Monitoring long-tailed bat (*Chalinolobus tuberculatus*) activity and investigating the effect of aircraft noise on bat behaviour in a modified ecosystem

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They are the scatterlings of Africa

Each uprooted one

On the road to Phelamanga

Where the world began

I love the scatterlings of Africa

Each and every one

In their hearts a burning hunger

Beneath the copper sun...

Johnny Clegg

I dedicate this thesis to the 'scatterlings' of Africa and the long-tailed bats of the Hamilton region…may you thrive against the odds!

Abstract

Echolocating bats are one of the most diverse and cryptic mammalian groups. Individuals are typically small, nocturnal, highly mobile, and rely on high frequency (>20 kHz) vocalisations (i.e. echolocation pulses and social calls) inaudible to humans. It is estimated that a quarter of the more than 1,200 recognized bat species are threatened, which has largely been attributed to habitat loss through anthropogenic activities. Therefore, a need exists to improve our understanding of bat behaviour, habitat use and how anthropogenic activities might impact bats, especially in modified habitats. A primary aim of New Zealand's Bat Recovery Plan (1995) is to develop ways to effectively monitor bats to define distributions and identify conservation needs for specific populations: this would better focus bat management and conservation strategies. My research objectives were to: monitor the spatial and temporal activity patterns of long-tailed bats (*Chalinolobus tuberculatus*; LTBs) at two exotic forest fragments on the edge (Hammond Bush) and outskirts (an oak fragment) of Hamilton City (North Island, New Zealand) and conduct a field-based playback experiment to assess whether aircraft noise alters bat activity.

In **Chapter 2**, I monitored the spatial and temporal foraging activity of LTBs across different: nights; seasons; habitats; microhabitats (both vertical and horizontal dimensions); and varying environmental conditions, including an anthropogenic variable (frequency of aircraft overflights at the oak fragment). Foraging activity was variable over time, but nightly peaks occurred between the first and third hours after sunset. Pass rates were significantly higher at both habitats during spring and summer compared with winter. At the oak fragment, significantly more bat detections were recorded when detectors were placed at a height of 4-7m (compared with 15-30m); a similar non-significant trend was observed at Hammond Bush. A greater proportion of bat passes were recorded in microhabitats containing water bodies and open spaces. Mean nightly temperature was the only significant positive predictor of bat activity (at the oak fragment only). To maximise LTB detections in future monitoring studies so that resources can be better focused, I recommend that bats be monitored: 1.) during warmer months; 2.) on warmer nights; 3.) by placing detectors at heights of 4-7m; and 4.) by placing detectors in forested habitats near open spaces and water bodies.

In **Chapter 3,** I concurrently monitored LTB activity at four rural and urban sites over three consecutive seasons and conducted a presence/absence survey at 11 sites along the rural-urban interface of Hamilton City. I sought to apply monitoring recommendations at different habitats and determine how LTBs are distributed in relation to distance from anthropogenic structures (e.g. roads and houses) and riparian margins. LTBs used multiple rural and urban sites across successive seasons; however, bat activity was lower at sites not situated adjacent to the Waikato River compared with sites on the riverbank. I detected LTBs at eight of 11 sites surveyed confirming that this species is more widely distributed in the Hamilton region than previously shown. I did not detect bats at urban sites surrounded by roads and houses. Both proximity to riverine habitat and anthropogenic structures (e.g. roads) may influence LTB distribution and habitat use.

In **Chapter 4**, I showed that in addition to echolocation pulses, bat detectors also record some in-flight LTB calls. I classified LTB calls and tracked three common call types (chirps, pulses and buzzes) over the LTB breeding season (December-March). Pulses and buzzes were recorded around the time of female pregnancy to lactation, and lactation to juvenile volancy, respectively. These calls were only recorded at the oak fragment and were often associated with multi-bat echolocation sequences. Pulses and buzzes may be situation-specific social calls mediating interactions between reproductive females. Chirps were frequently recorded (89% of calls were chirps) across all months at both sites. Chirps may be more generally associated with foraging behaviour (e.g. aiding echo discrimination) as peaks in chirps overlapped with foraging activity. Tracking in-flight calls should alert researchers to sites of likely social importance to LTBs. Call function/s should be further investigated using playback experiments.

In **Chapter 5**, I used a combination of correlative and experimental playback methods to investigate whether aircraft activity and noise alters the evening activity of free-living LTBs. Correlative data revealed that low-altitude aircraft activity overlapped with bat activity at the oak fragment. Bat activity decreased during and after aircraft passes but this trend was not statistically

significant. It also appears that bats decrease their activity more during louder aircraft passes. Playback trials revealed that simulated aircraft noise did not significantly alter bat behaviour compared with baseline activity levels and a silent control. Results suggest that aircraft noise may not disturb LTB behaviour or mask high frequency echolocation pulses.

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Chapter 1

General Introduction

My M.Sc research involved monitoring the spatial and temporal activity patterns of long-tailed bats (*Chalinolobus tuberculatus*, Gray 1843; Chiroptera: Vespertilionidae; referred to from here on as LTBs) on the edge and outskirts of Hamilton City (North Island, New Zealand) to improve monitoring protocols in modified environments: I also conducted a field-based playback experiment to assess whether aircraft noise alters the evening activity of bats.

This introductory chapter will provide a brief background into conservation biology as a discipline and highlight some of the challenges associated with conserving cryptic threatened species. I will look at the requirements needed to monitor animal populations and explain why monitoring is an essential conservation tool. I will explain why monitoring animals in the urban ecosystem is so important to determine how human activities influence wildlife behaviour. I will then focus my attention on the specific effects anthropogenic noise might have on wildlife. Following this, I will provide a brief overview of the diversity and ecology of bats and the natural history of LTBs. I will also highlight the benefits and limitations associated with methods commonly used to monitor bats around the world and in New Zealand. Finally, I will outline the aims and format of this thesis.

1.1 Conservation challenges for cryptic threatened species

Conservation biology is best viewed as a multi-disciplinary science (Groom *et al.* 2006; Meine *et al.* 2006). Successfully addressing conservation issues requires an integrated, goal-oriented approach that considers ecological, political, economic and social domains (Brechin *et al.* 2002; Robertson & Hull 2001). However, conservation biology is also a crisis discipline (Soulé 1985). Species extinctions are occurring at unprecedented rates making conservation biology an ever more crucial discipline (Ehrlich 1995; Glowka *et al.* 1994; Soulé & Kohm 1989). The threats facing wildlife are diverse and complex, ranging from illegal poaching (e.g. Hayward 2009) and deforestation (e.g. St-Laurent *et al.* 2009) to inbreeding (e.g. Miller *et al.* 2009) and climate change (e.g. Prowse *et al.* 2009). Inevitably, the problems facing conservationists are many as they are multifaceted, complex and urgent (Barry & Oelschlaeger 1996). The need to act quickly in the face of uncertainty is often a reality for conservationists and managers (Meffe 2001). However, crisis decision-making can also be misguided with the potential to derail conservation efforts for a species or population (Brechin *et al.* 2002). A case in point is the recent local extinction of proboscis monkeys (*Nasalis larvatus*) from an Indonesian reserve. In a last-minute attempt to prevent the extinction of this local population due to habitat destruction, conservation authorities translocated the remaining individuals from the reserve to nearby unprotected habitats without undertaking any prior assessments of the protection status or quality of release habitats (Meijaard & Nijman 2000). This resulted in the death or illegal smuggling of translocated individuals and the extinction of the local population. This case highlights how a lack of important information (e.g. release habitat quality) can easily result in misguided, inadequate decision-making.

For cryptic threatened species the conservation challenges are especially acute. By definition, threatened species are those facing varying degrees of risk of extinction (i.e. critically endangered, endangered or vulnerable in status) and are characterised as having small and/or fragmented populations (International Union for Conservation of Nature (IUCN) 2001; Mace & Lande 1991). Threatened species are often also cryptic in nature or hard to detect and observe. This may in part be due to small population sizes but is also typically due to one or more behavioural (e.g. migratory), morphological (e.g. camouflage) and/or ecological (e.g. restricted site occupancy) characteristic/s of a species that makes collecting information about it problematic (Chadés *et al.* 2008). As a result, these species tend to be of the highest conservation priority yet remain the most data deficient (IUCN 2008). This invariably complicates conservation efforts (Rodrigues *et al.* 2006). There is clearly a real need to obtain information about these animals, as resources either need to be focused elsewhere in the case of extinction or intensive, immediate and integrated conservation efforts need to be implemented quickly in order to avert the loss of a local population or species (Chadés *et al.* 2008). Without adequate information conservationists risk failing to account for cryptic threatened species in decision-making because it is sometimes assumed that populations are already regionally or functionally extinct (e.g. ivory-billed woodpecker (*Campephilus principalis*; Stokstad, 2007)). In other cases, population sizes may be so low that resources are indeed shifted from managing a species to surveying for its occurrence. For example, presence/absence monitoring undertaken in Kerinci Seblat, Sumatra successfully detected sun bears (*Helarctos malayanus*) in felled forests considered of low conservation priority and commonly assigned to oil palm plantations (Linkie *et al.* 2007). This monitoring

data will be vital to guiding and re-thinking conservation plans for this species in more degraded habitats. Wherever possible, cryptic threatened species that depend on *in situ* conservation efforts should be monitored in order to guide conservation and management strategies (Caro 2007, 1999).

Monitoring cryptic threatened species

Monitoring animals may be defined as a detection-based process involving the collection and analysis of repeated observations and measurements of individual/s, population/s or species (Elzinga *et al.* 2001). Monitoring can provide valuable information about a species' status (e.g. Shekelle & Salim 2009), behaviour (e.g. Wearmouth & Sims 2009), distribution (e.g. King & Gurnell 2005), population trends (e.g. Graening *et al.* 2010), current and potential threats (e.g. Welbergen *et al.* 2008) and whether management and conservation actions are successful (e.g. Bain & French 2009). Before collecting data for any monitoring project, researchers need to decide on which species or population/s to monitor and what methods or strategies to use that will best achieve monitoring objectives. Each of these requirements is addressed in turn.

Threatened species should be monitored above more resilient species of lower conservation concern because they are data deficient, often the most sensitive and responsive to habitat alterations and may serve as good 'surrogate' species (e.g. indicator, keystone, or flagship species) for conservation initiatives (Fleishman & Murray 2009; Regan *et al.* 2008; Caro & O' Doherty 1999). Monitoring species that serve as reliable indicators of change may enable researchers to circumvent the need to monitor all species in an environment on the premise that the needs of one (e.g. habitat requirements) also represents the needs of others (Regan *et al.* 2008; Favreau *et al.* 2006). For example, distribution data

for the endangered Scops owl (*Otus scops*), a cryptic and data deficient species, revealed that conservation efforts for this species (e.g. encouraging agricultural practices that prevent the loss of grassland habitat) would likely yield benefits for biodiversity at multiple ecological scales in the Swiss Alps (Sergio *et al.* 2009). Monitoring cryptic threatened species is thus often a key first step in many conservation processes. For example, presence/absence data for small carnivores of high conservation concern in Northern Laos detected 14 species that led to the establishment of a 3000 km^2 ecological protection zone (Johnson *et al.* 2009).

Choosing an optimal monitoring method is equally important and requires: 1.) an understanding of the biology of the species of interest (e.g. terrestrial and aquatic species will require different monitoring approaches); 2.) identification of the most important information needs for effective conservation action; and 3.) inspection of available resources (Joseph *et al.* 2006). Monitoring methods are diverse and designed to provide researchers with specific information. This can range from presence/absence data for multiple species (e.g. camera traps for birds and mammals; Stein *et al.* 2008)), abundance data for a single species (e.g. capture-recapture surveys; Straley *et al.* 2009), to behavioural data for one or more representative individuals (e.g. movements patterns using radio-telemetry; Runciman *et al.* 1995). Using multiple monitoring methods will likely increase the amount and type of data collected, however, in practice multi-method approaches may not always be financially and technically feasible. Developing cost-effective yet innovative and optimal designs for monitoring high priority species may provide a better means of using available resources in ways that maximise data collection (for case studies see Haddad *et al.* 2008; Nowicki *et al.* 2008). Ultimately, monitoring programmes can provide reliable and valuable

information about species of high conservation priority, which should forestall crisis decision-making (Fischer *et al.* 2009). Collecting and interpreting data and implementing conservation strategies will also need to be sensitive to the ecological context in which a species or local population/s occurs. For instance, threatened species living in native forest ecosystems and highly modified human-dominated ecosystems will require different conservation and management strategies that vary in focus and urgency.

Monitoring cryptic threatened species in an urban context
The rate of global urbanisation is higher than ever before (United Nations, 2008). Urban ecosystems are characterised by a suite of variables that may not be encountered in unmodified ecosystems including housing density, artificial lighting and anthropogenic noise. These variables are often subject to rapid change within and around urban environments with the potential to impact wildlife (Pickett *et al.* 2001; Theobald *et al.* 1997). Little is known about the effect and scale of anthropogenic activities on wildlife, but it is evident that animals must either adapt or abandon environments where anthropogenic impacts are high (Warren *et al.* 2006; Brumm & Slabbekoorn 2005). This is especially concerning for cryptic threatened species known to reside in or near human-dominated environments, as these species may be particularly sensitive to anthropogenic disturbances (e.g. Harveson *et al.* 2007; Riley *et al.* 2003; Kerley *et al.* 2002).

Noise is one anthropogenic variable that has been shown to disturb a wide range of animal taxa living in or near human-dominated environments, including anurans (Parris *et al* 2009), fish (Smith *et al* 2004), birds (Slabbekoorn & Ripmeester 2008) and echolocating bats (Schaub *et al.* 2008). Different noise

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sources can occur in urban environments, ranging from vehicle traffic (e.g. train, car and aircraft noise) to amplified music and construction noise. Each noise source will invariably have different acoustic and temporal properties (e.g. loudness, frequency range and duration), which in turn may affect wildlife in different ways. For example, wildlife may be less likely to habituate to noise that is irregular, loud and sudden in onset (e.g. aircraft noise) compared with more continuous noise (e.g. air conditioning compressors; Brumm & Slabbekoorn, 2005). It is also important for researchers to differentiate between the different effects anthropogenic noise may have on wildlife. Noise may affect individuals in one of two broad ways: 1.) by disrupting normal behaviour patterns (e.g. startle response); and 2.) masking important animal sounds used for communication, foraging and/or orientation. For example, boat traffic has been shown to disrupt the foraging behaviour of bald eagles (*Haliaeetus leucocephalus*; Stalmaster & Kaider 1998), while noise produced by boats likely interferes with the echolocation pulses of some marine mammals (e.g. killer whales (*Orinus orca*); Holt & Noren 2009). Some species (e.g. blackbirds (*Turdus merula*); Nemeth & Brumm 2009) are able to compensate for signal masking by adjusting the pitch and amplitude of their calls when anthropogenic noise levels are increased, while other species simply avoid areas with high levels of noise, sometimes at the expense of being able to use important habitats like foraging grounds (e.g. Florida manatees (*Trichechus manatus latirostrus*); Miksis-Olds *et al.* 2007). It may not always be appropriate to assume that taxonomically related species respond to anthropogenic noise in similar ways. For example, European tree frogs (*Hyla arborea*) exposed to vehicle noise showed no call plasticity (i.e. individuals did not alter call properties to compensate for anthropogenic noise; Lengagne 2008);

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however, southern brown tree frogs (*Litoria ewingii*) were found to adapt to vehicle noise by calling at a higher pitch (Parris *et al.* 2009). Investigating the species-specific effects of anthropogenic noise using different research methods would likely yield the most conclusive information about how animals respond to noise. For example, correlative data could reveal whether a species actually alters its behaviour in response to vehicle traffic, while playback experiments broadcasting noise back to individuals could provide more insight into how noise, a specific stressor associated with vehicle traffic, influences wildlife behaviours.

Monitoring cryptic threatened wildlife of high conservation priority in the urban ecosystem is pertinent to conservation biology in the 21st century as any improvements to existing knowledge has great potential to guide management and conservation efforts for these species (e.g. Turner 2003). Research into the potential impact anthropogenic variables have on wildlife are also increasingly important as this information provides additional insight into how wildlife are impacted by or adapt to human activities (e.g. Bright *et al.* 2004).

1.2 The diversity and ecology of bats

Bats are the only mammals capable of powered flight (Feldhamer *et al.* 2007). Second only to the Rodentia, the Chiropteran order is recognized as the most diverse mammalian order with more than 1,200 identified species worldwide (Feldhamer *et al.* 2007). Of those species more than 900 belong to the suborder Microchiroptera, or microbats (the remaining species belong to the suborder Megachiroptera or non-echolocaters; Pough *et al.* 2005; Kunz & Pierson 1994). Microbats rely on echolocation - an active sensory system in which individuals emit laryngeal sounds (typically of high frequency; >20 kilohertz (kHz)), which reverberate off objects in the local environment and return to echolocaters in the

form of echoes (Au & Simmons 2007; Schuller & Moss 2004; Sales & Pye 1974). Echolocation aids foraging, navigation and possibly even communication (e.g. Jones 2005; Fenton 2003a; Leonard & Fenton 1984; Fenton *et al.* 1976) and likely evolved in microbats as the primary sensory modality in an environment where vision was insufficient (Jones & Teeling 2006; Simmons & Stein 1980; Novick 1977).

Bats are found on every continent except Antarctica and occupy a diverse range of trophic niches (Wilson 1973). Bats may be carnivorous (e.g. fish-catching bats (*Noctilio leporinus*)), insectivorous (e.g. aerial hawking bats like the northern bat (*Eptesicus nilssonii*) and gleaning bats like little big-eared bats (*Micronycteris megalotis*)), nectivorous (e.g. Mexican long-tongued bats, (*Choeronycteris mexicana*)), frugivorous (e.g. short-tailed fruit bats (*Carollia perspicillata*)), and even sangivorous or blood feeding (e.g. vampire bats (*Desmodus rotundus*); Neuweiler 2000; Kunz & Pierson 1994; Kunz & Fenton 1982)). Despite many negative public perceptions and misconceptions, bats provide a multitude of ecological services including controlling insect densities, acting as keystone seed dispersers and pollinators as well as serving as important 'surrogate' species particularly for habitat disturbance (e.g. Cleveland *et al.* 2006; Fenton *et al.* 1992; Cox *et al.* 1991). However, given their nocturnal and volant (i.e. mobile) nature bats remain one of the most misunderstood and challenging to monitor animal groups (Fenton 1997). As a result the behaviour, ecology and conservation needs of most bat species remains poorly investigated and often unaccounted for in management decision-making (Fenton 2003b).

1.3 Long-tailed bats

Only two surviving bat species can be found in New Zealand – lesser short-tailed

bats (*Mystacina tuberculata*; STB) and LTBs – which together form the entirety

of New Zealand's native terrestrial mammal fauna (O'Donnell 2005). Both bat

species are endemic to New Zealand and are of high conservation priority (Molloy

1995; Molloy & Davies 1994; Daugherty *et al.* 1993).

Physical description

LTBs are small mammals that vary in size and morphology according to sex, age,

season and geography (Daniel 1990). Males tend to be smaller (ca. 8-10g) and

darker in colour (short, ca. 7mm, black velvety fur around the head with light and

dark-brown under and upperparts, respectively) compared with larger (up to 16g

when pregnant but typically 10-12g when not pregnant), lighter-coloured females

(chestnut upper and under parts that may have white tips; Figure 1.1; O'Donnell

2001a; Dwyer 1962). The weight of individuals may vary nightly by as much as

3g depending on individual foraging success and flight activity and seasonally as

individuals accumulate fat reserves before colder winter months (O'Donnell

2001a). LTBs may conserve energy throughout the year by entering torpor (i.e.

short term inactivity in which the metabolism is slowed; O'Donnell 2005). These

states of inactivity tend to last for prolonged periods during winter months

(O'Donnell 2005, 2001a).

Females are distinguished as reproductive if nipples are conspicuous

(nipples remain pronounced after females have given birth once) and non-

reproductive if nipples remain absent (O'Donnell 2001a). Volant juveniles are

recognized by their small size, black fur and patches of bare skin, but once

phalangeal epiphyses fuse after 3-4 months of age distinguishing the young of the

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year becomes difficult (O'Donnell 2001a). Forearm lengths range between 37-46mm (O'Donnell 2005). Wingspan and wing depth ranges from 270-280mm and 49-54mm, respectively (O'Donnell 2005). The ears are small and rounded with pronounced grooves in the inner pinnae and the nose is flat and small. The long v-shaped interfemoral tail membrane and lip-lobules at the corner of the mouth are important distinguishing features of this species (O'Donnell 2005).

Figure 1.1 Photograph of a male LTB captured in Kinleith Forest, Tokoroa, North Island, New Zealand (reprinted with permission by K.M. Borkin, Auckland University).

Taxonomy, conservation status and threats
LTBs belong to the superfamily Vespertilionoidae and the family Vespertilionidae (vesper, evening or common bats; Feldhamer *et al.* 2007). The Vespertilionidae is the largest bat family with 37 genera and more than 350 species. The *Chalinolobus* genus (pied, wattled or long-tailed bats) has 16 identified species, five of which can be found in Australia, New Caledonia, Norfolk Island and Papua-New Guinea and nine in Southern Africa (O'Donnell 2005, 2000a; Daniel 1990). LTBs are thought to be most closely related to Gould's wattled bat

(*Chalinolobus gouldii*) and are also commonly referred to as long-tailed wattled bats or Pekapeka (Molloy 1995; Daniel 1990). Long-tailed bats are thought to have colonised New Zealand from Australia following a random dispersal event (i.e. likely windblown across the Tasman Sea; O'Donnell 2005). This species has thus been evolving in isolation in New Zealand for more than a million years or since the Pleistocene.

LTBs are classified internationally as vulnerable (IUCN 2010) and locally as threatened or of secondary conservation priority (Molloy & Davies 1994). Populations are thought to have declined by as much as 30% over the last 10 years with the likely extinction of the species in the medium future should no conservation action be taken (O'Donnell 2000a; IUCN 2001). The primary threats facing this species are habitat loss through logging and forest fragmentation (O'Donnell 2000a). LTBs rely on tall old-growth native and exotic trees for roosting and with large scale removal of lowland forests for agriculture purposes and urban development, population declines are inevitable (Sedgeley & O'Donnell 1999). Roost disturbance, predation and competition for roosts by introduced mammalian pest species (e.g. *Rattus* spp. and brushtail possums (*Trichosurus vulpecula*)) also contribute to population declines (Pryde *et al.* 2006; O'Donnell 2005, 2001a, 2000a). Long-tailed bats are also predated on by moreporks (*Ninox novaeseelandiae*) - the only known extant natural predator of this species (Borkin & Ludlow 2009). Captive husbandry of LTBs has been successful in a few cases but *in situ* conservation efforts are recognized as most important for this species (O'Donnell 2005). LTBs are protected under the Wildlife Act 1953 (Molloy 1995).

Present distribution

From historical anecdotes and preliminary monitoring it is clear that LTBs are now rare or absent from many areas where they once were common (O'Donnell 2001a, 2000a; Molloy 1995; Dwyer 1962; Hutton 1872). In the South Island (S.I.) LTBs may still be found in Fiordland (e.g. Eglinton Valley), Geraldine, South Canterbury and on Steward Island (O'Donnell 2005, 2000a; Molloy 1995). In the North Island (N.I.) LTBs are more widespread with populations still found in the central N.I. (e.g. Pureora Forest Reserve, Tokoroa, King Country), Hawkes Bay, Waitakere Ranges and Great and Little Barrier Islands (Borkin & Parsons 2009; O'Donnell 2005, 2002; Molloy 1995).

Echolocation calls and foraging behaviour

LTBs are forest-dwelling aerial insectivores (O'Donnell 2001a). Individuals use high frequency-modulated (i.e. calls passing through a frequency range; FM) echolocation pulses (Parsons *et al.* 1997). Echolocation pulses are used by LTBs for navigation and orientation as well as for identifying and tracking small insect prey (e.g. midges, mosquitoes and small moths) which are caught on the wing or in tail membranes and devoured mid-flight (O'Donnell 2005; Daniel 1990). The mean fundamental frequency of foraging LTB echolocation pulses is ca. 39.7 kHz with the mean high and low frequency components concentrated around ca. 65.2 kHz and 35.1 kHz, respectively (Parsons *et al.* 1997). Echolocation pulses may be divided into search phase pulses, pre-buzz/terminal phase pulses and feeding buzzes, which differ in spectral and temporal characteristics (less so for search phase and terminal phase pulses). Search phase pulses are steep, downward, FM sweeps with a mean inter-pulse interval of ca. 104 ms and are used by bats to locate and track prey as well as for general orientation and navigation purposes (Parsons 1997; Parsons *et al.* 1997). Feeding buzzes are short (ca. 4.5 ms) FM

sweeps used to target prey during the final capture-phase of insect pursuit (Parsons *et al.* 1997). Echolocation frequencies have been shown to vary between different populations and may also vary according to sex, age and behavioural situation (Parsons 1997; Parsons *et al.* 1997). LTBs have a manoeuvrable flight pattern and are moderately fast fliers capable of speeds of up to 60km/h (O'Donnell 2005). Individuals are known to forage over water bodies, farmland and along riparian and forest margins (O'Donnell *et al.* 2006; O'Donnell 2000c; Daniel 1990).

Social behaviour, reproductive biology and survivorship
LTBs form complex social groups (O'Donnell 2005, 2001a). Individuals may be colonial or solitary roosting and frequently switch between roosts (average roost switching rates may be as high as once every 1.8 days in native rainforest habitats; O'Donnell 2000b; Sedgeley & O'Donnell 1999). In temperate native forests, males have been shown to be more solitary roosting (37% communal) compared with females (63% communal; O'Donnell & Sedgeley 1999). This is likely due to higher thermoregulatory demands in females particularly during pregnancy and lactation. Roosting groups have been described as highly structured and of small average roost sizes (ca. 35 individuals; O'Donnell 2005). However, in Grand Canyon Cave (Te Kuite, N.I) as many as 400 LTBs may use this cave as a night roost with non-random aggregations of individuals within the cave likely reflective of smaller daytime roost units (i.e. during the day individuals are thought to break-up into smaller social groups and roost in nearby trees; O'Donnell 2002; Daniel & Williams 1983). In Eglinton Valley, individuals are known to form non-random social groups, which may range in size from tens to hundreds of individuals (O'Donnell 2000b). Groups overlap in range and likely

form much larger deme populations of unknown sizes (i.e. interbreeding occurring across local groups; O'Donnell 2000b). The home range of LTBs is also one of the largest for an echolocating bat species with males and females known to have home ranges as large as 5629 ha and 1361 ha, respectively (O'Donnell 2005, 2001b).

Female LTBs synchronously give birth to a single pup each spring (November-December) in communal maternity roosts after reaching sexual maturity (1-2 years of age; O'Donnell 2005, 2001a; Sedgeley 2001). Sex ratios at birth are thought to be equal and suckling non-volant pups can be carried by females in-flight until they are as much as 80% of the female's body weight (O'Donnell 2005). Young begin to fly soon after birth at about 5-6 weeks of age (O'Donnell 2005). LTBs are long-lived relative to their small size and are thought to survive for as long as seven years (Pryde *et al.* 2006; O'Donnell 2005). Social calls mediating social interactions (e.g. roost switching, group formation and maintenance, dispersal, mating and mother-pup contact) remain unidentified.

1.4 Monitoring bats

Bats are commonly monitored using one of two broad methods. These include: 'trapping and tracking', which involves catching bats in mist nets or harp traps with the option of subsequently tracking individuals using radio-telemetry; and 'acoustic detection', which relies on ultrasonic detectors that passively detect and record bat echolocation pulses. Each monitoring method has specific limitations and benefits.

The 'trap and track' method is useful for obtaining important data about community assemblages, species diversity, home range, roost site locations, sex

ratios and relative abundance of species (e.g. Russo *et al.* 2005; Russo *et al.* 2004). However, the limitations of this method include: 1.) invasiveness; 2.) reliance on specialist equipment and techniques (e.g. harp traps, mist nets and handling protocols); 3.) limited applicability to inaccessible habitats over long time periods; and 4.) trap avoidance by echolocating bats with recapture rates likely declining over consecutive trapping nights, which in turn may result in small sample sizes and skewed sex ratios (MacSwiney *et al.* 2008; Berry *et al.* 2004).

Monitoring bats using ultrasonic detectors is useful because: 1.) devices are non-invasive (Ahlén & Baagøe 1999; Kuenzi & Morrison 1998); 2.) many detectors can be used repeatedly at one or more sites and can monitor individuals in remote or difficult to access habitats; 3.) monitoring can be undertaken over long periods of time and is limited only by the availability of detectors and research effort (Kuenzi & Morrison 1998); 4.) large areas can be monitored concurrently; 5.) useful information about real-time bat activity patterns, habitat use as well as species diversity is often obtainable (Preatoni *et al.* 2005; Russo & Jones 2002); and 6.) devices are relatively inexpensive and easy to use. The main disadvantages of using detectors is that information about abundance, sex ratios and roost site location is not directly obtainable from recorded data and bats can only be detected within a restricted detection range of detectors. Detectors also cannot discriminate between individuals. Both monitoring methods can be used individually although used in combination they tend to provide the most complete species inventories and reliable bat activity patterns (MacSwiney *et al.* 2008; O'Farrell & Gannon 1999; Kuenzi & Morrison 1998; Mills *et al.* 1996). However, using both monitoring methods is often not feasible. Other common bat monitoring methods may involve visual (e.g. bat counts during roost emergence;

Warren & Witter 2002) and auditory surveys (i.e. bat detections using hand-held ultrasonic detectors; Fenton *et al.* 1987), which may improve knowledge about bat distribution patterns and population trends. It is important for researchers to be aware of the limitations and benefits associated with each monitoring method before deciding on the most appropriate method to use (Gannon *et al.* 2003; Sherwin *et al.* 2000; O'Farrell & Gannon 1999).

Monitoring bats in New Zealand

Advances in technology have made studying bats in New Zealand more accessible, which in turn has seen an increase in the amount of research undertaken for both species (O'Donnell 2001a). This has largely been attributed to the manufacturing of automated digital heterodyne bat monitoring detectors (Stag Box III, The Department of Conservation; O'Donnell & Sedgeley 1994; referred to from heron as detectors). Detectors (Figure 1.2) are custom made in New Zealand and are designed to measure bat activity by detecting and recording the fundamental echolocation frequencies (frequency of peak amplitude) used by each species (Figure 1.2; Lloyd 2009). Each detector is capable of concurrently recording the echolocation pulses emitted by both species on two separate frequency channels – LTBs on 40 kHz and STBs on 28 kHz (Lloyd 2009). There is little overlap in the echolocation frequencies used by each bat species making this dual-monitoring approach both appropriate and effective in New Zealand (Parsons 1997). Echolocation pulses are recorded with an exact date (year/month/day) and time (hour/minute/second) stamp, which provides information about when bats were active. Monitoring bats with detectors is now the more preferred approach in New Zealand, however, effective field-based methods for monitoring bats using detectors is still in the developmental stage (Molloy 1995). One of the primary

aims of New Zealand's Bat Recovery Plan (1995) is to extensively monitor bats in order to define distributions and identify the conservation needs of specific populations, which in turn should focus management strategies (Greaves *et al.* 2006; Molloy 1995).
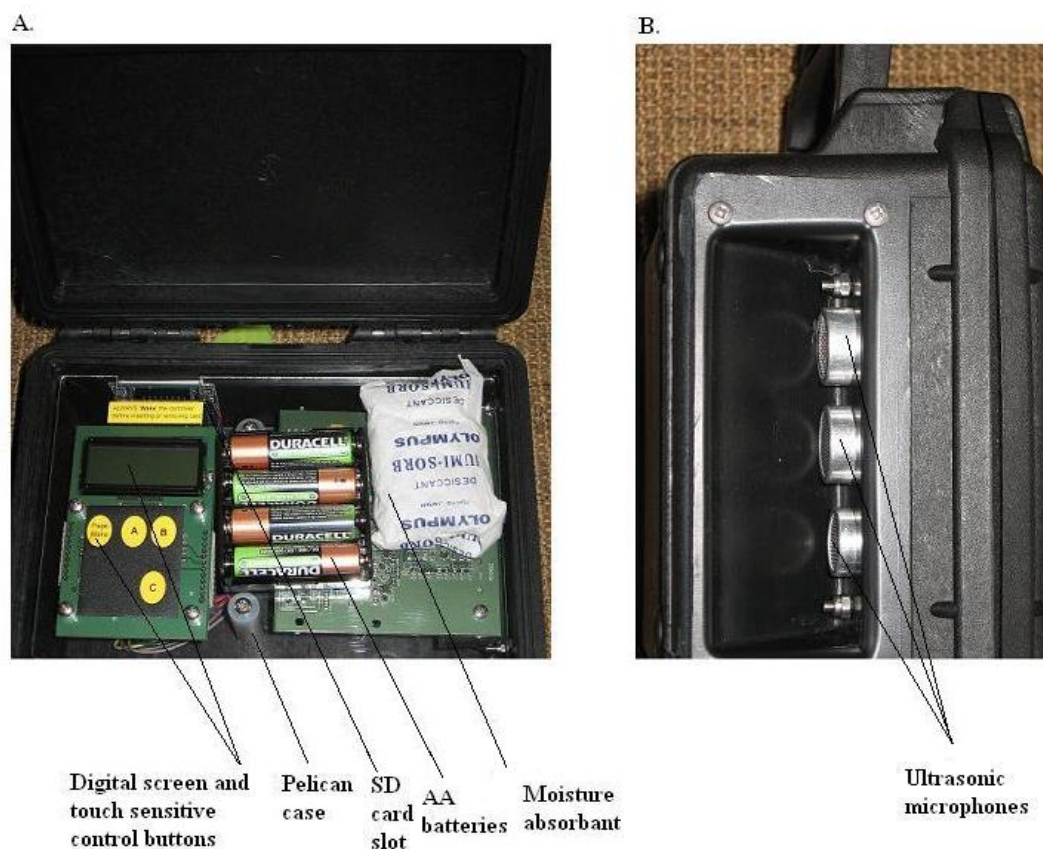
Figure 1.2 Automated heterodyne bat monitoring detector (Stag Bat Box III) used to record LTB and STB echolocation pulses. The front-on view of an open detector reveals internal components (A.) and the lateral view reveals the ultrasonic microphones (B.), which concurrently detect LTB and STB echolocation pulses on a 40 and 28 kHz recording channel, respectively.

1.5 Aims and format of thesis

The aims of this thesis are four-fold. My first aim was to provide recommendations for monitoring foraging LTBs in modified ecosystems using detectors (**Chapter 2**). I developed a stratified monitoring design that allowed me to concurrently measure bat activity across different habitats and microhabitats

(both horizontal and vertical dimensions). Foraging LTBs were intensively monitored over a nine month period (July-March) at two small forest fragments: an open area situated near native bush on the suburban edge of Hamilton City; and an oak (*Quercus robur*) fragment on the rural outskirts of the city near the airport. I sought to identify the best time of the night, season, height of detector placement, microhabitat features and environmental conditions in which to encounter LTBs. Knowing when and where foraging bats are most active can allow researchers to maximise and improve recording opportunities of LTB echolocation pulses for bioacoustic analyses. This information can also improve bat capturing efforts when trapping is required (e.g. using mist nets). Wildlife managers should thus use monitoring recommendations to better focus available resources (e.g. time and equipment) so that LTBs can be more effectively conserved in modified habitats.

The second aim of this thesis was to demonstrate how LTB monitoring recommendations developed in Chapter 2 could be practically applied at multiple sites across the southern urban-rural interface of Hamilton City (**Chapter 3**). I conducted short-term concurrent LTB monitoring (five night sessions) at four habitats (one urban and rural site with and without known LTBs) over three successive seasons to determine if a less intensive sampling regime could still provide accurate information about LTB foraging patterns. I also used monitoring recommendations to conduct a presence/absence survey at 11 urban and rural habitats, so that bat habitats and distribution patterns could be better elucidated. Being able to quickly and accurately track bat activity and identify the most important habitats used by bats using a standardised monitoring protocol would improve conservation and management strategies for this protected species.

The third aim of this thesis was to identify, categorise and monitor the use of rarely recorded in-flight LTB calls – an additional data output from bat detectors not previously characterised (**Chapter 4**). In-flight calls differ from stereotypical echolocation pulses and may have social functions mediating complex interactions between individuals. This monitoring project was undertaken at the same field sites using the same stratified monitoring design detailed in Chapter 2. The temporal and spatial use of the three most common in-flight calls was intensively tracked over four months of the LTB breeding season (December-March). This is the first study to track non-echolocation calls through space and time using detectors. This additional information output could be used to non-invasively identify habitats of likely social importance to bats during certain times of the breeding season when individuals may be most sensitive to disturbance. I also identify the best time of the night, height of detector placement and microhabitat features in which to encounter in-flight calls so that future bat monitoring studies can maximise and improve recordings of these calls. Future studies should determine call function/s using playback experiments and examine the potential use of bat calls as 'acoustic lures' in other bat conservation efforts (e.g. improving bat capturing and translocation efforts).

The fourth and final aim of this thesis was to test whether free-ranging LTBs altered their evening activity in response to aircraft noise (**Chapter 5**). I predicted that both real and simulated aircraft noise would reduce LTB foraging activity, as measured by changes in echolocation pass rates. I used both correlation methods and a playback experiment to address this issue. For the playback experiment, I exposed bats to three stimuli including: five minutes of blackbird calls (a non-human acoustic disturbance; control 1); five minutes of

silence (control 2); and five minutes of aircraft noise. Each five minute playback stimulus was flanked by a ten minute pre-playback silent period and two five minute post-playback silent periods. Bat response was measured as the change in per minute echolocation passes recorded across all three stimuli. This study provides information about how anthropogenic activity might affect cryptic threatened wildlife in urban ecosystems. This study also demonstrates how information about when and where bats are most active can be used to guide applied experimental studies that seek to address conservation issues in a cryptic threatened species.

This thesis has been formatted as a collection of four papers written for publication in scientific journals. The flanking general introduction (**Chapter 1**) and discussion (**Chapter 6**) chapters have been written to integrate the four middle chapters. These general chapters are not intended for publication but rather to assist with making the thesis a cohesive document. Some repetition across chapters should be anticipated.

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Chapter 2

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Tracking long-tailed bat activity using a stratified design in modified habitats: Recommendations for monitoring

2.1 Abstract

Monitoring animal populations is important for formulating management strategies. I developed a stratified monitoring design that enabled the spatial and temporal changes in long-tailed bat (*Chalinolobus tuberculatus*; LTB) activity to be tracked at two exotic forest habitats on the urban edge and rural outskirts of Hamilton City, New Zealand so that peaks in bat activity could be identified. Bats were monitored across different: nights ($N = 217$); seasons ($N = 4$); microhabitats (both vertical and horizontal dimensions); and varying environmental conditions, including an anthropogenic variable – aircraft overflights. Bat activity peaked during the first and third hours after sunset. Pass rates were significantly higher at both rural ($P < 0.001$) and urban ($P < 0.001$) habitats during spring and summer compared with winter. At the rural site, significantly ($P < 0.001$) more bat detections were recorded when detectors were placed at heights of 4-7m compared to height of 15-30m; a similar non-significant trend was observed at the urban site. A greater proportion of bat passes were recorded in microhabitats containing water bodies and open spaces compared with a microhabitat with no water body. Mean nightly temperature was the only significant positive predictor ($P = 0.009$) of bat activity at the rural site only. To maximise LTB detections using detectors it is recommended that LTBs be monitored: 1.) during warmer months; 2.) on warmer nights; 3.) by placing detectors at a height of 4-7m; and 4.) by placing detectors in forested habitats near open spaces and water bodies. Knowing when and where foraging bats are most active could guide future studies that seek to maximise and improve: recordings of LTB echolocation pulses; and bat trapping rates (e.g. mist netting). Wildlife managers should thus use monitoring recommendations to better focus available resources (e.g. time and equipment) so

that this cryptic threatened bat species can be more effectively conserved in modified habitats.

2.2 Introduction

Monitoring animal populations is important for formulating effective management strategies (Groom *et al.* 2006; Soulé & Kohm 1989). This is especially important, yet challenging, for cryptic threatened species (Regan *et al.* 2008; Rodrigues *et al.* 2006). Threatened species face high risks of extinction and are often difficult to monitor due to small population sizes and one or more behavioural (e.g. secretive behaviour), morphological (e.g. small size) or ecological (e.g. restricted ecological niche) trait that makes data collection problematic (Chadés *et al.* 2008; IUCN 2008, 2001). Challenges commonly associated with monitoring cryptic threatened species include: poor detection and recapture rates; populations confined to remote, inaccessible habitats (e.g. alpine species; Gonzalez-Voyer *et al.* 2001); loss of life or habitat disturbance using invasive techniques (e.g. flipper banding of marine species; Dugger *et al.* 2006; Nichols & Seminoff 1998); and reliance on specialist and expensive equipment (e.g. satellite tracking; Geschke & Chilvers 2009). As a result, cryptic threatened species tend to remain data deficient, which in turn hinders effective conservation and management efforts for these species (e.g. Bain & French 2009; Shekelle & Salim 2009; Linkie *et al.* 2007; Meijaard & Nijman 2000). It is therefore of increasing importance to develop optimal and innovative monitoring methods for species of conservation priority that are: cost effective; non-invasive; and provide information about populations that can guide

conservationists and managers alike (Fischer *et al.* 2009; Regan *et al.* 2008; Ewen & Armstrong 2007; Joseph *et al.* 2006).

Bats are a difficult group of animals to manage due to their nocturnal and mobile nature (O' Shea *et al.* 2003; Fenton 1997, 2003). As a result, the behaviour, distribution and conservation needs of many bat species remain poorly understood (Feldhamer *et al.* 2007; Mickleburgh *et al.* 2002). It is estimated that a quarter of the more than 1,200 identified bat species are globally threatened, primarily due to habitat loss (Feldhamer *et al.* 2007; Mickleburgh *et al.* 2002). As a result, many bat species now depend on highly modified, human-dominated ecosystems to survive (e.g. Miller 2003; Lumsden *et al.* 2002), including urban ecosystems. Nevertheless, management and conservation efforts for bats in modified habitats typically remain absent or misguided due to a lack of knowledge, particularly regarding how bats use urban landscapes and habitats (O' Shea *et al.* 2003).

Some bat species thrive in urban environments. For example, big brown bats (*Eptesicus fuscus*) gain thermal benefits from roosting in buildings compared to natural rock crevices (Lausen & Barclay 2006) and the rare African bat (*Otomops martiensseni*) is abundant in a city compared with other parts of its range (Fenton *et al*. 2002). On the other hand, many bat species fair poorly in urban environments due to both direct (e.g. road mortality (Lesinski 2008) and persecution (Hadjisterkotis 2006)), and indirect impacts (e.g. lack of roosting or foraging resources; Sparks *et al.* 2005; Gerell & Lundberg 1993). Some bat species that live in or near cities depend heavily on less disturbed urban spaces (e.g. forested areas with low housing densities areas and parks; Gaisler *et al.* 1998). These habitats are often dispersed around or within the urban matrix and are typically characterised by specific landscape elements favoured by roosting

and/or foraging bats (e.g. natural riparian margins; Hein *et al.* 2009; Gerht & Chelsvig 2004; Glendell & Vaughan 2002; Verboom 1998; Kurta & Teramino 1992). However, even within more secluded habitats bat diversity and activity can be lower compared with rural and natural habitats (e.g. Johnson *et al.* 2008; Avila-Flores & Fenton 2005; Kurta & Teramino 1992). This may be due to a combination of factors including: the presence and absence of habitat features within the local environment (e.g. availability of roost trees; Bartonička & Zukal 2003); prey availability (e.g.: Kurta & Teramino 1992); social factors (e.g. sex-based habitat partitioning; Safi *et al.* 2007; Lumsden *et al.* 2002); and the influence of both environmental and anthropogenic variables (e.g. artificial lighting; Scanlon & Petit 2008). Indeed, bat activity has been shown to vary in response to changes in: environmental variables (e.g. temperature and rainfall; Parsons *et al.* 2003; Vaughan *et al.* 1997); prey availability (Lang *et al.* 2006; Hecker & Brigham 1999); and anthropogenic disturbances such as artificial lighting (e.g. Scanlon & Petit 2008) and vehicle noise (e.g. Schaub *et al.* 2008). Therefore, in order to fully appreciate how bats use modified habitats, specific monitoring designs need to account for bat activity at multiple temporal and spatial scales. Knowing when and where bats are most likely to be encountered would allow wildlife managers to maximise bat detection and capture rates, thereby better focusing available resources. The relationship between bat behaviour and environmental and anthropogenic factors also needs to be elucidated in order to better predict bat activity patterns.

In New Zealand there are only two extant bat species – long-tailed bats (*Chalinolobus tuberculatus*; LTBs) and lesser short-tailed bats (*Mystacina tuberculata*; STBs), which form the entirety of New Zealand's native terrestrial

mammal fauna (O'Donnell 2005; Daugherty *et al.* 1993). Developing specific field-based monitoring methods for each bat species is of high priority but is still in the developmental stages (O'Donnell *et al.* 2006; Molloy 1995; Molloy & Davies 1994; Dwyer 1962). Like most bat species, New Zealand bats are monitored using one of two broad methods: 1.) trapping and tracking (i.e. mist-netting or harp trapping bats followed by radio-tracking of select individuals); and 2.) acoustic detection and recording of bat echolocation pulses using detectors. Trapping and tracking is useful as it enables the identification of home ranges, roost sites and relative abundance – information not directly obtainable from detectors (MacSwiney *et al.* 2008; O'Farrell & Gannon 1999). Unlike the trapping and tracking approach, detectors provide a means of non-invasively monitoring bat activity over extended time periods across multiple sites (O'Farrell *et al.* 1999). In New Zealand this approach is becoming the more feasible and accessible method to study bats (Lloyd 2009; O'Donnell & Sedgeley 1994). The principle behind heterodyne bat detection is being able to remotely detect bats by transforming high frequency echolocation pulses (sounds >20 kHz emitted by bats during foraging and navigation) into audible lower frequency sounds heard by humans (Ahlén & Baagøe 1999; O'Farrell *et al.* 1999; Fenton 1994; O'Donnell & Sedgeley 1994).

LTBs are small forest-dwelling aerial insectivores that rely on high frequency echolocation pulses (fundamental frequency of ca. 40 kHz) for orientation and foraging (O'Donnell 2001a; Parsons *et al.* 1997; Parsons 1997). LTB populations are characterised as small (i.e. tens to hundreds of individuals), fragmented and widely distributed throughout New Zealand (O'Donnell 2005; Daniel 1990). This species is listed as vulnerable with widespread population

declines attributed to habitat loss and fragmentation (IUCN 2010, 2001; Hutson *et al.* 2001; O'Donnell 2000a; Molloy 1995; Molloy & Davies 1994).

I used bat detectors arranged in a vertically and horizontally stratified manner to monitor LTB foraging activity at two exotic forest habitats on the urban edge and rural outskirts of Hamilton City. I sought to develop practical monitoring recommendations by identifying the best time of the night, season, microhabitat features, height of detector placement and environmental conditions in which to use detectors so that LTB echolocation detections could be maximised. This information should improve LTB detection and capture rates by allowing wildlife managers to more efficiently focus research effort at times and places of highest bat activity. This information should thus guide future monitoring, management and conservation strategies for this cryptic and protected bat species, especially in modified habitats.

2.3 Methods and Materials

Site descriptions

Hamilton City (North Island, New Zealand; 37°47'S, 175°17'E; Figure 2.1A) is one of the few remaining cities in New Zealand to still support a resident population of LTBs (Dekrout 2009). This is despite The Hamilton Ecological District being one of the most ecologically degraded in New Zealand (Clarkson & McQueen 2004). I intensively monitored LTB activity over nine months between July 2009 and March 2010 at two field sites on the edge and outskirts of Hamilton City. Both sites are small exotic forest fragments separated by ca. 4 km and are flanked by the Waikato River (Figure 2.1A). The first is a ca. 1.2 hectare (ha) old-growth oak (*Quercus robur*) fragment situated on private property on the

immediate rural fringes of Hamilton City (Figure 2.1B; referred to from here on as the oak fragment). The second site is a ca. 0.3 ha open area adjacent to a 1 ha native forest remnant located on the residential edge of Hamilton City (Figure 2.1C; referred to from here as Hammond Bush).

The oak fragment is situated on an elevated river terrace ca. 2.5 km north east from the runway of Hamilton International Airport (HIA). The site lies in the wider Mangakotukutuku gully system and slopes steeply (14° elevation) toward the east from a higher terrace to a lower terrace (Figure 2.1B). Old growth oak trees (mean ± SE diameter 60.1 ± 3.22cm (standard 10 x 10 vegetation plots); > 100 years old (ring counts of felled trees)) dominate the site. Most of the mature oak trees have canopy heights of >25m and are of high stocking density with more than 200 stems distributed throughout the fragment. Agricultural land flanks the site to the south, east and west and the Waikato River and associated riparian margins lie to the north. Apart from the Waikato River, three minor water bodies (i.e. a pond, creek and irrigation channel) are situated to the south and east of the site. Native vegetation including cabbage trees (e.g. *Cordyline australis*) and small totara trees (*Podocarpus totara*) are sparsely distributed around water bodies and riparian margins.

Hammond Bush is a native forest remnant situated in a medium density urban subdivision in the residential suburb of Hillcrest (de Lange 1996; Figure 2.1C). The site is situated in the Mangaonua gully system, which together with the Managkotukutuku gully creates a continuous riparian ecotone (Clarkson & McQueen 2004; de Lange 1996; Figure 2.1A). This ecotone includes the city's southern urban areas and surrounding peri-urban and rural regions (including the oak fragment), which are all bisected by the Waikato River. Despite its small size

(1 ha), Hammond Bush is floristically the richest native forest remnant in Hamilton city, supporting ca. 145 native plant species (Clarkson & McQueen 2004). The forest is classified as a mixed broadleaf forest of primary succession status dominated by pukatea (*Laurelia novae-zelandiae*) and tawa trees (*Beilschmiedia tawa*; Clarkson & McQueen 2004; de Lange 1996). The Waikato River flanks the site to the west. At the southern end of the reserve is a much smaller open area dominated by old-growth exotic trees including, alders (*Alnus* sp.), grey willows (*Salix cinerea*), *Acacia* sp., *Eucalyptus* sp. and pines (*Pinus radiata*). A small channel is situated to the north of this area. This area is poor draining due to slowly permeable underlying silt sheets, resulting in rain water frequently collecting above the ground (de Lange 1996). LTB monitoring was restricted to this exotic open area of Hammond Bush.

LTB monitoring was undertaken at these two sites because both habitats have confirmed LTB roosts (Dekrout 2009) and are situated in close proximity to one another in a defined ecotone with similar landscape features (i.e. old-growth exotic trees, flanking river margins and internal water bodies). The availability of equipment restricted site replication.

A.
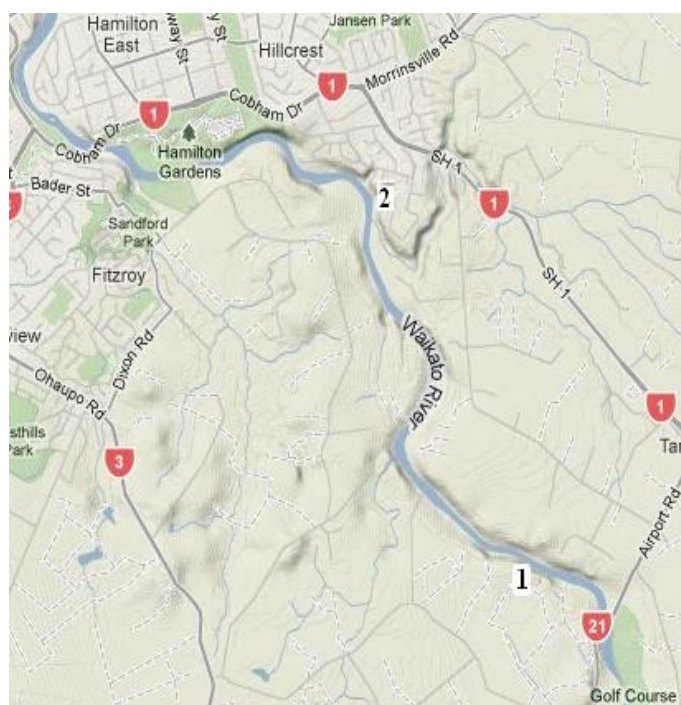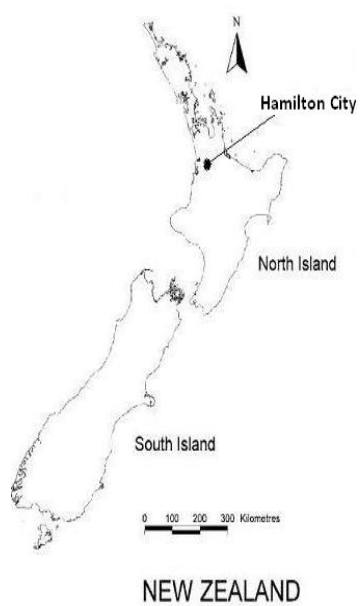
B.
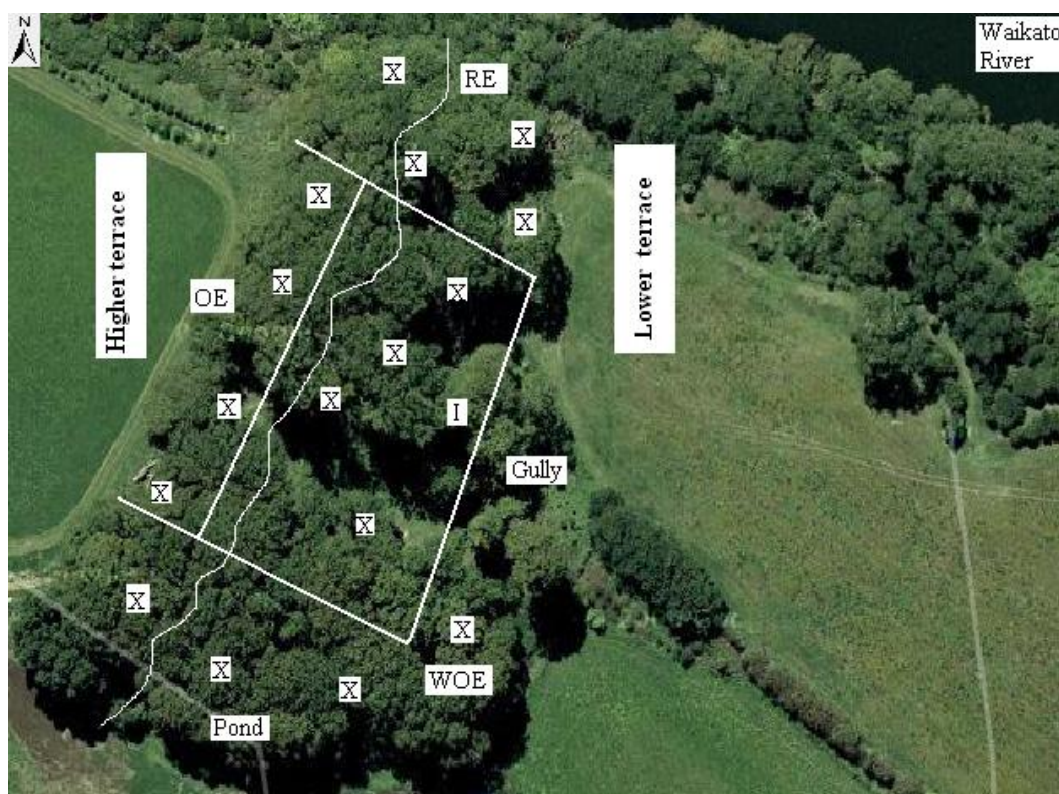
C.

Figure 2.1 Map of New Zealand (A) showing the location of Hamilton City and an aerial map highlighting the close proximity of the oak fragment (1) and Hammond Bush (2) within the urban-rural interface of the city. Aerial photographs show the monitoring set-up at the B.) oak fragment and C.) open area at the southern end of Hammond Bush. An X marks all trees setup with a rope and pulley system (see below).

Monitoring design and equipment

The oak fragment was divided into four proportionally representative microhabitats based on the site's habitat features (i.e. the presence/absence of water bodies, open spaces and elevation; Figure 2.1B). Microhabitats included: 1.) an open edge to the north west situated on the higher river terrace and containing no internal water bodies (OE); 2.) an open edge to the south east, containing internal water bodies (i.e. open edge with water; WOE); 3.) an interior dominated by a large central clearing surrounded by trees on all sides next to a small gulley (I); and 4.) a river edge to the north (RE; see Appendix I for detailed descriptions

and measurements of each microhabitat). I assumed that at least some of the microhabitats delineated at this site would be comparable with microhabitats at other modified habitats. In each microhabitat I selected four tall mature oak trees (N = 16 trees) to setup a rope and pulley system. This was used to hoist bat detectors up to varying heights: a lower height of ca. 4-6m and a higher height of ca.15-30m (Figure 2.2). Trees were selected on the basis of: safety and security for tree climbing purposes; height of the tree (> 25m to increase the chance of detectors independently monitoring bats at each height); and the distance between selected trees in the same microhabitat (i.e. trees were at least 25m apart to increase the chance of detectors independently monitoring bats at different trees). The vertical arrangement of the detectors (Figure 2.2) enabled concurrent monitoring of LTB activity within the air space between the ground and the mid-story (0-20m) as well as from the mid-story to above the canopy (>20m; for other vertical bat monitoring designs see Wallace 2006; Menzel *et al.* 2005; Weller & Zabel 2002). I assumed that each detector independently monitored bats. All detectors were orientated to face upward at ca. 45°C from the horizon to maximise bat detection (Weller & Zabel 2002). At the open area at Hammond Bush I replicated this monitoring set-up in four alder trees of lower heights (ca. 15-25m; Figure 2.1C). It was not possible to select taller trees at this site due to safety concerns for climbers. Microhabitats were also not delineated at this site because the area was too small, but the habitat was most comparable with the I and RE microhabitat.

Pulley

Higher Tier: (15-30m)

Rope-line

Lower Tier: (4-7m)
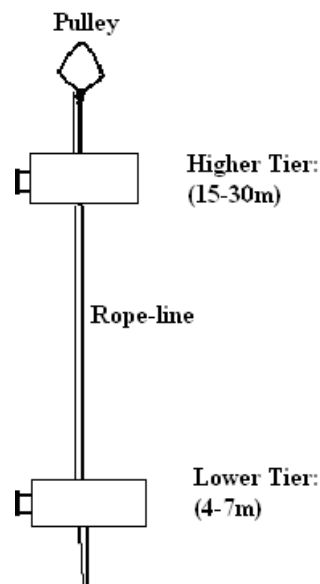
Figure 2.2 Schematic of the rope and pulley system used to hoist detectors up selected trees. Detectors concurrently monitored LTBs at a lower (ca. 4-6m) and higher height (ca. 15-30m).

Ten automated heterodyne bat detectors (Stag Bat Box III, The Department of Conservation) were used to monitor LTBs. The main components of each detector included: a waterproof casing (Pelican 1120, Torrance, USA); a power source (four 1.2V, AA batteries); ultrasonic microphones; a digital screen and touch sensitive buttons; an audio recorder; and a mechanism to initiate and end recordings (Lloyd 2009; O'Donnell & Sedgeley 1994). Detectors were made with similar sensitivities and it was assumed that each detector had an equal chance of detecting LTB echolocation pulses (Lloyd 2009). Detectors were calibrated to have the same time and date settings (NZST) and were pre-set to automatically start monitoring LTBs 30 minutes before sunset until 30 minutes after sunrise (start and stop times were updated once every two weeks). No more than ten detectors (i.e. five detector pairs) were used to concurrently monitor LTBs at both field sites. This resulted in only one randomly chosen tree out the four selected trees in each microhabitat having a detector pair monitoring bats at

any one time. Thus all five detector pairs concurrently monitored LTB activity at Hammond Bush and within each of the four microhabitats at the oak fragment. Detector pairs were assigned to different: trees (4 x 4 Latin square; row = tree number, column = visit); and microhabitats (at the oak fragment) or Hammond Bush (5 x 5 Latin square; row = pair, column = visit, treatment code = microhabitat/Hammond Bush) every three to five days. Detectors were also alternated between lower and higher tiers on each rotation. This rotation scheme was used to reduce the influence of potentially confounding factors or interactions (e.g. the same tree and detector pair having a spurious interaction). However, equipment failure and availability as well as theft of ropes at Hammond Bush sometimes meant that not all five detector pairs could concurrently monitor bat activity. In fact 34% of monitoring nights had fewer than 5 detector pairs. Only 23% and 10% of monitoring nights had fewer than 4 and 3 detector pairs, respectively. On nights with fewer than five detector pairs, one or more randomly selected microhabitats at the oak fragment were excluded from the monitoring regime. Despite this, I was still able to monitored bats with no less than two detector pairs at any one time. Concurrent monitoring was always undertaken at the oak fragment and Hammond Bush to enable site comparisons. LTB activity was monitored on as many nights as possible, irrespective of weather conditions. This was undertaken over four successive seasons: winter (July and August); spring (September, October and November); summer (December, January and February); and autumn (March). All LTB echolocation passes were recorded on the 40 kHz channel of detectors. Recorded passes were stored onto Secure Digital cards (2GB, SanDisk) as WAV files for later analyses.

Data collection and classification

Echolocation pulses

I sorted all recorded LTB echolocation sound files by visual and auditory inspection of waveforms using BatSearch 1.02 Software ® (The Department of Conservation, 2008, New Zealand). Sound files were sorted into either: LTB echolocation passes, defined as a series of two or more high frequency echolocation pulses emitted by flying bats (Au & Simmons 2007; Fenton *et al.* 1998; Parsons *et al.* 1997; Fenton 1994), or non-bat sounds (e.g. wind, rain or insect generated background noise) that were discarded. Echolocation passes were classified as either: 1.) search phase pulses with relatively low pulse repetition rates (mean inter-pulse interval of ca. 104 milliseconds) likely used to locate and track prey (Figure 2.3A; Parsons *et al.* 1997); or 2.) feeding buzzes consisting of a series of very rapidly emitted pulses (mean inter-pulse durations of ca. 4.5 ms) used to determine the range of prey immediately prior to capture (Figure 2.3B; Parsons *et al.* 1997). This classification enabled a basic indication of the different LTB foraging activities. For example, feeding buzzes indicated that prey was being pursued, whereas search phase pulses could indicate that bats were commuting or searching for prey (Parsons *et al.* 1997). When two or more feeding buzzes were recorded on a single sound file (i.e. one bat pass), I considered this to represent a single prey capturing event and conservatively classified the file as only one feeding buzz. Search phase pulses preceding feeding buzzes were never classified as independent search phase passes (i.e. only as feeding buzzes) to avoid double classifying a single bat pass. Similarly, when the echolocation pulses of two or more LTBs overlapped on a single sound file, I classified the file as being only one bat pass as the number of independent search phase sequences could not always be distinguished. All LTB echolocation pulses were recorded

with a date (day/month/year) and time (hour/minute/second) stamp. I inspected the time stamps of every echolocation pass recorded at a lower and higher height to ensure that they did not overlap in time. On occasions when this did occur, I only classified the echolocation pulse recorded with the greatest clarity and intensity indicating the more likely height of bat flight relative to the detector's position.
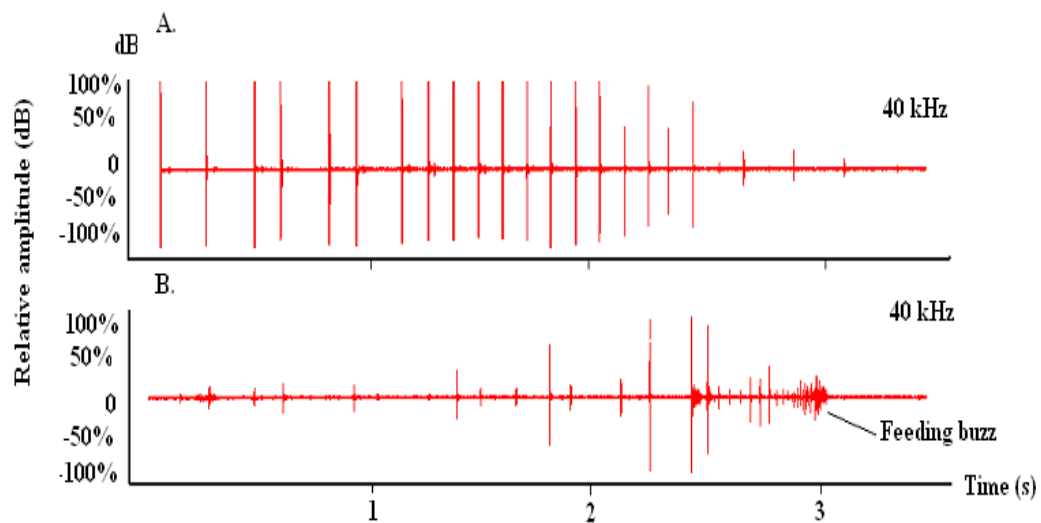
Figure 2.3 Waveforms of LTB foraging echolocation pulses recorded using heterodyne bat detectors. Pulses include a: A.) 40 kHz search phase pulse - the more common LTB echolocation pulse; and B.) 40 kHz search phase pulse culminating in a feeding buzz - a series of rapid pulses indicating prey pursuit and potential capture.

Environmental and anthropogenic variable/s

Data for a range of environmental variables collected at hourly intervals was retrieved from the national weather station located at HIA (agent number 2112; network number C75834; MetService, National Institute for Water and Atmosphere's, Ltd (NIWA); www.cliflo.niwa.co.nz). Environmental variables of interest included mean nightly: 1.) temperature (°C); 2.) relative humidity (%); 3.) precipitation (mm); 4.) wind speed (m.s^{-1}); 5.) relative cloud amount (octa); and 6.)

lunar illumination (%). Two hygrochrones (*i*-Buttons, DS1923-F5; Embedded Data Systems, Ltd.) were also secured at heights of 4m and randomly rotated around selected trees with rope and pulley set-ups at each habitat between August and October to independently measure hourly temperature (°C) and relative humidity (%) at the habitat scale. Given the proximity of the oak fragment to HIA, I also recorded the number of aircrafts that flew directly over the oak fragment throughout the night on 43 nights (this was not repeated at Hammond Bush due to little aircraft activity observed near this site). Aircrafts were recorded between July 2009 and February 2010 from the central clearing in the I microhabitat using an omnidirectional ultrasonic microphone (Sennheisser, MZK 8000) connected to a digital audio recorder (722 SoundDevices, WI, USA). Recordings were saved as uncompressed monaural WAV files (16-bit, 44.1 kHz sample rate) and viewed in Audition (Adobe Systems, San Jose, CA, USA).

Statistical analyses

Nightly and monthly activity patterns
I calculated the mean number of search phase pulses and feeding buzzes recorded during each hour after official sunset (NZST; MetService; NIWA). Data was sorted according to season and kept separate for each habitat. A non-parametric Krusal-Wallis test was used to compare variation in the number of LTB passes/active minute/night across each season. Passes/active minute (i.e. the minute during which one or more LTB passes is recorded)/night is a more robust measure of how active bats are when they are active (see Miller 1999).

Detector height and microhabitat patterns
I used a factorial ANOVA (2 x 2 between-groups ANOVA; dependant variable: number of bat passes; independent factors: month and tier height) to determine if

placing detectors at a lower or higher height made any significant difference to the number of LTB detections. Data was kept separate for each habitat to identify site-specific trends. A factorial ANOVA (dependant variable: number of bat passes; independent factors: season and microhabitat) was also undertaken to investigate if LTBs used microhabitats differentially over consecutive seasons at the oak fragment.

Predictors of bat activity

Backward stepwise multiple regression analyses were used to determine which continuous environmental variables or combination of variables served as the most reliable predictor/s of LTB activity. The number of bat passes/night was held as the dependant variable. These multivariate analyses enabled each variable to be tested by removing one variable at a time while holding all other variables included in the model in place. Mean nightly rainfall, temperature, % relative humidity, % lunar illumination, cloud amount and wind speed were included in each analysis. Analyses were undertaken separately for Hammond Bush ($N = 159$ nights) and the oak fragment ($N = 173$). I repeated the regression analysis for select nights ($N = 43$) in which the number of aircraft passes/night could be included as an additional independent variable at the oak fragment. I also determined if there was any difference in the mean nightly temperature and % relative humidity recorded independently at each habitat using hygrochrones (*i*-Buttons) compared with the same data obtained from a weather station situated <5 km from each field site (paired t-test; dependant samples). This provided an indication of how variable environmental conditions might be at the habitat scale despite even short distances between field sites and weather stations from which environmental data is commonly retrieved.

All data was log-transformed where necessary to achieve normality or near normality (Kolmogorov-Smirnov and Shapiro-Wilk's W test). *Post-hoc* analyses were undertaken using Tukey tests. Statistical analyses were completed using STATISTICA® 8.0 (Statsoft Inc, Tulsa, OK, USA) with the level of significance held at 0.05. Means are presented as ± SE throughout the paper.

2.4 Results

In total both field sites were monitored for over 2,300 hours during nine months of LTB monitoring. LTBs were detected during every month of monitoring at both habitats. Bats were detected on ca. 84% of monitoring nights at the oak fragment (183/217 nights) and Hammond Bush (180/217). A total of 22,833 LTB echolocation passes were recorded and classified (11,077 and 11,756 at Hammond Bush and the oak fragment, respectively). A total of 1,472 (6.4%) LTB passes could conclusively be classified as including feeding buzzes.

Nightly and monthly activity patterns

Overall, bat activity peaked between the first and third hours after official sunset at both habitats during all seasons (Figure 2.5). A bimodal activity pattern with an additional peak in LTB activity 3-4 hours before sunrise was observed during spring, summer and autumn (Figure 2.5). This was most evident at the oak fragment. Feeding buzzes were rarely recorded relative to search phase pulses. During winter at the oak fragment a clear peak in feeding buzzes was evident during early evening hours (Figure 2.5).

LTB activity was highly variable between nights and seasons. Activity was generally characterised by distinctive peaks and crashes over successive monitoring nights across all seasons (Figure 2.4). In extreme instances, the number of bat detections recorded on a single detector varied from 0 to 400 passes

over two consecutive monitoring nights with no change to detector position. Large peaks in activity were typically followed by one or more days of reduced bat activity, although this trend was not consistent as smaller more regular peaks in activity could persist for longer periods of time (e.g. 20 days).

Bat activity peaked in spring at both the oak fragment (2,654 passes in September) and Hammond Bush (1,626 passes in November). The number of bat passes/active min/night was significantly higher in spring and summer compared with winter at both Hammond Bush (Kruskal-Wallis, $H = 35.05$, $P < 0.001$) and the oak fragment ($H = 33.37$, $P < 0.001$, Table 2.1 and Figure 2.4). The longest consecutive monitoring period without any bat detections at each site was three nights. Pre-sunset bat passes were recorded on only five separate occasions during summer.
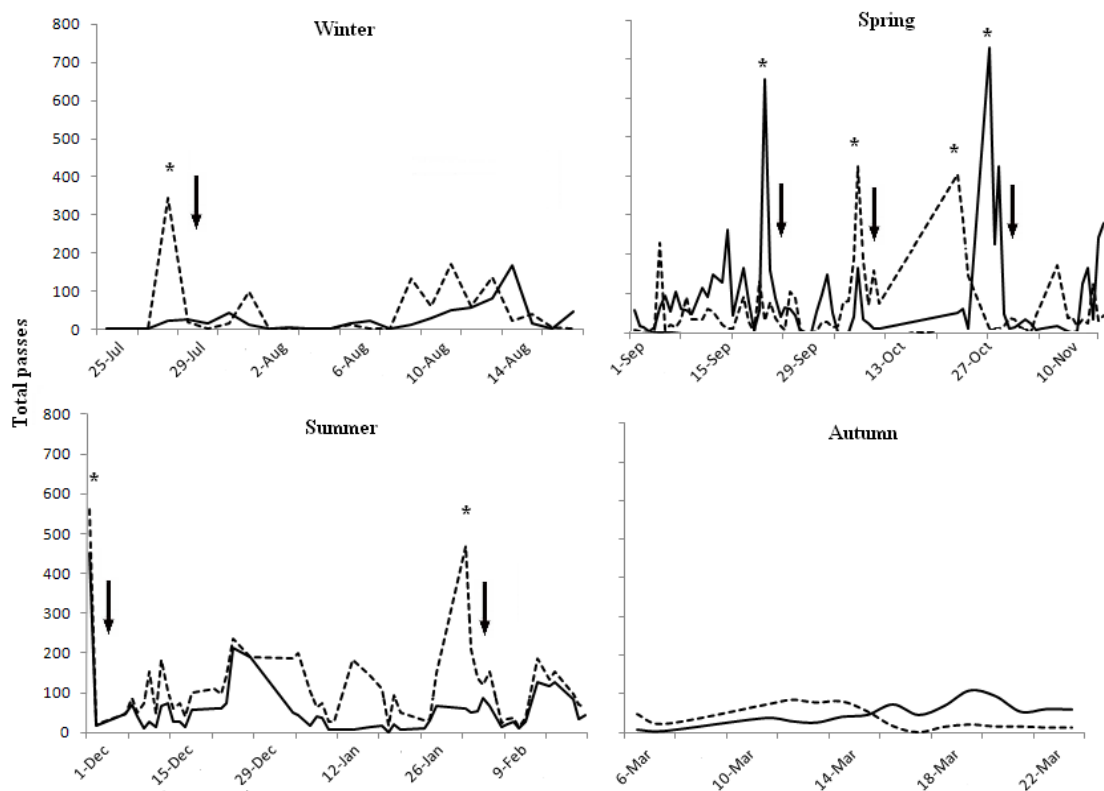
Figure 2.4 Total number of bat passes recorded during each monitoring night at the oak fragment (dashed line) and at Hammond Bush (solid line) across consecutive seasons (i.e. winter (July - August); spring (September-November); summer (December-February) and autumn (March).

Table 2.1 The mean number of LTB passes/active min/night calculated for each concurrently monitored habitat in each season. Seasons that do not differ significantly (Krusal-Wallis, $P > 0.05$) in bat pass rates are marked by the same letter in each row.

	Hammond Bush	Oak Fragment
Winter	0.81 ± 0.04^{a}	0.71 ± 0.11^{a}
Spring	1.37 ± 0.75^{b}	1.97 ± 0.2^{b}
Summer	1.35 ± 0.05^{b}	1.66 ± 0.06^{b}
Autumn	1.42 ± 0.07^{b}	1.26 ± 0.03^{a}
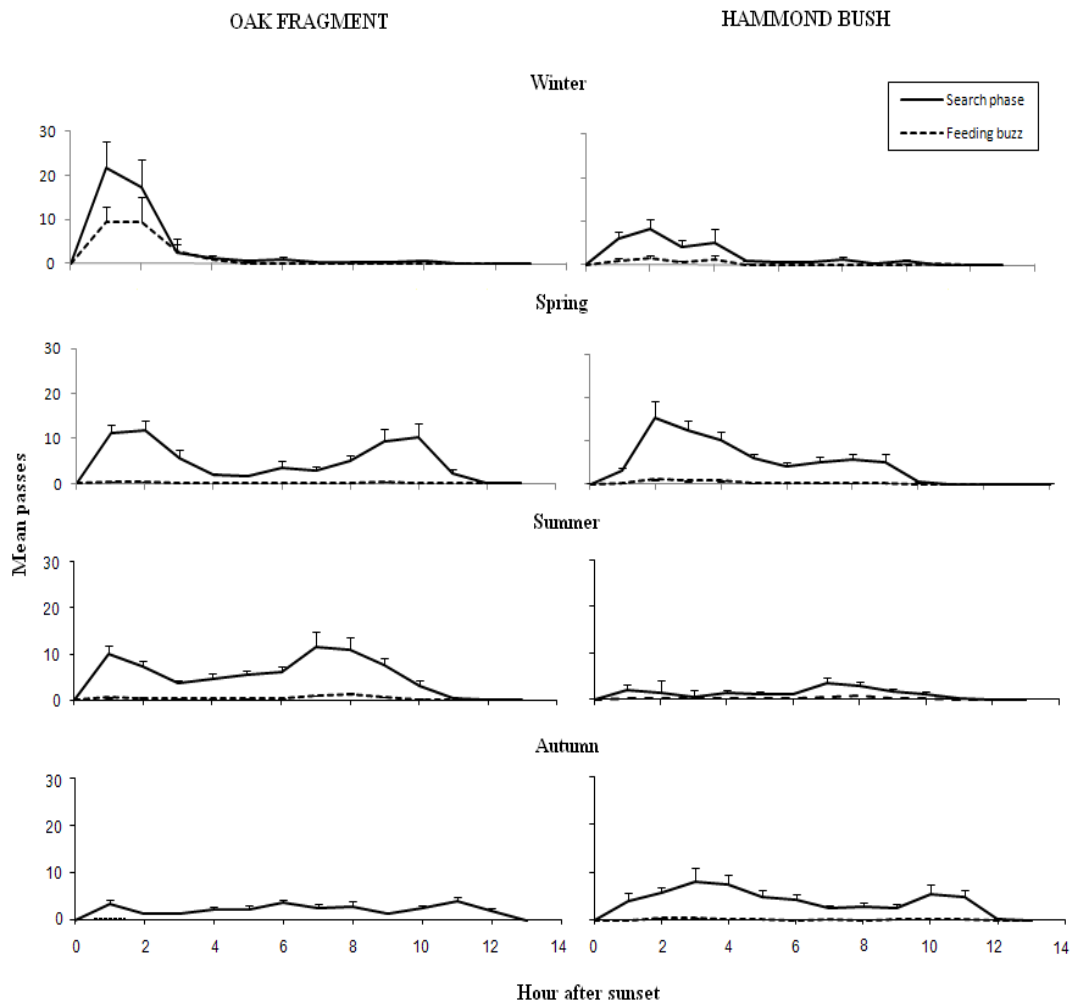
Figure 2.5 Mean number of search phase pulses (solid line) and feeding buzzes (dashed line) recorded for each hour after official sunset at each habitat across all four seasons monitored.

Detector height and microhabitat patterns

At the oak fragment significantly more LTB passes were detected at a lower height compared with higher heights (ANOVA, $F_{1, 365} = 43.6$, $P < 0.001$); at Hammond Bush no significant difference ($F_{1, 302} = 0.1$, $P > 0.05$) was detected between heights. At both sites the number of bat passes at higher heights increased during spring, summer and autumn. The number of LTB detections varied according to the different months of monitoring at the oak fragment ($F_{8, 365} = 2.66$, $P = 0.007$) and Hammond Bush ($F_{8, 302} = 2.79$, $P = 0.005$). One assumption with ANOVA is that samples are independent. The two detectors

placed at each height could not independently monitor bats, especially at Hammond Bush where trees were of a lower height. However, I did inspected all bat passes recorded at each height to ensure that if passes did overlap in time that one was excluded from the analysis.
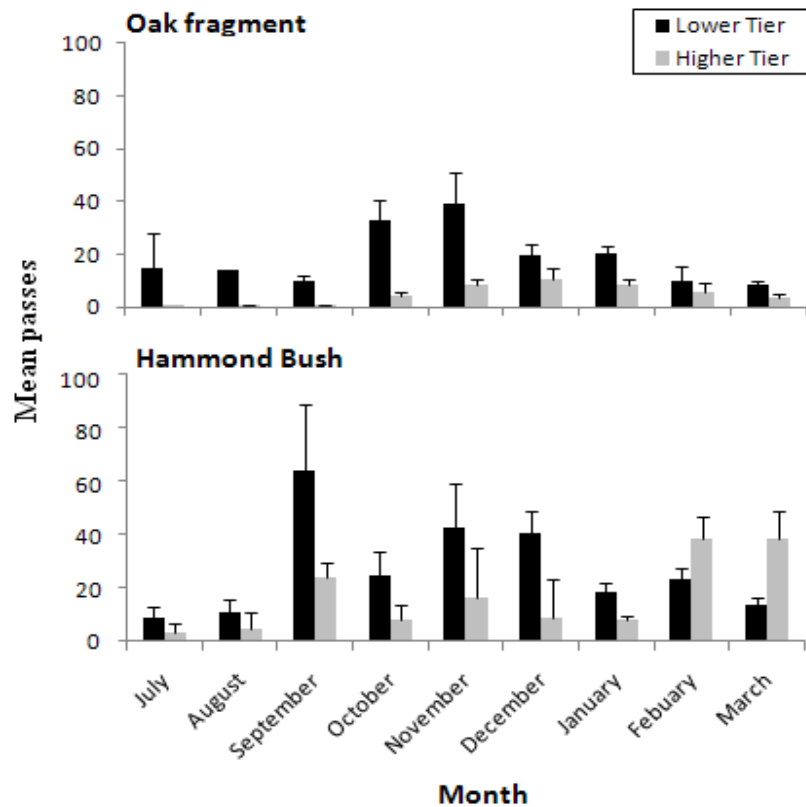
Figure 2.6 Mean number of bat passes recorded at each site at the lower (ca. 4-7m; black bars) and higher heights (ca. 15-30m; gray bars) for each month of LTB monitoring.

LTB activity was non-randomly distributed across microhabitats at the oak fragment. The number of bat passes recorded in the OE never accounted for more than 20% of all bat passes. A significant interaction between the use of microhabitats by LTBs and season was detected (season*microhabitat, $F_{9, 571} = 2.19$, $P = 0.02$; Figure 2.7). This suggests that LTBs may use different microhabitats at different times of the year. During winter 60% of all LTB passes were recorded in the I microhabitat. During spring there was near equal use of the

RE, WOE and I microhabitat (ca. 31% of all passes in each microhabitat). During summer and autumn 43% and 60% of LTB passes were recorded in the WOE and RE, respectively (Figure 2.7).
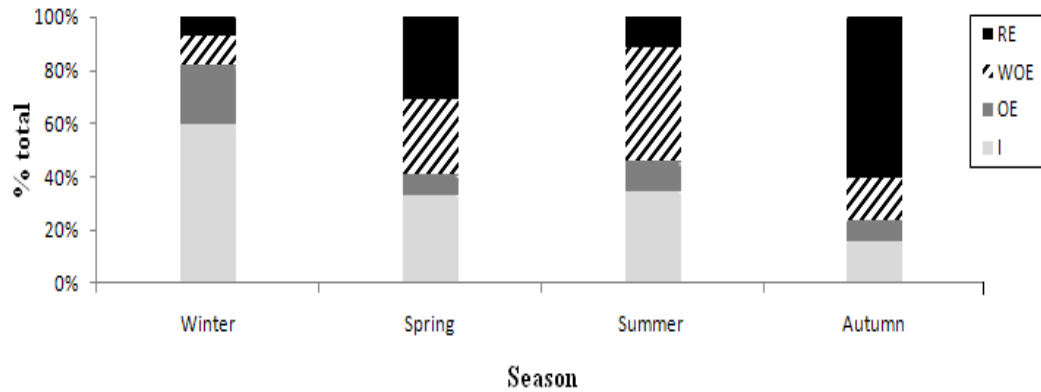
Figure 2.7 The proportion of LTB passes recorded in each microhabitat at the oak fragment over four successive seasons.

Predictors of bat activity

At Hammond Bush no environmental variables were found to be significant predictors of bat activity (stepwise multiple regression, multiple $r^2 = 0.18$, $P = 0.54$). At the oak fragment bat activity was significantly positively correlated with mean nightly temperature (standard partial regression coefficient = 0.2, multiple $r^2 = 0.04$, $F_{2, 170} = 3.63$, $P = 0.009$). When the regression analysis was repeated for select nights for which the number of aircraft passes/night could be included, mean nightly temperature (0.46, $r^2 = 0.31$, $F_{2, 40} = 9.12$, $P = 0.001$) was once again the only significant predictor of bat activity. There was a significant difference ($P < 0.05$) between mean nightly temperature and % relative humidity data obtained from the nearest weather station (MetService, NIWA) and *i*-Buttons rotated within each habitat. On average nightly temperature and % relative

humidity were 0.58 ± 0.15°C warmer and 6.66 ± 1.05% more humid at the habitat scale compared with environmental data logged at the weather station.

2.5 Discussion

Nightly and monthly activity patterns

LTB foraging behaviour was characterised by a series of regular peaks and crashes in activity over the entire study period at both the rural and urban habitats. This fluctuating activity pattern is consistent with the foraging behaviour previously described for LTBs (e.g. O'Donnell *et al*. 2006; O'Donnell 2000c) and some other aerial insectivorous bat species (e.g. Scanlon & Petit 2008; Parsons *et al.* 2003). Differential peaks in LTB activity likely represents variation in foraging effort, which in turn may be complexly linked with changes in ephemeral prey availability and environmental conditions (see below; O'Donnell 2000c). I observed no major differences between LTB activity at the urban and rural habitats. This finding was not unexpected as a previous radio-tracking study showed that LTBs do move between these two sites using the Waikato River and associated riparian margins as a connecting corridor (Dekrout 2009) but is counter to studies that have documented higher bat activity at rural sites compared with urban parklands (e.g. Johnson *et al.* 2008; Gaisler *et al.* 1998; Kurta & Teramino 1992; Geggie & Fenton 1985).

Pre-sunset bat emergence was recorded on only five occasions during summer and detections were never earlier than 30 minutes before sunset. Daniel (1990) also reported LTBs leaving their roosts before sunset and O'Donnell (2000a, b) reported LTBs emerging as early as 54 minutes before sunset in Fiordland (S. I., New Zealand). It is likely that pre-sunset emergence in bats may

result in increased predation risk from predators such as moreporks (*Ninox novaeseelandiae*; see Fenton *et al.* 1994; Jones & Rydell 1994). At both field sites and across all seasons LTB activity peaked during the first 1-3 hours after official sunset. Peaks in foraging activity during early evening hours is not uncommon for insectivorous bat species as individuals need to accumulate energy after emergence before performing other activities (e.g. flying between habitats; Kunz & Fenton 1982; Kunz 1974). Greater availability of flying insect prey and warmer evening temperatures may also explain initial peaks in foraging activity (Milne *et al.* 2005; Bartonička & Zukal 2003; Jones & Rydell 1994). LTB activity decreased during the middle portion of the night across all seasons. Flight can be energetically expensive and discontinuous nightly activity likely represents bursts of foraging activity interspersed with periods of night roosting in which individuals rest, digest food and socialise between foraging bouts (Murray & Kurta 2004; Bartonička & Zukal 2003; Speakman & Thomas 2003). Night roosts may differ from day roosts; however Dekrout (2009) revealed that roost re-use tends to be higher in and around Hamilton City, a modified roost-limited environment, compared with native ecosystems where roost trees are more readily available (e.g. O'Donnell 2000b).

As bats approach and attempt to capture insect prey, echolocation pulse rates increase terminating in feeding buzzes (Griffin *et al.* 1960). Feeding buzzes represent discrete insect-capturing attempts and are regularly used as a more conclusive measure of feeding activity for insectivorous bats (Miller 1999; Thomas & West 1989; Griffin 1958). Unsurprisingly, feeding buzzes only accounted for a small percentage ($< 7\%$) of recorded LTB passes, which made it difficult to identify clear long-term trends for these foraging sequences (see

similar cases in Gannon *et al.* 2003; Glendell & Vaughan 2002). The obvious exception was during winter where a peak in feeding buzzes was evident. During colder winter months LTBs, like other temperate bat species (e.g. big brown bats; Hamilton & Barclay 1994), enter torpor (facultative heterothermy) during which individuals reduce their body temperatures to conserve energy. Bats are known to periodically rouse from this state to forage (Willis 2006). Distinctive peaks in feeding activity during winter likely represent LTBs embarking on brief but intense foraging bouts to maintain and replenish energy reserves (e.g. Turbill 2008). LTBs were always detected by the fourth night of consecutive monitoring at both sites even during winter (see Borkin and Parsons 2009 for a similar finding).

In spring and summer significantly greater LTB pass rates were detected at both habitats. This is consistent with previous reports for seasonal LTB activity trends in other parts of New Zealand (e.g. O'Donnell *et al.* 2006, O'Donnell 2001b, 2000c), with few exceptions (e.g. Borkin & Parsons 2009). Increased bat activity during spring and summer is likely linked with warmer nightly temperatures, increased insect availability and reduced thermoregulatory costs (see below; Speakman & Thomas 2003; O'Donnell 2000c). In spring, summer and autumn an additional peak in foraging activity was observed before dawn. Bimodal peaks in bat activity have also been observed in several bat species (e.g. Cel'uch & Kropil 2008; Erkert 1982), including LTBs (Griffiths 2007; O'Donnell 2005) and likely represent bats returning to day roosts before sunrise. Bimodal activity patterns in bats have also been linked with reproductive status. For example, in pipistrelle bats (*Pipistrellus pipistrellus*) bimodal activity was observed during lactation when energy demands are greater compared with

unimodal peaks in activity at other times of the year (Swift 2009). This may

explain more pronounced bimodal activity patterns at the oak fragment during

spring and summer (i.e. pregnancy-lactation; see below).

Detector height and microhabitat patterns

Echolocation and flight are closely synchronised in aerial insectivorous bats,

which in turn may influence how bats make use of habitats and microhabitats

(Holderied *et al.* 2008; Verboom *et al.* 1999). Foraging LTBs have highly

manoeuvrable flight and the wing morphology (i.e. medium wing loading and

aspect ratios) and echolocation pulse structure (i.e. intense broadband frequency-

modulated pulses) of LTBs is typical for aerial hawking bat species adapted to

foraging in sparsely cluttered open edge habitats (O'Donnell *et al.* 2006;

O'Donnell 2001a; Parsons *et al.* 1997). Indeed, previous studies have shown that

LTB activity can vary between habitat types (e.g. roads, grasslands and forest

edges; Borkin & Parsons 2009; O'Donnell *et al.* 2006; O'Donnell 2000b) but no

study has examined the differential use of microhabitats by LTBs (i.e. within

habitat use of vertical and horizontal space). Both sites monitored in this study can

be broadly described as exotic riparian forest fragments that are sparsely cluttered

(i.e. a habitat type where foraging LTBs have frequently been observed; Borkin &

Parsons 2009; O'Donnell 2005; Griffiths 1996; Dwyer 1962). However, even

within these habitats bat activity was found to vary, significantly in some cases, in

relation to both the use of vertical airspace and horizontal microhabitats

characterised by different habitat features (e.g. presence of water bodies and open

spaces).

At the oak fragment significantly more LTB passes were recorded when

detectors were placed at lower heights compared with higher heights. A similar,

albeit non-significant, trend was observed at Hammond Bush. This is likely due to a combination of two factors. Firstly, selected trees with rope and pulley setups were not as tall (< 25m) at Hammond Bush as those at the oak fragment (> 30m), which invariably influenced LTB detection rates at higher heights (Appendix I). Secondly, the open area at Hammond Bush is characterised by a large open space flanked by trees compared with the oak fragment that is densely stocked with trees and flanked by large open spaces. LTBs may prefer to fly at lower heights at the oak fragment in order to avoid more obstacles (i.e. structural clutter from branches and leaves) higher in the canopy that might limit flight manoeuvrability and alter echolocation signals through sound attenuation and pulse-echo overlap (Wallace 2006; O'Donnell 2005; Broders *et al.* 2004; Kalcounis *et al.* 1999; Verboom & Spoelstra 1999; Griffin 1971). A seasonal effect in vertical bat activity at both habitats was also observed; during spring, summer and autumn more LTB passes were recorded at higher heights compared with winter. This may be linked with increased temperatures and greater insect activity at higher elevations (see studies by Collins & Jones 2009; Broders *et al.* 2006; Hecker & Brigham 1999).

LTB activity was non-randomly distributed among microhabitats at the oak fragment. The percentage of bat passes recorded in the OE microhabitat was never more than 20% of all recorded passes during each season of monitoring. The OE is the only microhabitat situated entirely on the elevated river terrace lacking a flanking water body (Figure 2B; Appendix I). This microhabitat is also the most exposed to prevailing westerly winds that may influence temperature – a positive predictor of LTB activity at this site (see below). Verboom and Spoeltra (1999) showed that the proportion of pipistrelle bats flying along the leeward side

of tree lines increased in response to both the relative velocity and direction of wind. Minimising wind exposure may reduce flight costs for foraging bats (Racey & Swift 1985). The availability of water bodies in the other three microhabitats also likely contributes to decreased bat activity in the OE. Insect concentrations have been shown to increase as the distance to water bodies decreases (Fukui *et al.* 2006). Aerial insectivorous bats, like LTBs, exploit insect concentration over both natural and modified water sources (e.g. Vindigni *et al.* 2009; Verboom *et al.* 1999; Krusic *et al.* 1996). Moreover, some bat species may require up to 20% of their daily water intake from drinking (Kurta *et al.* 1990; Speakman & Racey 1989).

During winter 60% of all LTB passes recorded at the oak fragment occurred within the I microhabitat. This sheltered microhabitat is characterised by a small clearing surrounded by a barrier of trees on all sides, which likely acts as a buffer against wind, colder temperatures and could also reduce visual detection of bats by predators such as moreporks known to occur at this site. Reported incidents of bat predation by moreporks are rare (e.g. Borkin & Ludlow 2009) but bats that remain in more vegetated areas are likely to be less conspicuous to aerial predators (see Fenton *et al.* 1994; Jones & Rydell 1994). During autumn 60% of all LTB passes recorded at the oak fragment occurred within the RE microhabitat. LTBs actively accumulate fat reserves before winter (O'Donnell 2005), and increased bat activity near riparian margins may be related to bats tracking higher densities of ephemeral insect prey over the river at this time of the year (e.g. Warren *et al.* 2000).

Given that microhabitat variation in bat activity was only investigated at one site in this study, this data should be viewed as preliminary. Further

investigations into the use of microhabitats by LTBs at other habitats are needed before generalising these findings. Nevertheless, LTBs are clearly responsive to small-scale habitat features, which can influence bat detection rates at fine spatial scales (e.g. Patriquin *et al.* 2003). This has implications for future monitoring studies as microhabitat variation is often unaccounted in acoustic bat monitoring (see Gannon *et al.* 2003; Sherwin *et al.* 2000).

Predictors of bat activity
Identifying environmental and anthropogenic variables that influence bat behaviour can help explain observed variability in activity patterns. I found that the only significant environmental predictor of LTB activity was mean nightly temperature (at the oak fragment only). This finding is consistent with other studies, which found that changes to ambient temperatures influences bat activity (e.g. Scanlon & Petit 2008; Milne *et al.* 2005; Parsons *et al.* 2003; O'Donnell 2000c). However, the site-specific influence of temperature is intriguing and lends support to a previous speculation that male and female LTBs likely use different habitats along the southern urban-rural interface of Hamilton City, at least during part of the year (see Dekrout 2009). Females of many temperate bat species have higher thermoregulatory constraints associated with delayed parturition, lactation and foetal development compared with fewer constraints for spermatogenesis and testicular development in males (Speakman & Thomas 2003; Lumsden *et al.* 2002; Barclay 1991). Sex differences in thermal requirements may explain observed behavioural differences in bat activity patterns and habitat use (Senior *et al.* 2005; Racey & Entwistle 2000). For example, Broders *et al* (2006) showed that female northern long-eared bats (*Myotis septentrionalis*) and little brown bats had foraging and roosting areas 3.4 and 6.1 times larger than males, respectively. In

LTBs varying thermal requirements between the sexes likely explains different roosting densities with females being more communal than males (Sedgeley 2001; O'Donnell & Sedgeley 1999; Sedgeley & O'Donnell 1999). Previous bat trapping undertaken at Hammond Bush (summer and autumn 2004-2007) revealed an extreme male capture bias (23 males: 1 female; Dekrout 2009). This might suggest that females prefer to use rural habitats more than urban habitats; however, no bats have been caught at the oak fragment despite numerous attempts making it impossible to compare sex ratios between these sites. It is also important to note that the small scale at which trapping was undertaken and the likelihood of trap avoidance by female LTBs could easily skew sex ratios (MacSwiney *et al.* 2008; Berry *et al.* 2004; O'Farrell & Gannon 1999; Kuenzi & Morrison 1998). Moreover, LTBs are known to regularly move between these two habitats (Dekrout 2009). Nevertheless, if site-specific temperature dependence reflects differential use of habitats by male and female LTBs, this may explain some of the observed variation in LTB activity patterns. For example, a greater peak in feeding buzzes at the oak fragment during winter may indicate that overwintering females in rural habitats make less use of torpor compared with males as torpor potentially reduces milk production and foetal growth rates. This has been shown in other temperate bat species (Dietz & Kalko 2005; Russo *et al.* 2004; Hamilton & Barclay 1994).

Insect availability also likely influences LTB activity in and around Hamilton City as shown in a previous study (Dekrout 2009). O'Donnell (2000) found that overnight temperature was a better predictor of LTB activity compared with invertebrate activity in native rainforest habitats; however, it is unlikely that LTBs respond independently to each of these variables as temperature typically influences insect abundance (e.g. Scanlon 2005). Wind speed, cloud cover, %

lunar illumination, % relative humidity and rainfall were not significant predictors of LTB activity, consistent with some studies (e.g. Scanlon & Petit 2008; Hecker & Brigham 1999; Hayes 1997; Vaughan *et al.* 1997). In other cases, one or more of these variables have been shown to influence bat activity (e.g. Jung & Kalko 2010; Parsons *et al.* 2003; Lackie 1984). Importantly, I failed to take into account the number of hours during the night that the moon was out for and the effect that cloud cover may have had on overall lunar illumination (see Milne *et al.* 2005; Hayes 1997). This should be re-considered in future studies. It is also important to bear in mind that environmental variables can affect bat behaviour in species-specific and complex ways (e.g. Jung & Kalko 2010; Scanlon & Petit 2008; Avila-Flores & Fenton 2005). For example, Hecker and Brigham (1999) found that bats flew higher in the forest as moonlight increased, which in turn was explained by changes to insect behaviour in response to varying lunar conditions. When evaluating the relationship between environmental conditions and animal activity patterns, researchers also need to be aware of variation at the habitat-scale. I found a significant difference between nightly temperature and % relative humidity logged at both habitats compared with the same data obtained from a weather station < 5km from each of the study sites. These discrepancies can introduce potential inaccuracies in results.

Due to the close proximity of the oak fragment to the runway of HIA (2.5km), I predicted that aircraft activity might disturb nightly bat activity at this site. Variables associated with low-altitude aircraft overflights including flashing lights, changes to air pressure and noise; all have the potential to disrupt animal behaviour and mask animal signals that are important for foraging and orientation (see examples by Pepper *et al.* 2003; Krausman *et al.* 1998; Trimper *et al.* 1998;

Weisenberger *et al.* 1996). I found that the number of aircraft pass/night (i.e. the frequency of aircraft activity) was not a significant predictor of bat activity at the oak fragment. This suggests that aircraft activity may not alter LTB activity at this site, which may be linked to high frequency echolocation pulses used by LTBs not being masked by lower frequency aircraft sounds (Jones 2008; Schaub *et al.* 2008). However, further research is needed to verify this (see Chapter 5).

Recommendations for monitoring LTBs in modified habitats

Effective management of cryptic threatened species is often hindered by a lack of adequate data collection methods. Ultrasonic detectors are a relatively new and effective means to monitor bat activity in New Zealand (O'Donnell & Sedgeley 1994). In order to improve and maximise LTB detections using bat detectors in highly modified habitats such as fragmented urban and rural ecosystems I recommend that LTBs be monitored: 1.) during warmer months; 2.) on warm nights; 3.) by securing detectors at a height of 4-7m; and 4.) by placing detectors in forested habitats near open spaces and water bodies (e.g. rivers or ponds).

Restricted site replication is an important limitation of this study as only two habitats were intensively monitored. I acknowledge that LTB activity is temporally and spatially heterogeneous and this was evident from the results. Moreover, LTBs are highly mobile animals that have extremely large home ranges – up to 19km (Dekrout 2009; O'Donnell 2001a, b). Therefore any definitive predictions of LTB habitat use in modified habitats would be premature (see Gannon *et al.* 2003; Sherwin *et al.* 2000); however, intensive monitoring of bats in this study does provide confidence in the observed activity trends at both sites (see Hayes 1997). It is important that further monitoring be undertaken at sites both within and around Hamilton City (Chapter 3) as well as other modified

environments throughout New Zealand. This is important to determine how effective and applicable this monitoring protocol is at other habitats and modified environments.

Conclusion

In human-dominated environments a lack of effective and standardised protocols for monitoring bats invariably limits effective management and conservation efforts for these animals. As far as I am aware this is one of the longest and most intensive acoustic bat monitoring studies undertaken in a modified environment and the first study to consider both vertical and horizontal microhabitat use in a New Zealand bat species. I aimed to identify basic LTB activity trends and patterns of habitat and microhabitat use in order to develop practical LTB monitoring recommendations that can be applied to modified habitats where this protected species may occur. Increased awareness of when and where bats are most active would better guide researchers seeking to maximise and improve recordings of LTB echolocation pulses for bioacoustic analyses and for detector-based monitoring purposes (e.g. presence/absence surveys; Chapter 3). This information should also guide researchers wanting to increase bat capturing success rates and improve LTB surveys using trapping techniques (e.g. placing mist nets in microhabitats most used by bats). Co-ordinating field-experiments to coincide with times of the highest bat activity would also maximise bat response data and optimise research effort (Chapter 5). Recommendations are thus anticipated to better focus available resources (e.g. equipment and research effort) and guide future monitoring, management and conservation strategies for LTBs in modified ecosystems. This is important as there is currently no management plan for this protected species in modified environments.

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Chapter 3

'Bats in the backyard': Applying long-tailed bat monitoring recommendations to the urban-rural interface of Hamilton City, New Zealand

3.1 Abstract

Being able to effectively obtain useful behavioural information about animal populations (e.g. knowing when and where animals are most active) can better inform management decisions (e.g. allocating available resources). I used automated bat detectors to apply long-tailed bat (*Chalinolobus tuberculatus*; LTB) monitoring recommendations (developed to maximise echolocation detections in modified habitats; Chapter 2), in two different ways. First, I conducted a short-term concurrent monitoring study to identify basic nightly and seasonal LTB activity trends at rural and urban sites with and without a confirmed LTB presence. Second, I conducted a LTB presence/absence survey at 11 rural and urban sites across the urban-rural divide of Hamilton City. I wanted to determine if: 1.) monitoring recommendations are applicable at other modified and native forest fragments; 2.) short-term concurrent monitoring (i.e. a less intensive sampling regime) can still provide accurate nightly and seasonal activity trends (compared with activity trends from a more intensive monitoring study; Chapter 2); 3.) LTBs are more widely distributed in and around Hamilton City then previously shown; and 4.) proximity to river margins and anthropogenic structures likely influences bat activity and distribution. Concurrent monitoring revealed that bats do use multiple rural and urban sites even within a single night across successive seasons. Nightly trends in bat activity were mostly consistent with those presented in a more intensive monitoring study (Chapter 2) demonstrating that although reduced sampling effort does make data more variable, basic activity patterns are still accurate. I recorded LTBs at eight out of 11 surveyed sites (73%) confirming that bats are more widely distributed in and around Hamilton City than previously shown using hand-held detector surveys. Relative bat activity was consistently higher (> 40 passes/night) at sites nearest to the river (≤ 50m) compared with sites

further (≥ 1km) from the river (< 20 passes/night). Bats were not detected at urban sites surrounded by roads and houses closest to the city centre but were detected at rural sites near roads. Proximity to riparian margins, habitat connectivity and the presence of anthropogenic structures likely influences LTB habitat use and distribution patterns in this modified landscape. Effective bat monitoring in human-dominated environments should better focus conservation strategies such as protecting habitats and landscape features most important to bats.

3.2 Introduction

It is becoming increasingly important to develop and apply monitoring methods that provide a means of quickly obtaining useful information about target populations. This is especially valuable for cryptic threatened species known to reside in or near human-dominated environments (Chadés *et al.* 2008; Regan *et al.* 2008). For example, knowing when and where individuals are most active can improve detection and capture rates, which in turn could provide more robust data sets that better inform management and conservation policy-making.

Bats are a challenging group of animals to monitor because they are mobile, nocturnal and typically rely on high-frequency (> 20kHz) echolocation pulses inaudible to humans (Fenton 2003, 1997; Kunz & Fenton 1982). As a result, the behaviour, distribution and conservation needs of many bat species often goes unaccounted for in management and conservation decisions (Feldhamer *et al.* 2007; Mickleburgh *et al.* 2002). Effectively managing bats is often limited by a lack of standard inventory and monitoring protocols. Wildlife

managers are thus faced with the task of improving bat monitoring techniques and designs so that information about bat distribution patterns and use of available habitats can be increased (Chapter 2; Gerht & Chelsvig 2004; O' Shea *et al.* 2003; Verboom *et al.* 1999; Verboom 1998).

Many bat species survive in human-dominated landscapes including agricultural land (e.g. Lumsden *et al.* 2002), managed pine plantations (e.g. Borkin & Parsons 2010; Miller 2003) and urban environments (e.g. Scanlon & Petit 2008; Avila-Flores & Fenton 2005). The successful exploitation of urban ecosystems by bats depends on species-specific roosting and foraging requirements (Sparks *et al.* 2005; Duchamp *et al.* 2004; Gerht & Chelsvig 2004). For instance, white-striped free-tailed bats (*Molossid tadarida*) have roost sites that are widely dispersed throughout Brisbane City, Australia but individuals may rely on more restricted foraging areas near riparian margins (Rhodes & Catterall 2008). Conversely, species like brown long-eared bats (*Plecotus auritus*) appear to have restricted roost sites but more dispersed foraging ranges in cities (Entwistle *et al.* 1997). Some bat species may use rural forest habitats more than urban areas (e.g. parklands; Sparks *et al.* 2005; Kurta & Teramino 1992) but the opposite is true in other cases (e.g. Gerht & Chelsvig 2004).

The use of urban landscapes by bats may be influenced by a range of interacting variables, including the proximity of natural (e.g. forest fragments) and artificial (e.g. streetlights) features characterising local habitats and microhabitats (Chapter 2; Johnson *et al.* 2008; Gerht & Chelsvig 2003). For example, insectivorous bat species are known to concentrate their foraging activity around

water bodies, which is thought to be linked with greater insect availability (e.g. Vindigni *et al.* 2009; Avila-Flores & Fenton 2005; Brooks & Ford 2005; Ciechanowaski 2002). The influence of anthropogenic variables (e.g. housing density) on wildlife is also of growing concern (Jung & Kalko 2010). Structures like roads may influence how animals use available habitats (e.g. Speziale *et al.* 2008). Certain bat species have been shown to be adversely affected by artificial lighting (Stone *et al.* 2009; Scanlon & Petit 2008; Downs *et al.* 2003) and vehicle traffic (Kerth & Melber 2009; Jones 2008; Schaub *et al.* 2008), which may influence bat movement and habitat use patterns.

Only two bat species are found in New Zealand – long-tailed bats (*Chalinolobus tuberculatus*; LTBs) and lesser short-tailed bats (*Mystacina tuberculata*; STBs; O'Donnell 2005). LTBs are aerial insectivores that use native and exotic old-growth trees for roosting purposes (O'Donnell 2005; O'Donnell & Sedgeley 1999; Sedgeley & O'Donnell 1999). This species is classified as 'vulnerable' (IUCN 2010; Molloy 1995; Molloy & Davies 1994; O'Donnell 2008, 2000a) because of ongoing population declines attributed to habitat loss through agricultural and urban expansion (O'Donnell 2001a, 2000a). Hamilton City (North Island, New Zealand) is recognized as one of the few remaining cities in New Zealand to still support a population of LTBs (Dekrout 2009). This is despite the Hamilton Ecological District being one of the most degraded in New Zealand with ca. 1.6% of the original vegetation remaining (Clarkson & McQueen 2004). In order to improve conservation and management strategies for local LTB populations in modified environments like Hamilton City, information about bat activity trends, habitat use and distribution patterns is needed (Chapter 2; Molloy

1995; Molloy & Davies 1994).

Advances in bat monitoring devices (Stag Bat Box III; The Department of Conservation) have made it possible to non-invasively monitor bats in New Zealand (O'Donnell & Sedgeley 1994). In addition to providing presence/absence data, valuable information about nightly, seasonal and spatial bat activity trends can also be measured from echolocation pass rates (Chapter 2; Gannon *et al.* 2003; Sherwin *et al.* 2000). However, detectors do not provide information about bat abundance, sex ratios and specific roost locations (O'Farrell & Gannon 1999; O'Donnell & Sedgeley 1994). Guidelines for improving and maximising detection rates in the field using detectors are still in the developmental stage (Chapter 2; Molloy 1995).

In Chapter 2, I developed practical LTB monitoring recommendations for improving bat detections using automated detectors in modified habitats. The recommendations proposed in this study included: 1.) monitoring LTBs on warmer nights; 2.) monitoring LTBs during warmer seasons (i.e. austral spring and summer); 3.) placing detectors at a height of 4-7m; and 4.) placing detectors in forested habitats near water bodies and open spaces. In this study I implemented these recommendations using two different bat monitoring strategies: 1.) a short-term concurrent monitoring study, which sought to identify basic nightly and seasonal LTB activity trends at rural and urban sites with and without a confirmed LTB presence (Dekrout 2009); and 2.) a LTB presence/absence survey at 11 rural and urban sites situated on either side of the urban-rural divide of Hamilton City. I wanted to determine if: 1.) monitoring recommendations are

applicable to other modified and native forest fragments so that I could better comment on the broader applicability of this monitoring protocol (i.e. were bats detected and were activity patterns comparable to those at sites with known LTBs?); 2.) short-term concurrent monitoring (i.e. a less intensive sampling regime) can still provide accurate nightly and seasonal activity trends (compared with activity trends in a more intensive study; Chapter 2); 3.) LTBs are more widely distributed in and around Hamilton City then previously shown using hand-held detector surveys (Dekrout 2009); and 4.) proximity to river margins and anthropogenic structures likely influences bat activity and distribution. This study will improve current knowledge about LTB habitat use and distribution patterns in the Hamilton region and demonstrate how LTB monitoring recommendations can be applied in modified environments using non-invasive acoustic approaches.

3.3 Methods and Materials

Site selection

LTBs have only previously been confirmed at two sites in and around Hamilton City: one rural forest (an oak fragment) and one urban park (Hammond Bush; Chapter 2; Dekrout 2009). In this study I conducted LTB monitoring at 11 forested habitats situated ≤ 5km on either side of the southern urban-rural divide of Hamilton City (Figure 3.4). All sites were selected on the basis of: 1.) presence of old-growth native and/or exotic trees (typically used by roosting LTBs; Sedgeley & O'Donnell 1999); 2.) presence of flanking open spaces (typically used by foraging LTBs; O'Donnell 2005; Parsons 1997); 3.) distance from anthropogenic structures including roads and houses (i.e. potential barriers of bat movement and habitat use); 4.) distance from riparian margins; and 5.) distance from other sites monitored in this study with bats (i.e. habitat connectivity). Therefore, all sites had old-growth trees and flanking open spaces but were of

varying distances from both the river, anthropogenic structures, and other habitats that were monitored (Figure 3.4; Appendix I).

Concurrent monitoring

At four sites, two urban parklands (Hammond Bush and Sandford Park) and two rural forest fragments (the oak fragment and Whewell's Bush), I concurrently monitored LTBs over three successive seasons: spring (October 2009); summer (January-February 2010); and autumn (March-April 2010). I ensured that the two sites with known LTBs (i.e. the oak fragment and Hammond Bush) were always monitored for comparative purposes (monitoring at these sites was conducted independently from the monitoring study presented in Chapter 2). LTBs could only be concurrently monitored at three sites at any one time due to a limited number of detectors. Equipment limitations also meant that I could not monitor Sandford Park during spring. Therefore, during each season (except spring) I conducted two concurrent monitoring sessions considering all site combinations (i.e. Hammond Bush and the oak fragment and Whewell's Bush or Sandford Park). Each monitoring session consisted of five consecutive monitoring nights (total N = 25 nights).

Presence/absence survey

I conducted a LTB presence/absence survey at all 11 sites (including the four sites concurrently monitored; see above). Additional sites included: Mystery Creek golf course, Humarie Park, Hillcrest Park, the campus of The University of Waikato, the Hamilton Gardens, Hamilton Cemetery and Claudelands Bush (Jubilee Park). All sites have flanking natural (e.g. river) and/or artificial water bodies (e.g. artificial ponds), except Hillcrest Park. Some sites are connect to other monitored sites by the Waikato River and the associated riparian margins (i.e. the Hamilton

Gardens, Hamilton Cemetery and Mystery Creek golf course), while other sites are more isolated, further from the river and closer to anthropogenic structures (i.e. Humare Park, Hillcrest Park and Claudelands Bush). Three sites have native kahikatea (*Dacrycarpus dacrydiodes*) remnants (i.e. Whewell's Bush, Hillcrest Park and Claudelands Bush) while all the others are exotic.

Site descriptions

Rural sites

The oak fragment (ca. 1.2 ha) is situated on an elevated river terrace ca. 2.5 km north east of Hamilton International Airport (HIA; Figure 3.4). The site lies within the wider Mangakotukutuku gully system. Old growth oak trees (*Quercus robur*; mean ± SE diameter 60.1 ± 3.22cm (standard 10 x 10 vegetation plots); > 100 years old (ring counts of felled trees)) dominate the site. Most trees have canopy heights of > 25m and have a high stocking density with > 200 stems distributed throughout the site. Agricultural land flanks the site to the south, east and west and the Waikato River and associated riparian vegetation lie to the north. Two minor water bodies (i.e. a pond and gully) are situated to the south and east and a larger pond and irrigation channel lie to the south of the site. Monitoring was restricted to open edges closest to the artificial water bodies and the river (i.e. WOE and RE), which have previously been shown to have higher bat activity compared with other areas (Chapter 2). Native vegetation including cabbage trees (*Cordyline australis*) and small totara trees (*Podocarpus totara*) are sparsely distributed around water bodies and riparian margins. LTBs use the oak fragment throughout the year (Chapter 2).

Whewell's Bush is an old-growth native kahikatea remnant situated near Matangi (a town south west of Hamilton City; Figure 3.1). The site is a

Department of Conservation scientific reserve and is ca. 11.5 ha in size making it considerably larger than the oak fragment. The site is flanked by agriculture land on all sides. Historically, this remnant was poor draining with rain-fed water characteristically collecting on the surface; however water was drained from the site for agricultural purposes by digging trenches alongside the forest. The site is now considerably drier and supports dry land vegetation species (e.g. Mahoe, *Melicytus ramiflorus* and tawa, *Beilschmiedia tawa*) that dominate the understory. Two small roads flank the site to the north (Tauwhare Rd) and west (Swallow Ln.). Unlike the other sites, Whewell's Bush is situated at least 3km east of the Waikato River and is separated from other habitats by a motorway (SH1; Figure 3.1). Detectors were placed near to the forest edges, on the assumption that bat activity would be higher there than in the more cluttered forest interior (Chapter 2).

LTBs were also monitored at Mystery Creek golf course during the presence/absence survey. This site is situated on elevated river terraces and is flanked by the Waikato River and a main road (Airport Rd; Figure 3.4). The site has several tall exotic trees (e.g. *Pinus radiata*) sparsely distributed between many large open spaces (e.g. golf greens). Detectors were secured adjacent to a parking lot that is flanked by both the main road and the river.
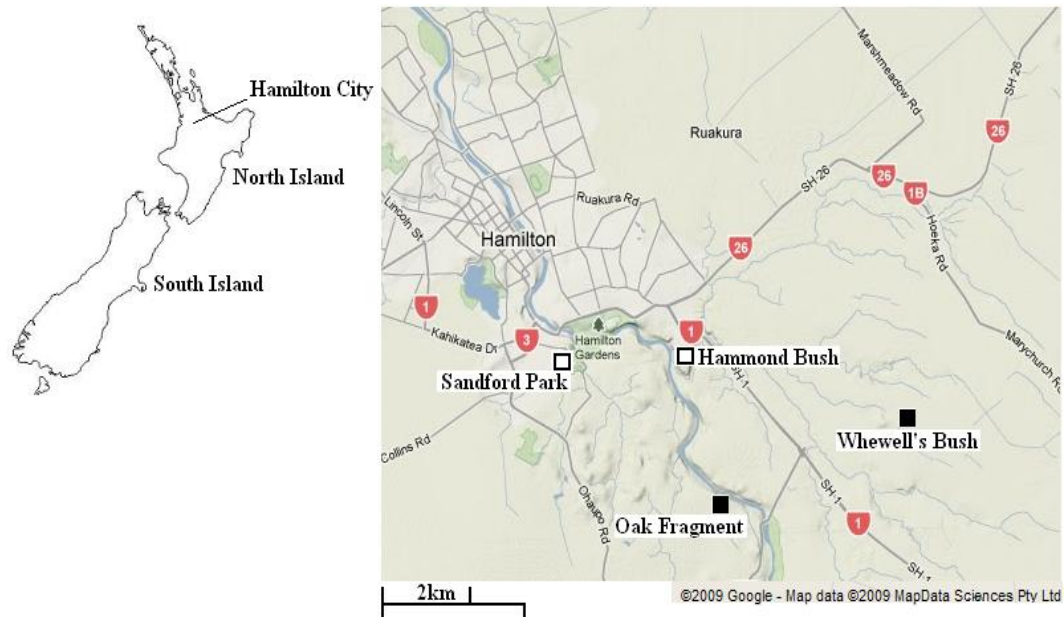
Figure 3.1 Map of New Zealand and an aerial view of southern Hamilton showing the location of the rural (solid squares) and urban sites (open squares) where LTBs were concurrently monitored over three successive seasons. Note the relative distances between the sites and their proximity to the Waikato River.

Urban sites

Hammond Bush (1 ha) is a native forest remnant situated in a medium density urban subdivision in the suburb of Hillcrest (Figure 3.1; de Lange 1996). The site is situated in the Mangaonua gully system, which together with the Managkotukutuku gully creates a continuous riparian ecotone (Clarkson & McQueen 2004; de Lange 1996). This ecotone includes the city's southern urban areas and surrounding peri-urban and rural regions including the oak fragment,

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Mystery Creek golf course, Hamilton Gardens, Hamilton Cemetery, Sandford Park and surrounding gullies, which are all bisected by the Waikato River (Figure 3.4). Despite its small size, Hammond Bush is floristically the richest native forest remnant in Hamilton City, supporting ca. 145 native plant species (Clarkson & McQueen 2004). The forest is a mixed broadleaf forest of primary succession status dominated by native pukatea (*Laurelia novae-zelandiae*) and tawa trees (Beilschmiedia tawa; Clarkson & McQueen 2004; de Lange 1996). The Waikato River flanks the site to the west. At both the southern and northern end of the reserve are much smaller (ca. 0.3 ha) open areas dominated by old-growth exotic trees including, alders (*Alnus* sp.), grey willows (*Salix cinerea*), *Acacia* sp., *Eucalyptus* sp. and pines (*Pinus radiata*). LTB monitoring was restricted to these less cluttered open areas. LTBs are active in Hammond Bush throughout the year (Chapter 2; Dekrout 2009). LTBs are also known to move between the oak fragment and Hammond Bush using the Waikato River as a connecting corridor (Dekrout 2009; Figure 3.1).

Sandford Park (21.58 ha) is situated within the wider Mangaonua gully system and is just ca. 1 km and ca. 2km from the Waikato River and Hammond Bush, respectively. The area is situated in a medium density urban subdivision in the suburb of Fitzroy. The area consists of a network of gullies supporting both old-growth exotic and native vegetation (e.g. mamuka (*Cyathea medullaris*) and totara). I restricted monitoring to areas containing stands of exotic old-growth pine trees situated near open spaces and water bodies such as creeks and storm water channels. Monitoring was undertaken near pine stands off Manor and Annabel Pl and Peacockes Rd.

In addition to these two urban parks, I also monitored LTBs at several
other urban sites including the Hamilton Gardens (48 ha) and Hamilton Cemetery
(14 ha) situated immediately adjacent to one another on an elevated river terrace.
Approximately 1km on either side of both these sites is Hammond Bush and
Sandford Park (Figure 3.4). Large open spaces and tall old-growth exotic trees
(mainly pine trees) are clustered in small areas at these sites, which can mainly be
found on the southern end of the gardens nearest to the cemetery. I restricted LTB
monitoring to this area where I secured detectors in tall (>25m) pine trees
overlooking the river. I also secured detectors in acacia trees overlooking a gully
on the southern end of Humarie Park (1.13 ha). This site is ca. 1km from the river
and is flanked by several small roads (e.g. Cranwell Pl. and Berkley Cres), two
main roads (Cambridge Rd and Morrinsville Rd) and medium density housing
within the suburb of Hillcrest (Figure 3.4). I also secured detectors at the
University of Waikato campus (68 ha) in tall-old growth pine and eucalypt trees
near an artificial lake (near Chapel Lake) and sports field (near Bleakley Park).
Houses and roads (Hillcrest Rd and Knighton Rd) surround the University (Figure
3.4). Detectors were also secured in two old-growth kahikatea fragments -
Hillcrest Park and Claudelands Bush (Figure 3.4). Hillcrest Park (7.5 ha) is
flanked by houses and a roads (e.g. Masters Ave). Claudelands Bush (5.2 ha) is an
isolated forest remnant situated closest to the city centre and surrounded by main
roads (Boundary Rd and Brooklyn Rd) and medium-high density housing (Figure
3.4). I placed detectors near the forest edge at both sites facing open fields.

Monitoring procedure

Concurrent monitoring

For each five night monitoring session, two detectors were secured to low-lying

branches or the base of trees at a height of 4-7m using cable ties (203 x 4.6mm, Elmark) and padlocks. Detectors were placed near water bodies and open spaces and were orientated upward at 45° from the horizon (Weller & Zabel 2002). Care was taken to ensure that detectors faced the direction with the least amount of vegetation (i.e. clutter). Detectors were secured at a different place within each site during each monitoring session. Detectors were separated by at least 150m to ensure independent monitoring of bats (O'Donnell *et al.* 2006). Detectors were set to start monitoring LTBs 30 minutes before sunset until 30 minutes after sunrise. I tried to restrict monitoring to warmer nights that were forecast to have minimum temperatures of at least $\geq 10°C$ (www.metservice.com/national/). The start and stop times of each detector were re-calibrated before each five night monitoring session. All detectors are custom made in New Zealand (The Department of Conservation, Wellington, New Zealand) with similar sensitivities (Lloyd 2009). LTB echolocation pulses were recorded with an exact time (hour/minute/second) and date (year/month/day) stamp and were stored onto SD cards (San Disk, 2GB) for later analyses. All echolocation pulses were sorted from non-bat sounds (e.g. wind and rain generated noise) by visual and auditory inspection of waveforms using BatSearch 1.02 software (The Department of Conservation, Wellington, New Zealand).

Presence/absence survey
A different monitoring schedule was devised for the presence/absence survey. Each site (including the four sites concurrently monitored; see above) was monitored only once over three consecutive nights during summer (February) using two detectors spaced 150m apart. Detectors were secured and orientated in the same manner described above. Due to limited equipment availability I could

not concurrently monitor bats all 11 sites.

Statistical analyses

For each five night concurrent monitoring sessions I pooled LTB echolocation passes recorded on both detectors at each site. I calculated the total number of LTB passes recorded during each monitoring night at each site and the mean number of bat passes/min during each hour after official sunset across all monitoring nights. I kept data separate for each season. I used a non-parametric Krusal-Wallis test to determine if the number of bat passes/night differed significantly across each season at each site. *Post-hoc* analyses were performed using Tukey tests. For the presence/absence survey at the 11 sites, I calculated the mean number of LTB passes/night.

3.4 Results

Concurrent monitoring

A total of 2,510 LTB passes were recorded at all four sites concurrently monitored over the three successive seasons. LTB activity was not equal at these sites: 57% and 33% of all passes were recorded at Hammond Bush and the oak fragment, respectively. Only 6% and 4% of all LTB passes were recorded at Whewell's Bush and Sandford Park, respectively. A total of 100 LTB passes could be conclusively classified as feeding buzzes (ca. 4% of all recorded LTB passes), 57% and 27% of which were recorded at Hammond Bush and the oak fragment, respectively.

LTB activity was also not equal across the three successive seasons. At the oak fragment significantly (Krusal-Wallis, *Post-hoc test*; $H = 8.34$, $P < 0.05$) more bat passes/night were recorded during spring and summer compared with autumn (Table 3.1; Figure 3.2). Conversely, at Hammond Bush significantly (*Post-hoc*

test; $H = 7.41$; $P < 0.05$) more bat passes were recorded during autumn compared with spring and summer (Table 3.1; Figure 3.2). The percentage total of LTB passes at Whewell's Bush and Sandford Park was never more than 10% at each site during each season (Table 3.1).

Nightly LTB activity peaked between the first and third hours after official sunset across all seasons, with few exceptions (e.g. Sandford Park in summer and Whewell's Bush in autumn; Figure 3.3; see Chapter 2 for a similar result). Several additional smaller or equal peaks in bat activity were also observed throughout the night, especially before dawn. During autumn LTB activity was consistently high throughout the night at Hammond Bush compared with the more stereotypical peak and crash pattern normally characteristic of nightly LTB activity.
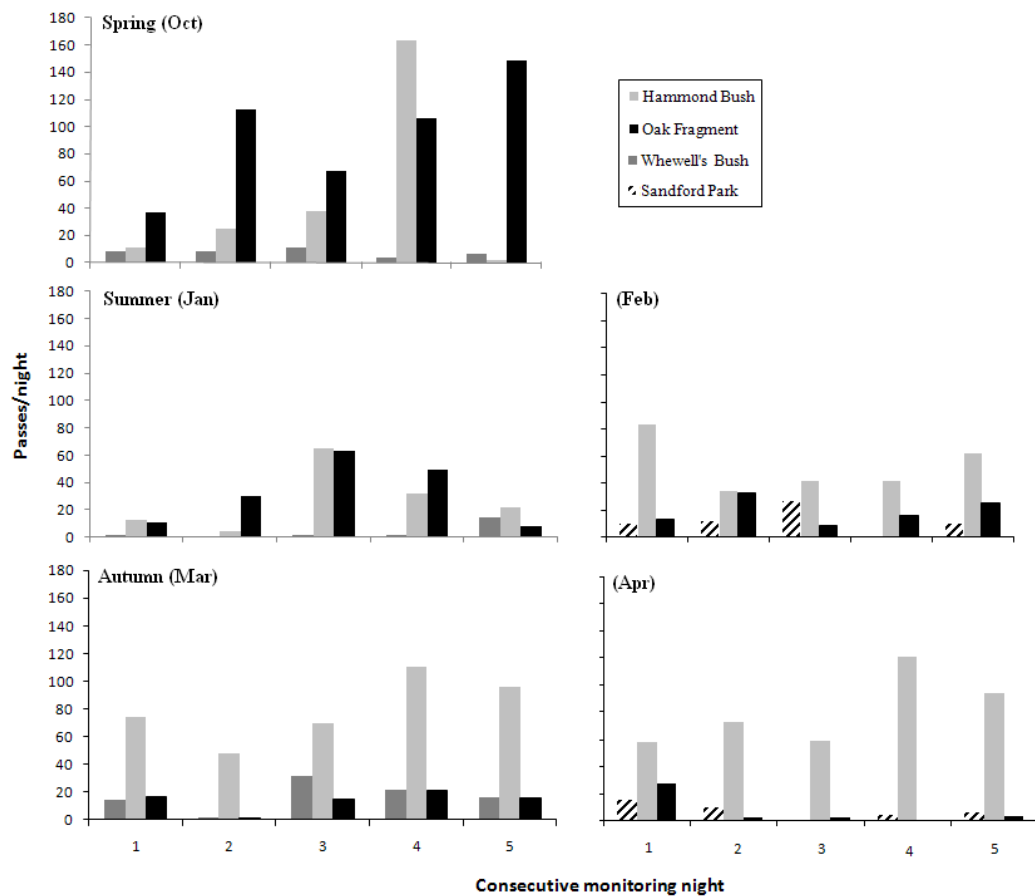
Figure 3.2 The total number of LTB passes recorded on each consecutive monitoring night at three concurrently monitored sites during spring, summer, and autumn. Due to limited detector availability only three sites could be concurrently monitored at any one time (i.e. Hammond Bush and the oak fragment and Whewell's Bush or Sandford Park). Each five-night concurrent monitoring session is presented separately.
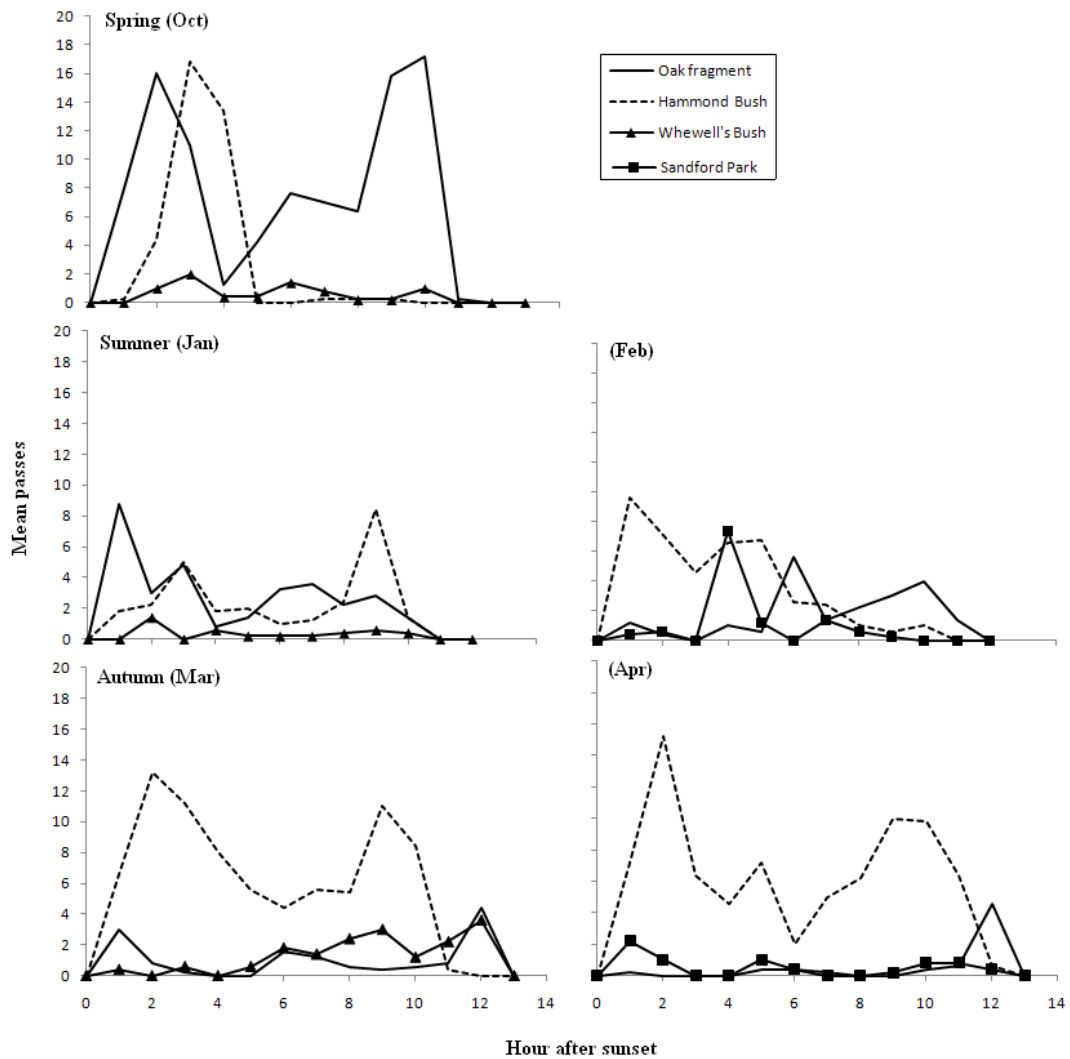
Figure 3.3 The mean number of LTB bat passes recorded for each hour after official sunset at three concurrently monitored sites over three successive seasons. Each five-night concurrent monitoring session is presented separately.

Presence/absence survey

A total of 728 LTB passes were recorded at the 11 habitats during this survey.

LTBs were detected at eight out of the 11 sites surveyed (73%). No bats were

detected at Hillcrest Park, The University of Waikato campus and Claudelands

Bush (Figure 3.4). On average, < 20 LTB passes/night were recorded at Humare

Park, Sandford Park, Whewell's Bush and Mystery Creek golf course (Figure 3.5).

On average, > 40 LTB passes/night were recorded at Hammond Bush, the oak

fragment, Hamilton Gardens and Hamilton cemetery (Figure 3.5; Appendix I).

Table 3.1 The percentage total LTB passes for each site during each season. The seasons with the same letter in each row do not differ significantly (Krusal-Wallis, *Post-hoc*, $P < 0.05$) in the number of bat passes recorded per night at that site.

Season	% total of all passes	Site			
		Oak fragment	Hammond Bush	Whewell's Bush	Sandford Park
Spring	30	63^a	32^a	5^a	-
Summer	29	54^a	35^a	3^a	8^a
Autumn	41	10^b	79^b	8^a	3^a
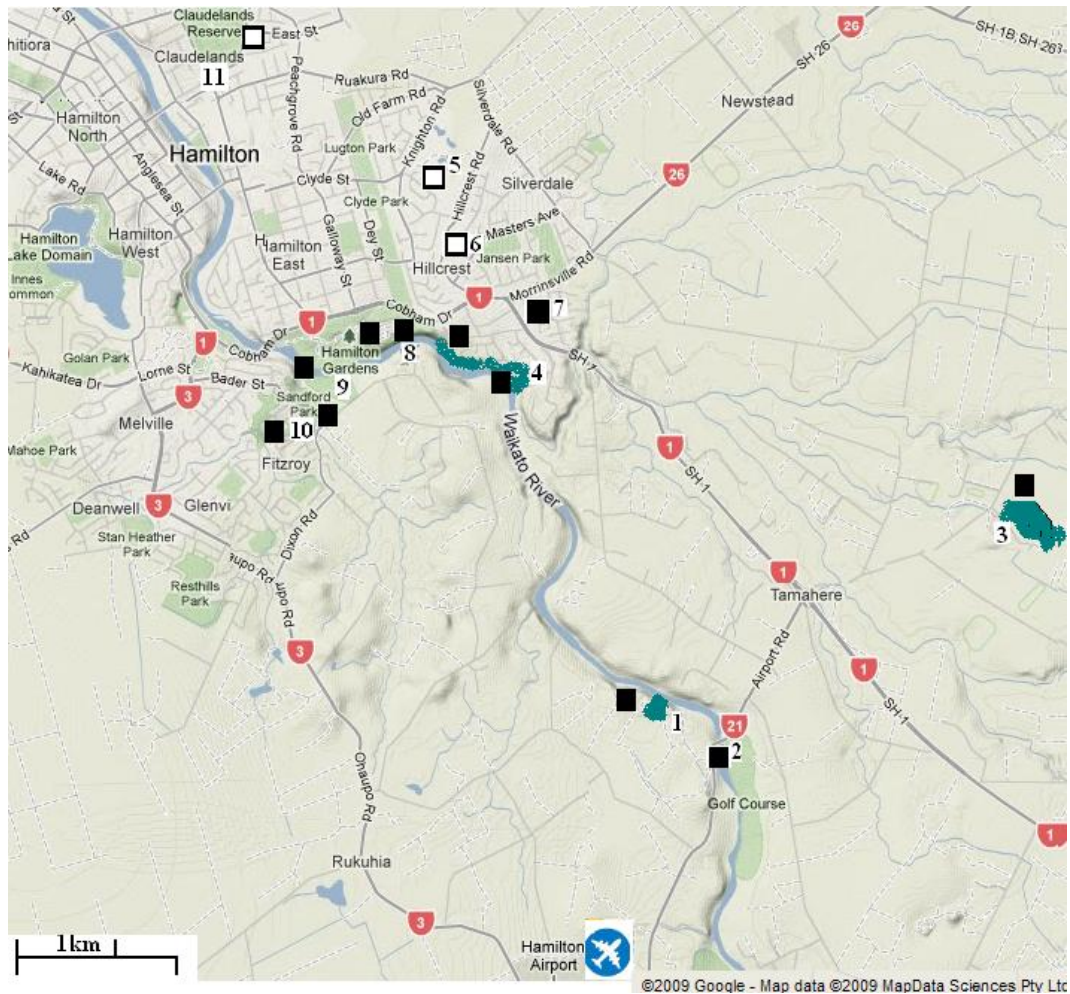
Figure 3.4 An aerial map showing the 11 forest sites situated along the southern urban-rural interface of Hamilton City where the LTB presence/absence survey was undertaken. Solid and open squares represent sites where LTBs were and were not detected, respectively. Rural sites included the oak fragment (1), Mystery Creek golf course (2) and Whewell's Bush (3). Urban sites included Hammond Bush (4), The University of Waikato campus (5), Hillcrest Park (6), Humarie Park (7), Hamilton cemetery (8), Hamilton Gardens (9), Sandford Park (10) and Claudelands Bush (11). Note the relative proximity of each site to the Waikato River.
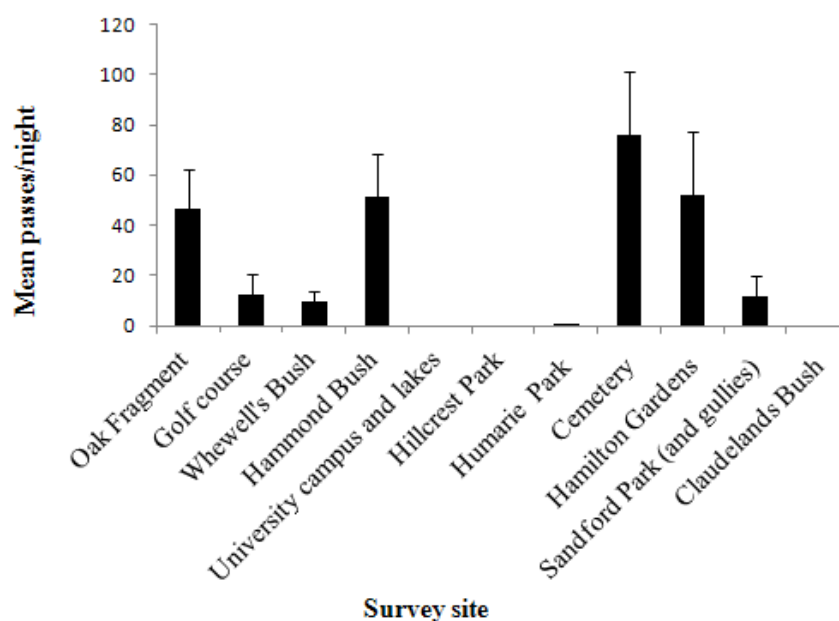
Figure 3.5 Mean ± SE number of LTB passes/night recorded on detectors at each of the 11 surveyed forest sites

3.5 Discussion

Concurrent monitoring

Concurrent monitoring revealed that LTBs do use multiple urban and rural sites in and around Hamilton City even within a single night. LTBs have one of the largest home range sizes for an echolocating bat species with males and post-lactating females known to have maximum ranges as large as 5629 ha and 1361 ha, respectively (O'Donnell 2005, 2001b). LTBs have also been shown to move between riparian habitats using the Waikato River as a connecting corridor (Dekrout 2009). Therefore, given access to a number of available habitats and the mobile nature of this species it is unsurprising that individuals would use multiple habitats, especially habitats connected by riparian margins. However, the differential use of habitats by bats is most interesting and could be related to a range of interacting variables from the availability of ephemeral insect prey (e.g. Kurta & Teramino 1992) to anthropogenic 'barriers' (e.g. artificial light) that potentially alter bat activity (e.g. Stone *et al.* 2009).

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I found that the number of LTB passes (i.e. relative bat activity) was highest at sites closest (> 50m) to the river (i.e. the oak fragment and Hammond Bush) compared with sites further (≥ 1km) from the river (i.e. Whewell's Bush and Sandford Park). LTBs appear to concentrate their activity at sites that are closer to riverine habitat (e.g. Warren *et al.* 2000), rather than on the basis of urban-rural divisions as shown in other studies (e.g. Johnson *et al.* 2008; Avila-Flores & Fenton 2005; Gaisler *et al.* 1998; Kurta & Teramino 1992). LTBs are known to use open edge riverine habitats over more cluttered habitats (e.g. forest interiors) as this likely allows for more manoeuvrable flight performance, especially during foraging (O'Donnell 2005; Parsons 1997; Parsons *et al.* 1997). Small ephemeral insect prey is also known to make up a considerable portion of LTB diet (Dekrout 2009; O'Donnell 2000b) and may also be more concentrated near riparian margins (e.g. Fukui *et al.* 2006). LTBs likely consume many insects over a short period of time to maintain energy levels needed for flight, which in turn would require foraging effort to be concentrated in areas that support high concentrations of prey. This would explain why more LTB passes were recorded at Hammond Bush and the oak fragment. In fact, 84% of all feeding buzzes were recorded at Hammond Bush and the oak fragment. It is possible that LTBs may use Whewell's Bush and Sandford Park for roosting rather than foraging purposes, which would explain why fewer LTB passes were detected at these two habitats.

Significantly more bat passes were recorded at Hammond Bush during autumn compared with spring and summer. In fact, 85% of all feeding buzzes recorded during autumn were detected at Hammond Bush. Higher concentrations of bat activity at Hammond Bush likely represents foraging bats spending more time in optimal foraging habitat (i.e. open areas with high insect densities) in

order to accumulate fat reserves before colder winter months (see also bat pass rates/season presented in Chapter 2; O'Donnell 2005). This would also explain why nightly activity at this site was more continuous during autumn, compared with the more stereotypical peak and crash pattern of activity observed during other seasons. It has also been suggested that male and female bats differentially use certain habitats during certain parts of the year (see Dekrout 2009; see other studies documenting sex-based habitat partitioning in echolocating bats; Safi *et al.* 2007; Senior *et al.* 2005; Grindal *et al.* 1999). Dekrout (2009) found that sex ratios at Hammond Bush were highly male-biased (22 males: 1 female) during spring and summer, which suggests that females may rely on rural sites over urban parklands for maternity purposes as rural forest fragments typically support more old-growth roost trees. During spring and summer significantly more bat passes were recorded at the oak fragment compared with autumn. This may reflect increased foraging activity by lactating females as energy demands increase at this time of the year (see also Chapter 2; Mackie & Racey 2007; Lumsden *et al.* 2002; O'Donnell 2002; Sedgeley 2001; Racey & Swift 1985).

It is likely that within-habitat features (e.g. amount of vegetation and open spaces) characterising each habitat also influenced bat detection rates in this study. Parsons (1996) showed that detection rates could be affected by the amount of vegetation or clutter surrounding detectors. Care was taken to place detectors in areas with the least amount of clutter at each site; however, it is possible that LTBs may prefer to use specific microhabitats at Sandford Park and Whewell's Bush that were not where my detectors were placed (see Chapter 2). This could explain the consistently low detection rates at both sites. Future LTB monitoring should be undertaken for longer periods of time at these sites in order to determine

the microhabitats bats use (see Chapter 2; Johnson *et al.* 2008; Avila-Flores &
Fenton 2005; Gerht & Chelsvig 2003). This should enable researchers to place
detectors in specific areas so that detection rates can be maximised, which in turn
would make habitat comparisons more accurate.

LTB activity peaked between the first and third hours after official sunset
at each site across all seasons. This is consistent with LTB activity trends
documented in Chapter 2; however, there was more variation in the number and
time of activity peaks compared with the same data collected more intensively (i.e.
for a longer time period using more detectors; see Figure 2.5, Chapter 2).
Increasing sampling effort makes data more robust, however, I also appreciate that
limited resources (e.g. equipment availability) can often restrict sampling effort.
Therefore, I recommend that LTBs be monitored for at least five nights in order to
maximise the chance of detecting bats and improve the accuracy of nightly and
seasonal activity trends; however, wherever possible, bat monitoring should be
undertaken for as long as possible. This is not only important for concurrent
monitoring but also for presence/absence surveys that risk reporting an absence of
bats at a given site due to limited sampling when in fact this may not be the case.

Presence/absence survey

LTBs were detected at five out of the seven urban sites monitored. Relative bat
activity was highest (> 40 passes/night) at urban sites immediately adjacent to the
Waikato River, compared with lower bat activity (< 20 passes/night) at urban sites
further from the river (e.g. Sandford Park and Humarie Park). This finding is
consistent with data obtained from the concurrent monitoring study discussed
above (see also Dekrout 2009). Insectivorous bats, including LTBs (Griffiths 2007;
O'Donnell 2005; Daniel 1990; Dwyer 1962) frequently use riparian zones (e.g.

Williams *et al.* 2006; Warren *et al.* 2000; Kurta & Teramino 1992), which likely serve several important ecological functions for bats. Firstly, they provide individuals with a source of insect prey and drinking water (e.g. Racey & Swift 1985). The abundance of emergent insects has been shown to increase with decreasing distances to riparian margins (e.g. Fukui *et al.* 2006). Secondly, rivers and riparian vegetation are important connecting corridors facilitating bat movement (e.g. Hein *et al.* 2009). With the exception of Whewell's Bush, all the sites with confirmed LTB presence are connected by the Waikato River and fall within a continuous riparian ecotone (Dekrout 2009; Clarkson & McQueen 2004). Finally, riparian zones support structural habitat (e.g. topographical complexity and old-growth trees) favoured by roosting and foraging individuals (Sedgeley & O'Donnell 2004; O'Donnell 2001a; O'Donnell & Sedgeley 1999; Daniel 1990). Linear landscape features such as rivers can also be important navigational references for commuting bats (e.g. Verboom *et al.* 1999; Verboom 1998).

Failure to detect LTBs at three urban sites surrounded by roads and houses (i.e. Hillcrest Park, the university campus and Claudelands Bush) suggests that anthropogenic structures and/or activities may also influence LTB activity. Dekrout (2009) also failed to detect LTBs at Claudelands Bush and identified that housing density, road density and artificial lighting negatively correlated with LTB activity in Hamilton City. It is likely that a combination of anthropogenic variables (e.g. light and vehicle traffic), a lack of connectivity with other habitats, and other variables not considered in this study (e.g. mammalian pest density) collectively influence how LTBs make use of available habitats in this human-dominated environment. Stone *et al* (2009) experimentally demonstrated that streetlights disrupted the commuting behaviour of lesser horseshoe bats

(*Rhinolophus hipposideros*). Kerth and Melber (2009) showed that motorways can restrict habitat access in certain bat species and bat casualties from road traffic have also been documented (Gaisler *et al.* 2009; Lesinski 2008). Roads also flank two out of the three rural sites surveyed (i.e. Whewell's Bush and Mystery Creek golf course) but I still detected LTBs at these sites, albeit at lower activity levels compared a rural site not flanked by roads or houses (i.e. the oak fragment). It is possible that lower light levels in rural areas may explain why LTBs use rural sites but not urban sites flanked by roads. More experimental studies using playback techniques are needed to better understand the effect anthropogenic variables (e.g. vehicle noise and light) have on LTB behaviour and habitat use patterns in and around Hamilton City (see Chapter 5 for an example of how this might be achieved; see also Kerth & Melber 2009; Stone *et al*. 2009; Schaub *et al*. 2008; Shirely *et al*. 2001 for other examples).

This study confirmed that LTBs do use multiple habitats in and around Hamilton City. Bat activity was not restricted to a single urban park (i.e. Hammond Bush) as previously reported following 13 monthly hand-held detector surveys at 18 inner city green spaces (Dekrout 2009). The reason for this discrepancy in results is likely due to the different monitoring methods employed in each study. Hand-held bat detector surveys are limited in that they depend heavily on operator-effort for only brief periods of time and detectors are highly directional and subject to execution errors (e.g. adjustments to frequency settings can result in bats not being detected; de Oliveira *et al*, 1999). In this study I used remotely operating detectors that: store recorded echolocation pulses for later inspection; provide a standardized method for bat detection and survey; and can be used throughout the night over consecutive days across multiple sites (Lloyd

2009; O'Donnell & Sedgeley 1994; Thomas & West 1989). Acoustic bat monitoring is a relatively simple, affordable and effective way to quickly obtain useful behavioural information about LTBs. However, it is important to note that researchers using detectors to compare habitat use patterns at different sites should keep sampling effort constant across all sites (i.e. monitor sites for the same amount of time using the same number of detectors) as demonstrated in this study. Failing to do so can influence the number of LTB detections, which could skew data (Gannon *et al.* 2003; Sherwin *et al.* 2000; Thomas & West 1989). It is also important to note that just because LTBs are not detected at a given habitat does not necessarily mean that bats do not use that habitat. Other intensive LTB presence/absence surveys should be undertaken to better ascertain how LTBs are distributed throughout this modified environment. It is possible that LTBs are more widespread than shown in this study. Future bat surveys should focus on forested habitats situated adjacent to or near the Waikato River as well as native and exotic rural forest remnants on the outskirts of the city.

Conclusion

I applied practical LTB monitoring recommendations developed in Chapter 2 in two different ways in this study. Firstly, I demonstrated that concurrent monitoring at multiple sites can provide useful information about the temporal and spatial activity patterns of bats. Secondly, a presence/absence survey showed that bats are more widespread in the Hamilton region than previously thought. It still remains unclear how specific anthropogenic variables such as vehicle traffic, housing density and artificial lighting affect bat behaviour in this human-dominated environment and future research should investigate this using experimental approaches (i.e. playback techniques; see Chapter 5). Understanding

how anthropogenic variables affect wildlife is important as urban areas continue to expand worldwide (United Nations 2008). This study suggests that distance from riparian margins, habitat connectivity and the presence of anthropogenic structures (e.g. roads and houses) likely influences how LTBs are distributed and use available habitats in and around Hamilton City. Improvements to our knowledge of how LTBs make use of modified landscapes should enable researchers to better focus available resources, such as monitoring and protecting habitats and landscape features most important to bats.

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Chapter 4

Tracking the use of in-flight long-tailed bat calls: An additional data output from automated heterodyne bat detectors

4.1 Abstract

Bats are among the most 'acoustically-oriented' mammals, relying on complex vocalisations for both orientation (echolocation pulses) and communication (social calls). In this paper, I demonstrate how automated heterodyne bat detectors, already widely used in New Zealand to monitor native bat species by recording stereotypical echolocation sequences, can also be used to track in-flight calls emitted by long-tailed bats (*Chalinolobus tuberculatus*; LTB). I classified modified (heterodyned) LTB calls by visual and auditory inspection of basic waveforms. I tracked the use of the three most common call types (chirps, pulses and buzzes) over four months of the LTB breeding season (December-March) at two exotic forest fragments on the edge and outskirts of Hamilton City. I found that pulses and buzzes were predominately recorded around the time of pregnancy-lactation and lactation-juvenile volancy, respectively. Both pulses and buzzes were only ever detected at one of the two sites concurrently monitored. Pulses were frequently (ca. 42%) associated with multi-bat echolocation sequences and buzzes were the most infrequently (only 3% of recorded calls) recorded call type. I speculated that pulses and buzzes may be discreet situation-specific social calls mediating interactions between reproductive females and/or young. Unlike, pulses and buzzes, chirps were more frequently recorded (89% of calls were chirps) across all months of monitoring at both sites. I speculated that chirps may be more generally associated with foraging activity (i.e. echolocative). Future studies are needed to better elucidate call function/s using playback experiments.

Keywords: acoustic monitoring, bat detector, call function, *Chalinolobus tuberculatus*, habitat partitioning, social interactions.

4.2 Introduction

Signals provide individuals with the means to mediate social interactions (Bradbury & Vehrencamp 1998; Rogers & Kaplan 1998; Krebs & Dawkins 1984). Many animal taxa have evolved vocalisations for this purpose. Vocal signals might be used to attract a mate (e.g. male advertisement calls in bird-voiced treefrogs (*Hyla avivoca*); Martinez-Rivera & Gerhardt 2008), recognize and warn conspecifics (e.g. alarm calls used by collared pikas (*Ochotona collaris*); Trefry & Hik 2009), or challenge competitors (e.g. songs used by swamp sparrows (*Melospiza georgiana*) during aggressive male-male encounters; Ballentine *et al.* 2008). In many cases vocal signals may serve discreet situation-specific functions (e.g. predator alarm calls in vervet monkeys (*Chlorocebus pygerythrus*); Seyfarth *et al.* 1980).

Bats are among the most diverse and gregarious mammalian orders (Feldhamer *et al.* 2007; Bradbury 1977b). Many bat species are group-living and exhibit diverse and complex social behaviours (Kerth 2008; Wilkinson 2003; Kunz & Pierson 1994), including: reciprocal food sharing in vampire bats (*Desmodus rotundus*; Paolucci *et al.* 2006; Wilkinson 1990); mass communual breeding in Mexican free-tailed bats (*Tadarida brasiliensis*; McCracken 1993; McCracken & Gustin 1987); and territoriality and harem defence in male sac-winged bats (*Saccopteryx bilineata*; Behr *et al.* 2009). A diverse range of vocalisations may mediate these and other social interactions. For example, male sac-winged bats produce complex 'songs' outside roost territories. Songs may contain both 'noisy' broadband calls directed toward other males in territory defence and low-frequency tonal calls for appeasement and female attraction (Behr & Helversen 2004; Davidson & Wilkinson 2004). Males of other bat

species (e.g. Nathusius' pipistelles (*Pipistrellus nathusii*; Russ & Racey 2007); the common pipistrelle (*Pipistrellus pipistrellus*; Lundberg & Gerill 1986); hammer-headed bats (*Hypsignathus monstrosus*; Bradbury 1977a); African false vampire bats (*Cardioderma cor*; McWilliam 1987); and lesser noctule bats (*Nyctalus leisleri*; von Helversen & von Helversen 1994)) also produce complex advertisement or mate attraction calls. In white-winged false vampire bats (*Diaemus youngi*) individuals use frequency-modulated (FM; calls passing through a frequency range) 'isolation calls' (i-calls) to attract conspecifics, which often results in antiphonal vocal exchanges between individuals (i.e. alternating duet-like vocal behaviour; Carter *et al.* 2008). Similar antiphonal exchanges have been shown to mediate mother-pup reunions in greater horseshoe bats (*Rhinolophus ferrumequinum*; Matsumara 1981; Matsumara 1979), lesser fish-catching bats (*Noctilio alberventris*; Brown *et al.* 1983) and greater spear-nosed bats (*Phyllostomus hastatus*; Bohn *et al.* 2007). Low-frequency screech calls in greater spear nosed bats have also been shown to co-ordinate foraging amongst group members (Boughman & Wilkinson 1998; Wilkinson & Boughman 1998). These examples highlight the diversity in the structure and function of bat social calls. However, these studies are among the few that have classified and investigated social call structure and/or function in a subset of the more than 1,200 recognized bat species. This is not surprising given the cryptic and nocturnal nature of most bats (Fenton 1985). Although complex vocal repertoires are anticipated for many bat species, they remain largely undocumented or poorly understood.

Echolocating bats (microbats) are one of the few known vertebrates that rely on vocalisations for both orientation and communication (Fenton 1985; Sales

& Pye 1974). As a result, microbat vocalisations are often classified as being either: 1.) echolocation pulses/sequences used for foraging and orientation (i.e. actively produced sounds (typically of high frequency; >20 kHz), which individuals use to compare returning echoes within their local environment); or 2.) social calls (i.e. signals used specifically for communication; Fenton 2003). However, this strict classification of microbat vocalisations into two broad functional categories is likely an oversimplification when applied to most species (Fenton 1985; Gould 1977; Möhres 1967). Indeed, a number of studies have shown that echolocation calls may reveal important details about echolocater behaviour (e.g. feeding buzzes reveal foraging behaviour) and identity including: age (Masters *et al.* 1995); sex (Sawyer & Burnett 2006); size (Barclay *et al.* 1999); group affiliation (Kazial *et al.* 2001; Pearl & Fenton 1996); and even lactation state (Kazial *et al.* 2008b). These details have been shown to be used opportunistically (e.g. identify location of prey; Hickey & Fenton 1989; Leonard & Fenton 1984; Barclay 1982) and co-operatively (e.g. mutual recognition of group members; Kazial *et al.* 2008a; Kazial & Masters 2004) by listening conspecifics. Similarly, many bat species use social calls in-flight for communication and it is equally likely that these calls may serve an orientation or foraging function (Fenton 2003).

The long-tailed bat (*Chalinolobus tuberculatus*; LTB) is one of only two surviving bat species endemic to New Zealand. Individuals rely on broadband FM echolocation sequences (ca. 40 kHz) for orientation and in-flight foraging (O'Donnell 2001a; Parsons *et al.* 1997). However, the social call repertoire of this species remains undocumented. LTB social groups have been described as highly structured and of small average sizes (ca. 35 individuals; O'Donnell 2005). In the

Eglinton Valley (South Island; S.I.) individuals are known to form non-random social units that vary in size from tens to hundreds of individuals (O'Donnell 2000a). Social units may overlap in range forming larger deme populations (i.e. interbreeding occurs across local social groups; O'Donnell 2000a). It is unclear how males attract females for mating. Reproductive females typically form maternity colonies and synchronously give birth to only a single pup, which they nurse until volancy (O' Donnell, 2005). Females become pregnant in austral spring (October-November) and give birth in late spring/early summer (November-December; Figure 4.1; Dekrout 2009; O'Donnell 2001a). It is thought that species-specific i-calls are used to maintain mother-young contact as reported for other bat species (O'Donnell 2001a).
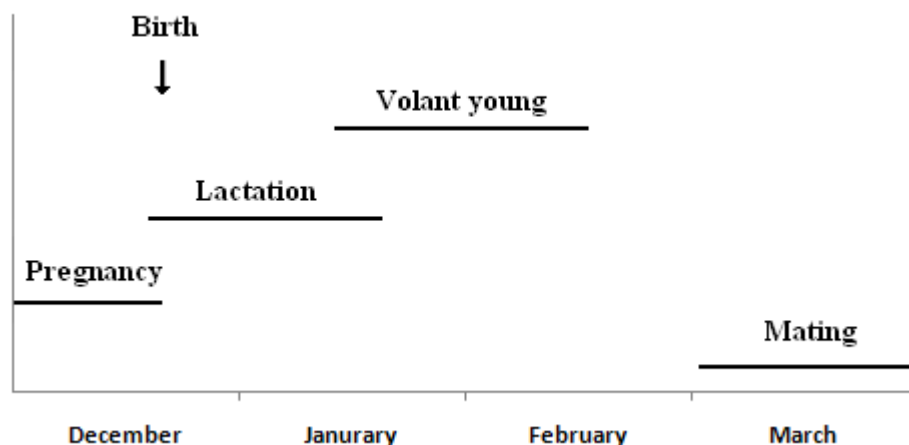
Figure 4.1 Reproductive stages for LTBs over the four month monitoring period as inferred from data collected for LTBs in the Eglinton Valley (S.I.; O'Donnell 2005; 2002a; 2001a) and the Grand Canyon Cave (N.I.; Dekrout 2009).

I am unaware of a study that has identified or categorized LTB calls that differ from stereotypical echolocation sequences. The aims of this chapter were: 1.) to identify and categorise in-flight LTB calls recorded on detectors by visual and auditory inspection of waveforms only; 2.) monitor the use of the three most

common call types over four months of the LTB breeding period at two exotic

forest fragments in Hamilton City (N.I., New Zealand); and 3.) provide basic

monitoring recommendations aimed at maximising detection rate for in-flight

calls in modified habitats. Bat researchers and wildlife managers that rely on

detectors to monitor LTBs in New Zealand could use this information to: 1.)

improve recordings of non-echolocation LTB calls for bioacoustic analyses; and

2.) identify habitats of importance to aggregating bats at certain times of the year

(e.g. lactation and juvenile volancy) when individuals may be most sensitive to

human disturbances (e.g. trapping). Thus, better understanding the vocal

repertoire of a species can provide insight into the social behaviour of individuals

(e.g. reproduction patterns), which in turn could better guide conservation efforts

(e.g. identifying and protecting habitats used by aggregating and/or breeding

individuals). I speculate on call functions based on the temporal and spatial

calling patterns obtained from recorded data; however, I recognize that this can

only be properly elucidated using experimental playback techniques. I discuss

how future studies might use playback to determine LTB call functions and

explore the potential for unmodified bat calls to be used as 'acoustic lures' in bat

conservation initiatives such as encouraging residency in artificial 'bat houses' in

roost limited environments and aiding the capture and translocation of individuals.

4.3 Methods and Materials

Call recording

LTB calls were passively recorded between December 2009 and March 2010 (i.e.

austral summer to autumn) using automated heterodyne bat detectors (Stag Box

III, The Department of Conservation). Bat detectors are custom made in New

Zealand and are designed to concurrently detect and record the stereotypical

foraging echolocation sequences emitted by both native bat species on two

frequency channels – 28 kHz for lesser short-tailed bats (*Mystacina tuberculata*;

STBs) and 40 kHz for LTBs (Lloyd 2009; O'Donnell & Sedgeley 1994). There is

little overlap between the echolocation frequencies used by each bat species

making this dual-monitoring approach both appropriate and effective in New

Zealand (Parsons 1997). In-flight calls used by LTBs are also inadvertently

recorded on the 28 kHz channels of bat detectors. Detectors only record a 'slice'

of specific LTB calls that have frequency components falling within the restricted

detection range of the 28 kHz channel. Calls may be described as ultrasonic (>20

kHz) of unknown function/s emitted by flying LTBs (i.e. calls are concurrently

recorded with 40 kHz echolocation sequences; see Table 4.1). Calls have also

been detected as individuals leave roosts using hand-held bat detectors (Bat4

detector, Magenta Electronics Ltd., UK) set to ca. 30 kHz (personal observations).

Detectors automatically record and store sound files (i.e. bat passes) onto Secure

Digital disks (2GB; SanDisk) in WAV format for later analyses. All calls are

automatically converted into a lower frequency that is audible to humans. This

heterodyning process modifies the spectral and temporal properties of all recorded

calls

In-flight LTB calls were concurrently monitored (i.e. the same sampling effort) at two small exotic forest fragments on the edge and outskirts of Hamilton City including a: 1.) ca. 1.2 ha old-growth oak (*Quercus robur*; mean diameter 60.1 ± 16.4 cm) fragment on the rural outskirts of the city; and 2.) ca. 0.3 ha open area flanking a native forest remnant on the urban edge of the city (i.e. Hammond Bush; Chapter 2). At the oak fragment four microhabitats were delineated based on landscape features (e.g. presence of water bodies; Chapter 2), which included: an open edge (OE); an open edge with water bodies (WOE); an interior (I); and a river edge (RE). The same monitoring set-up and rotation scheme detailed in Chapter 2 was used in this study. Briefly, this entailed setting up a rope and pulley system in 20 trees across both sites (four alder (*Alnus* sp.) trees at Hammond Bush and four mature oak trees in each of the four microhabitats at the oak fragment). Rope and pulley systems enabled detectors to be hoisted up trees in a two-tier vertical arrangement (i.e. a detector at a lower (4-7m) and higher (15-30m) height). Ten detector pairs with similar sensitivities were rotated between selected trees across all microhabitats every 3-5 days. Therefore detector pairs concurrently recorded LTB calls at each field sites and within each microhabitat at the oak fragment. All detectors were calibrated to start monitoring LTBs 30 minutes before sunset until 30 minutes after sunrise on as many nights as possible irrespective of weather conditions.

Call classification

Each call was recorded with an exact time (hour/minute/second) and date (day/month/year) stamp. Calls were viewed and identified by both visual and auditory inspection of the waveforms using BatSearch 1.02 Software (The Department of Conservation, Wellington, New Zealand). LTB calls were

classified as being either: 1.) stereotypical LTB echolocation sequences recorded on the 40 kHz channel of detectors with no 28 kHz call component (i.e. search phase pulses or feeding buzzes; Table 4.1); 2.) LTB calls recorded on the 28 kHz channel of detectors with an associated 40 kHz echolocation component (i.e. in-flight LTB calls); and 3.) non-bat sounds (e.g. rain, wind or insect generated noise files) that were discarded. All LTB calls were classified into one of three broadly defined categories based on how similar calls sounded and looked in waveform format (i.e. no meaningful quantitative measurements of call parameters was possible). Call categories included chirps, pulses (not related to echolocation sequences) and buzzes (more prolonged buzzes that differ from rapid feeding buzzes; Table 4.1). For each call I noted if there was an associated: feeding buzz indicating insect pursuit and potential capture (Griffin *et al.* 1960); whether two or more echolocation sequences were simultaneously recorded indicating that more than one bat was flying at the same time; and if more than one call type was emitted in sequence (i.e. a combination of call types on the same sound file). Several infrequently recorded calls (i.e. chattering outside a known LTB roost and a 'spring' call; Table 4.1) were also identified and classified in an 'other' category but could not be tracked due to small sample sizes. For comparative purposes, I also identified all echolocation pulses (i.e. 40 kHz recordings with no 28 kHz calls) that had two or more bats in-flight simultaneously (see Chapter 2). All calls were identified and classified by the same researcher (see Table 4.1 and Appendix II to view and listen to representative call types).

Statistical analyses

I calculated the mean number of calls in each call category for every hour of monitoring after official sunset (NZST; data retrieved from the National Climate

Database, National Institute for Water and Atmosphere, www.cliflo.niwa.co.nz).
Data was kept separate for each field site and month of monitoring. I calculated
the percentage total of calls in each call category that had an associated: feeding
buzz; two or more bats in-flight simultaneously; and/or combinations of different
call types recorded on the same sound file. I repeated this for stereotypical
echolocation sequences (i.e. only 40 kHz recordings) recorded over the same
monitoring period for comparison (see Chapter 2 for these details).

Detector height and microhabitat patterns

I calculated the mean number of calls recorded in each microhabitat at the oak
fragment during each hour after sunset. I used a factorial ANOVA (i.e. 2 x 2
between-groups ANOVA; dependant variable: number of bat calls; independent
factors: month and tier height) to determine if placing detectors at a lower or
higher height made any difference to the number of LTB calls detected. Data was
kept separate for each habitat to identify site-specific trends in LTB detection
rates. A factorial ANOVA (dependant variable: number of bat passes;
independent factors: season and microhabitat) was also used to investigate if the
number of LTB calls detected differed according to the microhabitat in which
detectors were placed.

All data was log-transformed where necessary to achieve normality or near
normality (Kolmogorov-Smirnov and Shapiro-Wilk's W test). *Post-hoc* analyses
were undertaken using Tukey tests. Statistical analyses were completed using
STATISTICA® 8.0 (Statsoft Inc, Tulsa, OK, USA) with the level of significance
held at 0.05. Means are presented as ± SE throughout the paper.

Table 4.1 Representative waveforms for stereotypical LTB echolocation sequences and in-flight LTB calls as recorded on automated bat detectors. Both the 28 and 40 kHz recording channels are presented for each waveform.

Call categories	Waveforms
I.) Stereotypical echolocation sequences	
A.) Search phase pulses	
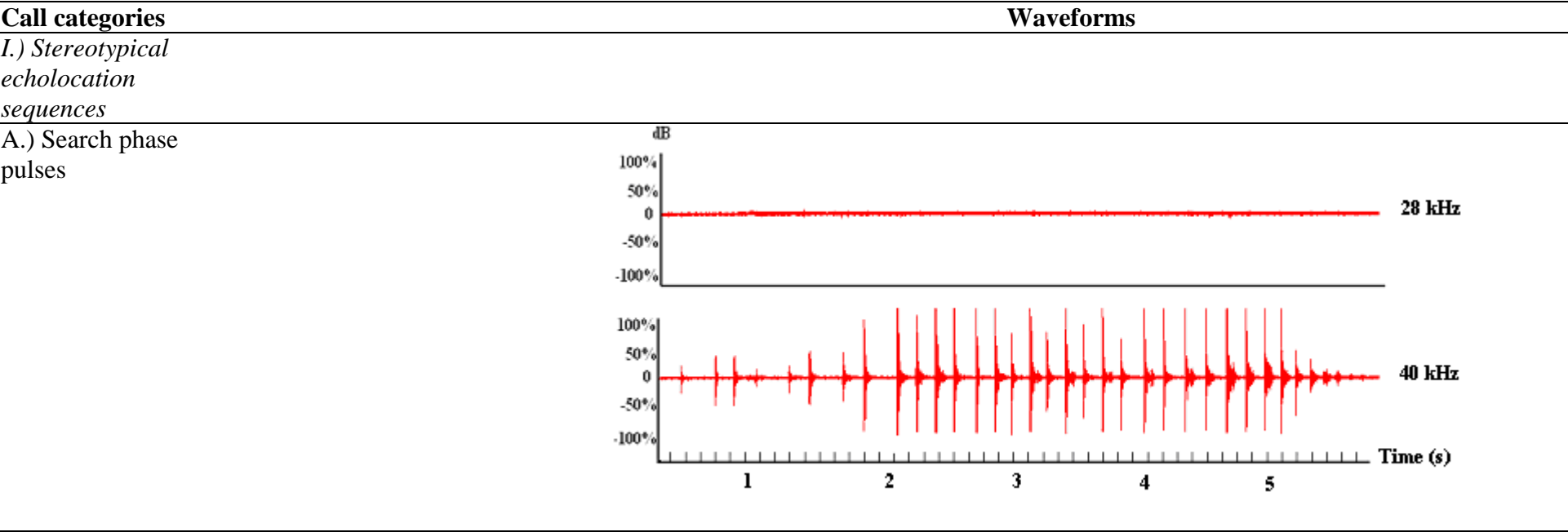
B.) Feeding buzzes
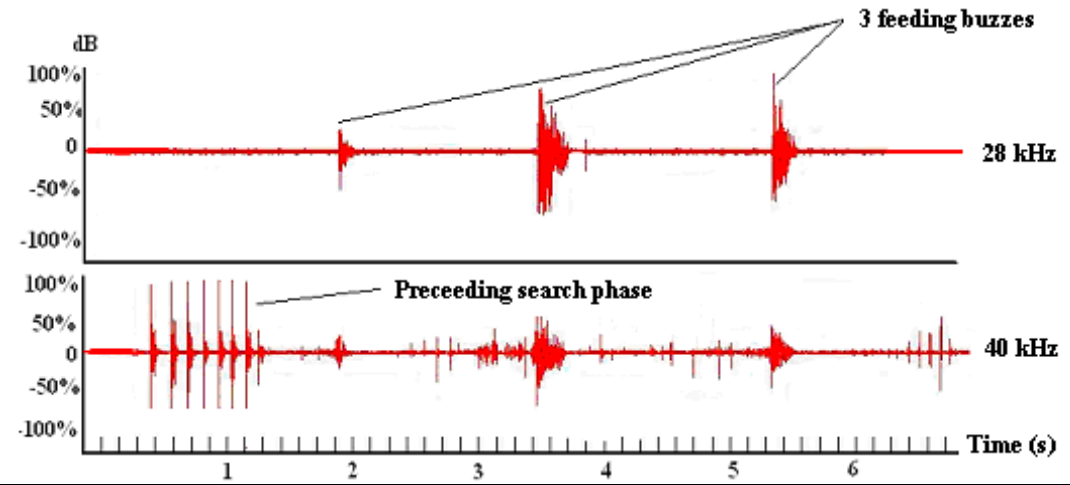
II.) In-flight calls

A.) Chirps
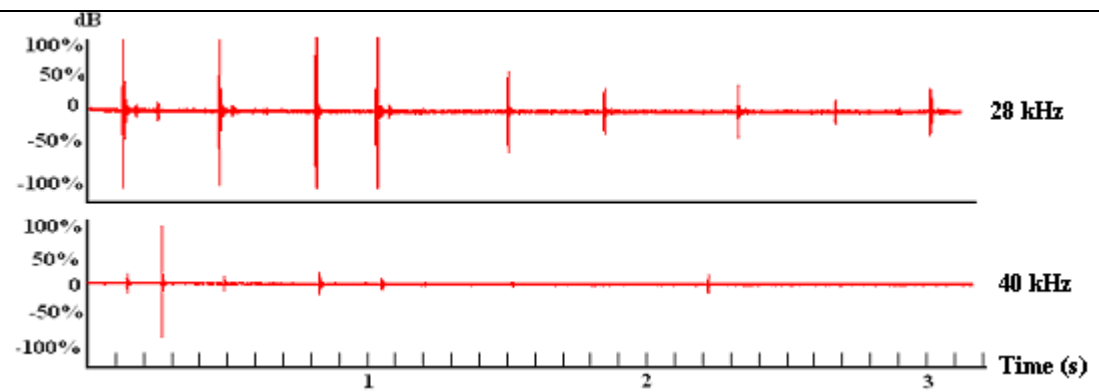
B.) Pulses
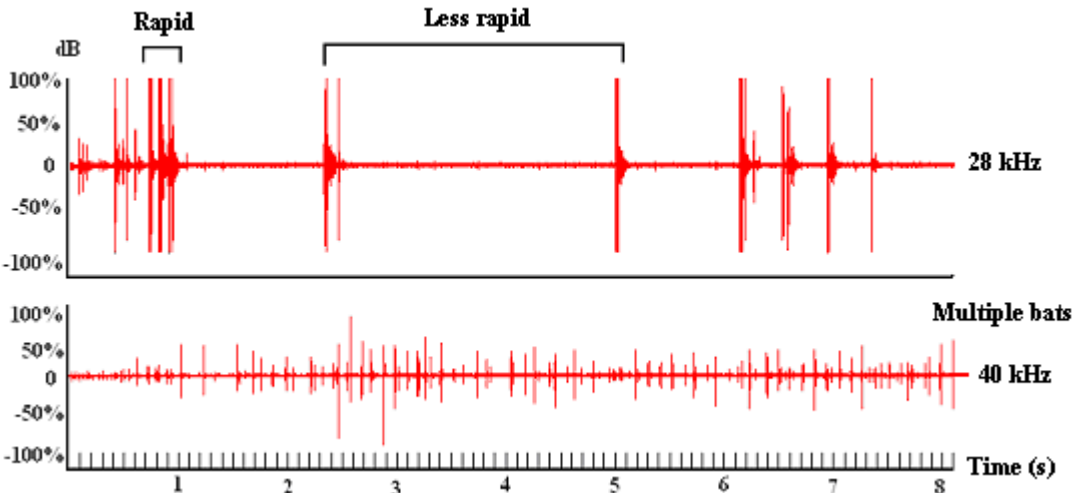
C.) Buzzes
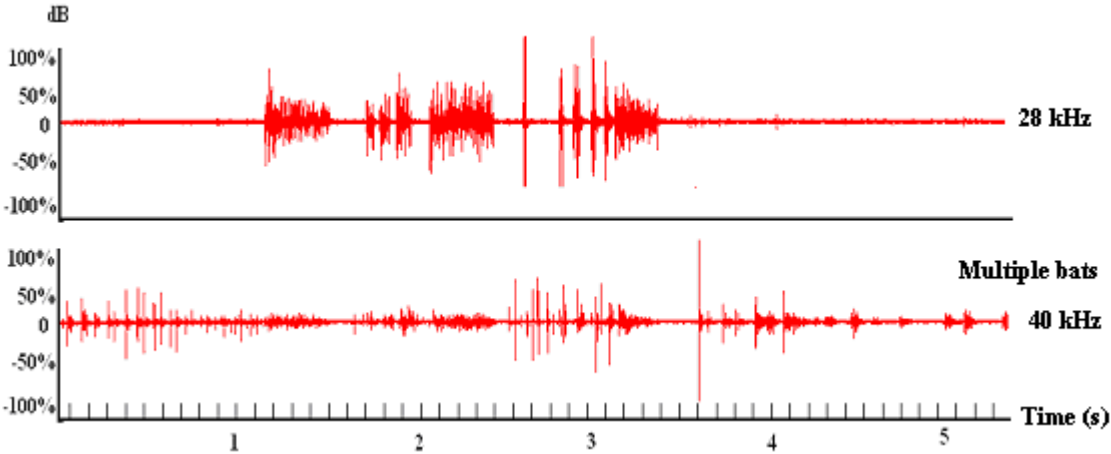
D.) Other calls   a.) Combination sequence
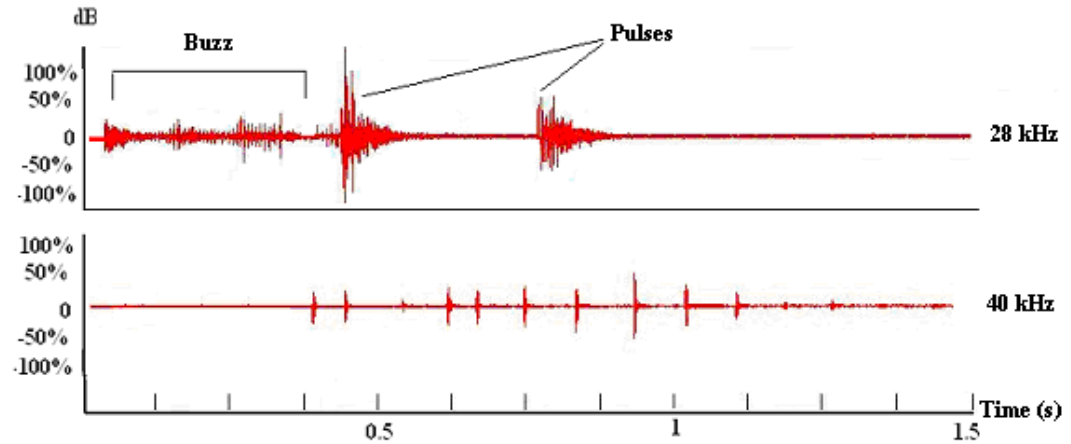
b.) Chattering outside a
known LTB roost (recorded
without 40 kHz echolocation
component)
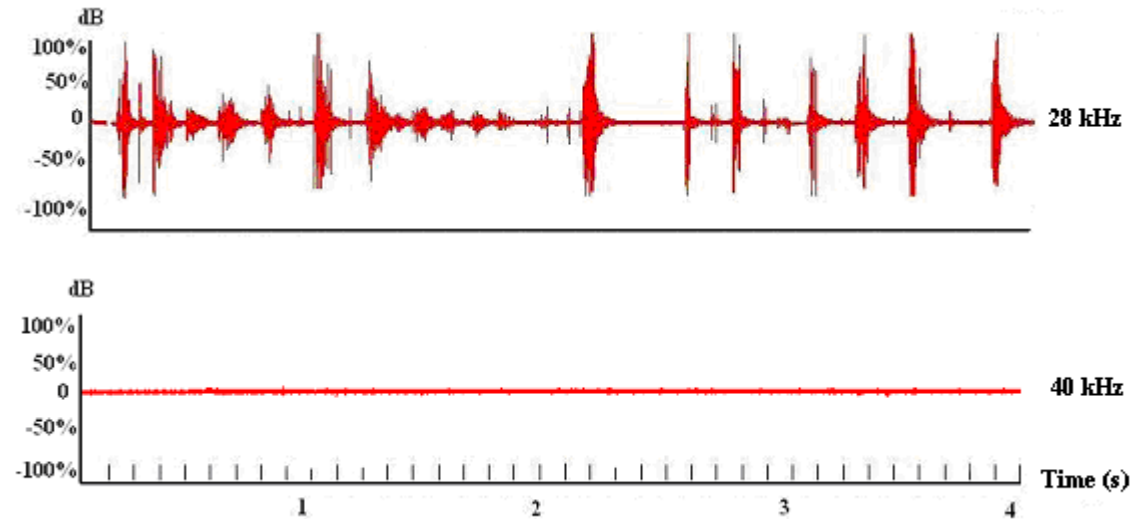
c.) 'Spring' call
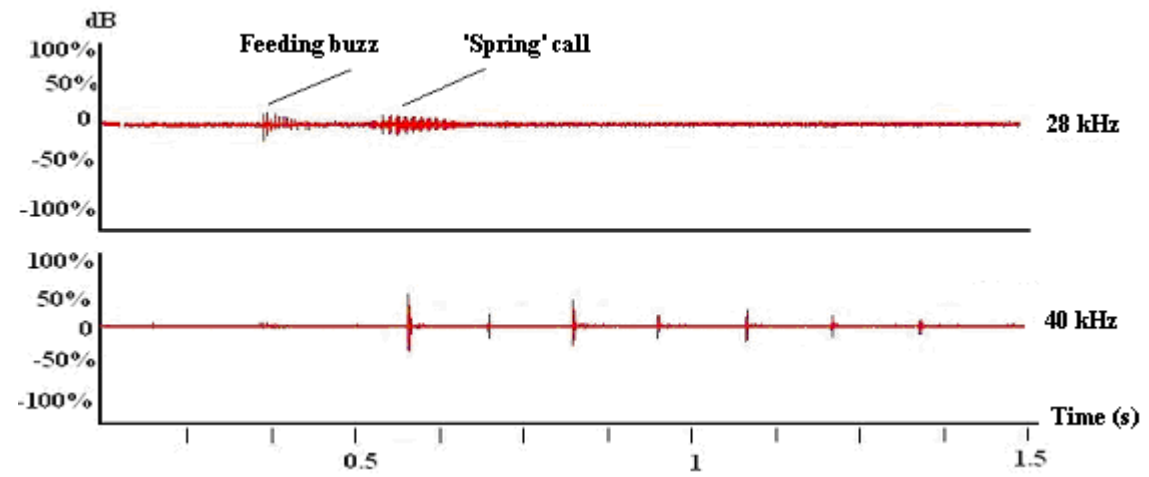
3.4 Results

A total of 1,157 in-flight LTB calls were recorded during 91 nights of monitoring over four consecutive months of monitoring. The greatest percentage of calls was recorded during December (43%); numbers decreased during January (24%) and February (25%) and was lowest by March (8%). A total of 259 stereotypical echolocation sequences with two or more bats flying together were also classified during this period.

Chirps

Chirps were the most frequently recorded call type accounting for 89% of all recorded calls (Figure 4.2). Chirps were recorded during all four months of monitoring and were first identified on detectors as early as August 2009 (Chapter 2). Chirp sequences consisted of two or more 'whistle-like' calls emitted singularly with varying pulses intervals (Table 4.1). Only 4% of chirps had two or more bats in-flight simultaneously (Figure 4.3A). Chirps that had two or more bats flying at the same time were most common during January (3% of chirps; Figure 4.3A). Chirps were rarely associated with feeding buzzes ($< 7\%$ of chirps; Figure 4.3B).

Pulses

Pulses consisted of multiple (1-22 pulses/sound file) intense-sounding 'squeal-like' sounds of varying inter-pulse intervals (Table 4.1). This call type accounted

for 8% of all recorded calls. Pulses were almost entirely recorded during December and January, which accounting for 98% of all recorded pulses (only 2 sound files contained pulses in February and none in March; Figure 4.2 and 4.3). Pulses with two or more bats flying together at the same time made up 43% of all recorded pulses (Figure 4.3A). Between December and January the number of pulses recorded with a feeding buzz increased from 3.9% to 11.1% (Figure 4.3B).

Buzzes

Buzzes were the most infrequently recorded call type accounting for just 3% of recorded calls (Figure 4.2). Buzzes were stereotypical consisting of multiple staccato 'zip-sounds'. These calls were more prolonged compared with rapid echolocative feeding buzzes, which distinguished the two call types (Table 4.1). During December no buzzes were recorded with two or more bats in-flight or with associated feeding buzzes (Figure 4.3A and B). However, during January and February the percentage of buzzes with two or more bats increased to 46% and 40%, respectively (Figure 4.4A). The percentage of buzzes associated with feeding buzzes (identified on the 28 kHz channel) increased from 8% to 20% between January and February (Figure 4.4B). No buzzes were recorded during March.

Other calls

On very rare occasions (0.01% of recorded calls) combinations of call types were recorded on the same sound file (e.g. pulses and chirps). I also recorded other calls that could not be conclusively classified into one of the other three call categories. These included chattering outside a known LTB roost and a 'spring' call (recorded on a single occasion following a feeding buzz; Table 4.1). All of these calls were recorded at the oak fragment only.

Echolocation sequences

The percentage of echolocation sequences with two or more bats in-flight at the same time increased from 16% to 32% between December and January (Figure 4.4B). Similarly, between February and March the percentage increased from 23% to 34%. Echolocation sequences with two or more bats in-flight that also contained a feeding buzz increased progressively from 9% in December to 11% and 20% in January and February, respectively. In March only 2% of multi-bat echolocation sequences had associated feeding buzzes.
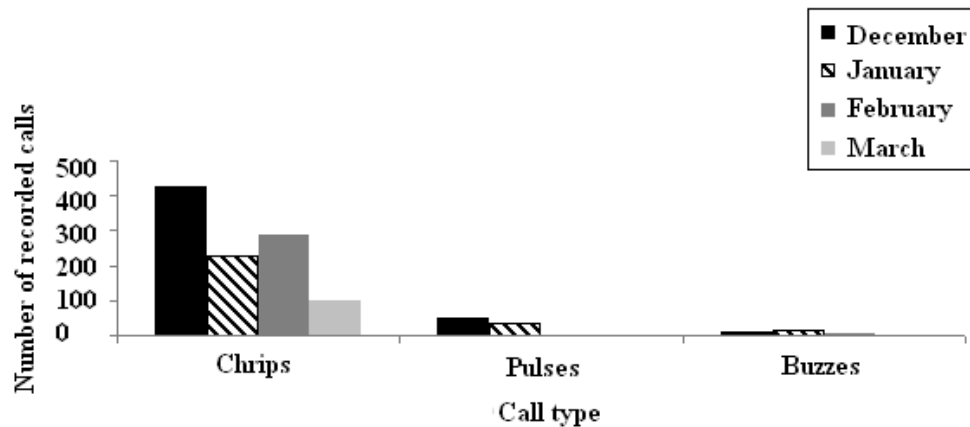
Figure 4.2 The number of recorded calls for each call type (chirps, pulses and buzzes) during the four months of the LTB breeding season.
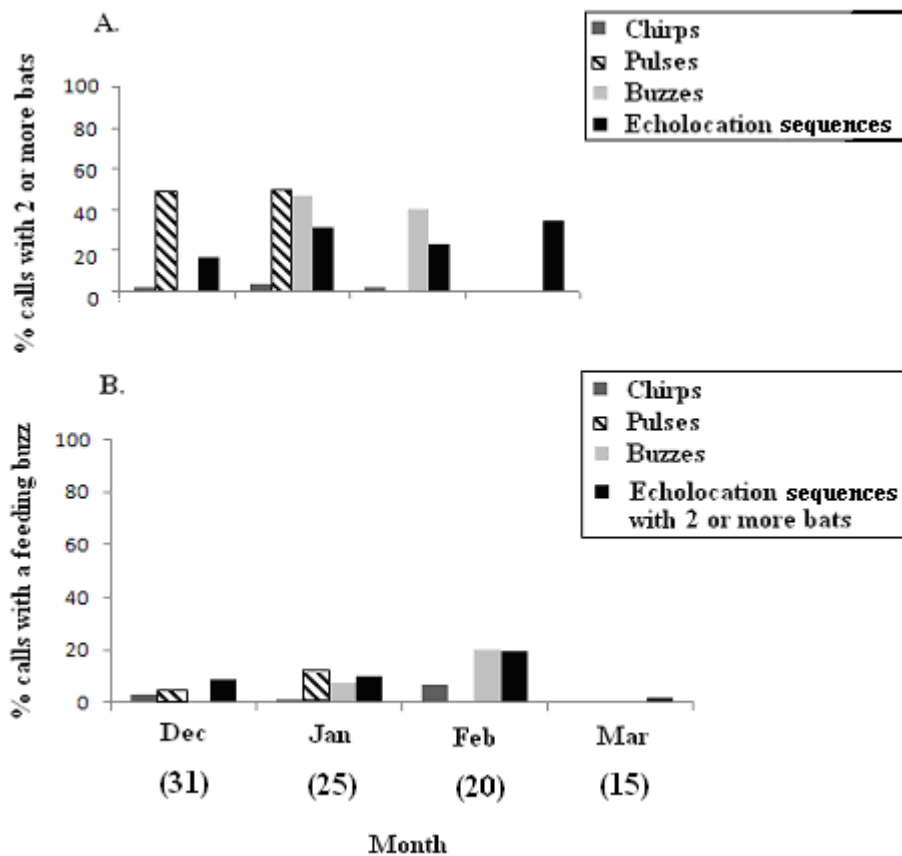
Figure 4.3 The percentage total of calls for each call type that had A.) two or more bats in-flight simultaneously (i.e. multi-bat echolocation sequences) and B.) associated feeding buzzes during each month of call monitoring. The number of days of call monitoring in each month is presented in brackets.

Across habitat patterns

Hammond Bush

The only in-flight call recorded at this site was chirps (Figure 4.4). Chirps were regularly recorded throughout the night across all months of monitoring. The number of chirps peaked between the first and third hours after sunset and again before dawn, which is consistent with foraging activity reported for LTBs at this site (see Figure 2.5, Chapter 2). Multi-bat echolocation sequences were infrequently recorded at Hammond Bush (Figure 4.4).

Oak fragment

LTB call diversity at the oak fragment was greater compared with Hammond Bush (Figure 4.4). All call types were recorded at this site, including infrequently recorded calls such as chattering, spring calls and various combination sequences (except during March when only chirps were recorded; Figure 4.4). Pulses were almost exclusively recorded during December and January. Buzzes were almost exclusively recorded during January and February. Pulses and buzzes peaked after dusk and again before dawn and were regularly associated with multi-bat echolocation sequences. The number of in-flight calls and multi-bat echolocation sequences were generally reduced by February.
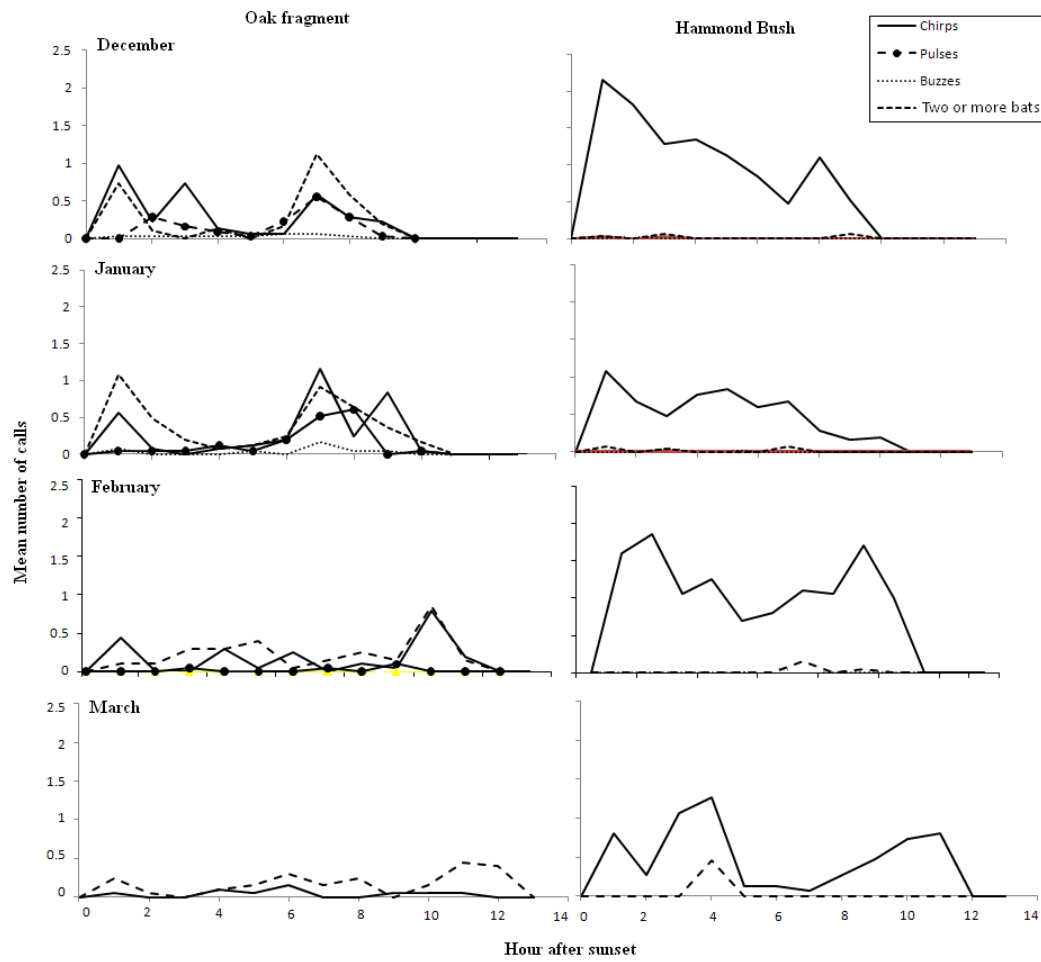
Figure 4.4 Mean number of calls recorded during each hour after sunset for each call type (including echolocation sequences with two or more bats in-flight at the same time).

Within habitat patterns

Detector height and microhabitat patterns

There was no significant difference between the number of in-flight calls recorded at different tier heights during each month of monitoring at both Hammond Bush ($F_{1, 133} = 0.03$, $P > 0.05$) and the oak fragment ($F_{1, 98} = 0.49$, $P > 0.05$; Figure 4.5). However, call behaviour was not randomly distributed across microhabitats at the oak fragment (Figure 4.6). Significantly ($F_{3, 368} = 4.83$, $P = 0.003$) more in-flight calls were recorded in the WOE microhabitat compared with all other microhabitats with little variation across the different months of monitoring. In

December, January and February 72%, 40% and 52% of all in-flight calls were recorded in the WOE, respectively. However, in March only 30% of calls were recorded in the WOE while 55% were recorded in the RE.
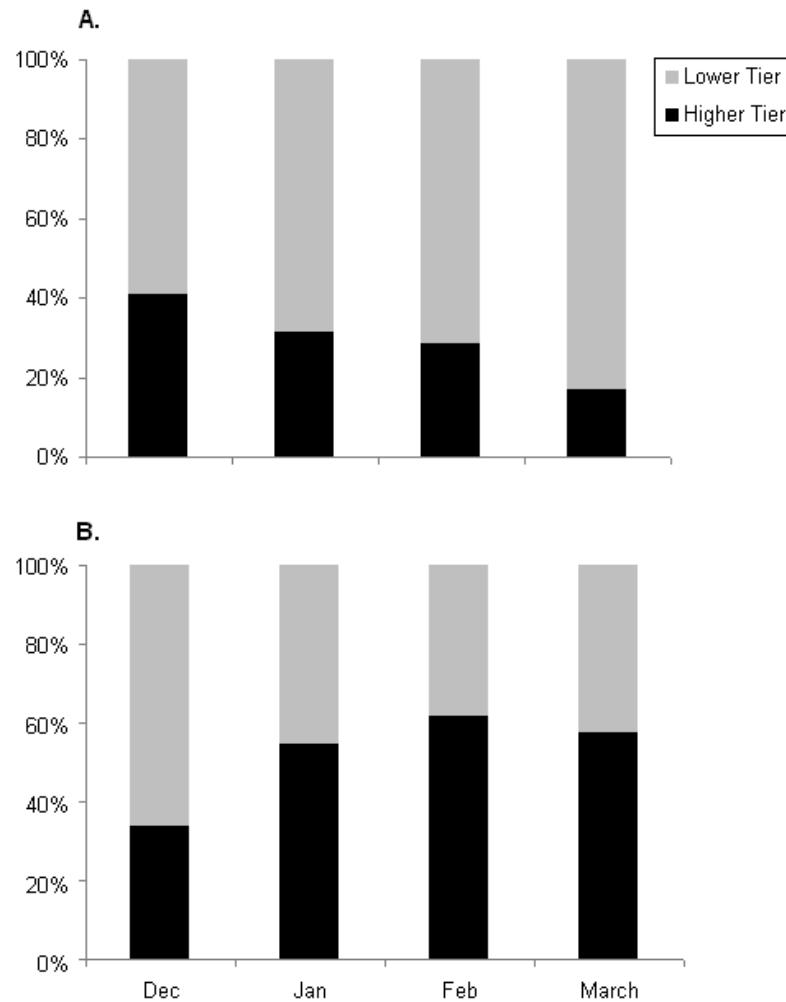
Figure 4.5 The percentage total calls recorded at a lower (4-7m) and higher (15-30m) height at each site across the four months of monitoring
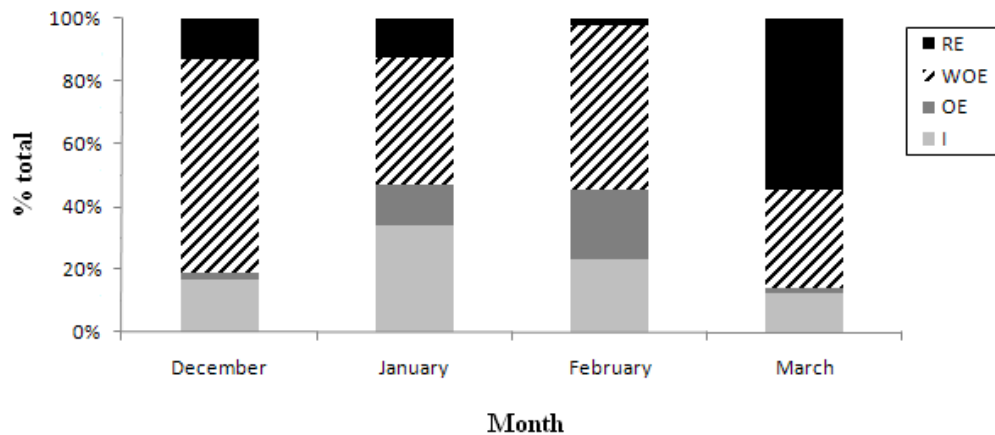
Figure 4.6 The percentage total LTB calls recorded in each microhabitat at the oak fragment over the four months of monitoring.

4.5 Discussion

Monthly and nightly call patterns

Bats are known to emit complex vocalisations for social and echolocative purposes (Fenton 2003). Therefore, the function of the LTB call types categorised and tracked in this study either serve a social (i.e. communicative) and/or echolocation (e.g. foraging) function. It would be an oversimplification to conclude that LTBs calls serve one or the other function, at least not from the data passively obtained from detectors (for discussions on this issue see Pfalzer & Kusch 2003; Barclay 1999; O'Farrell *et al.* 1999; Fenton 1985; Gould 1977; Möhres 1967). Indeed, I can only speculate on the function/s each LTB call type may serve based on the temporal and spatial calling patterns revealed by recorded data (and what has been documented in other echolocating bat species). In order to determine call function/s, further investigations will be necessary.

The use of certain in-flight calls by LTBs appears to be associated with certain reproductive stages, which in turn may be influenced by different social behaviours (e.g. communal roosting). Pulses were almost exclusively recorded

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during December and January when female LTBs transition from a state of pregnancy to lactation (O'Donnell 2005, 2001a). During both of these months ca. 50% of all pulses were concurrently recorded with multi-bat echolocation pulses. Comparatively, only ca. 35% of echolocation sequences not associated with in-flight calls were recorded with two or more bats flying together at the same time. During January pulses had the highest percentage (11%) of associated feeding buzzes compared with all other call types. Like many other temperate bat species (Speakman & Thomas 2003; Kurta *et al.* 1990; Racey & Swift 1985) the metabolic costs for female LTBs increases during pregnancy and lactation (O'Donnell 2002a, 2001a). Female LTBs typically form maternity colonies in communal roosts and synchronously giving birth to a single pup that is nursed until volancy (O'Donnell 2002a; Sedgeley 2001). It is possible that pulses may be social calls that facilitate co-operative interactions between communal members of a maternity colony, as shown for the calls of other bat species (e.g. screech calls in greater spear-nosed bats; Boughman & Wilkinson 1998; Wilkinson & Boughman 1998). Active (and passive) information transfer between non-randomly associated colony members about the location of resources (e.g. roost sites and ephemeral prey concentrations) could enable many bats to mutually exploit patchy resources (e.g. Kerth & Reckardt 2003; Adams & Simmons 2002; Kerth & König 1999; Wilkinson 1992; but see Kerth *et al.* 2001).

It is also possible that pulses and/or buzzes may be social calls mediating aggressive interactions between conspecifics. Agonistic interactions are often associated with competition for resources (e.g. prey or roosts), which may be limited within a small habitat, like the oak fragment, especially at a time when energetic demands are high (i.e. during pregnancy and lactation). Some aerial

insectivorous bat species are known to passively eavesdrop on the feeding buzzes of foraging conspecifics, which may reveal details about prey location and abundance (Dechmann *et al.* 2010; Gillam 2007; Fenton 2003; Surlykke *et al.* 2003; Barlow & Jones 1997). This can results in gleaning conspecifics that take advantage of this information being chased by other foraging bats (Budenz *et al.* 2009; Bayefsky-Anand *et al.* 2008; Hickey & Fenton 1989; Balcombe & Fenton 1988). Social buzzes that are often spectrally and temporally similar to feeding buzzes are known to mediate agonistic interactions in other bat species (e.g. Mexican free-tailed bats; Schwartz *et al.* 2007). Indeed, the proportion of buzzes that were associated with multi-bat echolocation sequences and feeding buzzes at the oak fragment increased in January and February at a time when young learn to fly and forage (O'Donnell 2001a). It is possible that this call type is used to appease or intimidate conspecifics during foraging bouts. Stereotypical calls like buzzes are often associated with discreet situation-specific social contexts (e.g. 'intimidation buzzes' in the pallid bat (*Anthrozous pallidus*; Orr, 1954) and in-flight 'grumbling sequences' in false vampire bats (*Megaderma lyra*; Leippert, 1994; see also Andrews *et al*. 2006; Barclay & Thomas 1979; Suthers 1965). This could explain why buzzes were recorded relatively infrequently in comparison to the other call types (for similar rarely recorded call types in other bat species see Ma *et al.* 2006 and Habersetzer 1981).

Unlike, pulses and buzzes, chirps were recorded during all months of monitoring and were more common than the other call types, accounting for 89% of recorded calls. This suggests that chirps may not be discreet situation-specific calls but may be more generally associated with in-flight activities like foraging and orientation (i.e. echolocative). Peaks in chirps also overlapped with foraging

peaks after dusk and before dawn (see Chapter 2). In some bat species (e.g.

emballonurid bats in Central America; Jung *et al.* 2007) individuals use

alternating low and high search phase frequencies that are thought to aid echo

discrimination in the presence of conspecifics or in certain habitat types. Chirps

may serve a similar function in LTBs. A greater percentage of chirps recorded at

Hammond Bush may be related to individuals using lower and longer

echolocation sequences in a more open habitat, compared with higher and shorter

echolocation sequences at the more cluttered oak fragment. Longer and lower

frequencies experience less atmospheric attenuation and can improve target

detection over greater distances in open habitats (Wund 2005; Ibáñez *et al.* 2004;

Fenton 2003; Obrist 1995; Simmons & Stein 1980). It remains unclear how LTBs

compensate for echo overlap when flying in the presence of conspecifics. In other

bat species the most well documented 'jamming avoidance' response involves

individuals modifying one or more spectral and/or temporal echolocation

parameter/s (e.g. fundamental frequency or call duration), which creates a more

personalised 'signature' that can be used to discriminate their own echoes from

those of others (Bartonička *et al.* 2007; Bates *et al.* 2008; Jones *et al.* 1994;

Ratcliffe *et al.* 2004; Ulanovsky *et al.* 2004). It is possible that lower frequency

chirps may be used to compensate for acoustic interference during multi-bat

flights; however, very few chirps (< 4%) were recorded with two or more bats

flying together at the same time. I cannot exclude the possibility that chirps serve

a social function like maintaining contact between two or more individuals (e.g.

Fenton *et al.* 2004; Kössl *et al.* 1999; Gould 1973). It is has been suggested that

male bats maintain small foraging territories at Hammond Bush and there also are

accounts of LTBs producing low frequency (20-30kHz) 'songs' during the mating

season (personal communication, Dr. A. Dekrout, Dr. S. Parsons, Auckland University). Perhaps chirps are low frequency components of a more complex in-flight advertisement or territorial 'song' (for examples of this vocal behaviour in other bats see Safi 2008; Sachteleben & von Helversen 2006; Park *et al.* 1996). This could explain why the mean number of chirps/hour was higher at Hammond Bush (compared with the oak fragment).

Across habitat call patterns

There was a clear difference in the diversity of call types recorded at each of the two concurrently monitored habitats, especially during December and January. At Hammond Bush, I never recorded pulses or buzzes. These calls were only recorded at the oak fragment along with combination sequences and other less common call types. It is possible that males and females use different habitats at least during certain times of the year (i.e. sex-based habitat partitioning). Habitat partitioning is not uncommon in temperate bat species (for examples see Mackie & Racey 2007; Safi *et al.* 2007; Senior *et al.* 2005; Lumsden *et al.* 2002). This may explain the differential use of different call types across these two habitats. It is possible that reproductive females and young use the oak fragment as a maternity site where densely stoked old-growth trees situated further from anthropogenic structures (e.g. streetlights and houses; Chapter 3) likely support roosts with favourable microclimates (see Dekrout 2009). Reproductive females are known to select roosts with specific microclimate properties (i.e. warmer cavities), which incur energetic benefits for both females and young (Sedgeley 2001; Sedgeley & O'Donnell 1999). Radio-tracking studies undertaken in native forest ecosystems (e.g. Eglinton Valley, S.I.) have revealed that males tend to be more solitary roosting (37% communal) compared with females (63% communal;

Sedgeley 2001; O'Donnell 2000a; Sedgeley & O'Donnell 1999). This could explain why higher incidents of multi-bat echolocation pulses were recorded at the oak fragment (compared with Hammond Bush). Indeed, previous LTB trapping undertaken at Hammond Bush during summer months (2004-2007) revealed a highly male-biased sex ratio (22 males: 1 female; Dekrout 2009). More studies investigating how males and females use habitats across the urban-rural interface of Hamilton City would much better resolve these issues, which in turn would better guide management strategies (e.g. protecting important habitats used by aggregating bats).

Within habitat patterns
The home ranges for lactating female LTBs (median = 330 ha) and (medium = 237 ha) juveniles that have been volant for ca. >2 weeks are among the smallest reported for this species (O'Donnell 2001a, b). However, after two weeks of volancy, juveniles and post-lactating females tend to increase their movements considerably (median = 2,006 ha; O' Donnell, 2001b). In modified and highly fragmented environments like the Hamilton region, rich foraging and roost habitats can be small and interspersed. As a result, lactating and recently volant juveniles may have very restricted home ranges. Indeed, at the microhabitat level significantly more LTB calls were recorded within the WOE compared with all other concurrently monitored microhabitats at the oak fragment. The WOE is characterised as an uncluttered area flanked by an open edge and water bodies (i.e. pond, irrigation channel and gulley). These microhabitat features likely support higher concentrations of ephemeral insect prey, especially during warmer months (Fukui *et al.* 2006; Ciechanowaski 2002; Kurta *et al.* 1990), while also providing shelter from aerial predators (i.e. moreporks (*Ninox novaeseelandiae*)) known to

occur at this site (Chapter 2; Borkin & Ludlow 2009). Indeed, several LTB roosts have been located in this area (Appendix I). However, during March more calls were recorded in the RE. This probably reflects juveniles and females increasing their home ranges and spending a greater proportion of their time foraging around and moving between riverine habitats and more distant forest tracts (e.g. Whewell's Bush and Pirongia nature reserve; Chapter 2 and 3). Future radio-tracking studies would better elucidate these patterns of activity.

Recommendations for monitoring LTB calls in modified habitats
In order to improve detection rates for LTB calls in modified habitats using detectors, it is encouraged that LTBs be intensively monitored from the onset of female pregnancy until after juveniles are volant (November/December - February). Knowing when and where LTBs are most likely to be emitting calls would allow researchers to improve recordings of calls for bioacoustic analyses. This would also allow wildlife managers to identify habitats that are of likely social importance to bats during certain parts of the year (i.e. pregnancy, lactation and juvenile volancy) when individuals may be most sensitive to disturbance (e.g. tree removal). Multiple detectors should be used to monitor bats at forested habitats (e.g. Hammond Bush and the oak fragment). Detectors should monitor bats throughout the night where possible, or at dusk (1-3 hours after official sunset) and dawn (7-10 hours after official sunset) where peaks in calling behaviour are most common. Detectors should be placed in areas near open spaces and water bodies. Placing detectors at a height of 4-7m would be most practical, but did not significantly improve call detection rates when compared with placing detectors at a higher height (15-30m). This is in contrast to the findings reported for echolocation sequences in Chapter 2 where more pulses were recorded at lower

heights. A likely explanation for this is that calls of a lower frequency attenuate less rapidly in air compared with echolocation pulses (Siemers 2006; Sales & Pye 1974; Griffin 1971). This may have resulted in calls being recorded on multiple detectors (i.e. at both heights). When monitoring LTB calls using detectors it is encouraged that only those calls with an associated echolocation sequence concurrently recorded on the same sound file be considered in analyses. This should ensure that recorded calls are not from an alternative source (e.g. wind, rain or insect generated 'noise' files).

Future research

Determining call functions

Heterodyne bat detectors used in this study only recorded a small 'slice' of specific LTB calls that have frequency components falling within the restricted detection range of the 28 kHz channel. Therefore, recorded calls likely represent only a subset of a variety of calls used by LTBs. Indeed, captive LTBs have been heard emitting calls with a frequency of 15-20 kHz that would not be detected on the narrowband recording channels of bat detectors (personal observation; see also Dwyer 1962). Heterodyne detectors modify the temporal and spectral properties of recorded calls, which restricts further bioacoustic analyses such as generating spectrograms with actual call properties (e.g. peak amplitude; Parsons *et al.* 2000). Call classifications and descriptions are thus under-representative of both the full vocal repertoire of LTBs and the complex temporal and spectral properties of unmodified LTB calls. Nevertheless, being able to recognize the basic waveforms of LTB calls is useful for wildlife managers and bat researchers in New Zealand that rely on detectors to survey and monitor bats. However, it would be worth developing and incorporating an algorithm into the automated bat detector system

that is capable of compressing broadband ultrasonic calls recorded on a wider frequency band (e.g. 15-50 kHz) into audible frequencies for human listening, whilst also maintaining the temporal and spectral properties of bat calls (see Koay *et al.* 2004 for an example of such an algorithm). This would allow for further discrimination of call types on the basis of unmodified acoustic properties (e.g. pulse repetition rates; see Sawyer & Burnett 2006; Burnett *et al.* 2001; Masters *et al.* 1995).

In order to determine the function of in-flight LTB calls, researchers should make use of experimental playback techniques undertaken in natural contexts. Playback provides a means of manipulating which stimuli subjects are exposed to at different times and locations (McGregor 2000; Catchpole 1992). Playback is commonly used to study communication in birds (e.g. Fitzsimmons *et al.* 2008) and anurans (e.g. Arch *et al.* 2009) but less attention has been dedicated to cryptic echolocating bat species. However, with the availability of bat detectors behavioural responses of even cryptic bat species can be quantified by measuring changes in echolocation (and call) pass rates (see Chapter 5; Fenton 1998; O'Donnell & Sedgeley 1994). For instance, in order to investigate whether pulses facilitate co-operative foraging in lactating female LTBs at certain times of the year, researchers might record (using an ultrasonic microphone to maintain spectral and temporal call properties) and broadcast pulses to flying bats during these times (using an ultrasonic speaker). Measuring changes in multi-bat echolocation sequences and in-flight call rates during the playback of pulses and one or more control stimuli (e.g. silence) would allow researchers to determine how responsive bats are to this specific call type (e.g. Dechmann *et al.* 2010; Russ *et al.* 2005). Coupled with observational data such as the relative distance of bats

to broadcasting speakers (obtained from infra-red video recordings), the social context (e.g. co-operative vs. aggressive encounters) in which certain calls function would be much better elucidated (for examples of similar set-ups used for echolocating bats in the field see Dechmann *et al.* 2010; Kazial *et al.* 2008a; Barlow & Jones 1997; Wilkinson 1992; Balcombe & Fenton 1988). Once it can be determined if and how bats respond to specific call types at certain times of the night and year, then acoustic playback lures could potentially be developed and applied to bat conservation strategies that have for the most part remained unexplored (but see Ruffell & Parsons 2009; Ruffell *et al.* 2009; Weinberger *et al.* 2009; Ruffell *et al.* 2007; Constantine 2003; Tomich 1986). Strategies might include: minimising bat dispersal following translocation (for an example from avian literature see Molles *et al.* 2009); increasing bat residency in artificial roosts (bat houses) in roost-limited environments (e.g. Hamilton City; Brittingham & Williams 2000); and increasing bat capture rates using trapping techniques as shown by Hill & Greenway (2005).

Conclusion

This study has demonstrated that automated heterodyne bat detectors already widely used to monitor bats throughout New Zealand by non-invasively recording echolocation sequences, can also be used to obtain data about in-flight LTB calls. Echolocating bats use complex vocalisations for both foraging and communication purposes and LTBs are no exception. Being able to track the use of in-flight calls provides an additional data output and a non-invasive 'window' into the likely social behaviours of this otherwise cryptic threatened bat species (e.g. identifying which habitats are important to aggregating bats). As far as I am aware this is the first study to intensively track the use of multiple call types by a

bat species over a breeding season using non-invasive bat detectors. Future studies should seek to record and analyse unmodified LTB calls; determine call function/s using playback experiments; and explore the use of bat calls as potential acoustic lures in bat conservation initiatives (e.g. bat translocation).

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Chapter 5

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'Noisy neighbours': Do long-tailed bats alter their evening activity in response to aircraft noise?

5.1 Abstract

The effect of anthropogenic disturbances on wildlife behaviour is of growing concern, especially in urban ecosystems. Human-generated noise such as vehicle traffic is one such disturbance that has the potential to alter animal activity patterns and mask important signals in a diverse range of taxa including birds, anurans, marine mammals and echolocating bats. I used a combination of field-based correlation and playback methods to investigate whether aircraft activity and noise alters the evening activity of long-tailed bats (*Chalinolobus tuberculatus*) - a cryptic threatened New Zealand bat species. Correlative data revealed that low-altitude aircraft activity overlapped with evening bat activity at a forest fragment situated near the runway of an international airport. Bat activity decreased during and after low altitude aircraft overflights but this trend was not statistically significant when compared with pre-aircraft bat activity. Weaker evidence revealed that bats may respond differentially to aircrafts of varying loudness, but this remained inconclusive due to small sample sizes. Recordings confirmed that only low levels of high frequency sounds were produced by aircrafts. This suggests that aircraft noise is unlikely to mask LTB echolocation; however it remains unclear whether LTBs can perceive loud aircraft noise of lower frequency and whether this disturbance alters bat activity. Playback experiments revealed that playback stimuli had a statistically significant effect on the overall change in bat activity/min at both sites; however, simulated aircraft noise did not significantly alter bat behaviour when compared with baseline activity levels and a silent control. Results suggest that aircraft noise does not appear to alter LTB activity but further investigations are needed to determine the

effect of other variables associated with low altitude aircraft overflights on bat activity (e.g. flashing lights and changes to air pressure).

5.2 Introduction

The impact of urbanisation on the amount of usable habitat available to wildlife is now well documented (e.g. Laurance 2010; Shochat *et al.* 2004; Riley *et al.* 2003; Marzluff 2001; Wang *et al.* 2001; Lehtinen *et al.* 1999; Theobald *et al.* 1997). Of increasing concern is the influence human activities may be having on wildlife behaviour. Cryptic threatened species known to reside in or near urban ecosystems may be particularly sensitive to anthropogenic disturbances (e.g. Harveson *et al.* 2007; Kerley *et al.* 2002). Features of urban ecosystems like housing density, artificial light and noise have the potential to adversely impact wildlife (e.g. Grigione & Myrkalo 2004; Harrison 1997). Noise in particular not only has the potential to disturb animals but may also mask vocalisations that are important for foraging, navigation and communication in a diverse range of taxa (Warren *et al.* 2006; Brumm & Slabbekoorn 2005). Noise may thus have longer-term impacts on animal activity budgets, habitat use, foraging and mating success and ultimately the survival of individuals (Warren *et al.* 2006; Brumm & Slabbekoorn 2005).

Studies investigating the effects of anthropogenic noise on wildlife activity tend to rely on one of two methods: field-based correlations; and controlled experiments using playback techniques. Correlation studies have shown that some marine mammals (e.g. killer whales (*Orcinus orca*); Holt & Noren 2009) adjust the pitch or amplitude of their signals (i.e. the Lombard effect) to compensate for

high levels of vessel noise (see also Tyack 2009; Buckstaff 2004; Foote *et al.* 2004; Costa *et al.* 2003). Similarly, birds like blackbirds (*Turdus merula*; Nemeth & Brumm 2009) and dark-eyed juncos (*Junco hyemalis*; Slabbekoorn *et al.* 2007) have been found to sing songs of higher frequencies in cities compared with forest populations (see similar avian studies by Halfwerk & Slabbekoorn 2009; Luther & Baptista 2009; Slabbekoorn *et al.* 2007; Katti & Warren 2004). Other species may simply avoid areas with high levels of anthropogenic noise (e.g. Miksis-Olds *et al.* 2007; Schick & Urban 2000; Reijnen & Foppen 1997). Correlative studies are often limited in that a range of extraneous variables occurring in the studied environment often go unaccounted for. More controlled experiments may overcome this limitation; however, lab-based tests may also be limited because captive individuals may not exhibit responses comparable to free-ranging individuals (e.g. Bee & Swanson 2007). The design and execution of field experiments assessing the effect of anthropogenic disturbance on free-ranging animals in natural contexts has not been fully explored. Combining both correlative and experimental methods will likely yield more conclusive results regarding the effect of anthropogenic noise on wildlife, however, few studies have adopted multi-method approaches (e.g. Conomy 1998).

Bats are a difficult group of species to study due to their cryptic, volant and nocturnal nature (Fenton 1997, 2003b). Bats are also one of the most 'acoustically-orientated' animal groups, relying on echolocation pulses and social calls for a range of activities including foraging, orientation and social interactions (Au & Simmons 2007; Jones & Holderied 2007; Fenton 2003a, 1994a, b, 1985; Gould 1977). In some bat species individuals may avoid foraging over turbulent water with high levels of ripple-generated noise despite greater insect availability

(Rydell *et al.* 1999; Mackey & Barclay 1989; von Frenckell & Barclay 1987). The effect of anthropogenic noise on bat behaviour has also recently been investigated using both correlative methods and playback experiments. Shirley *et al* (2001) found that the emergence time of Daubenton's bats (*Myotis daubentonii*) roosting in a church was significantly later during a music festival compared with other nights. Schaub *et al* (2008) used laboratory choice-tests to investigate the effect of vehicle noise on the foraging effort and success of greater mouse-eared bats (*Myotis myotis*); individuals chose not to forage in playback compartments broadcasting vehicle or vegetation noise (i.e. rustling reeds), preferring to forage in silent compartments. Importantly, greater mouse-eared bats rely on prey-generated sounds while foraging; bats that rely on echolocation pulses to capture prey may be less impacted by traffic noise due to little or no signal masking (Jones 2008).

I assessed whether aircraft noise influenced the evening foraging activity of long-tailed bats (*Chalinolobus tuberculatus*; LTBs), using both field-based correlations with real aircrafts and field-based playback experiments using simulated aircraft noise. LTBs are aerial insectivores that rely on high frequency (ca. 40 kHz) echolocation pulses to locate, track and capture insect prey in flight (Parsons 1997). LTBs are one of only two native bat species in New Zealand - which together form the entirety of New Zealand's terrestrial mammal fauna (O'Donnell 2005, 2001; Daugherty *et al.* 1993). LTBs are classified as vulnerable due to population declines resulting from widespread habitat loss and fragmentation (O'Donnell 2000a, b; Sedgeley & O'Donnell 1999). Playback experiments were conducted at two field sites on the edge (low levels of aircraft activity) and outskirts (high levels of aircraft activity) of Hamilton City (North

Island, New Zealand). I predicted that real aircraft activity and simulated aircraft noise would reduce bat activity, as estimated by changes in echolocation activity, in comparison to a naturally occurring disturbance stimulus (i.e. blackbird alarm calls; control 1) and silence (control 2). I also predicted that, due to habituation, bats at the airport site would be less influenced by aircraft noise than bats at the site with little aircraft activity.

5.3 Methods and Materials

Site descriptions and study population

Playback trials were conducted on free-ranging LTBs over 30 nights during the austral summer months of December (2009) and January (2010), when bats are most active (Chapter 2). Trials were conducted near Hamilton City (37°47'S; 175°17'E) at a 0.3ha open area situated on the residential edge of the city (residential site) and a 1.2ha old-growth oak (*Quercus robur*) fragment situated adjacent to the city airport (airport site). Both sites have resident LTBs that roost and forage at each site throughout the year (Chapter 2). The airport site has high levels of aircraft activity compared to the residential site. Large international and domestic Boeing 737 aircrafts as well as light propeller and turbo engine aircrafts fly directly over the airport site prior to landing at the runway. A flight academy is also situated adjacent to the airport site and trainee pilots and instructors frequently use the forest fragment as a landmark during flight training. Circuit and night flights are thus common in the area.
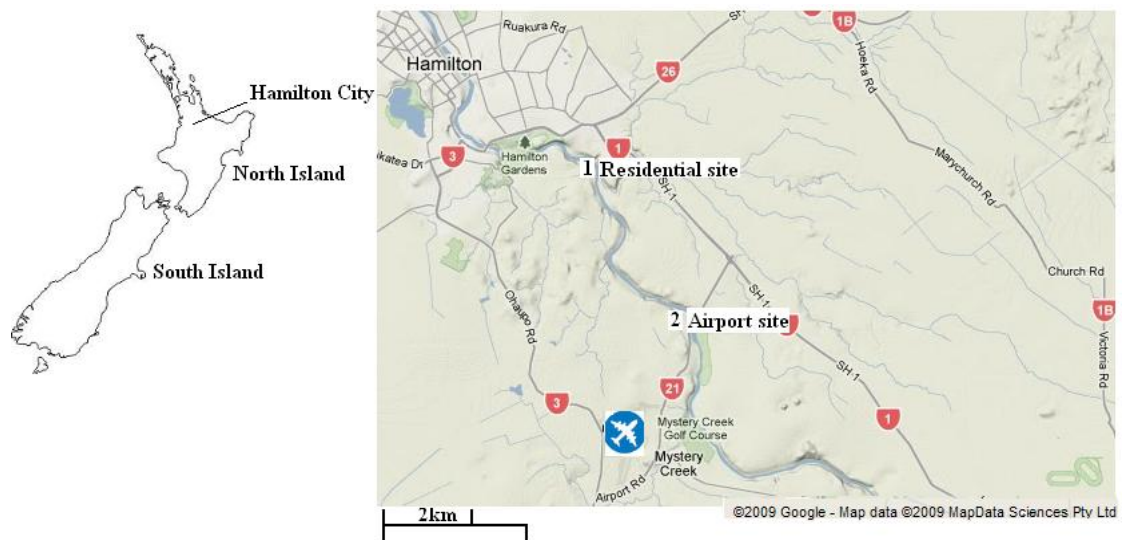
Figure 5.1 The study sites: 1.) residential site (Hammond Bush) situated on the suburban edge; and 2.) the airport site (the oak fragment), on the rural outskirts of Hamilton City. The sites are ca. 4 km from one another. The airport site is directly adjacent to the runway of Hamilton International Airport (ca. 3km; marked by the aircraft sign).

Correlative study

Low-altitude aircraft overflights were recorded continuously over 32 nights at the airport site between July 2009 and February 2010, irrespective of weather conditions. I used an omnidirectional ultrasonic microphone (Sennheisser, MZK 8000) connected to a digital audio recorder (722 SoundDevices, WI, USA) to record aircrafts. Recording equipment was placed in a central clearing with the microphone oriented upward and elevated to 2m using an extension pole. Recordings were saved as uncompressed monaural WAV files (16-bit, 44.1 kHz sample rate) and viewed in Audition (Adobe Systems, San Jose, CA, USA). Four pairs of bat detectors were positioned at least 25m apart in a two-tier vertical arrangement (i.e. a detector at a lower (4-7m) and higher (15-30m) height) to monitor bat activity during each night of aircraft recording (Chapter 2). I calibrated the time settings on the recorder to coincide with the time setting on all

bat detectors to ensure that comparisons could be carried out as accurately as possible.

Playback study

Three playback stimuli were broadcast to flying LTBs between emergence and no later than midnight, including: 1.) five minutes of blackbird calls (Figure 5.2A); 2.) a silent track (i.e. the exact same playback procedure with no broadcasted sound); and 3.) five successive aircraft passes (one per minute; Figure 5.2B). Playback stimuli were recorded using an omnidirectional microphone (Sennheisser, MZK 8000) connected to a digital audio recorder (722 SoundDevices, WI, USA). Each playback stimulus was flanked by a ten minute silent pre-playback period and a ten minute silent post-playback period; the post-playback period was further sub-divided into two five minute time segments for finer scale assessments of bat activity following playback (Figure 5.3). Only aircraft recordings with high signal-to-noise ratios were selected for playback. Recordings consisted of both Boeing 737s ($N = 3$) and turbo-powered aircrafts ($N = 2$). The mean $\pm$ SE peak amplitude calculated for all five aircraft recordings was 88.4 ± 2.08 dBA.

Blackbird alarm calls were presented as a familiar disturbance stimulus (control 1). Blackbirds are frequently heard calling after sunset and even after dark at both sites (personal observations; see Dabelsteen 1984). Calls were recorded after sunset on a single evening at the airport site. A series of blackbird alarm calls (see Andrew 1961) typically heard during evening hours were looped with brief periods of silence (5-15 seconds) to realistically simulate a five minute calling bout.

Background noise was filtered from all broadcasted sounds, including the silent track, using a high-pass frequency filter set at 200 Hz in Audition. Recordings were normalized to -1dB and ramped by fading in and out three seconds at the start and end of recordings.
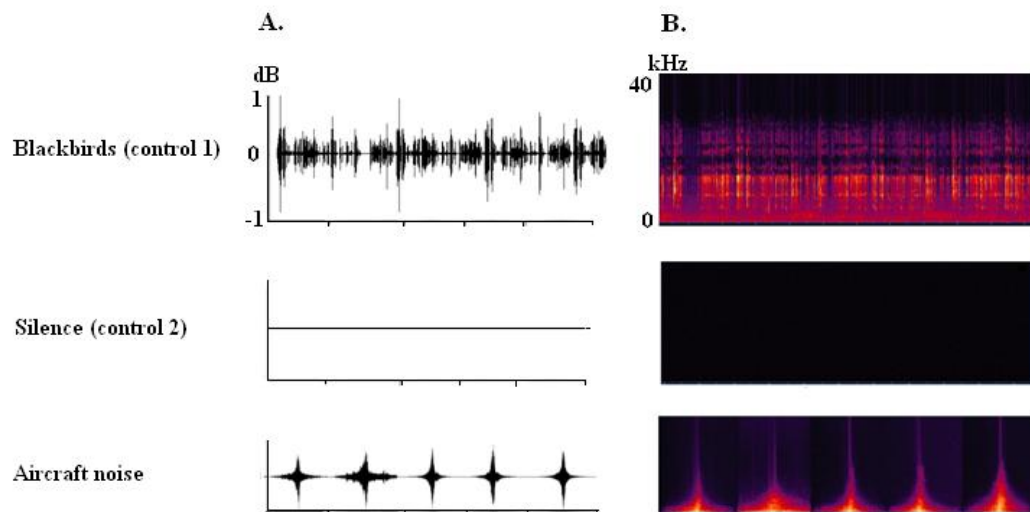
Figure 5.2 Waveforms, generated in SYRINX-PC (J. Burt, Seattle, WA, U.S.A; FFT length of 512 pts; Blackman window) A.) and spectrograms, generated in Audition B.) for the five minute playback of blackbird alarm calls (control 1); silence (control 2); and the five aircraft passes played back to flying LTBs.
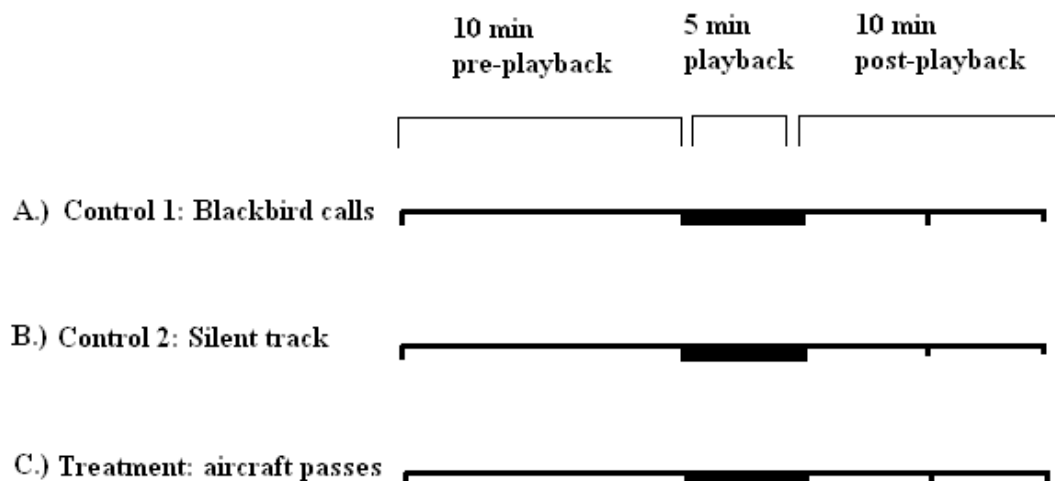
Figure 5.3 Playback design showing the 10 minute pre-playback silence, 5 minute playback and two five minute post-playback silence.

Only nights where all three 25 minute playback trials were successfully completed were included in analyses. The order in which playback stimuli were presented to bats was decided using a 3 x 3 randomised factorial design, ensuring that all six possible playback orders were presented at least once to bats at each site (i.e. six successful playback nights per site).

Playback stimuli were broadcast to bats using a single loudspeaker (base reflex, SP-636, Sherwood, USA) and an iPod (Apple, Cupertino, CA, USA) connected to an amplifier (CA115, TAO Corporation, Japan). The iPod and amplifier were housed in a waterproof case (Peli-Case®, Pelican Products Inc, Terrance, CA, USA) and a 12V car battery (G12-40, Synergy Power Solutions, Sunawee, GA, USA) powered the set-up. The speaker was hoisted to a height of between 15-30m using a rope and pulley system (Chapter 2). At the residential and airport site, rope and pulley systems were setup in four trees. At both sites, stimuli were broadcast from one of these four trees on each playback night in a rotated manner. All trees were at least 25m apart to ensure independent monitoring of bats. Blackbird calls and aircraft noise was broadcasted at ca. 90dB at 1m (Realistic sound level meter, Radioshack, AT.No. 33-2050 with slow response setting).

Trials began as soon as I detected a LTB pass (i.e. a series of two or more high frequency echolocation pulses separated by ca. 1 second; Fenton 1994b; Simmons & Stein 1980) on a hand-held bat detector (Bat4 detector, Magenta Electronics Ltd., UK) set to 40 kHz (i.e. the fundamental frequency of stereotypical LTB echolocation pulses; Parsons *et al.* 1997). Earphones were connected to hand-held detectors to ensure that sounds were not fed-back to bats. One or two field workers walked around the field site at a medium to slow pace

listening for bat passes. Workers listening for bats remained at least 50m from the playback set-up. Noise was kept at a minimum. After completing the first trail, the second and third 25 minute playback trials were only started after another LTB echolocation pass was detected on the hand-held detector. This resulted in varying inter-trial intervals (0-80 min). If other anthropogenic noises (e.g. loud music, fireworks and real aircraft passes) interrupted a trial then the trial was re-started. If other noises persisted, the playback night was abandoned. I did not broadcast stimuli to bats after midnight to avoid disturbing individuals during early morning peaks in activity (Chapters 2 and 4) and to avoid introducing temporal variation in bat activity (see Chapter 2 for an overview of nightly bat activity during summer). Playback trials were completed within one month to avoid introducing seasonal variation (Chapter 2). I also tried to select playback nights with similar environmental conditions, particularly warmer nights (Chapter 2).

Measuring bat response
I used three pairs of automated heterodyne bat detectors (Stag Box III, The Department of Conservation), arranged in a two-tier vertical arranged, to concurrently detect and record LTB echolocation pulses. Detector pairs were hoisted up three monitoring trees (15-35m in height) using rope and pulley systems set-up at each field site. Each monitoring tree was at least 25m from the other two monitoring trees and the tree from which stimuli were broadcast from. All six detectors were calibrated to automatically start monitoring bat activity 30 minutes before sunset until 30 minutes after sunrise. Sensitivity and time settings of all detectors were standardised. The researcher recording the start time of each playback trial ensured that their time settings coincided with those on all the bat detectors (NZST). All recorded sound files were automatically stored onto secure

digital cards (SanDisk Ultra, 2GB). LTB echolocation passes were recorded on the 40 kHz channel of bat detectors and were counted by visual and auditory inspection of waveforms using BatSearch 1.02 Software (The Department of Conservation, Wellington, New Zealand).

Statistical analyses

Correlation study

I calculated the mean number of direct aircraft passes recorded for each hour after official sunset during winter, spring and summer (Chapter 2). To investigate whether bat activity decreased in relation to real aircraft overflights, I calculated the mean number of echolocation passes recorded per minute (bat passes/min) on all bat detectors five minutes before; 1 minute during (i.e. aircraft disturbances were approximately 1 minute in length from first detection); and five minutes after each aircraft pass. Each aircraft passes were also classified into one of three relative loudness categories based on varying peak amplitudes including: 'loud' (< -18 to -8dB), 'moderately loud' (< -22 to -19dB) and 'least loud' (< -30 to -22 dB). A two-way ANOVA (STATISTICA 8.0, Statsoft Inc, 2008) was used to determine if bat activity changed significantly over each time period and if this trend differed relative to aircraft loudness.

Playback study

For each field site I calculated the overall change in LTB passes/min recorded on all detectors during and after the presentation of each playback stimulus (i.e. the difference between mean bat activity/min recorded during pre-playback periods (i.e. baseline levels) and bat activity recorded during playback and post-playback periods). I used an analysis of covariance (ANCOVA) to determine how significant changes in overall bat activity were between sites, playback stimuli

and across each playback time period. I accounted for the possibility that other independent environmental variables (covariates) might also explain changes in LTB behaviour by incorporating mean nightly temperature (°C), wind speed (m.s^{-1}), relative humidity (%), lunar illumination (%), cloud cover (octa) and rainfall (mm) recorded for each playback night into the analysis. Nightly means for all environmental variables were calculated from hourly data obtained from the national weather station located at the airport (agent number 2112; network number C75834; MetService, National Institute for Water and Atmosphere's, Ltd; www.cliflo.niwa.co.nz). The number of real overhead aircraft passes that resulted in playback trials being re-starting were also incorporated into the analysis. To investigate whether the number of bat passes/min changed significantly from baseline levels for each playback stimulus I performed a factorial ANOVA (i.e. 2 x 2 between-groups ANOVA; dependant variable: bat passes/min; categorical factors: site, playback stimuli and playback period). I also performed a separate factorial ANOVA for each site to determine if the number of bat passes/min recorded at a lower and higher heights changed significantly from baseline levels following exposure to each playback stimulus (i.e. a less obvious behavioural response; dependant variable: bat passes/min and categorical factors: playback stimuli, playback period and tier height). *Post hoc* analyses were performed using Tukey tests. All data was log-transformed to achieve normality or near-normality (Kolmogorov-Smirnov and Shapiro-Wilk's W test). Statistical analyses were completed using STATISTICA$^{®}$ 8.0 (Statsoft Inc, Tulsa, OK, USA) with the level of significance held at 0.05. Means are presented as ± SE throughout the paper.

Ethical note

The playback experiment was designed to be as non-invasive as possible.
Playback stimuli were presented only to free-flying animals at the two field sites
specified. This experiment was approved by the University of Waikato Animal
Ethics Committe under Protocol No. 770.

5.4 Results

Correlation study

The number of aircraft passes recorded at the airport site during winter (9 nights),
spring (14 nights) and summer (9 nights) was highest during the first three hours
after sunset, clearly overlapping with the first peak in bat activity following
emergence (Figure 5.4). I recorded a total of 28 instances when aircraft and LTB
activity overlapped. The overall trend on these occasions was one of decreasing
bat activity/min. Relative to pre-aircraft levels, bat activity decreased by 31% and
36% during (1 min) and after (5 min) aircraft passes, respectively; however, this
trend was not statistically significant ($F_{2, 25} = 0.623$, $P = 0.539$; Figure 5.5). Finer
scale analysis suggested that bat activity may have differed according to the
loudness of aircrafts. Bat activity decreased by ca. 58% during loud ($N = 9$) and
moderately loud ($N = 6$) aircrafts passes (Figure 5.6). Conversely, bat activity did
not decrease during aircraft passes of least loudness ($N = 9$). However, these
differences were also not statistically significant (time period, $F_{4, 88} = 0.67$, $P =
0.51$; aircraft loudness, $F_{4, 88} = 0.56$, $P = 0.58$; time period*aircraft loudness, $F_{4, 88}
= 0.224$, $P = 0.924$).
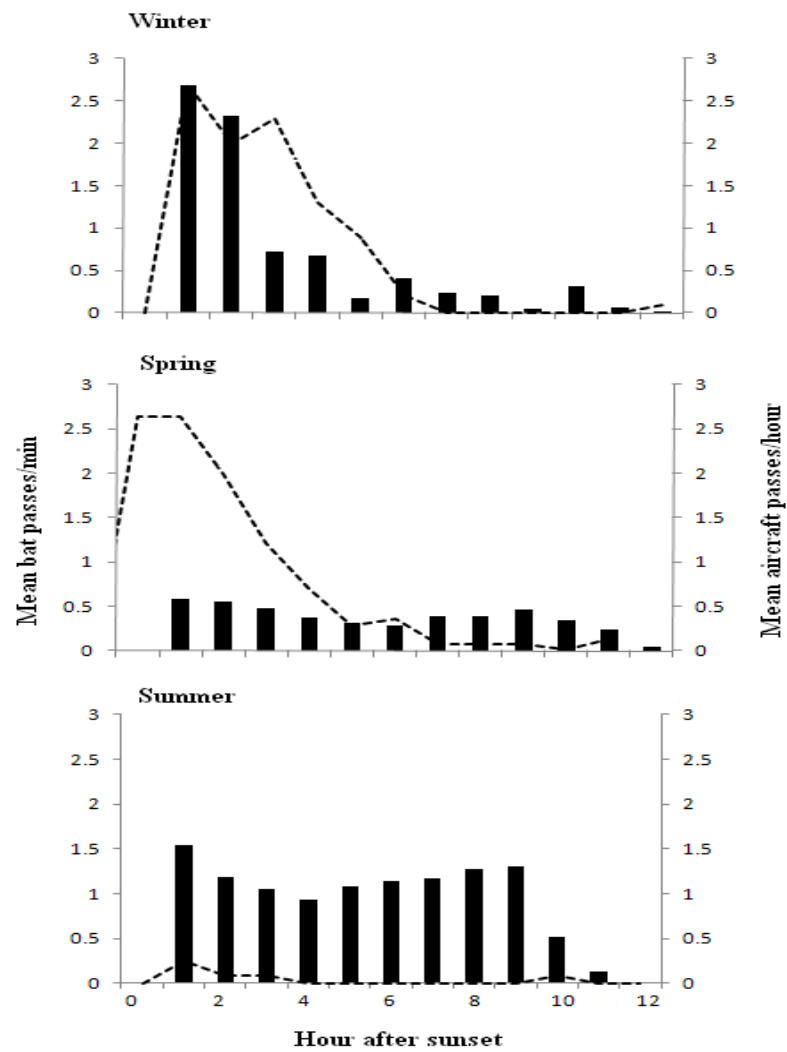
Figure 5.4 Mean number of bat passes recorded during each hour after sunset for winter, spring and summer (solid bars) at the airport site only. The mean number of aircraft passes recorded on select nights during the same season is superimposed over bat activity (dashed line).
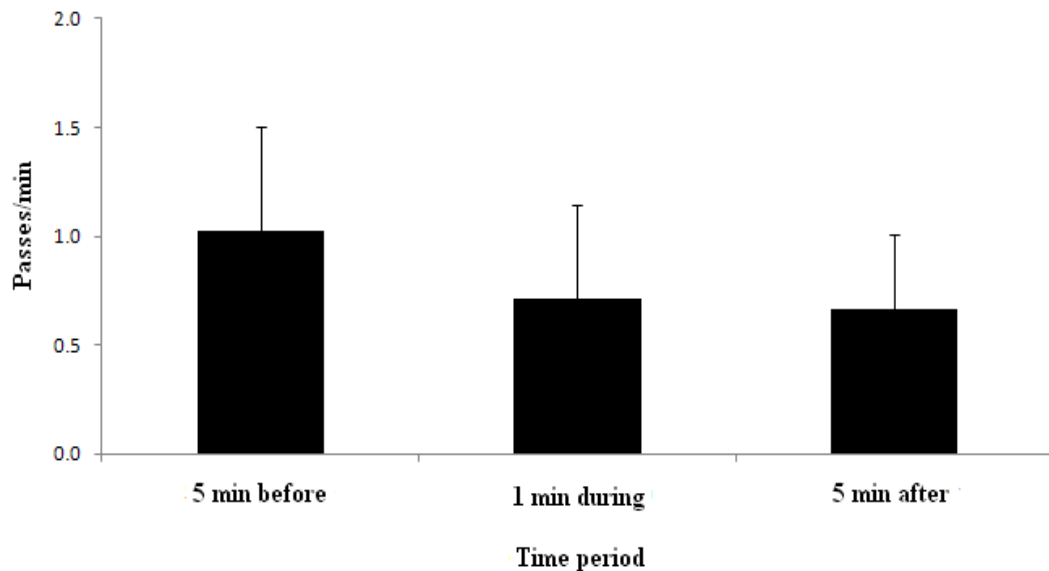
Figure 5.5 Mean number of bat passes/min recorded before, during and after each low-altitde aircraft passes of ca. 1 min durations at the airport site. Overall bat activity decreased during and after aircraft passes, however, this trend was not significant relative to pre-aircraft activity.
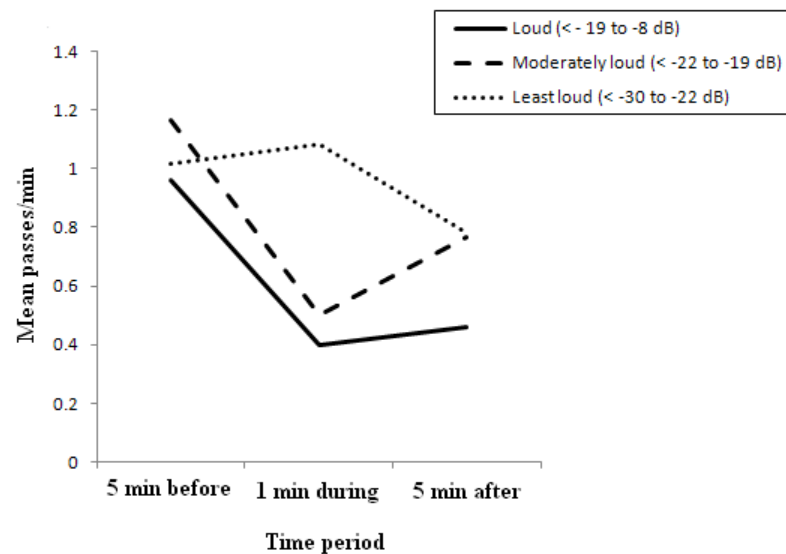
Figure 5.6 Mean number of bat passes/min recorded before, during and after real aircraft passes of varying loudness (i.e. peak amplitude).

Playback study

I recorded a total of 1,108 LTB bat passes (560 at the residential site; 548 at the airport site) on 12 successful playback nights. Playback stimuli had a significant effect ($F_{2, 34} = 8.26$, $P = 0.001$) on the overall change in bat activity/min at both

sites (Table 5.1). Changes to bat pass rates during and after the playback of blackbird alarm calls was significantly different from changes to bat pass rates during and after silence (*post hoc*, $P = 0.001$) and aircraft noise (*post hoc, P = 0.001*); however pass rates did not differ significantly between silence and aircraft noise (*post hoc, P = 0.99*, Figure 5.6). Changes in bat pass rates during and after exposure to all three stimuli were not significantly different from baseline pass rates (ANOVA, playback stimuli*playback period, $F_{6, 66} = 0.828$, $P = 0.55$). Bat activity did not decrease significantly more at the residential site after exposure to aircraft noise when compared with the airport site (difference of 33.3%, 70% and 8% in each of the respective five minute time periods following pre-playback silence; site*playback stimuli, $F_{2, 70} = 3.02$, $P = 0.054$; Figure 5.6).

Environmental variables incoporated into the ANCOVA revealed that wind speed ($F_{1, 11} = 11.43$, $P = 0.001$), relative humidity ($F_{1, 11} = 10.90$, $P = 0.001$), % lunar illumination ($F_{1, 11} = 9.57$, $P = 0.003$) and temperature ($F_{1, 11} = 6.20$, $P = 0.015$) were also likely to influence bat activity on playback nights; however, real aircraft passes were not ($F_{1, 11} = 0.16$, $P = 0.688$).

The number of bat passes/min recorded at lower and higher heights did not change significantly from baseline levels during and after the playback of all three stimuli at the residential site (playback stimuli*tier height, $F_{2,17} = 0.586$, $P = 0.558$; playback period*tier, $F_{3,69} = 0.234$, $P = 0.873$) and airport site (playback stimuli*tier, $F_{3,69} = 1.99$, $P = 0.142$; playback period*tier, $F_{3,69} = 0.92$, $P = 0.434$).

Table 5.1 Summary statistics for the ANCOVA that incorporate categorical variables and a range of covariate predictors of bat activity.

Effect	Degrees of freedom	*F*-statistic	*P*-value
Categorical predictors			
Playback stimuli	2	8.26	*0.001*
Site	1	1.763	0.188
Playback period	2	1.128	0.329
Site*playback stimuli	2	3.02	0.054
Site* playback period	2	0.19	0.827
Playback stimuli*playback period	4	0.211	0.932
Playback stimuli* site* playback period	4	0.284	0.888
Covariates			
Wind speed	1	11.43	*0.001*
% Rel. humidity	1	10.90	*0.001*
% Lunar illumination	1	9.57	*0.003*
Temperature	1	6.20	*0.015*
Rainfall	1	3.52	0.064
Cloud amount	1	0.48	0.492
Real aircrafts	1	0.16	0.688
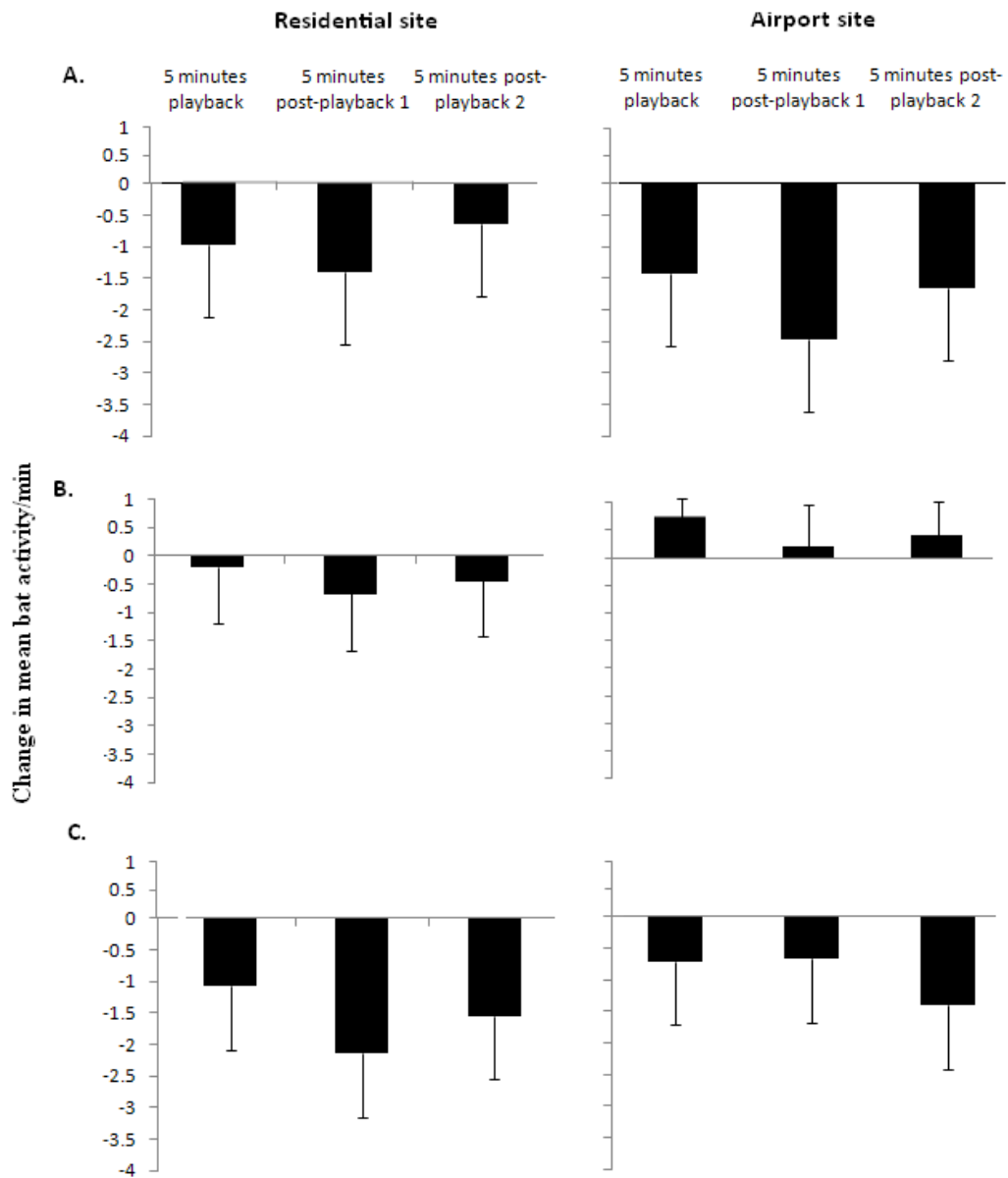
Figure 5.7 Changes in the mean number of bat passes/min at the residential ($N = 6$) and airport site ($N = 6$). Changes in LTB pass rates from baseline activity levels (i.e. ten minute pre-playback period) are presented for the five minute playback and two post-playback time periods for all three stimuli: A.) silence; B.) blackbird alarm calls; and C.) aircraft noise.
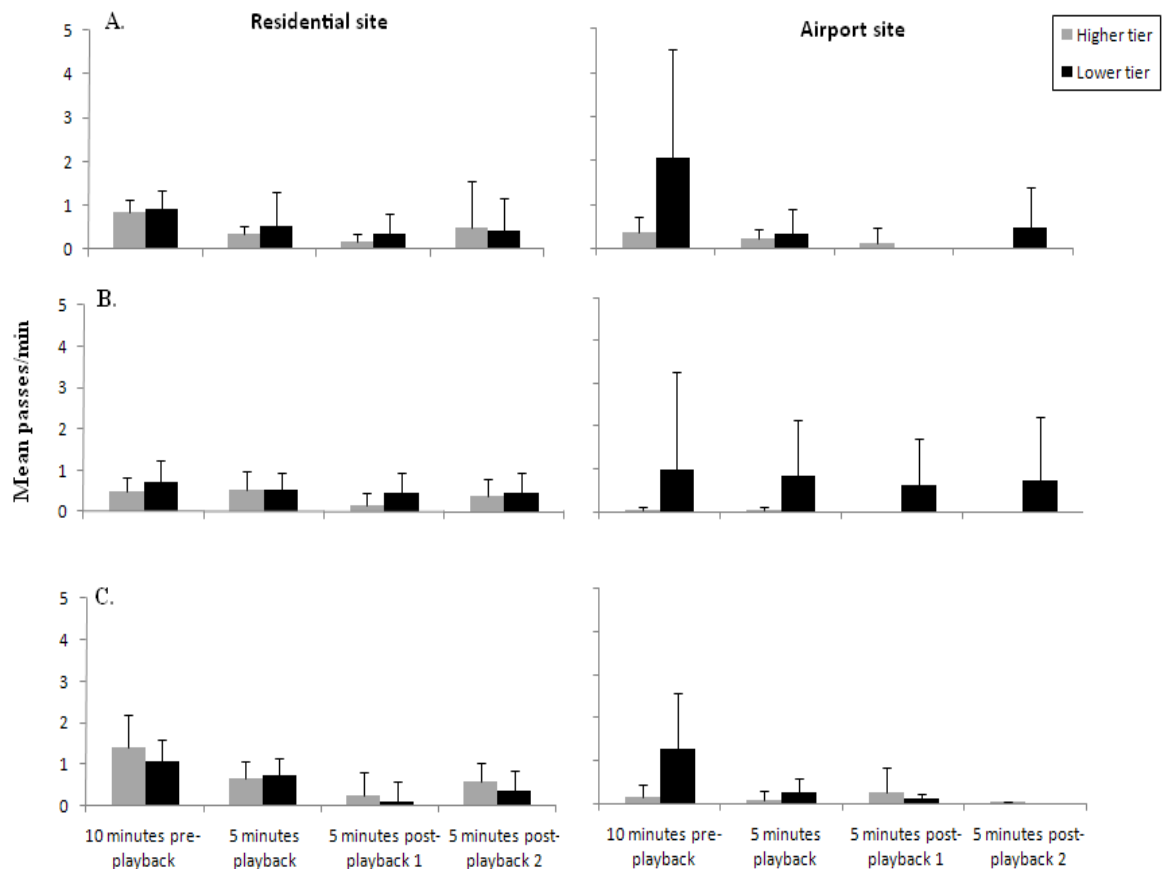
Figure 5.8 Mean number of bat passes/min recorded at each site at the lower (ca. 4-7m) and higher heights (ca. 15-30m) during each time periods for all three playback stimili: A.) silence; B.) blackbird calls; and C.) aircraft noise.

5.5 Discussion

I found that the average number of low-altitude aircraft passes/night at the airport site was highest during the first three hours after sunset, clearly overlapping with LTB activity. It has been shown that some echolocating bats do avoid anthropogenic disturbances such as vehicle traffic and light (Kerth & Melber 2009; Stone *et al.* 2009; Schaub *et al.* 2008; Shirley *et al.* 2001). Szewczak & Arnett (2006) also found that broadcasting an artificial ultrasonic sound deterrent to echolocating bats near wind farms significantly decreased bat activity rates. If LTBs were adversely affected by low-flying aircrafts I assumed that individuals would reduce their in-flight activity during and after aircraft overflights indicating an avoidance response (Schaub *et al*, 2008). Of primary concern was that bats

might decrease the time they spent performing normal behaviours such as in-flight foraging at resource-rich habitats as a result of this acute disturbance, which in turn could alter longer-term activity budgets and habitat use patterns (see Efroymson & Suter 2001).

Correlation study

Overall bat activity/min decreased by >30% during and after real aircraft passes; however this trend was not statistically significant when compared with pre-aircraft bat activity. Similar findings have been documented for mountain sheep (*Ovis canadensis nelsoni*; Krausman *et al.* 1998), caribou (*Rangifer tarandus*; Harrington & Veitch 1991), kit foxes (*Vulpus marcotis arsipus*; Bowles *et al.* 1995), Mexican spotted owls (*Strix occidentalis lucida*; Johnson & Reynolds 2002; Delaney *et al.* 1999) and osprey (*Pandion haliaetus*; Trimper *et al.* 1998). In all of these studies individuals did not significantly alter their behaviour after exposure to low-altitude aircraft overflights. However, other studies have found significant changes to wildlife behaviours after exposure to aircrafts (e.g. wood ducks (*Aix sponsa*) Conomy *et al.* 1998; bald eagles (*Haliaeetus leucocephalus*) Stalmaster & Kaiser 1997).

Finer scale investigations revealed that overall trends in bat activity may have differed according to the loudness of aircrafts: bat activity decreased by ca. 58% during aircraft passes with high amplitudes compared with no decrease in bat activity during aircraft passes of lower amplitude. Although these trends were not significantly different from each other, they do suggest that LTBs may respond to aircrafts of varying noise properties in different ways. This has been demonstrated in harlequin ducks (*Histrionicus histrionicus*) by positive dose-response curves (Goudie & Jones 2004). It is important to also note that there was no significant

difference between the mean number of bat passes/min during and after aircraft passes compared with pre-aircraft activity levels in each aircraft loudness category. Small sample sizes invariably reduced confidence in this finding. Multi-regression analysis undertaken in Chapter 2 also revealed that the number of aircraft passes/night (i.e. frequency of aircraft passes) was not significantly negatively correlated ($r^2 = 0.28$; $P = 0.46$) with the number of bat passes recorded on the same nights ($N = 43$). Overall, correlative data suggests that the presence of low-altitude aircraft overflights at the airport site does not appear to negatively impact LTB activity. Nevertheless, correlation data needs to be interpreted with caution as negative results do not necessarily mean that aircrafts have no effect on bat behaviour.

It has been suggested that relative to other animal taxa (i.e. birds (e.g. Nemeth & Brumm 2009); anurans (e.g. Parris *et al.* 2009); and marine mammals (e.g. Foote *et al.* 2004)) aerial insectivorous bats that rely on high frequency echolocation pulses for foraging and orientation might not be as adversely affected by traffic noise due to little or no overlap between high frequency echolocation and low frequency noise (Jones 2008; Schaub *et al.* 2008). From acoustic recordings I found that low-altitude aircrafts produced little ultrasonic sounds that would likely mask 40 kHz LTB echolocation pulses. Even if signal masking did occur one might expect LTBs to exhibit short term behavioural adaptations (e.g. signal modulation or site avoidance) to compensate for high levels of noise as demonstrated in other taxa (e.g. Nemeth & Brumm 2009; Parris *et al.* 2009; Foote *et al.* 2004). Indeed, numerous echolocating bat species have been shown to adjust one or more echolocation properties (e.g. frequency and call duration) during high levels of background noise as part of a 'jamming avoidance'

response (e.g. Bates *et al.* 2008; Gillam & McCracken 2007; Ibanez *et al.* 2004; Obrist 1995).

Without specific investigations into the auditory perception of LTBs (see Palakal & Wong 2004 for an example of how this might be achieved and Chittka & Brockmann 2005 for a discussion) it is difficult to conclude that individuals do not perceive low frequency aircraft noise. It likely that LTBs, like many other bat species that rely on broadband frequency-modulated echolocation pulses (Parsons 1997; Parsons *et al.* 1997), exhibit non-specialised auditory tuning and a basic cochlear anatomy (e.g. non-specialised gradients in basilar and tectorial membranes; Ulanovsky & Moss 2008; Vater & Kössl 2004; Moss & Sinha 2003). If so, then the auditory capacity of LTBs is unlikely to be restricted to a narrow frequency range as shown for some constant-frequency echolocaters (e.g. Mustached bats (*Pternotus parnelii*); Huffman & Henson 1991; Suga *et al.* 1987). LTBs also use a range of in-flight calls of lower frequencies (ca. 30 kHz and even <20 kHz; Chapter 4; see also Bohn *et al.* 2006 and Pollak *et al.* 2003). This suggests that LTBs would perceive low frequency aircraft noise that could potentially impact bat activity. However, correlative data does not provide sufficient information to determine this as it is difficult to identify if noise, a specific stressor associated with low altitude aircraft overflights, is responsible for changes in bat activity (Pepper *et al.* 2003; Efroymson & Suter 2001; Kempf & Hüppop 1996). Therefore, to more conclusively determine whether aircraft noise alters bat behaviour, more controlled experiments were necessary.

Playback study
Relative to pre-playback levels bat activity was reduced during and after the playback of aircraft noise and silence (i.e. no significant difference between

treatment and control 2); however, bat activity was significantly less reduced during and after exposure to blackbird alarm calls. This finding is counter to my initial prediction that bats would reduce their activity during and after exposure to simulated aircraft noise but not control sounds. It appears that LTBs are unaffected by blackbird calls, which was anticipated as these sounds occur naturally at both sites and are unlikely to be signals associated with bat predation or the availability of potential prey, which otherwise might have altered bat activity. However, a reduction in bat behaviour during and after silence was unexpected. This might have been due to errors in playback execution such as researcher presence and movement, but this was minimal and kept constant across all playback trials. It is possible that during silent trials, researcher disturbance may have been accentuated compared with the other trials as there was no playback stimulus to 'mask' researcher movement and associated noise. Another possible explanation is that high frequency sounds or static emitted inadvertently from the speaker while playing back the silent track reduced bat activity; however I failed to identify any additional sounds after careful inspection of all recordings. It is also possible that decreasing bat activity trends observed during and after the playback of silence (and aircraft noise) reflect natural variability in LTB activity over a 25 minute time period. LTB activity is highly variable even over short time periods and is characterised by a series of nightly peaks and crashes as individuals return to roosts, move between habitats or simply fall out of the detection range of detectors (Chapter 2; Dekrout 2009).

I also considered the influence environmental variables may have had on bat activity on successful playback nights and found that in addition to playback treatment; temperature, wind speed, % relative humidity and % lunar illumination

may also have influenced activity patterns as shown in other insectivorous bat species (e.g. Scanlon & Petit 2008; Lang *et al.* 2006; Verboom & Spoelstra 1999; Vaughan *et al.* 1997). In Chapter 2, mean nightly temperature was found to be the only positive predictor of bat activity (at the oak fragment only) over 173 nights. In the present study I only considered environmental variables over 12 nights, which is less likely to accurately reflect the predictors bats are most responsive to. Overall, no significant changes in bat pass rates during and after exposure to both silence and simulated aircraft noise suggests that aircraft noise has little, if any, negative impact on bat behaviour. This corroborates correlative findings. Observational evidence of bats roosting in noisy environments such as churches (e.g. Zahn 1999) and under bridges (e.g. Allen *et al.* 2010; Adam & Hayes 2000) is additional support to suggest that some echolocating bat species may be able to tolerate high levels of anthropogenic noise (see Schaub *et al*, 2008 and Shirely *et al*, 2001 for further discussions).

To better account for the unpredictability of bat activity in future field experiments, researcher might consider having shorter trial lengths (i.e. 5 min pre-playback, 1 min stimulus exposure and 5 min post-playback). This would enable experiments to be executed quicker with greater replication and would also better simulate natural aircraft overflights, at least in this modified habitat. Important characteristics of a stimulus are often altered during the manipulation procedure of experiments, which in turn might influence wildlife in unexpected ways. Playing back five of the loudest aircraft passes to bats in rapid succession lacked realistic temporal variation as real aircraft passes are more unpredictable in pass rates and noise properties. Similar concerns were highlighted by Bee & Swanson (2007) who found that playing back traffic noise during male tree frog (*Hyla chrysoscelis*)

calling resulted in decreased female orientation toward male signals; however simulation of vehicle traffic lacked temporal variation typical of real traffic noise.

I found no evidence to suggest that bats at the airport site were habituated to aircraft noise compared with bats at the residential site; however, during the playback of aircraft noise at the residential site bats decrease their activity by 70% more than bats at the airport site. Radio-tracking has shown that bats do move between the airport and residential habitats using the Waikato River as a connecting corridor (Dekrout 2009). I thus cannot rule out that the same individuals were exposed to playback trials at both sites, as there was no way to control for bat movement. Nevertheless, behavioural adaptations to aircraft noise are likely to be sound-specific rather than site-specific. More investigations will be needed to confirm this. A challenging, yet exciting, area of research would be to investigate the physiological response (e.g. heart rate) of free-ranging bats during and after exposure to anthropogenic disturbances (for examples in other taxa see Smith *et al.* 2004; Krausman *et al.* 1998; Weisenberger *et al.* 1996). One approach might be to develop remotely operating sensors capable of providing physiological measurements (for an example of this approach in a bird see Harms *et al.* 1997).

I also wanted to determine if bats respond to aircraft noise by flying at lower heights (i.e. a less obvious behavioural adaptation that increases the distance between flying individuals and the noise source). In other taxa less obvious behavioural adaptations to anthropogenic noise have been documented such as nocturnal signing in robins (*Erithacus rubecula*) at sites with high daytime noise (Fuller *et al.* 2007). I found no significant difference in the number of bat passes/min recorded at lower and higher heights during and after exposure to

aircraft noise relative to pre-playback levels and control stimuli. Further studies should explore the possibility that wildlife respond in less obvious ways to anthropogenic disturbances. This is challenging as a range of disturbances can effect wildlife in different and species-specific ways (Lengagne 2008; Schaub *et al.* 2008; Sun & Narins 2005; Richter *et al.* 2006; Conomy *et al.* 1998).

Field experiments should also seek to more realistically simulate anthropogenic disturbances. In addition to noise, other variables including flashing lights and changes to air pressure characterise aircrafts overflights after dark. Multi-modal playback approaches that broadcast combinations of different disturbance stimuli (e.g. flashing lights with and without aircraft noise), would more clearly identify the variables responsible for observed changes in bat pass rates. Some echolocating bats have been shown to avoid artificial light (Stone *et al.* 2009; Kuijper *et al.* 2008). Light from buildings and streetlights has also been identified as a negative predictor of LTB activity in and around Hamilton City (Dekrout 2009). Simulating the movement effect of sound could also be achieved using multi-speaker arrangements, as demonstrated in avian research (e.g. Mennill & Vehrencamp 2008). The potential for more direct and serious impacts of low-altitude aircraft overflights to flying bats especially in habitats near airports remains unclear but these may include bat strikes and barotrauma (i.e. internal haemorrhaging of the lungs) caused by changes in air pressure. Bat fatalities at wind farms due to barotrauma and bat strikes near airports have been previously documented (Parsons *et al.* 2009; Baerwald *et al.* 2008).

Conclusion

The effect of anthropogenic noise on wildlife behaviour is concerning, especially in and around human dominated environments like urban ecosystems. In this

study I designed a field-based experiment that avoided the need to handle or maintain animals in captivity. Given their threatened status and prioritized *ex situ* conservation needs, experimental studies undertaken on vulnerable cryptic species often require non-intrusive experimental approaches. This is the first study to investigate the effect of aircraft noise on the behaviour of an echolocating bat species. It is also one of the first to rely on field-based correlation and experimental approaches to more conclusively address this issue. Aircraft noise does not appear to negatively impact LTB activity patterns likely due a lack of signal masking. These findings are counter to that of Schaub *et al* (2008) who found that 'passive listening' greater mouse-eared bats did avoid vehicle noise in laboratory-based choice experiments. Aircraft noise is unpredictable and rapid in onset and it is not always possible to realistically simulate such an acute disturbance; however future studies should explore ways in which this might be better achieved in natural contexts. I have shown that it is possible to use multiple methods in a non-invasive way to address a complex conservation issue in a cryptic threatened species. Further studies should investigate the effect of different anthropogenic disturbances in other bat species.

5.6 References

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Chapter 6

General Discussion

In this final chapter I will discuss the implications of the research I presented in Chapters 2, 3, 4 and 5 and explore future research avenues. I will also address some of the limitations and assumptions of my research.

6.1 Study implications and future research

Developing and applying LTB monitoring recommendations in modified habitats

Better understanding the movement patterns of cryptic, data-deficient species is pivotal if practical steps are to be taken towards better conserving these animals and the habitats they depend on (Chadés *et al.* 2008; Lawler *et al.* 2006; Soulé & Kohm 1989). This is especially important for threatened wildlife known to reside in or near highly modified, human-dominated environments as the threats facing these animal populations are typically increased (Meine *et al.* 2006; Meffe 2001). For conservation biologists this often means developing innovative and effective ways to obtain basic behavioural information about target populations (Soulé 1985).

In **Chapter 2**, I developed a stratified monitoring design that enabled me to non-invasively and intensively track the activity patterns of LTBs - a nocturnal, threatened bat species (IUCN 2010; O'Donnell 2001). The echolocation pulses emitted by foraging bats were concurrently recorded on multiple automated heterodyne detectors (Lloyd 2009; O'Donnell & Sedgeley 1994). Detectors were arranged so that both the vertical and horizontal stratification of bat activity (i.e. habitat and microhabitat patterns) could be measured across different temporal scales (i.e. nightly and seasonal patterns). As far as I am aware, Chapter 2 is the first study to use a monitoring design that considers both the vertical and

horizontal use of microhabitats by a New Zealand bat species. This study is also one of the longest and most intensive acoustic bat monitoring studies undertaken thus far in a highly modified ecosystem (for other examples see Scanlon & Petit 2008; Avila-Flores & Fenton 2005). I found that the number of bat passes recorded on detectors varied even over relatively short distances within already small, fragmented (< 2 ha) habitats. Detectors placed at lower heights (4-7m) consistently recorded more LTB passes compared with detectors secured at higher heights (15-30m). Detectors placed in microhabitats situated near a flanking water body recorded more LTB passes than detectors placed in a microhabitat lacking a water body. These findings showed that LTBs are clearly responsive to fine scale microhabitat features characterising habitats. Determining how bats make use of within-habitat space has important implications for future bat monitoring studies: failing to account for the vertical and horizontal stratification of bat activity could weaken conclusions made about how bats use habitats, which in turn could potentially misguide management and conservation decisions (e.g. Collins & Jones 2009). This is especially concerning in modified environments where viable bat habitat is likely already reduced. For example, if detectors were placed in microhabitats infrequently used by foraging bats because of an absence of water and thus insect prey (see Fukui *et al.* 2006), little if any bat passes would be recorded (i.e. the microhabitat may be more important for roosting rather than foraging). This information could mistakenly be interpreted as indicating that the habitat is of no or little importance to bats. Subsequent management decisions such as tree removal or land clearance would be poorly informed and fail to take into account the ecological significance of the habitat. I have shown that it is important to recognize that bat activity can be spatially and temporally

heterogeneous and attempts to better account for this in future bat monitoring efforts would invariably better inform conservationists and managers alike (Hutson *et al.* 2001).

Although bat activity was variable in space and time, clear activity trends were also evident. Nightly LTB activity peaked between the first and third hours after sunset, and higher bat pass rates were recorded at both rural and urban sites during summer and spring compared with winter. I also conducted stepwise multiple regression analyses, a multivariate correlation technique, to identifying the environmental (and anthropogenic) variables/s likely influencing LTB behaviour at each site. Many insectivorous bats are known to alter their activity in response to a range of fluctuating environmental variables (e.g. Turbill 2008; Verboom & Spoelstra 1999; Hayes 1997), which in turn may be influenced by other factors occurring within the local environment such as: habitat complexity (e.g. structural vegetation clutter; Barclay *et al.* 1999); the presence of specific landscape elements (e.g. water bodies; Verboom *et al.* 1999); and anthropogenic activities (e.g. vehicle traffic and light; Bach *et al.* 2004; Kerth & Melber 2009; Stone *et al.* 2009). I found that mean nightly temperature was a significant positive predictor of LTB activity at the oak fragment only. Collectively, these trends in bat activity allowed me to develop practical monitoring recommendations aimed at maximising LTB detections in modified habitats using detectors. Monitoring recommendations are especially important for wildlife managers as it allows them to forecast the temporal and spatial activity of bats, which in turn enables available resources (i.e. research effort and available equipment) to be better allocated (Chadés *et al.* 2008). Knowing when and where bats are most active could allow researcher to improve recordings of LTB

vocalisations for bioacoustic analyses and improve bat capture rates using trapping techniques (e.g. mist netting). Therefore, monitoring recommendations should better inform researchers and managers about bat behaviour, allowing some of the challenges associated with monitoring a secretive, nocturnal species to be overcome.

A clear limitation encountered in Chapter 2 was that of restricted site replication. This was because of limited equipment availability and information about whether bats actually used other sites in the Hamilton region. In order for monitoring recommendations to be more broadly applicable to modified environments, I had to assume that LTB activity recorded at the two exotic sites monitored would be comparable to LTB activity at unmonitored sites with similar habitat features. To better address this assumption, it was an important and logical next step for me to apply the monitoring recommendations at other habitats so that I could better comment on the broader applicability of this monitoring protocol.

In **Chapter 3**, I applied LTB monitoring recommendations in two different ways. I conducted a short-term concurrent LTB monitoring study at four habitats (rural and urban sites with and without known LTBs) over three successive seasons, and a LTB presence/absence survey at 11 sites across the urban-rural interface of Hamilton City. Sites included exotic and native forest fragments of varying distances to: other viable habitats; the Waikato River; and anthropogenic structures such as houses and roads. I found that LTBs do use multiple rural and urban sites even during a single night across all the seasons monitored. I also detected LTBs at eight out of 11 sites surveyed confirming that LTBs are more widely distributed in and around Hamilton City than previously shown using hand-held detector surveys (Dekrout 2009). Future LTB monitoring

studies should thus make use of automated bat detectors and replicate monitoring set-ups at as many sites as possible so that more accurate conclusions about bat activity, habitat use and distribution patterns can be made (Williams *et al.* 2006; Gannon *et al.* 2003; Sherwin *et al.* 2000). It is important to bear in mind that just because bats were not detected in a habitat during the presence/absence survey does not necessarily mean that they do not use that habitat. Repeated surveys that maximise sampling effort (i.e. undertaken for longer time periods using multiple detectors) would reduce the risk of reporting an absence of bats when in fact this may not be the case. Nevertheless, it also needs to be recognized that intensive sampling regimes (Chapter 2) may not always be logistically possible. Sub-sampling regimes and bat surveys (Chapter 3) can clearly still provide valuable, albeit less robust, data about bat activity and distribution patterns (see Jackson *et al.* 2008 for a discussion).

Both concurrent monitoring and survey data revealed that relative bat activity was highest at sites situated immediately adjacent to the Waikato River that were connected to other viable habitats, compared with more isolated sites further from the river (Appendix I). I failed to detect any bats at urban sites surrounded by roads and houses, even at a densely stoked old-growth native remnant (i.e. Claudelands Bush). Proximity to riparian margins, habitat connectivity and the presence of anthropogenic structures likely complexly influences LTB habitat use and distribution patterns along the urban-rural interface of Hamilton City (see Bennett 1999). It is difficult to protect bat habitat without knowledge of the sites and landscape features that bats depend on. Therefore, without an effective method to survey bats and measure bat activity, managers risk underestimating viable bat habitats. This is especially concerning in

expanding urban ecosystems where the loss and fragmentation of habitat is already increased (see Ball 2002). I advocate that knowledge about LTB activity and distribution patterns can be improved by applying LTB monitoring recommendations at multiple sites in modified environments throughout New Zealand. Reducing uncertainty about cryptic threatened species like LTBs is vital for conservationists and managers alike (for case studies in other cryptic threatened species see Johnson *et al.* 2009; Shekelle & Salim 2009; Regan *et al.* 2008; Linkie *et al.* 2007; Joseph *et al.* 2006). It is anticipated that the development (Chapter 2) and application (Chapter 3) of LTB monitoring recommendations will better guide and inform future monitoring, management and conservation strategies, which in turn should forestall misguided crisis decision-making for this protected species (Meffe 2001). This is critical as no management plan or standard monitoring protocol currently exists for LTBs in modified environments (see Dekrout 2009).

Future research

Developing and applying an effective monitoring protocol for LTBs is an important step towards sustainably managing bat habitat (Chapters 2 and 3). However, effectively conserving this species in modified ecosystems will also depend on a committed and collaborative effort from multiple organisations, private landowners and members of the public (Trewhella *et al.* 2005; Brechin *et al.* 2002; Robertson & Hull 2001). For example, setting up a bat management plan for resource planning purposes is one practical approach that would help mitigate direct and indirect impacts associated with urban expansion (e.g. selective and whole-scale logging and changes to light regimes; O' Shea *et al.*; 2003; Turner, 2003; Theobald *et al*. 1997). A bat monitoring protocol would thus be an

important component of a larger adaptive species management framework. Efforts to increase local awareness about: bat habitat use; bat distribution patterns; and the threats facing local populations will also strengthen conservation initiatives (Fenton 2003; Medellín 2003; Mickleburgh *et al.* 2002; Hutson *et al.* 2001; Molloy 1995). This should involve raising the public profile of bats and including members of the public in restoration and conservation initiatives (e.g. the 'Project Echo' bat distribution database and awareness website for the Hamilton region; see www.ew.govt.nz/projectecho). Future research should also investigate whether LTBs could serve as a viable 'surrogate' species in conservation and land restoration initiatives (see Regan *et al.* 2008; Favreau *et al.* 2006; Caro & O' Doherty 1999). This could potentially enable researchers and managers to circumvent the need to monitor all species in an ecosystem on the premise that the needs of LTBs also represent those of other native fauna (e.g. LTBs as an 'indicator' species of habitat connectivity; or a 'flagship' species for riparian preservation and restoration; see Hein *et al*. 2009; Kalcounis-Rueppell *et al*. 2007; Medellín *et al*. 2000). Identifying and protecting significant ecological habitat in human-dominated environments can be challenging, but being able to prioritise monitoring for specific species that are especially sensitive to habitat alterations due to one or more specific habitat requirement/s (e.g. availability of roost trees), could make this task more achievable (see Home *et al.* 2009; Fleishman & Murray 2009; Thompson 2006; Carignan & Villard 2002; Poiani *et al.* 2000 for critical discussions).

Due to the cryptic nature of LTBs, conserving local populations will also depend on ongoing monitoring efforts using a standard monitoring protocol (Chapters 2 and 3). This is important if comparisons between data sets are to be

made accurately and if conservationists and managers are to be alerted to any significant alterations in bat activity and habitat use patterns over time, especially following changes to local environments. Future research should also focus on using baseline field datasets (e.g. Chapters 2 and 3; Appendix II) to develop predictive models for LTB habitat use and distribution patterns in defined areas (e.g. the Waikato Basin; see Greaves *et al.* 2006 for an example of a predictive spatial model for LTBs). This would better focus forest management and habitat restoration efforts (Visconti *et al.* 2010; Rhodes *et al.* 2006).

Tracking the use of in-flight LTB calls

In **Chapter 4**, I demonstrated that in addition to obtaining useful temporal and spatial data about LTB foraging activity, detectors can also 'glean' additional information by recording in-flight LTB calls. This study is the first to identify, describe and classify LTB calls that differ from more stereotypical echolocation pulses (Parsons *et al.* 1997). I intensively and concurrently tracked the three most common call types (pulses, buzzes and chirps) over four months of the LTB breeding season. I found that pulses and buzzes were predominantly recorded around the time of female pregnancy and lactation and lactation and juvenile volancy, respectively. These calls were only ever detected at the oak fragment. Pulses were also commonly associated with multi-bat echolocation sequences simultaneously recorded on a different detector channel (40 kHz). Female LTBs are thought to depend on maternity roosts in old-growth rural forest fragments on the outskirts of Hamilton City (Dekrout 2009; Chapter 2) and I therefore speculated that pulses and buzzes may represent discreet situation-specific social calls mediating interactions between gregarious reproductive females. Variation in across and within habitat call patterns provided insight into how LTBs use

different habitats and when and where individuals aggregate during certain times of the breeding season (i.e. call types associated with multi-bat echolocation pulses). This information can better focus conservation efforts as wildlife managers could be alerted to sites of importance to social bats using remotely operating bat detectors, which in turn would minimise disturbance of individuals during important reproductive stages.

A major limitation with only using detectors to monitor bats is that sex ratios and specific roost locations cannot be determined (Ahlén & Baagøe 1999; O'Farrell *et al.* 1999; Mills *et al.* 1996). Detectors are also unable to discriminate between individuals from echolocation or call data only, making abundance estimates impracticable. As a result, it still remains unclear how male and female LTBs use different habitats in the Hamilton region (Dekrout 2009). Using detectors in combination with trapping and tracking techniques would provide more insight into the social ecology of LTBs and how accurate call recordings reflect social interactions occurring at these habitats during certain times of the year (MacSwiney *et al.* 2008; O'Farrell & Gannon 1999; Kuenzi & Morrison 1998; Thomas & West 1989). Invasive trapping methods must, however, be employed with care as bats are fragile and handling can alter bat behaviours. The research objectives of each study should ultimately guide which method or combination of methods is used.

Future research

Identifying the factors (e.g. foraging or social) responsible for the differential use of microhabitats, habitats and local landscapes can better assist with managing cryptic bat species (Safi *et al.* 2007; Broders *et al.* 2006; Senior *et al.* 2005; Lumsden *et al.* 2002). LTBs have a slow reproduction output, are known to form

non-random social aggregation and depend on crucial resources like roosting and foraging habitat (Chapters 2, 3 and 4; Sedgeley 2001; O'Donnell & Sedgeley 1999; Sedgeley & O'Donnell 1999). Therefore, any impacts (e.g. tree felling) to fragmented forest habitats could have considerable negative consequences for local bat populations, especially sites of social importance (e.g. maternity roost sites and breeding grounds; Rhodes & Catterall 2008; Garroway & Broders 2007; Safi *et al.* 2007; Russo *et al.* 2004; Bradbury 1979). Actively protecting key roosting and foraging habitat used by aggregating bats should be a priority for wildlife managers. Future research should seek to further disclose how male and female bat species partition local environments so that conservation efforts can be better focused. Knowing which sites reproducing individuals use during certain key reproduction stages should forestall both direct and indirect impacts to these habitats. Moreover, better understanding how anthropogenic disturbances influence local bat populations is equally important if anthropogenic impacts are to be effectively mitigated.

Does aircraft noise alter the evening activity of LTBs?

The effect of anthropogenic disturbances on wildlife behaviour is of growing concern, especially in urban ecosystems (e.g. Jung & Kalko 2010; Slabbekoorn & Ripmeester 2008; Sun & Narins 2005; McKinney 2002). In **Chapter 5**, I used a combination of field-based correlation and playback methods to investigate whether aircraft activity and noise alters the evening activity of LTBs. This study is the first to investigate the effect of aircraft noise on the behaviour of an echolocating bat species. I demonstrated that it is possible to use multiple field-based research approaches that are non-invasive to address a complex conservation question in a cryptic threatened species. Given that most cryptic

threatened species have prioritized *ex situ* conservation needs, exploring less intrusive experimental approaches to test important research hypotheses is important so that researchers do not risk further loss of life to already threatened species. Correlative data revealed that low-altitude aircraft activity clearly overlapped with bat activity at the oak fragment, which is situated just 2.5km from the runway of an international airport. LTB activity decreased during and after low altitude aircraft overflights but this trend was not significant when compared with pre-aircraft bat activity. Playback experiments revealed that simulated aircraft noise did not significantly alter LTB behaviour when compared with baseline activity levels and a silent control. In environments where anthropogenic disturbance is common, animals are forced to either avoid or adapt to human activities (e.g. Jung & Kalko 2010; Warren *et al.* 2006). My findings suggest that aircraft noise does not negatively affect bat activity in this modified environment, which is likely due to low-frequency aircraft noise not masking higher-frequency LTB echolocation pulses.

This study also demonstrated that monitoring local populations can provide valuable data that can guide more applied field studies. I used the same stratified monitoring design developed in Chapter 2 for my field experiments. This allowed me to measure changes in bat activity at differing heights and in microhabitats shown to have a greater proportion of bat passes (i.e. microhabitats with open spaces and flanking water bodies). Moreover, being more aware about the times of the night (i.e. evening activity) and the seasons (i.e. warmer summer months; Chapter 2) during which LTBs are most active allowed me to coordinate experimental trials with peaks in bat activity so that bat response data could be maximised and research effort optimised. I was also aware that in addition to

playback stimuli, changes in environmental variables could also influence bat activity (Chapter 2) so I incorporated these factors into my analyses. Ultimately, monitoring data allowed me to make informed decisions during the design of this experiment and the analysis of my data. I was also better informed about how best to allocate available resources during field trials. I have shown that field experiments can be effectively designed and executed to answer pertinent conservation questions as they apply to a cryptic threatened species.

Future research

Additional field experiments are needed to further investigate the impact of anthropogenic variables (e.g. light and vehicle noise) on bat behaviour. In Chapter 3 I found that proximity to anthropogenic structures like houses and roads may partly explain why LTBs are less active, or absent in certain available habitats. Radio-tracking studies that specifically investigate LTB movement patterns in relation to roads and houses will shed more light on how these structures influence bat behaviour. More focused and controlled playback experiments are also needed to better quantifying how bats respond to specific disturbance stimuli. Anthropogenic disturbances can also be unpredictable in nature making it difficult to realistically simulate in experiments and future studies should also explore ways in which this can be better achieved (see Chapter 5).

6.2 Overall conclusion

Since the first acoustic surveys of bats (Ahlén & Baagøe 1999; Fenton & Bell 1981) the use of detectors has become a popular and effective bat monitoring tool. In all the research chapters presented in this thesis I have used detectors to non-invasively collect different types of information for LTBs. The data that I chose to collect varied according to the different research objectives of each chapter. Data

ranged from robust nightly and seasonal foraging trends and habitat and microhabitat use patterns (Chapter 2) to less robust presence/absence data and distribution patterns (Chapter 3). I also demonstrated that additional information about in-flight LTBs calls and multi-bat echolocation sequences can be gleaned from detectors (Chapter 4); and showed that changes in bat pass rates can be a useful measure of bat response in field experiments (Chapter 5). Monitoring bats using detectors has many benefits (e.g. easy to use and relatively inexpensive relative to other methods), but most importantly it allows researcher to collect useful information about bat behaviour with little intrusion on individuals and the habitats they depend on (Johnson *et al.* 2008). Future research should strive to strategically monitoring bats, which should involve: being cost effective; adopting an experimental or novel approach where possible; and focusing on threatened target species that are most sensitive to habitat alteration (Fischer *et al.* 2009; Ewen & Armstrong 2007; O' Shea *et al.* 2003; McKinney 2002; Robertson & Hull 2001).

Conservation biologists must ultimately seek to inform and guide species conservation and management policy-making (Angeloni *et al.* 2008; Regan *et al.* 2008; Robertson & Hull 2001). I have demonstrated how research aimed at reducing uncertainty about a cryptic bat species' behaviour, distribution, and response to local anthropogenic disturbance can practically guide conservation and management decision-making. This required insight into the ecology and behaviour of the target species (i.e. LTB activity trends, habitat use, distribution patterns and breeding and foraging ecology), but also sensitivity to more applied issues related to managing and conserving local animal populations in highly modified environments. It was important to translate information about LTB

behaviour into practical conservation and management strategies, which should in the end be developed and implemented. I showed that monitoring animal populations can be an effective conservation tool and provided practical ways to overcome some of the challenges associated with monitoring the cryptic threatened LTB. Ultimately, finding ways to better understand, manage and protect ecologically significant species that are vital components to local biodiversity is the most important and pressing goal in conservation biology today.

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Appendices

Appendix I

Table 1: <u>Characteristics and field measurements for the four microhabitats at the oak fragment and the open area at Hammond Bush. Measurements are presented as means ± SE</u>

Characteristics	Open Area (Hammond Bush)	Oak Fragment			
		Microhabitat			
		Open edge (OE)	Open edge with water (WOE)	Interior (I)	River edge (RE)
Approximated area (ha)	0.3	0.1	0.34	0.59	0.17
Number of trees/microhabitat	33 trees	28	55	50	30
Diameter at breast height (DBH; six 10x10 vegetation plots; cm)	63.66 ± 1.94	60.68 ± 2.83	64.08 ± 6.72	52.13 ± 5.74	63.94 ± 4.37
Closest distance to a water body (m; measured from	ca.10m to Waikato River	ca.14m to gully (~25 to Waikato River)	ca. 6m to pond (~12 to gully)	ca. 6m to gully	ca. 6m to gully (ca. 7-12m from Waikato

next nearest tree)					River)
Closest inter-tree distance (m)	14.61 ± 1.56	5.69 ± 0.45	7.88 ± 0.42	6.07 ± 0.29	5.89 ± 0.42
Lower tier height	4.51 ± 0.07	4.62 ± 0.31	4.64 ± 0.23	5.95 ± 0.35	4.92 ± 0.58
Higher tier height	16.32 ± 2.69	15.55 ± 1.81	23.47 ± 2.75	30.49 ± 3.13	20.27 ± 5.61
Native vegetation? (Yes/No)	Y	N	Y	Y	Y
Temperature (°C) (Hygrochrone measurements; July-Oct)	10.18 ± 0.39 (Sept-Oct)	8.24 ± 0.47	10.87 ± 0.88	8.27 ± 0.74	11.34 ± 0.38
Relative Humidity (%) (Hygrochrone measurements; July-Oct)	92.5 ± 0.97 (Sept-Oct)	91.53 ± 1.95	96.55 ± 0.95	92.83 ± 1.5	93.58 ± 1.28
Known LTB roost/s? (Yes/Not identified)	Y (Dekrout 2009)	Not identified	Yes (at least 2; personal observations; ca. 58 DBH; ca. 12m to gully)	Yes (at least 2; personal observation; A. Dekrout personal communication, Auckland University)	Yes (at least 2; personal observation; A. Dekrout personal communication, Auckland University)

Other landscape features	Situated on elevated terrace (incline ca.15° from lowest point); highest exposure to prevailing Westerly wind; crop grown on edge during summer	Situated mainly on lower terrace and extends upward onto higher terrace; crop grown on edge during summer	Situated on lower terrace; characteristic open clearing takes up ca. 25% of interior area	Situated on lower terrace and extends upward onto higher terrace; steep slope from end of microhabitat to the river (incline ca. 45°)

Table 2: <u>Summary of relative LTB activity/night at urban and rural sites surveyed for a LTB presence. The corresponding distances from the Waikato River, city centre and roads and/or houses flanked each sites are provided (only approximated values are given).</u>

Urban (U) or rural (R) site?	Distance to the Waikato River (from nearest point)	Distance to city centre (from nearest point)	Presence of roads (R) and/or houses (H)?	Relative number of bat passes/night
U	1km	1km	R + H	Bats not detected
	3km	3km	R + H	Bats not detected
	1km	3km	R + H	1
	0.5km	3km	R + H	12
	50m	4km	-	145
R	50m	8km	-	47
	50m	9km	R	13
	3km	11km	R	10