not more than 5 m tall in November 2015. The objective was to recreate a rainforest habitat on the overpass so that wildlife species would use it cross between the two nature reserves. Most of the traffic noise is inaudible from the centre of the overpass.

5.3.2 Pollution Standards Index (PSI)

As a measure of haze pollution each day, I obtained data on the 24-hour Pollutant Standards Index (PSI) from the National Environment Agency of Singapore (NEA), http://www.nea.gov.sg/anti-pollution-radiation-protection/air-pollution-control/psi (National Environment Agency 2016). An hourly PSI is given for each of five regions on the island – north, south, east, west and central. The PSI values from the central region were used as the overpass is within that region. The PSI is derived from six common atmospheric pollutants, which are calculated based on averaged concentrations: fine particulate matter (PM2.5), particulate matter (PM10), sulphur dioxide (SO_2), carbon monoxide (CO), ozone (O_3) and nitrogen dioxide (NO_2). PSI values up to 50 are considered good; 51-100 moderate; 101-200 unhealthy; 201-300 very unhealthy; and >300 hazardous. During the peak haze period the PSI reached 267, at which time Singapore residents were advised by the Government to avoid prolonged or strenuous outdoor physical exertion. I compiled PSI readings for four time periods with respect to the haze episode, hereafter known as "Before", "During", "3 weeks after" and "16 weeks after" (Table 5.1). These periods were defined by a combination of distinct changes in the Pollution Standards Index (PSI), and guided by NEA public advisories about the changing air quality. For analyses, I used the hourly PSI reading at 0800 hrs since this was the median of the PSI readings for our 2-hour morning acoustic recordings.

Table 5.1 Definition of events around the occurrence of haze in Singapore in 2015.

Event code	**Event**	**Period**	**PSI range**	**No. of recording days**
1	Before	11 Jan – 1 Feb 2015	31-68	22
2	During	24 Sep – 28 Oct 2015	97-267	21
3	3 weeks after	16 Nov – 14 Dec 2015	28-53	20
4	16 weeks after	29 Feb – 14 Mar 2016	37-55	15

5.3.3 Soundscape recordings

I deployed a Song Meter SM2BAT+ unit (Wildlife Acoustics Inc., USA) at the centre of the wildlife overpass with an acoustic microphone attached to a 1.8-metre aluminium pole. The pole extended the microphone above the short canopy leaving no obstruction from foliage or branches and a clear recording space around both microphones. The microphone, SMX-II, is both an omni-directional and audio broadband specification. The Song Meter unit was configured to record between 0700 and 0900 hrs each in .wav format at a sampling rate of 24 kHz and at 16 bits. A high pass-filter was applied at 180 Hz so excessive low-frequency sounds were attenuated and bird vocalizations could be adequately captured. The entire device was placed in a locked box and secured to a tree trunk, but with microphones exposed above the foliage.

5.3.4 Acoustic indices

Acoustic indices were adapted and developed from biodiversity assessment indices to estimate sound diversity produced from natural environments (Sueur *et al.* 2014). The basic premise of the application of acoustic indices is that communities with more vocal species equate to greater acoustic diversity, and biodiversity is positively correlated with acoustic diversity (Gage, Napoletano & Cooper 2001; Ji *et al.* 2007). Most acoustic indices act at the α-diversity level, and describe the richness and complexity of an acoustic community or landscape within group/site/period (Sueur *et al.* 2014). These indices can be further divided into three categories – complexity, intensity, and soundscape indices. In acoustics, the idea of ‘complexity’ is based on the assumption that a community or landscape acoustic output increases in complexity based on the number of vocal individuals and species; therefore, an index that accounts for the heterogeneity of sound should also be a proxy of animal acoustic activity (Sueur *et al.* 2014). This can be calculated in different ways, and many indices have been proposed in the relatively short time that soundscape ecology has been active as a discipline. Importantly, each index reveals a distinct characteristic of the soundscape, so using several complementary indices is preferable to relying on any single parameter to encapsulate the full variation in sound (Sueur *et al.* 2014). I generated three different complexity indices for the Singapore recordings (Table 5.2).

One of the earliest complexity indices developed was the **bioacoustic index**. It was designed to assess the relative abundance and composition of bird communities in the sub-montane ecosystems of Hawaii affected by exotic plant invasion (Boelman *et al.* 2007). The index calculates the area below the frequency spectrum above a specific decibel (dB) threshold and within a specific frequency range, and is a function of the sound level and the number of frequency bands used by the bird community (Boelman *et al.* 2007). The **acoustic complexity index** was developed later to serve as a direct quantification of soundscape complexity by calculating the variability of intensities of the sound recordings, despite the presence of constant anthrophony or human-generated noise (Farina & Pieretti 2014; Pieretti, Farina & Morri 2011). This index has been used to describe avian soundscapes (Farina, Pieretti & Piccioli 2011), to explore the association between these soundscapes and vegetation complexity (Farina & Pieretti 2014), and to investigate the influence of traffic noise (Pieretti *et al.* 2015). Pieretti, Farina & Morri (2011) discovered that this index correlates well with the number of bird calls, while eliminating aircraft noise overhead. The **acoustic diversity index** is also considered a useful proxy for species diversity. It is based on the Shannon index (Villanueva-Rivera *et al.* 2011), and is derived by dividing the frequency spectrogram into a number of bins (typically 10) and quantifying the proportion of signals in each bin above a volume threshold (typically – 50 dbFS) (Villanueva-Rivera *et al.* 2011; Sueur *et al.* 2014).

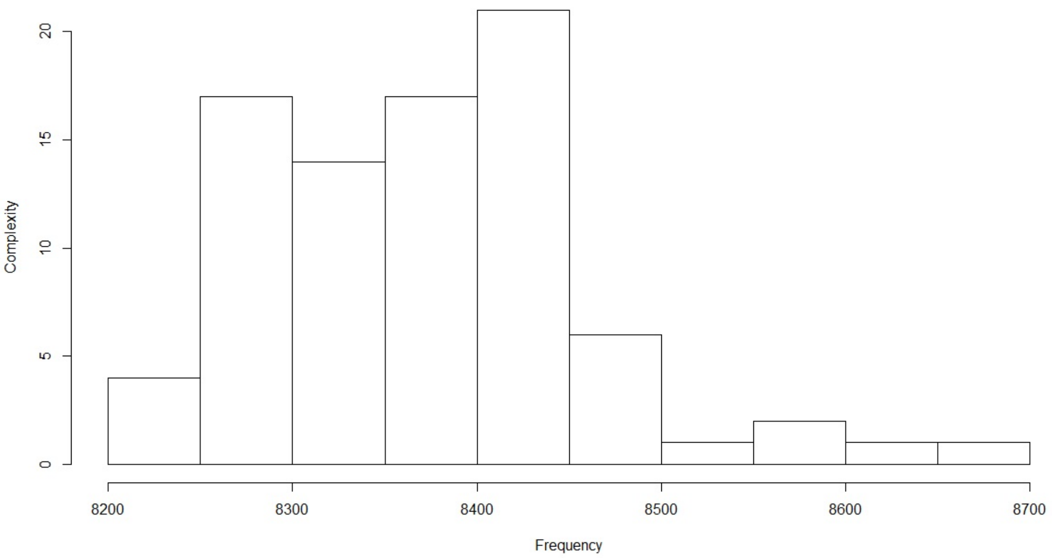
In addition to the three complexity indices I also quantified the **normalised difference soundscape index** (NDSI; Table 2). The NDSI is a true soundscape index in that it reflects the relative contribution of biophony compared to geophony and anthrophony. The calculation involves segregating the spectral profile of the soundscape into two main frequency bands between 0.2 and 2 kHz for anthrophonic sounds, and 2 kHz to 8 kHz for biophony respectively (Ji *et al.* 2007). The NDSI is calculated as a ratio of anthrophony to biophony and ranges from -1 to +1, with low and high values indicating the prevalence of anthrophony and biophony respectively. This index has been used to classify a large archive of online sound samples (Kasten *et al.* 2012), and to examine the soundscape changes over a period of four years in a lake habitat in North America with large soundscape time series datasets (Gage & Axel 2014). The NDSI values were high and stable throughout the four years of monitoring, which was expected of an environment uninhabited by humans.

5.3.5 Data processing and analyses

The daily two-hour recordings represented the dawn chorus and captured bird vocalizations and insect calls, such as those from cicadas and crickets. I checked all recordings prior to analyses to assess levels of rain activity at regular intervals within each file. Recordings from mornings with heavy rain were subsequently excluded from the study as bird activity (and hence vocalisations) is known to be reduced during rainy conditions (Robbins 1981). Each 2-hour recording was split into 12 files of 10-minute duration using WavePad v6.37 (NCH Software), and acoustic indices calculated for each of these 10-minute segments. Sensitivity analyses using recording segments of various lengths (10, 30 and 60-minute) for all four soundscape indices revealed that 10-minute segments gave the appropriate amount of variation across the duration of the dawn chorus as shown by histograms in Figure 5.1.

Signal settings for the four acoustic indices calculated are summarised in Table 5.3. Generation of acoustic data was performed in R, version 3.2.4 (R Core Team 2016) using the *multiple_sounds* function in the package 'soundecology' (Villanueva-Rivera & Pijanowski 2013), as well as the packages 'seewave', 'ineq', 'tuneR' and 'vegan'. Mean values of each soundscape index were calculated across the twelve 10-minute sound files recorded each morning, thereby producing a single average value for each index per day. The distribution of acoustic data across each event was checked for homoscedasticity (Levene's test) and visualised using violin plots using the R package ggplot2, and the residuals were checked for normality. The variance in mean acoustic data for each index was unequal between events, and so data did not fully conform to the assumptions of parametric tests. Kruskal-Wallis one-way ANOVAs were therefore used to determine if indices varied significantly between events, and pairwise Mann-Whitney tests were used to determine which events differed. A Bonferroni correction for the Mann Whitney tests was applied to control for Type 1 error across the six pairwise tests performed for each index. Linear models were then used to determine whether variation in each of the soundscape indices across the entire study period could be predicted by PSI. All statistical tests were performed in R, version 3.2.4 (R Core Team 2016).

(a) Acoustic complexity – 10-minute samples



(b) Acoustic complexity – 30-minute samples

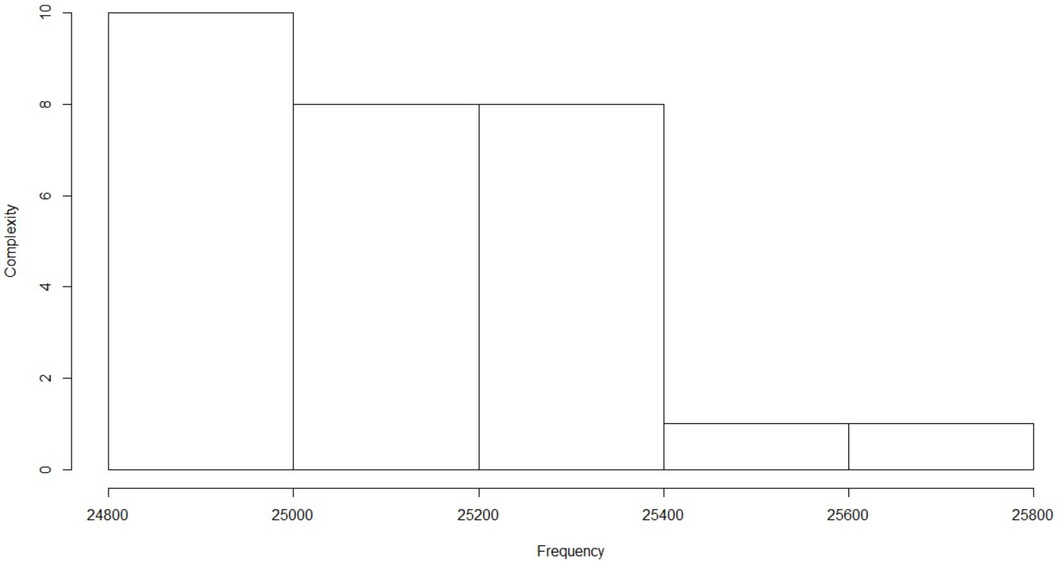
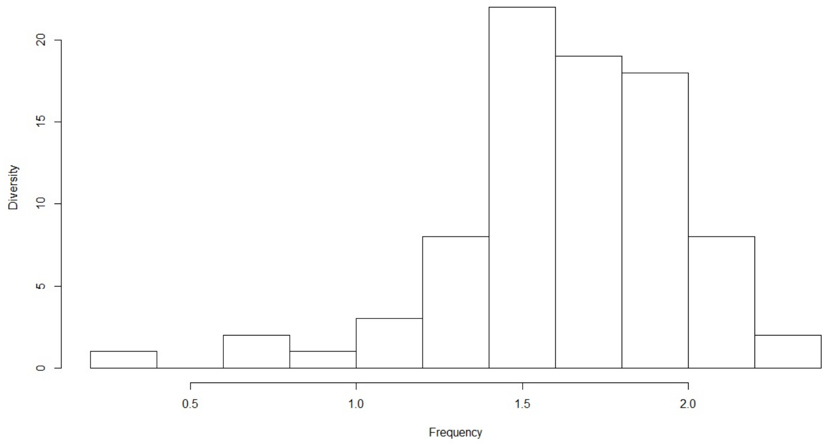
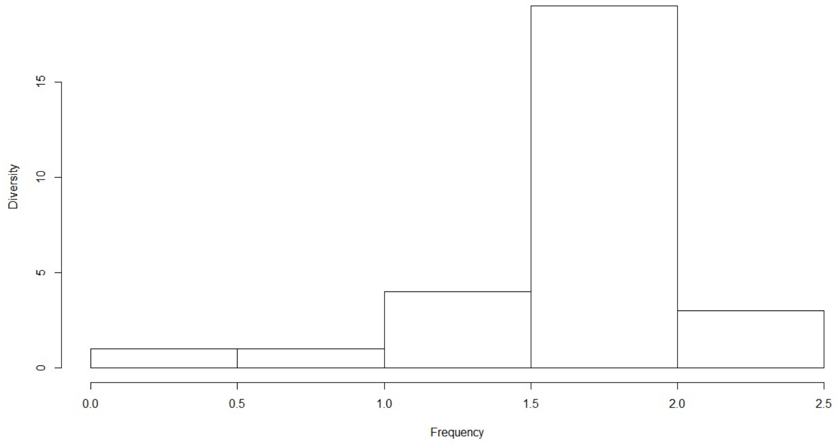


Figure 5.1 a-b. Histograms showing variation in frequency of the acoustic complexity index calculated on 10- and 30-minute sound recording segments from Singapore.

(c) Acoustic diversity – 10-minute samples



(d) Acoustic diversity – 30-minute samples



(e) Acoustic diversity – 60-minute samples

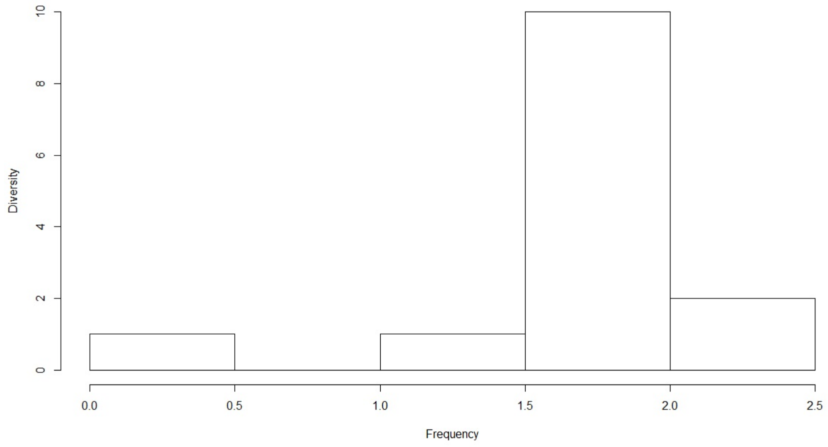
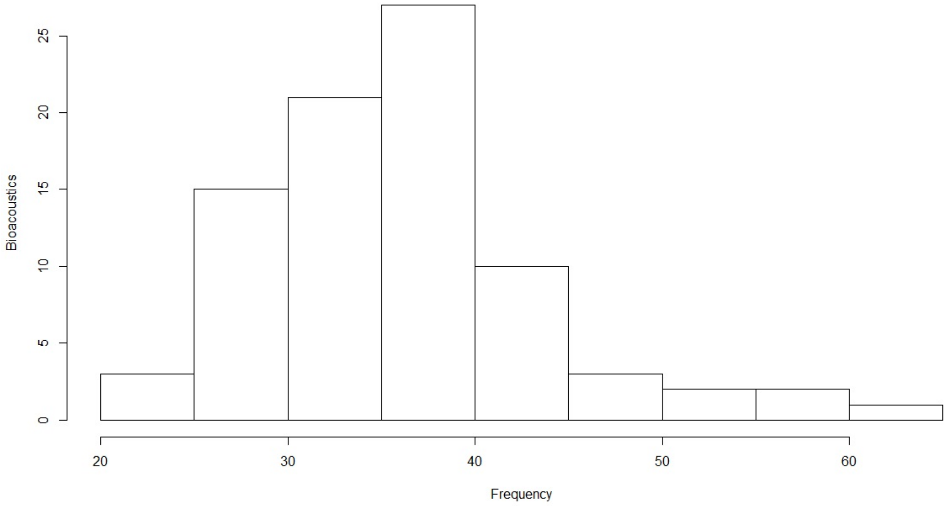
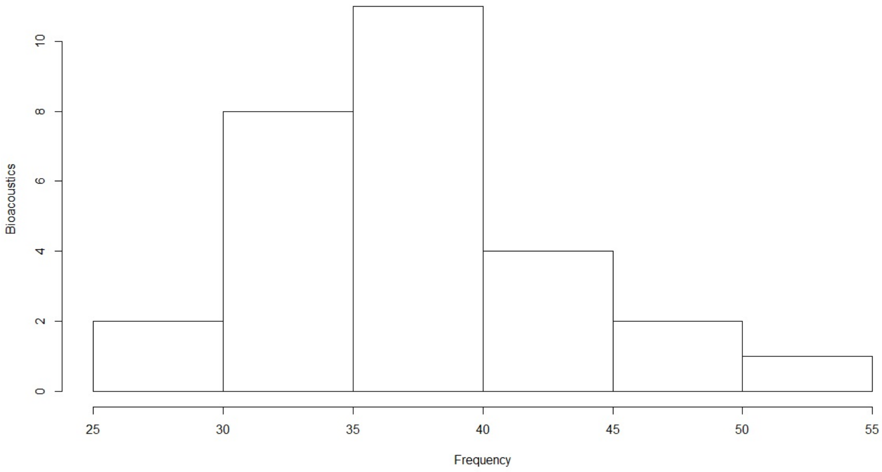


Figure 5.1 c-e. Histograms showing variation in frequency of the acoustic diversity index calculated on 10-, 30- and 60-minute sound recording segments from Singapore.

(f) Bioacoustic index– 10-minute samples



(g) Bioacoustic index – 30-minute samples



(h) Bioacoustic index – 60-minute samples

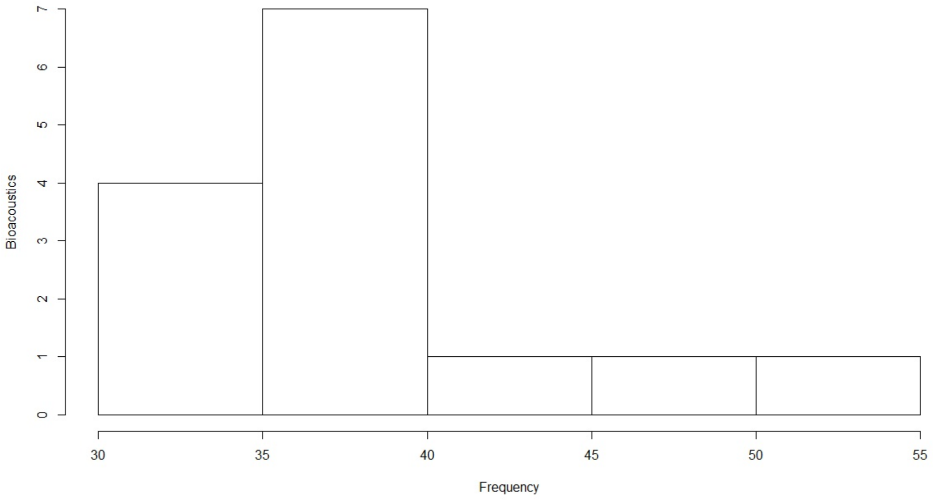
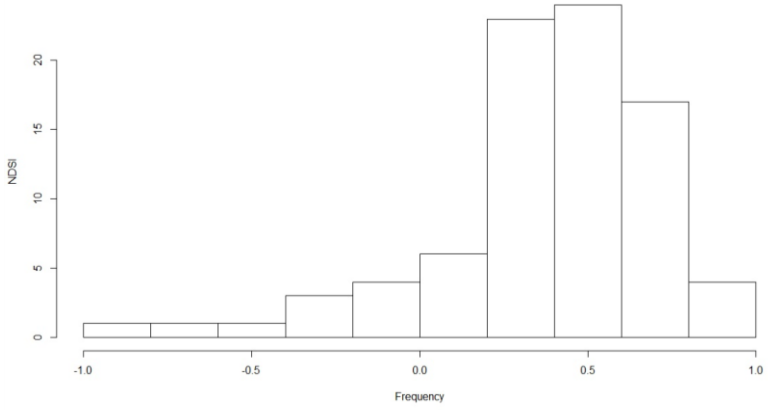
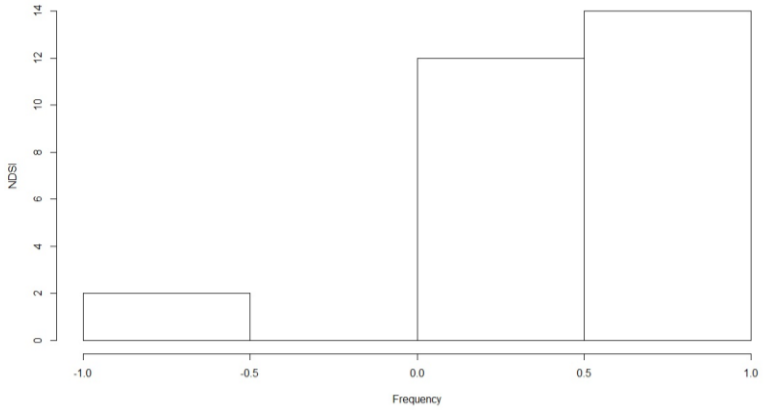


Figure 5.1 f-h. Histograms showing variation in frequency of the bioacoustic index calculated on 10-, 30- and 60-munite sound recording segments from Singapore.

(i) NDSI – 10-minute samples



(j) NDSI – 30-minute samples



(k) NDSI – 60-minute samples

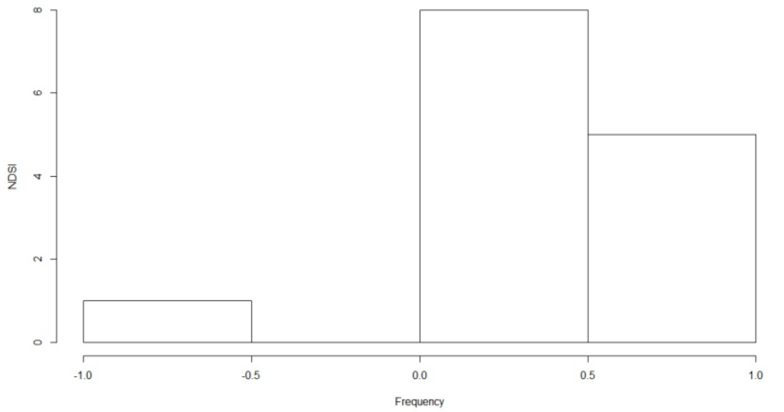


Figure 5.1 i-k. Histograms showing variation in frequency of the normalised difference soundscape index calculated on 10-, 30- and 60-munite sound recording segments from Singapore.

Table 5.2 Soundscape indices quantified form sound recordings collected in central Singapore between January 2015 and March 2016.

Index	**Purpose**	**Derivation**	**Reference**
Acoustic complexity (AC)	Rapid quantification of the typical complexity of biotic songs of a soundscape, despite the presence of anthrophony	Absolute difference (dk) between two adjacent values of intensity in a user-defined single frequency bin, which are then summed in the first temporal step of recording	(Farina and Pieretti 2014; Pieretti, Farina and Morri 2011)
Acoustic diversity (AD)	Good proxy for species diversity	Divides the frequency spectrogram into bins (default 10) and quantifies the proportion of signals in each bin above a threshold (default – 50 dbFS). Analogous to the Shannon index applied to these bins.	(Villanueva-Rivera *et al.* 2011; Sueur *et al.* 2014)
Bio-acoustic (BA)	Alpha diversity index for measuring relative avian abundance	Area under each curve in all frequency bands associated with the dB value that was greater than the minimum dB value for each curve. The area values are thus a function of both the sound level and the number of frequency bands used by the avifauna.	(Boelman *et al.* 2007)
Normalised Difference Soundscape Index (NDSI)	Estimate of the level of anthropogenic disturbance on the soundscape	Ratio of human-generated (anthrophony) to biological (biophony) acoustic components, defined by frequency bands.	(Kasten *et al.* 2012; Gage and Axel 2014)

Table 5.3 Settings used for the processing of the soundscape indices in R. Optimal parameters for each index were determined after sensitivity analyses on a subset of sound recordings.

Index	J (cluster size) (s)	Min freq (Hz)	Max freq (Hz)	dB threshold (Hz)	Freq step (Hz)	Anthro min (Hz)	Anthro max (Hz)	Bio min (Hz)	Bio max (Hz)
Acoustic complexity (AC)	10	—	11025	—	—	—	—	—	—
Acoustic diversity (AD)	—	—	11025	-30	1000	—	—	—	—
Bio-acoustic (BA)	—	2000	11025	—	—	—	—	—	—
Normalised difference soundscape (NDSI)	—	—	—	—	—	1000	2000	2000	11025

J: cluster size in seconds (e.g. a cluster size of 10 s will partition analyses into 10-second clusters); **Min freq:** minimum frequency used when calculating the value, in Hertz. Applied only to BA; **Max freq:** maximum frequency used when calculating the value, in Hertz. Applied to AC, AD and BA; **dB threshold:** threshold to use in the calculation and a dB of -30 dBFS was chosen as it was the most optimal based on a visual comparison of boxplots and histograms. Applied only to AD; **Freq step:** size of frequency bands. Soundscape studies typically use 1000 Hz bands; **Anthro min and Anthro max:** minimum and maximum values of the range of anthrophony (human-generated sound); **Bio min and Bio max:** minimum and maximum values of the range of biophony (biologically-generated sounds).

5.4 Results

Recordings were made for a total of 78 mornings between January 2015 and March 2016. Since post-haze data were not strictly independent of previous values recorded, the linear models were applied to a subset of data, (i.e. before and during the haze event). Acoustic activity was greatest in the pre-haze period across all soundscape indices (Figure 5.2). During the haze event, there was a significant and substantial decline in all acoustic indices. On average, soundscape metrics were 1.4 times higher before the haze than during the event for acoustic complexity, acoustic diversity and bioacoustic index while pre-haze NDSI was 5.5 times that measured during the haze. Three weeks after the haze event had passed, there was no significant change in acoustic diversity, bioacoustic index and NDSI, although there was a significant recovery of acoustic complexity, but not to the levels of pre-haze. This recovery continued three months after the smoke-haze event and reached pre-haze levels for bioacoustic index but not for the rest of the indices. In the three months post-haze period, acoustic complexity showed recovery levels that were intermediate between pre-haze and three weeks post-haze. Across the whole study period acoustic activity values were significantly and negatively correlated with daily pollution levels, with the highest PSI readings associated with the lowest values of soundscape metrics. The PSI was found to account for 48-62% of the variation in soundscapes.

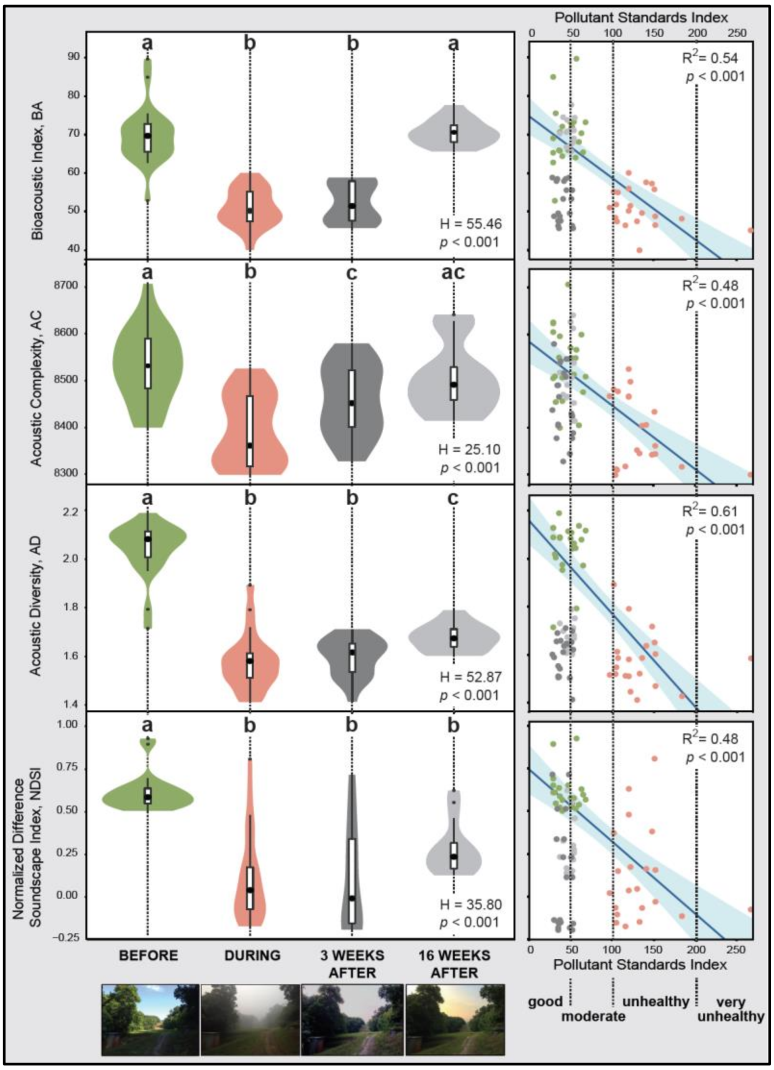


Figure 5.2 Daily variation in acoustic indices, and their association with air quality, before, during and after the 2015 El Niño forest fire smoke-induced haze event in Singapore. Left panels: violin plots show variation (median, range, kernel density; 25th–75th percentiles) in daily measures of dawn chorus acoustic activity ‘before’ (22 sample days), ‘during’ (21 sample days) and ‘after’ (20 and 15 sample days at 3 and 16 weeks respectively). A violin plot is a hybrid between a box plot and a kernel density plot, showing peaks in the data. It is more informative than a box plot because in addition to the median, inter-quartile range and the 95% confidence interval, the rotated kernel density plot on each side shows the distribution of the data. Different letters denote significant differences between sample periods, based on Kruskal-Wallis and post-hoc Mann-Whitney tests. Right panels: comprise regressions (+/- 95% CI, indicated by shaded area around line of best fit) of daily acoustic indices against the Pollutant Standards Index (PSI), Singapore's national standard for measuring air quality. Due to data non-independence issues associated with the two ‘after’ sample periods, the regressions are calculated from ‘before’ and ‘during’ the haze event. Dashed lines show the public health advisory PSI thresholds.

5.5 Discussion

It is estimated that forest and peat fires between June and October 2015 affected around 2.61 million hectares (The World Bank 2015) in Indonesia and resulted in the largest release of carbon since 1997 (Huijnen *et al.* 2016). While the health, economic, and greenhouse gas emission issues of regional fire and haze events have been well-documented, the impact of the haze on biodiversity and ecosystems has been relatively unstudied apart from anecdotal accounts by Kinnaird & O'Brien (1998) and Limin *et al.* 2006. My study presents a unique evaluation of the effects of the 2015 Southeast Asia forest fires on biodiversity and is the first to monitor natural soundscapes during a major air pollution event. The transboundary haze crisis had a negative impact on the natural soundscape in Singapore based on the responses of all four daily acoustic indices over the study period. A preliminary study in Central Kalimantan, Indonesia (Harrison *et al.* 2007) investigated how smoke affected forest dynamics by comparing leaf litter-fall in different years with various amounts of forest fire smoke and no smoke. The authors found that there was higher litter-fall in the year with smoke (2005-06) than in a year that was largely smoke-free (2000-01). They also speculated that high smoke levels may have amplified the effects of drought, and thereby caused more litter-fall as a response to physiological stress by forest trees (Harrison *et al.* 2007).

5.5.1 Suitability of acoustic indices to monitor biodiversity

The chosen indices used in my study appear to be ideal for monitoring tropical soundscapes in relation to the range of smoke pollution experienced in Singapore, as all metrics were significantly associated with PSI levels. Both bioacoustic (BA) and acoustic complexity (AC) indices were devised to capture mainly bird vocalisations, with the former measuring relative bird abundance and the latter measuring avian vocalisation dynamics in high-fidelity (or hi-fi) soundscapes (Boelman *et al.* 2007; Pieretti, Farina & Morri 2011). Rural areas provide good examples of hi-fi soundscape, in which a positive signal-to-noise ratio results from sounds that can be heard nearby and far away (Schafer 2004). Highly urban areas, on the other hand, tend to obscure the spread of sound and so typically do not conform to this pattern and would be termed as lo-fi soundscapes. My study would be somewhere in the middle of this soundscape but is perhaps more akin to the hi-fi soundscape (despite being above a road) due to rainforest habitat surrounding the recording location.

The acoustic complexity index is considered to be efficient at filtering out anthropogenic sounds and is able to describe the complexity of birdsongs competently in a given environment (Pieretti, Farina & Morri 2011). Hence, it is proposed that such a soundscape index has great potential for the monitoring of songbird communities faced with human disturbances, land use and climate changes (Pieretti, Farina & Morri 2011). The response of acoustic complexity to the haze event fitted these expectations - high pre-haze levels were significantly disrupted during the haze, and then recovered gradually over the post-haze period. However, the acoustic complexity levels three months after the haze did not recover to pre-haze acoustic complexity levels, indicating that some components of the ecological community continued to be absent or torpid. The bioacoustic index began high in the pre-haze period and fell significantly during the haze event. Bioacoustic levels did not recover by three weeks after the haze event, but had returned to pre-haze levels by 16 weeks.

Acoustic diversity and NDSI responded in a similar manner, in that the haze was associated with a major drop in each index with no return to pre-haze levels after 16 weeks post-haze. Generally, acoustic diversity index is seen as a good proxy for overall (vocal) faunal richness, because the sounds made by different animal species have different acoustic frequencies (Sueur *et al.* 2008; Pijanowski *et al.* 2011). A plausible explanation for acoustic diversity not recovering to pre-haze levels may be due to the absence of some non-avian species in the acoustic community. The NDSI, as a ratio of high frequency biological sound to lower frequency anthropogenic sound, is considered to be a measure of ecological health, with a healthy environment assumed to exhibit high levels of biological sound (Gage & Axel 2014). In their four year study of an uninhabited and relatively undisturbed island within a lake in Michigan, USA, Gage & Axel (2014) expected the NDSI to be high and stable across all years and their data confirmed their hypothesis with the median NDSI of about 0.6. The NDSI in my study began high at about a median of 0.58 and fell to -0.01 three weeks post-haze before recovering to 0.23 three months post-haze. The explanation for a lower NDSI is probably similar to that of the 3 months post-haze acoustic diversity index whereby the absence of non-avian species in the acoustic community resulted in a greater ratio of anthrophony to biophony.

5.5.2 Effects of atmospheric pollution on the Singaporean soundscape

The observed variation in soundscape indices in relation to the haze event suggests that the activity of animal species participating in the acoustic community has altered because of the air pollution. To the best of my knowledge, no other study has investigated the impacts of air pollution in this way. However, there is a single-species non-experimental study that examined the impact of heavy metal air pollution on the dawn signing behaviour of great tits *Parus major* (Gorissen *et al.* 2005). Here, it was revealed that male birds had less complex songs and a lower amount of singing during the dawn chorus in areas closer to the pollution source than places up to 4 km away from the source. It is not yet known how the pollutants physiologically affected songbird singing behaviour (Gorissen *et al.* 2005), but the behavioural cues clearly responded to environmental stress compared to bio-assays or morphological measurements (Zala & Penn 2004).

Although there are few studies on the impacts of atmospheric pollution on acoustic activity, research has been undertaken on the effects of sound pollution from anthropogenic sources. For example, in an open-cast mining area in Brazil species composition and spectral characteristics of animal calls were found to be different at two study sites — one near the mine and another far away — due to operation noises from mining machinery and transportation (Duarte *et al.* 2015). This study revealed higher levels of biophony in the site near the mine during the day, while higher biophony was experienced at night at the site distant from the mine. Overall, potential species richness was higher at the site away from the mine (Duarte *et al.* 2015).

The response of all four indices to the haze demonstrated a potential time lag in the recovery of the soundscape following the event in Singapore, despite an improvement in air quality. A time lag in species and ecosystem recovery after an environmental perturbation is common and it could be due to many reasons such as the low reproductive output of species (Elmqvist *et al.* 1994), drastic bio-geochemical changes in the environment (Stoddard *et al.* 1999), or a limited dispersal ability following habitat restoration (Cosentino *et al.* 2014). For example, Showman (1981) found that lichen improvement (as shown by the regrowth of injured thalli) happened only after two years of improving air quality and decreased SO_2 levels near a coal-fired power plant in Ohio, USA, and a minimum of four years was needed for lichen recolonization. Air pollutants and environmental contaminants are known to alter the life history phenotypes of organisms indirectly by modifying their operative environments (e.g. resource availability, thermal characteristics, predation risk) and/or directly by modifying the development and physiology of the organism itself (Congdon *et al.* 2001).

There are several possible reasons for the findings in Singapore. The time lag in the recovery of natural soundscapes (as measured by acoustic indices) in my study could possibly be due to the physiological stress of the species through inhalation of polluted air. The severe haze probably affected the health and fitness of some members of the acoustic community, which vocalised less and did not participate in the dawn chorus even though the air quality improved after the subsidence of the haze. In the study of the effects of haze on the singing of gibbons, Cheyne (2008) speculated that one possible reason for reduced singing in the primate be due to poorer health as a result of smoke inhalation giving rise to respiratory problems. She inferred this from studies on humans where over 90% of some 500 people affected by the 1997 fires had respiratory problems (Kunii *et al.* 2002). In my study, most of the species that contributed to the acoustic community at the recording site were probably birds and insects, and because there was no physical and intense heat damage to the habitats (unlike in areas close to the centres of burning in Indonesia), this could be a reason why the acoustic indices showed improvement in a relatively short time as the ecological community was largely intact. In contrast, Adeney *et al.* (2006) found that there were progressive changes in the bird community through visual surveys even in unburned forest plots in Sumatra because the intense heat (up to 45°C) and smoke caused abnormally high tree mortality five years post-fire thereby changing the vegetation structure and composition of the unburned plot. These findings suggest that the drivers of change in bird communities in unburned plots adjacent to burned plots are due to both the direct and indirect effects of fire and haze (Adeney *et al.* 2006). In forests affected by adjacent disturbance, the bird communities within may take up to a 100 years to stabilize as shown by long-term studies (Brooks, Pimm & Oyugi 1999; Castelletta, Sodhi & Subaraj 2010) probably due to a reduction in habitat area and edge effects (Murcia 1995).

5.5.3 Implications for biodiversity in other haze-affected parts of Southeast Asia

Despite the partial recovery in the soundscapes following the 2015 haze episode, the clear patterns of acoustic change revealed in Singapore indicate a potentially worrying trend elsewhere in Southeast Asia. My study was conducted around 300 km away from the centres of burning in peatland and forest landscapes of Borneo and Sumatra. In those areas pollutant levels during the 2015 El Niño were many orders of magnitude higher than in Singapore. For example, on 23 October 2015 at 4pm, the PSI levels in Palangkaraya in Central Kalimantan registered 2,251 (Chan 2015) compared to 124, the highest PSI recorded in Singapore at the same time point. Based on this day, smoke-haze pollution is at least 18 times more severe in some parts Indonesia than Singapore, and by extrapolation, the natural soundscapes in Indonesia would be much more severely affected by smoke-haze more drastically than Singapore. Monitoring the bioacoustic response to smoke and haze closer to fire sources to establish how wildlife communities are responding, and most importantly, whether they are recovering. Passive monitoring in this way has the added advantage that few field survey hours are needed, which is particularly important in fire prone areas, which are difficult and dangerous places to work. Acoustic monitoring, as demonstrated in Singapore, could therefore be a feasible way of monitoring wildlife safely and remotely, allowing field resources to be allocated elsewhere.

5.5.4 Recommendations for future soundscape monitoring

Although a clear response of the acoustic community to forest fire smoke has been demonstrated by this study, data were derived from a single site. Further recording efforts could therefore be improved upon by scaling up and establishing an array of acoustic sensors for long-term monitoring in more sites with varied geography and vegetation type, similar to the deployment of wireless sensor networks as proposed by (Marvin *et al.* (2016). The study could be readily replicated in various parts of Southeast Asia prone to forest and peat fires, or are subject to smoke-haze episodes annually, and could yield interesting insights into patterns of β diversity as well as α diversity. Interesting acoustic research questions for the Southeast Asian smoke-haze pollution would include:

- Do sites closer to fires/smoke-haze sources have lower acoustic diversity than sites further away?
- Do intact forests have a role to play in mitigating the impacts of smoke-haze to biodiversity at high to low PSI levels?
- How does the structure of burnt and unburnt forests correlate with soundscape activity?

There is great potential for the application of soundscape ecology to answer timely research questions in conservation, particularly in regions like Southeast Asia that are undergoing unprecedented levels of environmental change. As more data sets are collected in the region, we will have improved baseline understanding of multiple soundscapes, which is crucial in planning for soundscape conservation (Dumyahn & Pijanowski 2011) and quantifying the effects of environmental change.

5.6 References

Adeney, J.M., Ginsberg, J.R., Russell, G.J. & Kinnaird, M.F. (2006) Effects of an ENSO-related fire on birds of a lowland tropical forest in Sumatra. *Animal Conservation*, **9**, 292–301.

Anonymous. (2015) Operations at airport in Pekanbaru affected by haze, visibility down to 100m, SE Asia News & Top Stories - The Straits Times, http://www.straitstimes.com/asia/se-asia/operations-at-airport-in-pekanbaru-affected-by-haze-visibility-down-to-100m

Anwar, Z. (2015) Haze: Schools closure in Northern states tomorrow | New Straits Times | Malaysia General Business Sports and Lifestyle News. *New Straits Times*, **2016**.

Boelman, N.T., Asner, G.P., Hart, P.J. & Martin, R.E. (2007) Multi-trophic invasion resistance in Hawaii: Bioacoustics, field surveys, and airborne remote sensing. *Ecological Applications*, **17**, 2137–2144.

Brooks, T.M., Pimm, S.L. & Oyugi, J.O. (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology*, **13**, 1140–1150.

Canaday, C. (1996) Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation*, **77**, 63–77.

Carson, R. (1962) *Silent Spring*. Houghton Mifflin Harcourt.

Castelletta, M., Sodhi, N.S. & Subaraj, R. (2010) Heavy extinctions of forest avifauna in Singapore: lessons for biodiversity conservation in Southeast Asia. *Conservation Biology*, **14**, 1870–1880.

Chan, F. (2015) Indonesia set to evacuate kids in worst haze hit areas. *The Straits*

Times, **2016**.

Cheyne, S.M. (2008) Effects of meteorology, astronomical variables, location and human disturbance on the singing apes: Hylobates albibarbis. *American Journal of Primatology*, **70**, 386–392.

Cleary, D.F.R., Fauvelot, C., Genner, M.J., Menken, S.B.J. & Mooers, A.Ø. (2006) Parallel responses of species and genetic diversity to El Niño Southern Oscillation-induced environmental destruction. *Ecology Letters*, **9**, 304–310.

Cleary, D.F.R. & Grill, A. (2004) Butterfly response to severe ENSO-induced forest fires in Borneo. *Ecological Entomology*, **29**, 666–676.

Cochrane, M.A. (2003) Fire science for rainforests. *Nature*, **421**, 913–919.

Congdon, J.D., Dunham, A.E., Hopkins, W.A., Rowe, C.L. & Hinton, T.G. (2001) Resource allocation-based life histories: A conceptual basis for studies of ecological toxicology. *Environmental Toxicology and Chemistry*, **20**, 1698–1703.

Cosentino, B.J., Schooley, R.L., Bestelmeyer, B.T., Kelly, J.F. & Coffman, J.M. (2014) Constraints and time lags for recovery of a keystone species (Dipodomys spectabilis) after landscape restoration. *Landscape Ecology*, **29**, 665–675.

Duarte, M.H.L., Sousa-Lima, R.S., Young, R.J., Farina, A., Vasconcelos, M., Rodrigues, M. & Pieretti, N. (2015) The impact of noise from open-cast mining on Atlantic forest biophony. *Biological Conservation*, **191**, 623–631.

Dumyahn, S.L. & Pijanowski, B.C. (2011) Soundscape conservation. *Landscape Ecology*, **26**, 1327–1344.

Elmqvist, T., Rainey, W.E., Pierson, E.D. & Cox, P.A. (1994) Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain-forest.

Biotropica, **26**, 384–391.

Farina, A. (2008) *Principles and Methods in Landscape Ecology: Towards a Science of the Landscape*. BOOK, Springer Science & Business Media.

Farina, A. & Pieretti, N. (2014) Sonic environment and vegetation structure: a methodological approach for a soundscape analysis of a Mediterranean maqui. *Ecological Informatics*, **21**, 120–132.

Farina, A., Pieretti, N. & Piccioli, L. (2011) The soundscape methodology for long-term bird monitoring: A Mediterranean Europe case-study. *Ecological Informatics*, **6**, 354–363.

Fuller, R.A., Warren, P.H. & Gaston, K.J. (2007) Daytime noise predicts nocturnal singing in urban robins. *Biology Letters*, **3**, 368–370.

Gage, S.H. & Axel, A.C. (2014) Visualization of temporal change in soundscape power of a Michigan lake habitat over a 4-year period. *Ecological Informatics*, **21**, 100–109.

Gage, S.H., Napoletano, B.M. & Cooper, M.C. (2001) Assessment of ecosystem biodiversity by acoustic diversity indices. *The Journal of the Acoustical Society of America*, **109**, 2430.

Ghazali, R. (2015) Haze forces closure of three airport runways - Nation | The Star Online. *The Star Online*, 2015.

Gorissen, L., Snoeijs, T., Van Duyse, E. & Eens, M. (2005) Heavy metal pollution affects dawn singing behaviour in a small passerine bird. *Oecologia*, **145**, 504–509.

Grafe, T.U. (2005) Anuran choruses as communication networks. *Animal communication networks*, 277–299.

Harrison, M.E., Cheyne, S.M., Sulistiyanto, Y. & Rieley, J.O. (2007) Biological effects of smoke from dry-season fires in non-burnt areas of the Sabangau peat swamp forest, Central Kalimantan, Indonesia. *Carbon-climate-human interaction on tropical peatland. Proceedings of The International Symposium and Workshop on Tropical Peatland, Yogyakarta*, pp. 27–29.

Heil, A. (2007) *Indonesian Forest and Peat Fires: Emissions, Air Quality, and Human Health*. JOUR, University of Hamburg Hamburg.

Huijnen, V., Wooster, M.J., Kaiser, J.W., Gaveau, D.L.A., Flemming, J., Parrington, M., Inness, A., Murdiyarso, D., Main, B. & van Weele, M. (2016) Fire carbon emissions over maritime southeast Asia in 2015 largest since 1997. *Scientific Reports*, **6**, 26886.

Ji, W., Joo, W., Napoletano, B., Qi, J., Gage, S.H. & Biswas, S. (2007) Soundscape characteristics of an environment: a new ecological indicator of ecosystem health. *Wetland and water resource modeling and assessment: A watershed perspective* (ed. W. Ji), pp. 201–211. CRC Press, New York.

Kasten, E.P., Gage, S.H., Fox, J. & Joo, W. (2012) The remote environmental assessment laboratory's acoustic library: An archive for studying soundscape ecology. *Ecological Informatics*, **12**, 50–67.

Ketterings, Q.M., Wibowo, T.T., Van Noordwijk, M. & Penot, E. (1999) Farmers' perspectives on slash-and-burn as a land clearing method for small-scale rubber producers in Sepunggur, Jambi Province, Sumatra, Indonesia. *Forest Ecology and Management*, **120**, 157–169.

Kinnaird, M.F. & O'Brien, T.G. (1998) Ecological effects of wildfire on lowland rainforest in Sumatra. *Conservation Biology*, **12**, 954–956.

Kunii, O., Kanagawa, S., Yajima, I., Hisamatsu, Y., Yamamura, S., Amagai, T. & Ismail, I.T.S. (2002) The 1997 haze disaster in Indonesia: its air quality and health effects. *Archives of Environmental Health: An International Journal*, **57**, 16–22.

Lee, J.S.H., Jaafar, Z., Tan, A.K.J., Carrasco, L.R., Ewing, J.J., Bickford, D.P., Webb, E.L. & Koh, L.P. (2016) Toward clearer skies: challenges in regulating transboundary haze in Southeast Asia. *Environmental Science & Policy*, **55**, 87–95.

Limin, S.H., Rieley, J.O., Jaya, S. & Gumiri, S. (2006) The impact of forest fires and resultant haze on terrestrial ecosystems and human health in central Kalimantan, Indonesia. *Tropics*, **15**, 321–326.

Marlier, M.E., DeFries, R.S., Voulgarakis, A., Kinney, P.L., Randerson, J.T., Shindell, D.T., Chen, Y. & Faluvegi, G. (2013) El Nino and health risks from landscape fire emissions in southeast Asia. *Nature Climate Change*, **3**, 131–136.

Marvin, D.C., Koh, L.P., Lynam, A.J., Wich, S., Davies, A.B., Krishnamurthy, R., Stokes, E., Starkey, R. & Asner, G.P. (2016) Integrating technologies for scalable ecology and conservation. *Global Ecology and Conservation*, **7**, 262–275.

Michener, W.K., Baerwald, T.J., Firth, P., Palmer, M.A., Rosenberger, J.L., Sandlin, E.A. & Zimmerman, H. (2001) Defining and unraveling biocomplexity. *Bioscience*, **51**, 1018–1023.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, **10**, 58–62.

National Environment Agency. (2016) Historical PSI Readings, http://www.haze.gov.sg/haze-updates/historical-psi-readings

O’Brien, T.G., Kinnaird, M.F., Nurcahyo, A., Prasetyaningrum, M. & Iqbal, M.

(2003) Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest. *Animal Conservation*, **6**, 115–121.

Page, S.E., Siegert, F., Rieley, J.O., Boehm, H.-D. V, Jaya, A. & Limin, S. (2002) The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature*, **420**, 61–65.

Pieretti, N., Duarte, M.H.L., Sousa-Lima, R.S., Rodrigues, M., Young, R.J. & Farina, A. (2015) Determining temporal sampling schemes for passive acoustic studies in different tropical ecosystems. *Tropical Conservation Science*, **8**, 215–234.

Pieretti, N., Farina, A. & Morri, D. (2011) A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). *Ecological Indicators*, **11**, 868–873.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H. & Pieretti, N. (2011) Soundscape ecology: the science of sound in the landscape. *Bioscience*, **61**, 203–216.

R Core Team. (2016) R: A language and environment for statistical computing. ver. 3.2.4.

Reddington, C.L., Yoshioka, M., Balasubramanian, R., Ridley, D., Toh, Y.Y., Arnold, S.R. & Spracklen, D. V. (2014) Contribution of vegetation and peat fires to particulate air pollution in Southeast Asia. *Environmental Research Letters*, **9**, 94006.

Robbins, C.S. (1981) Bird activity levels related to weather. *Studies in Avian Biology*, **6**, 301–310.

Schafer, R.M. (2004) Audio Culture: Readings in Modern Music. *Audio Culture:*

Readings in Modern Music. (eds C. Cox & D. Warner), pp. 29–39. The Continuum International Publishing Group Ltd, New York.

Seow, J. & Hio, L. (2015) Haze forces closure of schools across Singapore, Environment News & Top Stories - The Straits Times , http://www.straitstimes.com/singapore/environment/haze-forces-closure-of-schools-across-singapore.

Showman, R.E. (1981) Lichen recolonization following air quality improvement. *Bryologist*, 492–497.

Siegert, F., Ruecker, G., Hinrichs, A. & Hoffmann, A.A. (2001) Increased damage from fires in logged forests during droughts caused by El Nino. *Nature*, **414**, 437–440.

Stoddard, J.L., Jeffries, D.S., Lükewille, A., Clair, T.A., Dillon, P.J., Driscoll, C.T., Forsius, M., Johannessen, M., Kahl, J.S. & Kellogg, J.H. (1999) Regional trends in aquatic recovery from acidification in North America and Europe. *Nature*, **401**, 575–578.

Sueur, J., Farina, A., Gasc, A., Pieretti, N. & Pavoine, S. (2014) Acoustic indices for biodiversity assessment and landscape investigation. *Acta Acustica united with Acustica*, **100**, 772–781.

Sueur, J., Pavoine, S., Hamerlynck, O. & Duvail, S. (2008) Rapid acoustic survey for biodiversity appraisal. *PLOS ONEe*, **3**, e4065.

Sutherland, W.J. (2006) *Ecological Census Techniques: A Handbook*. Cambridge University Press.

Tacconi, L. (2016) Preventing fires and haze in Southeast Asia. *Nature Climate Change*, **6**, 640–643.

The World Bank. (2015) The cost of fire : an economic analysis of Indonesia's 2015 fire crisis (English) | The World Bank, http://documents.worldbank.org/curated/en/2016/03/26010885/cost-fire-economic-analysis-indonesia’s-2015-fire-crisis

Thiollay, J.M. (1997) Disturbance, selective logging and bird diversity: A Neotropical forest study. *Biodiversity and Conservation*, **6**, 1155–1173.

Thompson, J.N., Reichman, O.J., Morin, P.J., Polis, G.A., Power, M.E., Sterner, R.W., Couch, C.A., Gough, L., Holt, R., Hooper, D.U., Keesing, F., Lovell, C.R., Milne, B.T., Molles, M.C., Roberts, D.W. & Strauss, S.Y. (2001) Frontiers of ecology. *Bioscience,* **51**, 15–24.

Truax, B. (2001) *Acoustic Communication*. Greenwood Publishing Group.

Uhl, C., Kauffman, J.B. & Cummings, D.L. (1988) Fire in the Venezuelan Amazon 2: environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos*, **53**, 176–184.

Velasco, E. & Rastan, S. (2015) Air quality in Singapore during the 2013 smoke-haze episode over the Strait of Malacca: Lessons learned. *Sustainable Cities and Society*, **17**, 122–131.

Villanueva-Rivera, L.J. & Pijanowski, B.C. (2013) R Package ‘soundecology’. *R Package ‘soundecology’*.

Villanueva-Rivera, L.J., Pijanowski, B.C., Doucette, J. & Pekin, B. (2011) A primer of acoustic analysis for landscape ecologists. *Landscape Ecology*, **26**, 1233–1246.

van der Werf, G.R., Dempewolf, J., Trigg, S.N., Randerson, J.T., Kasibhatla, P.S., Giglio, L., Murdiyarso, D., Peters, W., Morton, D.C., Collatz, G.J., Dolman, A.J. & DeFries, R.S. (2008) Climate regulation of fire emissions and deforestation in equatorial Asia. *Proceedings of the National Academy of*

Sciences of the United States of America, **105**, 20350–20355.

West, B., Flikkema, P., Sisk, T. & Koch, G. (2001) Wireless sensor networks for dense spatio-temporal monitoring of the environment: A case for integrated circuit, system, and network design. *2001 IEEE CAS Workshop on Wireless Communications and Networking*.

Whitmore, T.C. (1984) Tropical rain forests of the Far East, 2nd edn. Clarendon.

Zala, S.M. & Penn, D.J. (2004) Abnormal behaviours induced by chemical pollution: A review of the evidence and new challenges. *Animal Behaviour*, **68**, 649–664.

6. Discussion

6.1 Summary of findings

In this thesis, I first began with a review of the acoustic techniques used to study bats and devised guidelines to help researchers of Southeast Asia design and implement bat acoustic surveys (**Chapter 2**). I then applied these acoustic approaches to a study of road impacts on bats in forest and urban habitats (**Chapter 3**), and an investigation on the habitat value of green roofs to bats in the urban matrix (**Chapter 4**). For **Chapter 5**, I used techniques in soundscape ecology to understand the response of biodiversity (represented as an acoustic community) to transboundary smoke-haze pollution brought about by El Niño Southern Oscillation (ENSO)-induced fires in the Southeast Asian region.

In general, my study has confirmed that intense urbanisation has substantial impacts on the bat fauna of Singapore. Only four out of 20 known species of insectivorous bats were found to use the urban areas I surveyed in Singapore, while another two species were restricted to the rainforest nature reserves of the island. I found the overall bat activity recorded in the urban habitats of Singapore averaged 33 passes/night, which is slightly more than half of that recorded in the forest habitats (57 passes/night).

I tested the effects of major roads on bat activity (**Chapter 3**). I found that light levels negatively influenced bat activity in boh forest and urban habitats, and forest-dependent bat species could be experiencing a road barrier effect.

Due to the proliferation of green roofs in the urban landscape of Singapore in recent years, I investigated the habitat value of these compact green spaces for bats (**Chapter 4**). At a landscape scale, with models including variables describing the size, location and age of the green roofs, I found no relationship between bat activity and the planted area, but age and height were substantial negative predictors of bat activity. Bats were found to respond positively to structural features of the roof vegetation but not the presence of water bodies. Management operations of the green roofs such as pruning, and pesticide application had positive and negative effects on bat activity respectively. There was some evidence that the lack of vegetation in the immediate area of the roof (125 m buffer) negatively affected bat activity.

The outset of ENSO-induced fires in 2015 presented a unique opportunity to study the effects of smoke-haze pollution on biodiversity using a soundscape approach (**Chapter 5**). Using four acoustic indices collected over a year, I demonstrated that levels of ecological acoustic activity during the dawn chorus dropped sharply during the haze, and that this decline was significantly associated with levels of air pollution considered hazardous to human health. Acoustic disruption was clear across four common indices of soundscape activity, with only a partial recovery to pre-haze levels observed 16 weeks after the smoke had dissipated. My results demonstrate that large-scale air pollution crises may have underestimated and far-reaching impacts on biodiversity.

In this discussion, I bring together the themes that emerge from these investigations.

6.2 Acoustic sampling guidelines: towards a bat call library for Singapore

I have established guidelines for the acoustic sampling of bats in Southeast Asia in collaboration with three colleagues from the Southeast Asian Bat Conservation Research Unit (SEACRU). I have also provided a preliminary catalogue of full-spectrum calls for the insectivorous bat species encountered during my study in Singapore in **Chapter 2**. The list of bat detectors reviewed was not meant to be an exhaustive due to the rapid development in the field of acoustic equipment, especially in the last five years. As a manual of acoustic sampling guidelines for the bat workers of Southeast Asia, **Chapter 2** was meant to provide basic guidance and resources to encourage the building of call libraries and the use of acoustic monitoring to complement existing methods of bat surveys.

Bats are a critical component of the fauna of Southeast Asia — a biodiversity hotspot — and make up about 30% of the known mammal species in the region, and with levels of endemism reaching about 60% (Kingston 2010). New bat species are still being added to the Southeast Asian chiropteran inventory through the use of physical capture methods and molecular techniques coupled with specimen examination in museums (Kingston 2010). The use of bat echolocation call characteristics are increasing incorporated into the formal description of new species (e.g. Soisook *et al.* 2008; Douangboubpha *et al.* 2016) and in detailed studies of echolocation calls of little known species (e.g. Zsebok, Son & Csorba 2014). However, the use of echolocation calls in biodiversity surveys and community ecology studies are very few (e.g. Sedlock 2001; Phommexay *et al.* 2011). Given widespread land-use change and habitat loss in the region (Sodhi *et al.* 2004), Hughes *et al.* (2011) argued for the concurrent establishment of species inventories and monitoring protocols to prioritise areas for bat conservation. The SEACRU is cognisant of the conservation urgency and the research and monitoring gap in the adoption of acoustic methods in bat monitoring for the region. This is especially relevant given that two of the important research priorities identified through consensus for the conservation of Southeast Asian bats deal with cave-roosting bats and forest-dependent bats, and a common broad action plan for these two priorities involves improved long-term monitoring programmes of both bat assemblages and populations (Kingston 2010).

It has been recognised that ecological work or even basic monitoring work of bats using acoustic techniques has lagged far behind in most tropical countries, compared to the higher latitude countries (Walters *et al.* 2013). Based on the analysis of calls from a global bat call reference database called Echobank (Collen 2012), Walters *et al.* (2013) found that call similarity and call library coverage determined which regions best presented opportunities for acoustic monitoring. They found that the slow adoption of acoustic methods to study bats in tropical regions (which includes Southeast Asia) is attributed to the high numbers of closely related species and many of these species have call structures that are highly similar. This is in contrast to countries with a relatively lower diversity of bats in Eurasia, North Africa and the Middle East with low call similarities and a high call library coverage, which allows calls to be easily differentiated and identified (Walters *et al.* 2013). However, some bats of the genera *Myotis* and *Plecotus* are still challenging to differentiate based on call structure alone (Russ 2012).

The quest to build a global database of bat calls like Echobank is therefore very ambitious. In the short- to medium-term it may more practical to develop call libraries for a country or a regional group of countries. Even in a country with challenges of high bat diversity such as Thailand, it is possible to use acoustic methods to monitor certain bat families, notably those with species-specific bandwidths such as members in the families Rhinolophidae and Hipposideridae (Hughes *et al.* 2011). In Thailand of the 26 species of rhinolophid and hipposiderid bats examined for their calls, Hughes *et al.* (2011) could correctly classify 69% and 91% respectively using two call parameters — frequency with maximum energy (FMAXE) and call duration (D) — in a discriminant function analysis. Similarly, Phauk, Sarith & Furey (2013) evaluated the reliability of acoustic methods in identifying 13 bat species of rhinolophid and hipposiderid bats in Cambodia and reported a correct classification rate of 100% using the same methods. On the other hand, Hughes *et al.* (2011) cautioned about the identification of bats that use frequency-modulated (FM) components in their calls, especially in species-rich environments, because there was a high degree of misclassifications. Moreover, bats with FM call components exhibit both intra-individual and intraspecific variation in call structure. This identification challenge is further exacerbated when these bats fly in clutter, or when species alternate their calls, as exemplified by some emballonurid taxa (Hughes *et al.* 2011).

Both of my studies in **Chapters 3** and **4** took place in Singapore where the bat fauna is depauperate compared to neighbouring territories in Southeast Asia. Hence, acoustic monitoring was ideal given that 20 echolocating bat species are known to be present there, and no more than eight species commonly occur in both urban and forest environments (Table 2.6). In contrast, finding roosts and capturing some of these bat species is very challenging because some species are rare (e.g. *Rhinolophus lepidus*) or notoriously difficult to catch (e.g. *Saccolaimus saccolaimus* and *Taphozous melanopogon*). In the future, acoustic lures may be used in tandem with other physical catching methods such as harp traps and mist-nets to help build a complete bat call library. Elsewhere in the rainforests of Queensland, Australia, traps using acoustic lures show some promise, resulting in more bat captures of target species compared to control traps without lures (Hill, Armstrong & Barden 2015). In central Scotland, UK, Lintott *et al.* (2013) found a two to twelve-fold increase in trapping success of four species of insectivorous bats using acoustic lures in broadleaved and mixed woodland.

6.3 Mitigating the effects of roads on bats

My research from Chapter 3 supports the findings of other studies that demonstrate major roads to have a negative effect on bats. A major challenge for bat conservation is to improve permeability of roads to these animals without increasing the risk of vehicle collisions (Fensome & Mathews 2016). Underpasses have been found to be effective in reducing the barrier effect and reducing the roadkills for some bat species if the underpasses are spacious and coincide with flight paths along streams, woodland lanes or hedgerows (Boonman 2011; Abbott *et al.* 2015). Conversely, ‘bat gantries’ built over roads in the United Kingdom and Europe to increase road permeability for bats do not appear to have any benefit to bats, and may actually be counterproductive (Berthinussen & Altringham 2012). It has been discovered that only a very small proportion of bats used the gantries when encountered, where most of them crossed the road below the gantries at vehicle height, which places them at great collision risk (Berthinussen & Altringham 2012). The ineffectiveness of these gantries to improve road permeability for bats is attributed to inadequate environmental impact assessments, and this calls for more thorough investigations prior to the implementation of such purported mitigation measures (Abbott *et al.* 2015).

The effectiveness and feasibility of mitigation measures to increase road permeability for bats is also likely to be site-specific. For example, in a rural area in Indiana, USA, Bennett & Zurcher (2013) found that gaps more than 2 m encountered in the (bat) commuting route and vehicular noise caused bats to turn away from roads. These roads were classified as two-landed rural county roads measuring 4.2 m wide. Hence, the authors proposed two strategies for ameliorating the road barrier effect:

i) Connection of linear features bisected by roads by ensuring a continuous canopy between tree crowns;

ii) Restoration, enhancing and establishing linear features such as tree lines, hedgerows and fence lines to improve the permeability and soundscape of the overall landscape for bats.

In contrast to the highly urbanised situation in Singapore, the above recommendations may not be feasible given that the major roads in question are highways with six to eight lanes and at least 20-30 m wide, with no large trees planted in the centre road reservation due to safety reasons (Figure 6.1). In such cases, an overpass may be feasible to improve permeability for wildlife (including bats), but the use of such a mitigation measure to reduce the barrier effects of roads for bats are largely unproven (Abbott *et al.* 2015). However, several features of the overpass design and habitat connectivity to the surrounding is likely to encourage the use of overpasses by bats such as the strategic location on known flight path and preferably tall vegetation on the bridge (Altringham & Kerth 2016).

The Ecolink @BKE is a purpose built wildlife overpass in Singapore that took many years of planning and was finally built in 2013 (Chong, Yee & Yeo 2010; Figure 6.1). This wildlife overpass measures 64 m in length and has a width of 50 m, and it serves to re-connect two rainforest fragments which were separated by Bukit Timah Expressway in 1986. The vegetation planted on the overpass are rainforest plant species, which are selected to improve connectivity for target wildlife species such as pangolins and civets. My study in Chapter 3 demonstrated that forest-dependent bats such as *Rhinolophus lepidus* are restricted to forest habitats in Singapore, probably because of a road barrier effect. This is supported by acoustic monitoring using a stationary bat detector placed at the centre of the overpass during its construction, and every year after the overpass was completed (unpublished data). From these preliminary data *R. lepidus* did not appear to use the overpass until a year after it was completed, which could be due to the time needed for denser vegetation to form on the bridge before the bats would use the bridge as a crossing (Figure 6.1). This is a clutter-adapted species due to its low wing-loading and short, low aspect ratio wings, suggesting a slow and manoeuvrable flight (Pottie *et al.* 2005). Hence, it would need the cover and safety of the vegetation on the overpass to negotiate the landscape safely. The treatment of all future wildlife overpasses as designed experiments would allow firmer conclusions to be drawn about the effectiveness of overpasses in countering road impacts on bats and other wildlife species.

[R E D A C T E D]

Figure 6.1 The Ecolink@BKE — a wildlife overpass constructed in October 2013 to reconnect two rainforest fragments which was bisected by an eight-laned highway about 3 decades ago. Acoustic monitoring has shown that the forest-dependent *Rhinolophus lepidus* started using the overpass to cross the major road a year after its completion when the vegetation was still low. (Photos and graphics by National Parks Board (Singapore), Nick Baker and The Straits Times).

6.4 Green roofs as habitat for the conservation of bats and future studies

Chapter 4 is the first study to investigate the potential use of green roofs by tropical bats, and demonstrates that some species do use these features. It is notable that the bat species utilizing green roofs were all common, generalist taxa that have adapted well to the urban environment. However, it should be emphasized that common species often have key roles in ecosystem functioning due to their abundant nature (Gaston 2010), and in the case of bats, for their role as indicators of environmental degradation in urban areas (Russo & Ancillotto 2015). Therefore, is important to monitor common or widespread species as a potential first indication of environmental change impacts. In the UK, for example, it has been reported that even common urban-adapted bat species such *P. pipistrellus* and *P. pygmaeus* may decline in the face of increasing urban growth unless conservation measures are taken (Lintott *et al.* 2016).

With the increasing number of green roofs in cities worldwide, there is great potential for ecologists to be involved in green roof design for urban biodiversity conservation and better provision of ecosystem services (Blaustein, Kadas & Gurevitch 2016). Moreover, green roofs offer rather novel habitats for the testing and developing of ecological theories such as predicting species richness patterns on green roofs using island biogeography theory (IBT) (Blaustein, Kadas & Gurevitch 2016), and how to maximise and maintain diversity on roofs by drawing on niche theory in selecting plant groups for roofs (Vasl & Heim 2016). In particular, the application of IBT together with components of spatial ecology can increase our understanding of how the number of green roofs and their configuration enhances urban biodiversity through the provision of additional habitat. For example, Russo and Ancillotto (2015) recently hypothesized that along a gradient of increasing urbanisation, there are species-specific responses of bat fitness depending on how they are classified - urban-tolerant, urban sensitive, suburban habitat specialist and synurbic species (Figure 6.2A). Suppose there is a city-wide policy to increase greenspace cover, will increasing the number of green roofs (Figure 6.2B) in urban areas favour the fitness of the suburban habitat specialist species by extending the suburban habitat, and also the fitness of the synurbic species? With a proliferation of green roofs in cities globally, such a study design is possible with the incorporation of knowledge of use of green roofs by bats so far (Pearce & Walters 2012; Parkins & Clark 2015; Chapter 4). However, it must be noted that urban areas may also act as ecological traps for bats (Russo & Ancillotto 2015), such as through competition for limited prey items due to lower insect productivity in an urban environment (Coleman & Barclay 2012), or exposure to opportunistic predators such as raptors (Mikula, Hromada & Tryjanowski 2013). Therefore, further monitoring of bat assemblages on green roofs is needed to find out if species of conservation interest are lured out into the urban environment and subjected to reduced fitness as a result.

Future studies on the green roofs in Singapore should assess the nocturnal aerial insect diversity and abundance to find out the prey availability on roof for bats. This is because the availability and consumption of insects by bats may be influenced by roof characteristics such as the roof height and plant assemblages used, maintenance regimes and landscape factors. This mechanistic approach would give us a better understanding of the patterns of resource use by bats and account for the variation in bat activity between green roofs. With the miniaturisation of GPS loggers, it may also be possible to study the movement of bats on green roofs at a fine spatial scale provided the tagged bats return to their known roost in a roof or a building near the green roof. This should provide information about distances and routes travelled every night, and what urban features or greenspaces (including green roofs) the bats are using from their recorded flight paths. Williams, Lundholm & MacIvor (2014) evaluated six hypotheses that described the supposed benefit of green roofs in terms

[R E D A C T E D]

Figure 6.2 A. Hypothetical species-specific responses of bat fitness along a gradient of increasing urbanisation: (a) urban-tolerant species; (b) urban-sensitive species; (c) suburban-habitat specialist; (d) synurbic species. Bird’s eye view map of landscape below the fitness curves shows a change in colour from left to right. The cultivated fields in the rural areas are gradually replaced by impervious surfaces. Buildings are black rectangles and ellipses represent trees. B. Same urbanising gradient but with green cover (bright green) added to roofs on buildings. Circles represent shrubs or small trees. Note the change in the (hypothetical) fitness curve of the suburban-habitat specialist. Adapted from Russo & Ancillotto (2015).

of conserving biodiversity. They cautioned green roof proponents against over-selling the conservation benefits of green roofs until more comparative studies with ground habitats are conducted, and habitat connectivity within the urban environment purportedly provided by green roofs are investigated more thoroughly (Williams, Lundholm & Scott MacIvor 2014). One of the six hypotheses, that "green roofs can support species diversity, composition and abundances of organisms comparable to ground-level habitats", should be tested in the future with bats as well by comparing bat activity on roofs and ground habitats. The study could be expanded to include pteropodid bats (fruit and nectar bats) because there are food resources both on ground habitats and green roofs for them. Physical capture of these bats or/and the use of night-viewing devices (e.g. Vaughan 1976) are necessary to ascertain their presence on ground and roof habitats for these group of palaeotropical bats.

6.5 The use of eco-acoustics in environmental monitoring

Chapter 5 demonstrates the use of soundscape data to monitor an aspect of environmental change — trans-boundary smoke pollution as a result of El-Nino induced fires and its effects on biodiversity. Sueur & Farina (2015) has coined a term for this sort of investigation as eco-acoustics, an applied discipline in which sound is considered as a component that is studied at large spatial and temporal scales to answer questions about biodiversity conservation and ecology. My eco-acoustic study was opportunistic because I was due to cease my planned field work in my second season of road transects when the smoke-haze episode began. The pollutant index was deemed hazardous to health for field work for two months (September to October 2015), and so a contingency plan involving was needed. The recordings covered all biophony (sounds from biological sources) because I wanted to monitor the biodiversity that contributed to the soundscape community in that area. I followed the method of Pekin *et al.* (2012) in that I did not seek to model species richness by differentiating the sounds into different species or taxon groups. The purpose of my study was to use a rapid and automated data collection method to overcome the challenge of distinguishing all forms of sounds from biodiversity, and to have minimum exposure to the polluted air at that time.

If the objective of a study involving soundscapes is long-term monitoring, then a validation of acoustic sounds with ground surveys and identification of target acoustic taxa is required. For example, Grant and Samways (2016) recently assessed species richness of various biotopes in a global biodiversity hotspot in South Africa using eco-acoustics and found 65 singing species of birds, frogs and orthopterans (crickets and katydids) after some calibration. These species were found to be useful indicators in the conservation assessment of species in a mosaic of different land uses. In my study, I used a single sound recorder in my study over a year in the same forest location to examine the effect of smoke-haze on natural soundscape, but for long-term monitoring, a network of recorders in various vegetation or land-cover types would be useful to understand the diversity and variation of sounds in an entire landscape under various environmental conditions. This technique of employing an array of sound recorders collecting both ultrasonic and audible sounds is already underway in the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysia (see Ewers *et al.* 2011). This research programme complements current ecological field methods such as bird surveys and harp trap/mist net bat surveys to determine the effects of land-use change and fragmentation on tropical biodiversity.

With more episodes of haze expected in the future because of development and agricultural expansion in Southeast Asia, the passive monitoring of environmental change using eco-acoustics could have a crucial role to play in our understanding of the synergistic effects of biomass burning on ecosystem functions.

Indeed, Jaafar & Loh (2014) recognised the interlinked nature between atmospheric, terrestrial and marine ecosystems and called for more research efforts to be directed at investigating the effects of biomass burning on marine ecosystems in Southeast Asia, which has not been addressed so far. They listed some possible key impacts of biomass burning and transboundary haze on marine ecosystems such as nutrient enrichment and eutrophication from terrestrial and atmospheric inputs; sediment loading; reduction in photosynthetically active radiation (PAR) affecting the productivity of marine habitats (coral reefs, seagrass beds and mangroves); and a decrease in visibility in shipping lanes, which may cause an increase in shipping collision and result in an oil spill or the release of other hazardous substances thereby causing a marine environmental disaster (Jaafar & Loh 2014). Since the field of eco-acoustics is extremely versatile by allowing investigation to be undertaken in different media such as aerial, aquatic and even soil environments (Parsons *et al.* 2016), hydrophones (i.e. water-proof microphones) could be deployed in the coastal environment to study the effects of smoke-haze on the marine environment. For example, (Parsons *et al.* (2016) used eco-acoustics in the marine environment to qualify fish choruses and other marine associated sounds such as vessel/moorings noises and whale songs off the waters of Port Hedland in Western Australia. They identified a total of seven fish choruses and although they have not been identified, eco-acoustics show promise as a complementary tool in marine fauna monitoring in relation to environmental changes (Parsons *et al.* 2016).

6.6 Citizen science and the monitoring of urban biodiversity and soundscapes

During my study, the public whom I encountered while conducting my research activities were often surprised to find that bats are found in Singapore and in the urban environment. This is understandable as bats are nocturnal and cryptic animals. There is very little awareness generated about the presence of bats locally because are no bat-specific NGOs to promote bat conservation, and bats are not considered in development processes through legislation. However, Kingston (2015) has pointed out that feeding environmental knowledge to people alone is insufficient to promote behavioural change towards conservation of species. This is supported by a body of research from the social sciences (e.g. St John *et al.* (2010)), discussing the theoretical constructs underlying behavioural change. Perhaps actual encounters with bats either through a live animal display or a real-time view of a coloured sonogram with many call pulses may be more effective in engaging people apart from fact sheets or posters. For example, based on before-and-after questionnaire surveys at two bat-related events in North America, Hoffmaster, Vonk & Mies (2016) found that people knew more about bat ecology and conservation, perceived them in a positive way, and are more willing to take action to conserve them after attending a conservation event.

To sustain the interest in bats and their conservation, there needs to be constant engagement with the public. For example, “bat walks” in late spring and throughout summer are very well-run as a public outreach activity by various bat groups in the UK. The hugely successful National Bat Monitoring Programme (NBMP) in the United Kingdom involved over 3500 volunteers and collected valuable data to detect population changes over a period of 15 years in 10 bat species/species groups (Barlow *et al.* 2015). The time is perhaps opportune now in Singapore to raise awareness about urban biodiversity conservation using bats as a focal taxon due to their ubiquity and modest diversity in the urban environment with just a few common species. This could be achieved through bat walks and citizen science projects. In 2015, the National Parks Board of Singapore (NParks) launched a range of Community in Nature (CIN) citizen science programmes to involve the community in biodiversity monitoring and research programmes including the Garden Bird Watch, Butterfly Watch and BioBlitz, as part of the NParks CIN Biodiversity Watch and NParks CIN Biodiversity Survey @ Parks series (Wang, Lee & Low 2016). Bats could easily be added to some of these existing programmes as a group to be monitored using acoustic methods based on one or two common species in the urban environment. Similarly, given that sound samples are easily collected using stationary or handheld recording devices, soundscape ecology and biodiversity conservation can be promoted more widely by engaging the public in helping to manage the recorders, or getting them to be involved in citizen science projects involving soundscapes (Snaddon *et al.* 2013). My PhD data provide the basis for designing such initiatives using acoustic information.

6.7 References

Abbott, I.M., Berthinussen, A., Stone, E., Boonman, M., Melber, M. & Altringham, J.D. (2015) Bats and roads. *Handbook of Road Ecology*, 1st ed (eds R. van der Ree, D. Smith, & C. Grilo), pp. 290–299. John Wiley and Sons, Ltd.

Altringham, J. & Kerth, G. (2016) Bats and roads. *Bats in the Anthropocene: Conservation of Bats in a Changing World* Bats in the Anthropocene: Conservation of Bats in a Changing World. (eds C.C. Voigt & T. Kingston), pp. 35–62. inbook, Springer.

Barlow, K.E., Briggs, P.A., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., Walsh, A.L. & Langton, S.D. (2015) Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation*, **182**, 14–26.

Bennett, V.J. & Zurcher, A.A. (2013) When corridors collide: Road-related disturbance in commuting bats. *Journal of Wildlife Management*, **77**, 93–101.

Berthinussen, A. & Altringham, J. (2012) Do Bat Gantries and Underpasses Help Bats Cross Roads Safely? *Plos One*, **7**, e38775.

Blaustein, L., Kadas, G.J. & Gurevitch, J. (2016) Integrating ecology into green roof research. *Israel Journal of Ecology and Evolution*, **62**, 1–6.

Boonman, M. (2011) Factors determining the use of culverts underneath highways and railway tracks by bats in lowland areas. *Lutra*, **54**, 3–16.

Chong, K.Y., Yee, A.T.K. & Yeo, C.K. (2010) Biodiversity: linking Singapore's fragmented habitats. *Nature*, **465**, 289.

Coleman, J.L. & Barclay, R.M.R. (2012) Urbanization and the abundance and diversity of Prairie bats. *Urban Ecosystems*, **15**, 87–102.

Collen, A. (2012) *The Evolution of Echolocation. PhD Thesis*. University College London.

Douangboubpha, B., Bumrungsri, S., Satasook, C., Wanna, W., Soisook, P. & Bates, P.J.J. (2016) Morphology, genetics and echolocation calls of the genus Kerivoula (Chiroptera: Vespertilionidae: Kerivoulinae) in Thailand. *Mammalia*, **80**, 21–47.

Ewers, R.M., Didham, R.K., Fahrig, L., Ferraz, G., Hector, a., Holt, R.D., Kapos, V., Reynolds, G., Sinun, W., Snaddon, J.L. & Turner, E.C. (2011) A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 3292–3302.

Fensome, A.G. & Mathews, F. (2016) Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review*, **46**, 311–323.

Gaston, K.J. (2010) Valuing common species. *Science*, **327**, 154–155.

Hill, D.A., Armstrong, K.N. & Barden, P.A. (2015) Preliminary assessment suggests that acoustic lures can increase capture rates of Australian echolocating bats. *Australian Mammalogy*, **37**, 104–106.

Hoffmaster, E., Vonk, J. & Mies, R. (2016) Education to Action: Improving Public Perception of Bats. *Animals*, **6**, 6.

Hughes, A.C., Satasook, C., Bates, P.J.J., Soisook, P., Sritongchuay, T., Jones, G. & Bumrungsri, S. (2011) Using echolocation calls to identify Thai bat species: Vespertilionidae, Emballonuridae, Nycteridae and Megadermatidae. *Acta Chiropterologica*, **13**, 447–455.

Jaafar, Z. & Loh, T.L. (2014) Linking land, air and sea: Potential impacts of biomass burning and the resultant haze on marine ecosystems of Southeast Asia. *Global Change Biology*, **20**, 2701–2707.

Kingston, T. (2010) Research priorities for bat conservation in Southeast Asia: A consensus approach. *Biodiversity and Conservation*, **19**, 471–484.

Kingston, T. (2015) Cute, creepy, or crispy—How values, attitudes, and norms shape human behavior toward bats. *Bats in the Anthropocene: Conservation of Bats in a Changing World*, pp. 571–595.

Lintott, P.R., Barlow, K., Bunnefeld, N., Briggs, P., Roig, C.G. & Park, K.J. (2016) Differential responses of cryptic bat species to the urban landscape. *Ecology and Evolution*, **6**, 2044–2052.

Lintott, P.R., Fuentes-Montemayor, E., Goulson, D. & Park, K.J. (2013) Testing the effectiveness of surveying techniques in determining bat community composition within woodland. *Wildlife Research*, **40**, 675–684.

Mikula, P., Hromada, M. & Tryjanowski, P. (2013) Bats and swifts as food of the European kestrel (falco tinnunculus) in a small town in Slovakia. *Ornis Fennica*, **90**, 178–185.

Parkins, K.L. & Clark, J.A. (2015) Green roofs provide habitat for urban bats. *Global Ecology and Conservation*, **4**, 349–357.

Parsons, M.J.G., Salgado Kent, C.P., Recalde-Salas, A. & McCauley, R.D. (2016) Fish choruses off Port Hedland, Western Australia. *Bioacoustics*, **4622**, 1–18.

Pearce, H. & Walters, C.L. (2012) Do green roofs provide habitat for bats in urban areas? *Acta Chiropterologica*, **14**, 469–478.

Pekin, B.K., Jung, J., Villanueva-Rivera, L.J., Pijanowski, B.C. & Ahumada, J.A. (2012) Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest.

Landscape Ecology, **27**, 1513–1522.

Phauk, S., Sarith, P. & Furey, N.M. (2013) Cambodian bat echolocation: a first description of assemblage call parameters and assessment of their utility for species identification. *Cambodian Journal of Natural History*, **1**, 10–15.

Phommexay, P., Satasook, C., Bates, P., Pearch, M. & Bumrungsri, S. (2011) The impact of rubber plantations on the diversity and activity of understorey insectivorous bats in southern Thailand. *Biodiversity and Conservation*, **20**, 1441–1456.

Pottie, S.A., Lane, D.J.W., Kingston, T. & Lee, B.P.Y.-H. (2005) The microchiropteran bat fauna of Singapore. *Acta Chiropterologica*, **7**, 237–247.

Russ, J. (2012) *British Bat Calls: A Guide to Species Identification*. Pelagic Publishing.

Russo, D. & Ancillotto, L. (2015) Sensitivity of bats to urbanization: A review. *Mammalian Biology*, **80**, 205–212.

Sedlock, J. (2001) Inventory of insectivorous bats on Mount Makiling, Philippines using echolocation call signatures and a new tunnel trap. *Acta Chiropterologica*, **3**, 163–178.

Snaddon, J., Petrokofsky, G., Jepson, P. & Willis, K.J. (2013) Biodiversity technologies: tools as change agents. *Biology Letters*, **9**, 20121029.

Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K.L. (2004) Southeast Asian biodiversity: An impending disaster. *Trends in Ecology and Evolution*, **19**, 654–660.

Soisook, P., Bumrungsri, S., Satasook, C., Thong, V.D., Bu, S.S.H., Harrison, D.L. & Bates, P.J.J. (2008) A taxonomic review of Rhinolophus stheno and R. malayanus (Chiroptera: Rhinolophidae) from continental Southeast Asia: an evaluation of echolocation call frequency in discriminating between cryptic species. *Acta Chiropterologica*, **10**, 221–242.

St John, F. a V, Edwards-Jones, G., Jones, J.P.G. & A Moloney, K. (2010) Conservation and human behaviour: lessons from social psychology. *Wildlife Research*, **37**, 658–667.

Sueur, J. & Farina, A. (2015) Ecoacoustics: the ecological investigation and interpretation of environmental sound. *Biosemiotics*, **8**, 493–502.

Vasl, A. & Heim, A. (2016) Preserving plant diversity on extensive green roofs - theory to practice. *Israel Journal of Ecology and Evolution*, **62**, 103–111.

Vaughan, T.A. (1976) Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). *Journal of Mammalogy*, **57**, 227–248.

Walters, C.L., Collen, A., Lucas, T., Mroz, K., Sayer, C.A. & Jones, K.E. (2013) Challenges of using bioacoustics to globally monitor bats. *Bat Evolution, Ecology, and Conservation*, pp. 479–499.

Wang, J., Lee, B.P.Y.H. & Low, B. (2016) Citizen science and the urban ecology of birds and butterflies - A systematic review. *PLoS ONE*, **11**.

Williams, N.S.G., Lundholm, J. & Scott Macivor, J. (2014) Do green roofs help urban biodiversity conservation? *Journal of Applied Ecology*, **51**, 1643–1649.

Zsebok, S., Son, N.T. & Csorba, G. (2014) Acoustic characteristics of the echolocation call of the disc-footed bat, eudiscopus denticulus (osgood, 1932) (chiroptera, vespertilionidae). *Acta Acustica united with Acustica*, **100**, 767–771.