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**Lek breeding in the lesser short-tailed bat  
(*Mystacina tuberculata*): male courtship, female  
selection, and the determinants of reproductive  
strategies**



**Cory Alexander Toth**

A thesis submitted in fulfillment of the requirements for the degree of  
Doctor of Philosophy in Biological Sciences

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## Abstract

Bats (Mammalia: Chiroptera) are one of the most successful mammalian groups on Earth, and likely display the widest range of mating systems of all mammals. Despite this variety, one mating system appears to be underrepresented: lek breeding. Leks are characterised by aggregations of sexually-displaying males that are visited by receptive females for the sole purpose of fertilisation. To date only one bat species has been confirmed to breed using leks. In this study I investigate the possibility of lek breeding in a second bat species, the lesser short-tailed bat (*Mystacina tuberculata*) of New Zealand, using a variety of field and laboratory methods. Males in this species use “singing roosts” to sing during the breeding season, presumably to attract females. Through the use of radiotelemetry I show that females have large home ranges and dynamic roosting patterns. Through the use of video footage, spatial analyses, and passive-integrated transponder tags I confirm lek breeding in *M. tuberculata*; male singing roosts are aggregated spatially, are defended by males, and are visited by females for mating purposes. I also demonstrate that male singing roosts are aggregated around communal roosts used by the population, likely in response to the consistent high female densities in these areas. I analyse the characteristics of male songs and show that smaller males have higher song outputs than larger males. Furthermore, through the use of genetic analyses I show that smaller males have higher reproductive success than larger males, likely due to females selecting males with higher song outputs. Small size may permit males to expend less energy during their nightly activities, and thus they can expend more on courtship. Throughout the study I present many unique behaviours not described previously, including an alternative male strategy known as “timesharing” – multiple males sharing singing roosts. My results represent a useful description of sexual selection in a bat, as details of mating behaviour are known for only a fraction of bat species. I use my results to suggest conservation strategies for *M. tuberculata*, as well as to re-examine the apparent rarity of the mating system within the Order.

*This thesis is dedicated to three important women.*

*First, I dedicate this thesis to my mother, Deborah Toth, and my grandmother, Shirley Clark.*

*I'm sorry I moved halfway across the world, but hopefully reading this will help you understand why I did.*

*I also dedicate this thesis to Tertia Thurley. This project would not be even half the quality it currently is without your support over the years. Thank you.*

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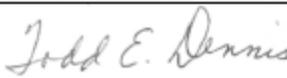
## CO-AUTHORS

Name	Nature of Contribution
Georgia Cummings	Assistance with: study design, field work, data analyses, editing of manuscript
Todd Dennis	Assistance with: study design, data analyses, editing of manuscript
Stuart Parsons	Assistance with: study design, field work, data analyses, editing of manuscript

## Certification by Co-Authors

The undersigned hereby certify that:

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- ❖ in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

Name	Signature	Date
Georgia Cummings		24/08/2015
Todd Dennis		26/08/2015
Stuart Parsons		26/08/2015
		<a href="#">Click here</a>
		<a href="#">Click here</a>
		<a href="#">Click here</a>

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### CO-AUTHORS

Name	Nature of Contribution
Todd Dennis	Assistance with: data analyses, editing of manuscript
David Pattemore	Assistance with: field work, editing of manuscript
Stuart Parsons	Assistance with: study design, field work, data analyses, editing of manuscript

### Certification by Co-Authors

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Name	Signature	Date
Todd Dennis		26/08/2015
David Pattemore		26/08/2015
Stuart Parsons		26/08/2015
		<a href="#">Click here</a>
		<a href="#">Click here</a>
		<a href="#">Click here</a>

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Chapter 4: Charming countertenors? The courtship songs of the lesser short-tailed bat (*Mystacina tuberculata*) display size-pitch allometry

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Extent of contribution by PhD candidate (%)

95

## CO-AUTHORS

Name	Nature of Contribution
Stuart Parsons	Assistance with: Study design, field work, data analyses, writing and editing of chapter

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Name	Signature	Date
Stuart Parsons		26/08/2015
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Chapter 5: Smaller males have higher reproductive success in a lek-breeding bat

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### CO-AUTHORS

Name	Nature of Contribution
Anna Santure	Assistance with: data analyses, editing of chapter
Stuart Parsons	Assistance with: study design, field work, data analyses, editing of chapter

### Certification by Co-Authors

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Name	Signature	Date
Anna Santure		26/08/2015
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Appendix A: Is lek breeding rare in bats?

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### CO-AUTHORS

Name	Nature of Contribution
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Name	Signature	Date
Stuart Parsons		26/08/2015
		<a href="#">Click here</a>



## General introduction

Empires fall, ids explode, great symphonies are written, and behind all of it is a single instinct  
that demands satisfaction.

– Sherwin B. Nuland, *How We Live*, p. 198

*Mystacina*, a curious breed

Not just for their habits to feed

For up high on his deck, the male sings in a lek

And the females, they service his needs

– Graeme Finlayson

## 1.1 The Breeding Behaviour of Bats

Bats (Mammalia: Chiroptera) provide a rich system of study for biologists. They are found on every continent (except Antarctica) and, with over 1,100 species, are second only to rodents as the most-specious group of mammals (Altringham 2011). The evolution of flight has promoted the adoption of the widest diversity of niches of any mammalian group (Kruttsch 2000), resulting in a myriad of unique forms and behaviours. For example, as bats are largely nocturnal the majority of species use echolocation rather than vision for navigation and foraging, a trait that has been studied since the late 1700s and is still generating new research questions today (Fenton 2013).

The mating systems of bats is an area that possibly has the widest potential for study. At the time of the last review, details of breeding behaviour were known for less than 7% of all bat species (McCracken and Wilkinson 2000). However, it appears as though mating system evolution operates similarly in bats and other mammals, namely being influenced by factors such as female density, female home range size, and female group stability (Clutton-Brock 1989; Clutton-Brock et al. 1993; Altringham 2011). Mating system evolution is further guided by the diversity of dietary niches and roosting behaviours bats exhibit (Kunz and Lumsden 2003), and as a result bats likely display the widest range of reproductive strategies of all mammals (Altringham 2011). For example, the spectral bat (*Vampyrum spectrum*) – the largest carnivorous bat in the world – has been hypothesised (although not confirmed) to be one of the few mammals to use obligate monogamy (Vehrencamp et al. 1977). A pair of *V. spectrum*, along with their young, were observed to cohabit for over a year. During the early evening, one adult would stay within the roost to guard the offspring while the other left to forage, potentially bringing prey back to provision the others (although this was not observed directly; Vehrencamp et al. 1977; McCracken and Wilkinson 2000). It is possible that this mating system has been adopted in *V. spectrum* because solitary females defend large

foraging areas. Thus, it is more energetically economical for males to attach themselves to single females rather than trying to defend multiple females over such large areas (Altringham 2011). Many species of bats, particularly those in the tropics, use harem defence strategies, with one or multiple males defending groups of females (McCracken and Wilkinson 2000). For example, males of several species of “tent roosting” bats modify leaves by chewing support structures to create “tents”, which are valuable roosting sites to females (e.g. Kunz and McCracken 1996). Males defend their tents against rivals, as tents attract groups of breeding females to which they can attach themselves (e.g. Kunz and McCracken 1996; Storz et al. 2000). Furthermore, some temperate species use a mysterious mating system referred to as “swarming”, where thousands of individuals of several species converge upon hibernacula sites during the late summer or autumn (e.g. Rivers et al. 2006; Furmankiewicz 2008). Mating is known to occur in swarms, and although mate choice appears to be superficially random (e.g. Thomas et al. 1979) there is evidence of skewed male reproductive success within them (Watt and Fenton 1995). In these examples the influence of foraging strategies, female density, and roosting behaviour on mating systems are clear.

## **1.2 Lek Breeding**

Lek breeding is one of the most interesting mating systems from a behavioural standpoint. In lekking species, groups of males will defend small, resource-free territories that are aggregated within a particular area of the available habitat (hereafter referred to as the lek) and produce sexual displays for visiting females. Females visit the lek to appraise male displays and select a mate. Classically, leks have been defined using four broad criteria (Bradbury 1977): 1) males are aggregated within the available habitat; 2) females do not receive resources from the males they mate with; 3) females are able to select their mates; and 4) males contribute no parental care to their offspring. However, with an increasing

number of species shown to use lek-like behaviour, it has been suggested that much more relaxed criteria be used to confirm lek breeding (see Höglund and Alatalo 1995). Regardless, leks have long been of great interest to behavioural ecologists for several reasons. Firstly, it is often unknown why males choose to aggregate in high densities, as it likely increases intrasexual competition and decreases individual reproductive success (Isvaran and St. Mary 2003). Secondly, as female mate choice is not confounded by resource ownership or the quality of the male as a paternal provider, male reproductive success is typified by an extreme skew in many lekking species (see Bradbury et al. 1985). Thus, leks offer an ideal system to study female selection for indirect benefits in free-living animals (Höglund and Alatalo 1995).

### **1.3 The Rarity of Lek Breeding in Bats**

Despite the range of behaviours observed in bats, lek breeding appears to be underrepresented in the Order. Only the hammer-headed bat (*Hypsignathus monstrosus*) has been confirmed to use leks (Bradbury 1977). *Hypsignathus monstrosus* is the largest bat in Africa and displays one of the most extreme cases of sexual dimorphism found in mammals; the larynx – used in the production of courtship calls – is three times larger in males than females (Langevin and Barclay 1990). During the night and early morning up to 130 males will aggregate along stretches of river and produce loud buzzing vocalisations and wing-flapping displays. Females will take large detours while travelling from their day roosts to their foraging grounds to visit calling sites and mate with males (Bradbury 1977).

The rarity of lek breeding in bats is something of a mystery. Many bat species possess all of the necessary prerequisites thought to be required for the evolution of leks (Höglund and Alatalo 1995): 1) males are emancipated from parental care; 2) resources required by females are indefensible; 3) fertilisation is internal; 4) males and females possess high

mobility; and 5) females can discriminate between males. In fact, bats appear better suited for lek evolution than birds, which have the highest number of lek-breeding species (Jiguet et al. 2000); many bird species require male parental care (Höglund and Alatalo 1995), whereas the evolution of male parental care appears to be precluded in bats (McCracken and Wilkinson 2000; but see Vehrencamp et al. 1977). Furthermore, leks are thought to form when females possess large home ranges and have high population densities, and resources required by females are indefensible (Clutton-Brock 1989). These conditions make it uneconomical for males to defend females or resources, requiring them to instead aggregate in areas with high female densities and use self-advertisement displays to attract mates (Emlen and Oring 1977; Bradbury et al. 1986; Bradbury et al. 1989). Large home ranges, high population densities, and indefensible resources are common traits in many temperate bat species (Barclay and Harder 2003; Kunz and Lumsden 2003), and thus it suggests that the rarity of lek breeding may be a result of the lack of information known for bat mating systems, rather than any factors precluding its adoption.

#### **1.4 *Mystacina tuberculata***

The lesser short-tailed bat (*Mystacina tuberculata*) is a threatened (O'Donnell et al. 2013), medium-sized (~10 – 20g), tree-roosting species endemic to New Zealand that exhibits characteristics suggestive of lek breeding, although the species' breeding behaviour has not been studied previously. In the summer months *M. tuberculata* establishes communal roosts containing some of the largest aggregations of all tree-roosting bats (Kunz and Lumsden 2003). During the breeding season (roughly September – May; Carter and Riskin 2006), males occupy small cracks in trees and sing, presumably to attract passing females. Male songs are audible to humans, but also extend to ultrasonic frequencies (Lloyd 2001). The “singing roosts” used by males have been reported to be clustered spatially, perhaps in

relation to high female densities (Winnington 1999), leading to suggestions that *M. tuberculata* is a lek breeder (Daniel 1990; Lloyd 2001).

Matching the suggestion of using a rare mating system, *M. tuberculata* also possesses a number of unique morphological and behavioural characteristics, likely as a result of its long evolutionary history on an isolated island. New Zealand began separating from Gondwana approximately 82 Ma, and by 70 – 80 Ma New Zealand was essentially a raft with an isolated terrestrial biota (Cooper and Millener 1993). As a result of this separation, combined with low levels of animal migrations from adjacent land masses, New Zealand has one of the highest levels of endemism on Earth (Gibbs 2006). Much of the modern biota of New Zealand is derived from the original Gondwana populations, including frogs, skinks, geckos, weta, tuatara, some spiders, terrestrial gastropods, ratites, and many plant groups (Cooper and Millener 1993). Furthermore, due to the islands' early separation from Gondwana, mammals were largely absent from New Zealand for much of its history. Bats – today represented by just *M. tuberculata* and the distantly-related long-tailed bat (*Chalinolobus tuberculatus*) – have been the only land mammals capable of settling in New Zealand naturally. Thus, when the ancestor of *M. tuberculata* – likely a relative of the noctilionoids (Kennedy et al. 1999; Teeling et al. 2003) largely found in South America today – reached New Zealand sometime after the Oligocene (25 – 37 Ma; Hand et al. 1998), they were able to evolve in an environment largely free of competition and predation (Gibbs 2006). As a result, *M. tuberculata* displays a number of characteristics and behaviours not seen in other species. For example, *M. tuberculata* has evolved the ability to fold its wings into a protective portion of its wing membranes, allowing it to walk quadrupedally (Riskin et al. 2006). It has been estimated that *M. tuberculata* spends approximately a third of its time foraging on the ground (Daniel 1976; McCartney et al. 2007), making it the most terrestrial bat in the world (Carter and Riskin 2006). *Mystacina tuberculata* also has a wide diet that is

dictated seasonal availability (e.g. Cummings et al. 2014), and includes nectar, pollen, fruit, and insects (Daniel 1976; Daniel 1979; Arkins et al. 1999). *Mystacina tuberculata* is the only fully temperate bat pollinator in the world, and is an important pollinator and seed disperser for many native plant species (Daniel 1976; Lloyd 2001; McCartney et al. 2007).

The potential use of lek breeding by *M. tuberculata* is of interest for three primary reasons: 1) it would be the discovery of a rare mating system virtually undescribed in Chiroptera; 2) it would provide the opportunity to determine the factors that have led to the evolution of the mating system, allowing for the investigation of other potential lek-breeding species with similar life histories; and 3) it would provide useful conservation cues (e.g. Morales et al. 2001). Furthermore, the use of a lek system by *M. tuberculata* would provide a valuable opportunity to study sexual selection in a bat given the general lack of such information in the majority of bat species, and the utility of lek systems for such studies. However, basic details of the breeding behaviour of *M. tuberculata* have yet to be studied, including whether or not the species fulfils the criteria for lekking outlined by Bradbury (1977), the characteristics of male songs, and if singing roosts actually serve a reproductive purpose.

## **1.5 Thesis Outline**

The aim of this thesis is to provide an overview of the mating behaviour of *M. tuberculata*, specifically to confirm or refute the occurrence of lek breeding in the species and, if confirmed, to identify the factors that may have led to its adoption. To do this I studied a population of *M. tuberculata* in the Pikiariki Ecological Area, in the central North Island of New Zealand during 2011 – 2014. The thesis is arranged as a series of stand-alone papers, and as such there is some degree of overlap between them. Two of the chapters, as well as an appendix, have been published in international journals (see chapter front page for details).

Because of this, the chapters of this thesis will differ in their style of writing and citation. I present four studies used to support the overall aim of my thesis.

In Chapter 2 I determine the home range size and roosting patterns of individual *M. tuberculata* in the Pikiariki Ecological Area using radiotelemetry. Female home range size and roosting behaviour are important determinants for bat mating systems, and as such a description of these behaviours provides insight into the reproductive strategies adopted by the species. These results are discussed in a framework of habitat use, as I present novel findings on the adoption of two habitat types (open space and exotic plantation) into the home ranges of *M. tuberculata* that have not been observed previously.

In Chapter 3 I investigate if the breeding behaviour of *M. tuberculata* meets the criteria of lekking proposed by Bradbury (1977). To do this I used spatial analyses to determine if male singing roosts are aggregated within the available habitat, and video cameras used in conjunction with passive identification techniques to determine if females visit singing roosts to mate with resident males, and if they receive resources when they do so. Furthermore I use spatial regression analyses to determine if singing roost locations are predicted by the location of communal roosts used by the population (i.e. areas of high female density), allowing for mechanisms of lek formation to be inferred.

In Chapter 4 I provide an overview of *M. tuberculata* singing behaviour, including an analysis of male song repertoires, the frequency characteristics of male songs, and male song output. As songs are likely the primary method of courtship for the species I suggest probable characteristics used for mate selection by females. This latter objective was accomplished by recording the songs of known (i.e. marked) males and regressing song characteristics against male morphometrics. I compare my findings to previous studies on other singing bat species, as well as to songbirds.

In Chapter 5 I use genetic analyses to determine male reproductive success to infer female selection criteria. Specifically I use my findings from Chapter 4 to investigate likely predictors of male reproductive success and discuss the use of several male reproductive strategies.

Chapter 6 summarises the principal findings of this study and places them within the context of management of a threatened species. I also discuss additional questions raised by my research that would be of interest for further study.

In Appendix A I critically examine the apparent rarity of lek breeding in Chiroptera. To do this I discuss and compare the determinants of mammalian mating systems, bat mating systems, and leks. I provide an overview of the current state of knowledge of bat mating systems, as well one of the most comprehensive and up to date lists of lek-breeding mammals, including bat species that likely display lek-breeding behaviour. I also discuss the utility of identifying lek-breeding bat species for conservation efforts. This Appendix was not included as a chapter proper because it is not a data chapter, and also does not serve specifically as an introduction or conclusion, but rather a commentary of the research as a whole.

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## **Adoption of alternative habitats by a threatened, “obligate” forest-dwelling bat in a fragmented landscape**

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## 2.1 Abstract

While they are among the most ecologically-important animals within forest ecosystems, little is known about how bats respond to habitat loss and fragmentation. The threatened lesser short-tailed bat (*Mystacina tuberculata*), considered to be an obligate deep-forest species, is one of only 2 extant land mammals endemic to New Zealand; it plays a number of important roles within native forests, including pollination and seed dispersal, and rarely occurs in modified forests. We used radiotelemetry to study the movements, roosting behavior, and habitat use of *M. tuberculata* within a fragmented landscape comprised of 3 main habitat types: open space (harvested forest and pastoral land), native forests, and exotic pine plantations. We found that the bats had smaller home-range areas and travelled shorter nightly distances than populations investigated previously from contiguous native forest. Furthermore, *M. tuberculata* occupied all 3 habitat types, with native forest being preferred overall. However, individual variation in habitat selection was high, with some bats preferring exotic plantation and open space over native forest. Roosting patterns were similar to those previously observed in contiguous forest; individual bats often switched between communal and solitary roosts. Our findings indicate that *M. tuberculata* exhibit some degree of behavioral plasticity that allows them to adapt to different landscape mosaics and exploit alternative habitats. To our knowledge, this is the first such documentation of plasticity in habitat use for a bat species believed to be an obligate forest-dweller.

## 2.2 Introduction

Habitat loss and the subsequent fragmentation that ensues have been shown to contribute significantly to loss of species globally (Ewers and Didham 2006). Many organisms that rely on unmodified tracts of forests for foraging, reproduction, and/or shelter risk population declines or extirpation through the removal of forest patches due to the effects of genetic isolation, microclimate change, and decreased availability of resources within patches (Saunders et al. 1991), as well as increased competition and predation from invasive species (e.g., Robinson and Wilcove 1994; Gibson et al. 2013). It comes as no surprise therefore that negative effects from fragmentation of important habitats have been reported for all major taxa (for reviews, see Offerman et al. 1995; Turner 1996; Laurance and Bierregaard Jr. 1997).

Not all organisms, however, experience negative effects from fragmentation of landscapes due to habitat loss (hereafter simply referred to as “fragmentation”) (Offerman et al. 1995; Laurance et al. 2002). For example, some open-habitat bird (Andren 1992; Stouffer and Bierregaard Jr. 1995b) and mammal (Malcolm 1997) species directly benefit from fragmentation, and frogs (Tocher et al. 1997) and butterflies (Brown Jr. and Hutchings 1997) can colonize areas that previously were unsuitable. Furthermore, some species are unaffected by moderate changes in habitat composition (e.g., Stouffer and Bierregaard Jr. 1995a; Pope et al. 2004), evidently possessing some degree of behavioral or ecomorphological plasticity that allows them to accommodate costs arising from fragmentation.

Bat communities are a major driving force of ecosystem dynamics in both temperate and tropical regions due to their wide range of foraging strategies and abundance of species (Altringham 2011). Thus, the responses of these communities to perturbations are of considerable interest to conservation management. Bats possess high mobility (which can offset the effects of fragmentation; Offerman et al. 1995; but see Harrison et al. 2013), yet they are vulnerable to environmental changes due their slow, ‘K-selected’ life-history

strategy (Barclay and Harder 2003). Research carried out to date examining the responses of bat species to habitat degradation has tended to examine multiple species simultaneously (e.g., Fenton et al. 1992; Estrada et al. 1993; Walsh and Harris 1996a; Schulze et al. 2000; Estrada and Coates-Estrada 2002; Cisneros et al. 2015). Bats are useful for such community-wide studies because they are readily captured or sampled through the use of automatic acoustic monitors (Lacki et al. 2007), and often occur in large numbers of both individuals and species. While community-wide studies facilitate inferences about the effects of habitat fragmentation over large spatio-temporal scales, they may lack sufficient spatial resolution (e.g., home-range area, foraging preferences, etc.) to determine effects on individual species. Few studies on bats have examined the effects of habitat fragmentation in detail (i.e., beyond passive detection) at the species level.

New Zealand presents interesting opportunities for the study of fragmentation effects on bat populations. With just two extant species – the long-tailed bat (*Chalinolobus tuberculatus*) and the lesser short-tailed bat (*Mystacina tuberculata*), both of which are of conservation concern (O'Donnell et al. 2010) – New Zealand has a low diversity of bats compared to other temperate islands of similar size (e.g., 31 species in Japan: Abe et al. 2008; 17 species in Great Britain: Altringham 2003). However, *M. tuberculata* plays an integral role in forest ecosystems that would otherwise be covered by several species due to its diverse and flexible foraging strategies. While *C. tuberculatus* is a strictly aerial insectivore (O'Donnell 2000), *M. tuberculata* is insectivorous, frugivorous, nectivorous, and pollinivorous (Daniel 1976, 1979; Ecroyd 1996; Arkins et al. 1999; Lloyd 2001; Pattemore and Wilcove 2012), choosing its foraging strategies in response to variation in food availability (Arkins et al. 1999; Cummings et al. 2014).

The role of native old-growth forests in the survival of *M. tuberculata* has been demonstrated explicitly (Daniel 1979), and notable populations have generally been found

only in large (> 1,000 ha), undisturbed tracts of indigenous forest (Lloyd 2001). O'Donnell et al. (2006) demonstrated that > 96% of recorded echolocation calls were within forest interiors in a South Island population. Communal roost trees selected by the species comprise the oldest and largest trees, and exclusively occur within forest interiors (Sedgeley 2003, 2006). The mating system of the species also requires native forest, with males occupying and defending clustered solitary roosts from which they sing to females (Daniel 1990; Toth and Parsons 2013). Male singing roosts have not been found in exotic tree species (C.A. Toth, pers. obs.). These life history traits, combined with echolocation call structure and a low wing loading and aspect ratio adapted to slow, highly maneuverable (gleaning) flight (Norberg and Rayner 1987), suggest *M. tuberculata* is adapted to living almost wholly within (but not limited to) forest interiors (Webb et al. 1998; Jones et al. 2003).

Unfortunately, New Zealand has been subject to intensive loss of native forests to forestry and agriculture. During the first three quarters of the 20<sup>th</sup> century the area covered by agricultural land and exotic tree plantations increased from 35% to 60% (Molloy 1980), and by 1993 52% of the land cover of New Zealand had been converted to farmland (Ministry for the Environment 1997). This loss of native forest cover has led to fragmentation of *M. tuberculata* habitat, yet how its populations continue to survive in and interact with such disturbed landscapes is unknown.

In this study we use radiotelemetry to describe the home ranges and roosting behavior of adult *M. tuberculata* within a fragmented landscape. We predicted negative effects of landscape fragmentation to manifest in bats in two ways: 1) an increase in home range size compared to individuals inhabiting contiguous forest if individuals need to range further to locate resources (e.g., Fraser and Stutchbury 2004), and 2) an increased fidelity to roosts if suitable roosting sites are scarce within the forest (e.g., Morrison 1978; Borkin et al. 2011).

## 2.3 Methods

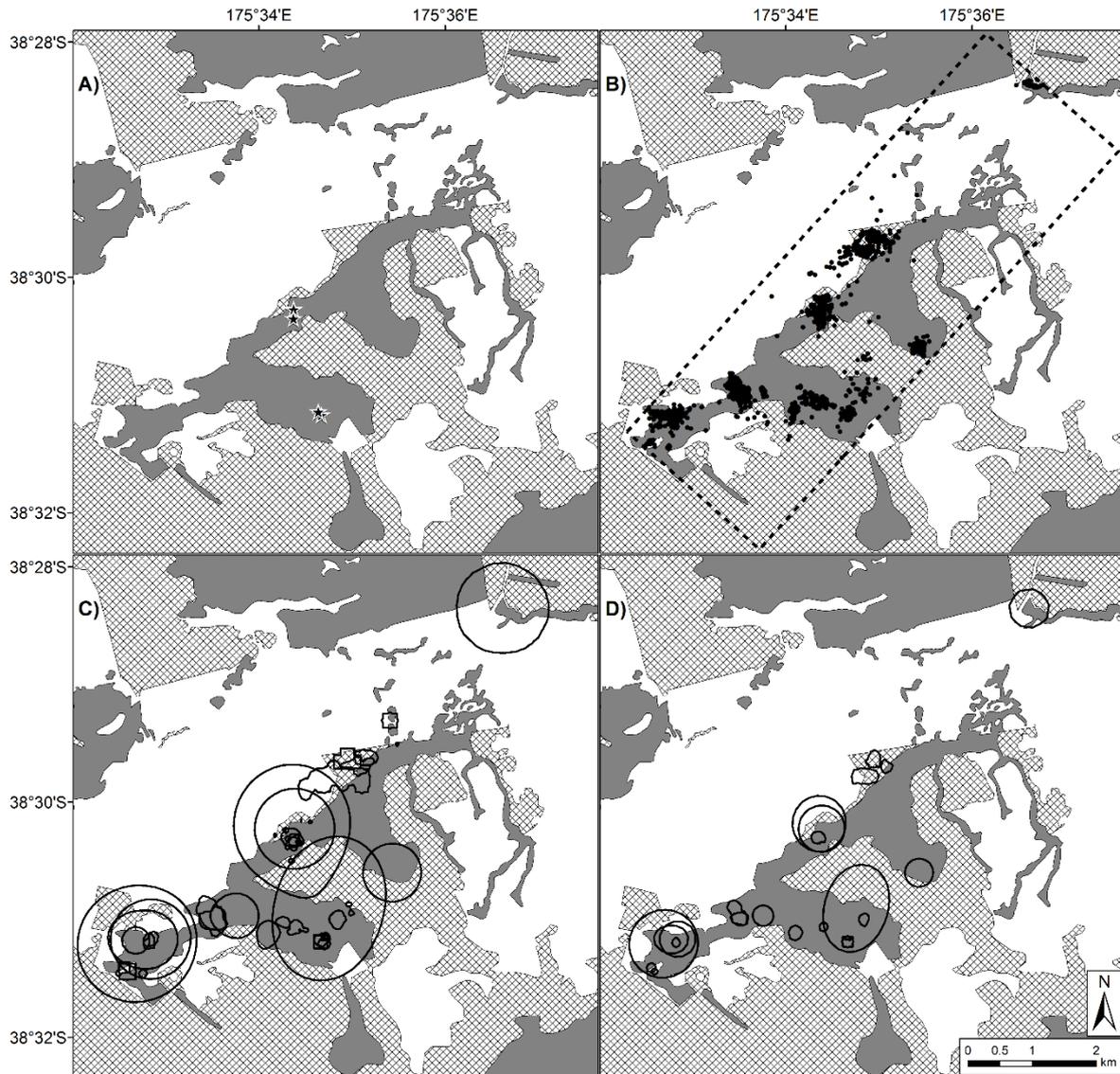
### 2.3.1 Study area

Our study was carried out in the Pikiariki Ecological Area of the Pureora Forest Park (38°26'S, 175°39'E), central North Island, New Zealand, between December and April 2011-12 and November and April 2012-13. Pikiariki is situated within the 78,000 ha Pureora Forest Park, and is comprised of approximately 450 ha of native, mature podocarp-hardwood forests bordered by exotic pine plantations (hereafter referred to as “exotic plantations”) and pastoral land (Wallace 2006) (Fig. 1a). Pikiariki was selectively logged until the 1980s creating a mosaic of different habitats within the study region, while the forest is characterized by a low canopy with a dense understory (Wallace 2006). Pikiariki is separated from the neighboring Waipapa Ecological Area to the north by a band of approximately 2 km of pastoral land and a state highway.

Pikiariki is home to approximately 700 *M. tuberculata* (Wallace 2006). At the time of our study 11 communal roosts had been located within Pikiariki, although only four were used by bats during this study (Fig. 1a).

### 2.3.2 Radiotelemetry

We affixed very high-frequency radio transmitters (model BD-2, Holohil Systems, Ontario, Canada) to 25 adult individuals ( $n = 10$  males,  $n = 15$  females) resulting in the successful tracking of 18 bats ( $n = 9$  males,  $n = 9$  females). Unsuccessful tracking attempts were due to transmitter failure ( $n = 2$ ), moisture damage to transmitters ( $n = 3$ ), and an inability to find the bats' nightly locations ( $n = 1$  male,  $n = 1$  female). We believe the latter male occupied an area of Pikiariki that was unreachable by foot, while the female may have been travelling to Waipapa, however this is unconfirmed. Although some females were tracked during the birthing period (December – January), only nulliparous females were fitted with transmitters.



**Fig. 1** - Habitat maps of the study area. A) The Pikiariki Ecological Area of the Pureora Forest Park, New Zealand. Dark gray sections indicate native forest, hatched sections represent exotic plantations, and white sections denote open spaces (composed of pastoral land and harvested forest). Stars mark the 4 communal roosts known to be used by the population during the course of this study. To the north of Pikiariki is the neighboring Waipapa Ecological Area where some bats were confirmed to visit nightly. B) Location fixes ( $n = 1,810$ ) for the 18 adult bats tracked during this study. The dashed line represents the smallest rectangle that encompasses all individuals' 100% MCPs and was used to define the study site during habitat selection analyses. C) Individual home ranges as determined by 95% fixed-kernel estimators. D) Individual home-range cores as determined by 50% fixed-kernel estimators.

We captured bats using a combination of mist nets sited along commuting routes and harp traps located at communal roosts, and deemed individuals suitable for tracking if the weight of the transmitter (approximately 0.6 g) did not exceed 5% of body weight (Aldridge and Brigham 1988) (mean weight of tracked animals was 13.8 g). We attached transmitters by clipping a small patch of fur between the shoulder blades and affixed with ADOS F2 contact

adhesive (CRC Industries, New Zealand). The capture and radiotracking of individuals was approved both by the University of Auckland Animal Ethics Committee and the New Zealand Department of Conservation, and followed the guidelines given by the American Society of Mammalogists (Sikes and Gannon 2011).

We released bats on the night of capture but initiated radiotracking the following evening to minimize handling effects (Withey et al. 2001). A maximum of two bats were tracked at any one time (on alternating nights). Tracking was accomplished via synchronized biangulation using two separate observers, each equipped with an Australis 26k Scanning Receiver (Titley Scientific, Australia) and a Yagi three-element antenna. The observers communicated via radio and thus location fixes were synchronized to within a few seconds. For each fix the observers noted their geographic coordinates (New Zealand transverse Mercator) using a global positioning system unit (GPS) and determined the bearing of strongest signal with a handheld compass (bearings were corrected later for local magnetic declination). Location fixes were taken at a minimum of one observation every 10 minutes, which we deemed an appropriate interval to ensure quasi-independent observations as the bats theoretically could fly across their range in < 10 minutes (*M. tuberculata* has been recorded flying at speeds over 44 km/hr; Christie 2006). Some location fixes were taken at intervals > 10 minutes as we were rarely able to track bats as they commuted to/from their day roosts, and sometimes bats would leave an area and were not re-located immediately. We tracked each bat following their emergence from their day roosts in the evening to the resumption of roosting in the morning, unless inclement weather prevented a full night's tracking. We determined the locations of day roosts via a close-approach method: a radio signal was followed until the tree the bat was roosting within could be identified from all directions at the lowest gain setting on the receiver.

We calculated bearing intersections from triangulation using LOAS Radio Telemetry Software 4.0 (Sallee 2004). Tracking continued for individuals on successive nights until an asymptote was reached in the incremental-area analysis of the minimum convex polygon (MCP) (Odum and Kuenzler 1955; Harris et al. 1990). Prior to analyses we screened data using a speed filter (set at 6 m/s, resulting in the removal of 19 location fixes) and calculated location errors (mean error = 54.7 m,  $SE = 19.1$  m; see Appendix B).

### 2.3.3 Home range and movement analyses

Using the telemetry fixes from each bat we calculated individual MCPs and fixed-kernel (FK) density estimators with the program Ranges8 (Kenward et al. 2008). Minimum convex polygons were primarily used for comparison of home-range size with previous radiotelemetry studies on *M. tuberculata* and for habitat selection analyses (see below), while FK density estimators were used as the primary means of home range calculation (see Worton 1987; Harris et al. 1990; Powell 2000; Börger et al. 2006; Nilsen et al. 2008; but also see Boyle et al. 2009). To account for potential location outliers, we defined home-range areas by their 95% FK contours (Laver and Kelly 2008) and core areas by 50% FK contours (Laver and Kelly 2008). For eight of the bats (four males and four females) the optimal smoothing factor for the FKs was calculated using least-squares cross-validation. For the remaining 10 bats the smoothing factor could not be optimized and so a multiplier of 1 was used instead (Kenward et al. 2008).

To quantify movements made by bats distances between location fixes were calculated using Ranges8. We calculated average distance travelled for each individual by summing nightly inter-location distances and averaging across the number of nights in which tracking data were collected. Furthermore, we divided inter-location distances into six distance categories (< 200 m, 200 – 399 m, 400 – 599 m, 600 – 799 m, 800 – 999 m, and >

1000 m) and expressed movements as percentages (e.g., 72% of movements were < 200 m, 18% between 200 – 399 m, 2% between 400 – 599 m, etc.). We then pooled percentage data for all individuals and performed pairwise Wilcoxon rank-sum tests using Holm-Bonferonni correction (Holm 1979) to compare distance classes.

#### *2.3.4 Habitat types*

For analyses of habitat usage we divided the Pikiariki study area into three broad categories: native forest, exotic plantations (primarily composed of *Pinus* spp.), and open space (composed of pastoral land and harvested forest). We obtained digital topographical maps (1:50000 scale) from Land Information New Zealand (<http://www.linz.govt.nz/>) and imported them into ArcMap 10 (Environmental Systems Research Institute, California, US). As the maps were created in 2009 we applied slight modifications based on personal knowledge of the study site to account for changes that occurred in the intervening time (namely a stand of pine that had been harvested after the map's release).

#### *2.3.5 Second- and third-order habitat selection*

We assessed habitat selection of individuals based on second- and third-order classifications. Second-order habitat selection compares habitats that occur within an individual's home range to the availability of those habitats within the wider landscape (i.e., habitat composition of home ranges), while third-order selection refers to the preference for habitats within an individual's home range and was estimated using telemetry location fixes (Johnson 1980). We conducted second- and third-order analyses of habitat selection in ArcMap 10 using a Euclidean distance-based analysis (Conner and Plowman 2001; see below). For these analyses we used 100% MCPs rather than 95% FKs as FKs are known to underestimate home-range area (Naef-Daenzer 1993; Seaman and Powell 1996); we deemed it more

appropriate to include potentially-unused areas into analyses than to disregard areas known to be used by individuals.

Second-order selection was determined for each bat by generating the smallest rectangle that encompassed all individuals' 100% MCPs and then dispersing 10,000 random points from a uniform distribution within that rectangle. We compared the average distance of random points that fell within a bat's home range to each habitat type to the average distance of all random points to each habitat type. Points falling within a habitat received a distance of zero. We then divided the average distance of the subset of points within a bat's MCP by the average distance of the random points resulting in a ratio for each bat in each habitat. A ratio  $< 1.0$  indicates that the habitat was preferred by that individual, while a ratio  $> 1.0$  indicates avoidance (Conner and Plowman 2001).

For third-order selection we calculated the mean distance of location fixes to each habitat type for each individual. We then divided this mean distance by the mean distance of random points to each habitat type throughout that individual's home range, which also resulted in a ratio that could be compared to 1.0 (i.e., no preference).

Prior to examining habitat preferences we tested male and female mean selection ratios for differences using Welch's *t*-tests (second-order selection) and Wilcoxon rank-sum tests (third-order selection). We assessed individual preferences for habitats by comparing the mean selection ratios for each habitat type against a ratio of 1.0 using Student's *t*-tests (second-order selection) and Wilcoxon signed-rank tests (third-order selection). We also determined relative habitat preferences (i.e., comparing habitat selection ratios to one another directly to determine a relative preference) by comparing mean selection ratios for each habitat using Welch's *t*-tests (second-order selection) and Wilcoxon rank-sum tests (third-order selection).

Prior to analyses we assessed all data for normality via Shapiro-Wilks tests. We conducted all statistical tests with R 3.01 (R Development Core Team 2013).

## 2.4 Results

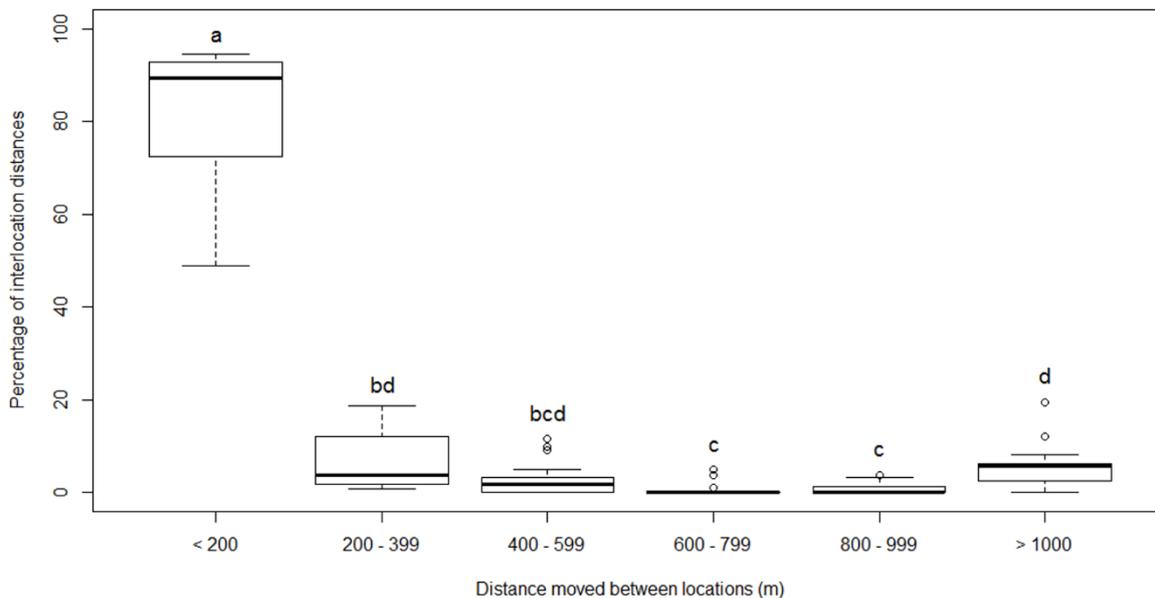
### 2.4.1 Home-range and core areas

Eighteen bats were tracked across 69 bat nights (mean = 3.1,  $SD = 0.8$  nights per bat) for a total of 1,810 location fixes (mean = 31.1,  $SD = 19.5$  fixes per night per bat; Table 1), ranging over 1,236.3 ha (Fig. 1b). Individual home ranges and home-range cores were extremely variable, ranging from 4.6 to 559.2 ha (mean = 91.8,  $SD = 140.6$  ha,  $n = 18$ ; Fig. 1c) and 1.3 to 146.9 ha (mean = 24.3,  $SD = 39.8$  ha,  $n = 18$ ; Fig. 1d), respectively (Table 1). To ensure that the variability in number of location fixes between individuals did not influence our measures of home-range area we performed a linear regression on both MCP and 95% FK size against the number of location fixes of each range estimate and found no significant association (MCP:  $F_{1,16} = 0.028$ ,  $P = 0.87$ ,  $R^2 = 0.0018$ ; 95% FK:  $F_{1,16} = 1.12$ ,  $P = 0.31$ ,  $R^2 = 0.007$ ; Appendix B). There was no statistically significant difference in the area of home ranges and home-range cores between the sexes (all  $P$ -values  $> 0.05$ ), so data were pooled for all subsequent analyses. Approximately 46% of all individual home ranges overlapped with those of others, averaging 7.8% overlap ( $SD = 18.4\%$ , range: 0 – 100%), while 13% of home-range cores overlapped, averaging 4.1% overlap ( $SD = 17.7\%$ , range: 0 – 100%).

Individuals travelled a mean distance of 7.1 km  $\pm$  3.3  $SD$  per night (range: 1.1 – 14.7 km,  $n = 69$  bat nights). Most movements (i.e., interlocation distances) were  $< 200$  m, and long-distance ( $> 1$  km) movements were more common than intermediate distances (Fig. 2). One male was found to leave Pikiariki nightly and travel to the neighboring Waipapa Ecological Area, a straight-line distance from the nearest communal roost of nearly 5 km.

**Table 1.** Summary information from radiotelemetry of 18 adult *Mystacina tuberculata* tracked in the Pikiariki Ecological Area through the summers of 2011 – 13.

	<b>Tracking Period</b>	<b>No. Days Tracked</b>	<b>No. Fixes</b>	<b>100% MCP (ha)</b>	<b>95% FK (ha)</b>	<b>50% FK (ha)</b>
Female 1	Dec 2011	11	159	261.9	22.8	8.0
Female 2	Feb 2012	3	19	43.8	8.4	2.3
Female 3	Feb 2012	3	44	63.1	11.5	2.6
Female 4	Feb – Mar 2012	4	115	169.7	65.3	15.3
Female 5	Mar – Apr 2012	5	46	506.3	559.3	146.9
Female 6	Apr 2012	5	59	309.6	312.4	109.5
Female 7	Apr 2012	4	74	51.3	40.8	8.2
Female 8	Dec 2012	3	94	14.3	4.6	1.3
Female 9	Apr 2012	3	87	18.5	15.2	3.7
<b>Mean (SD)</b>		<b>4.6 (2.6)</b>	<b>77.4 (42.3)</b>	<b>159.8 (169.1)</b>	<b>115.6 (192.7)</b>	<b>24.3 (39.8)</b>
Male 1	Nov – Dec 2012	5	121	54.4	10.2	3.2
Male 2	Jan 2013	4	77	548.5	160.4	28.4
Male 3	Jan 2013	3	117	85.7	15.2	7.0
Male 4	Jan – Feb 2013	3	125	639.1	60.4	9.5
Male 5	Mar 2013	2	126	338.0	122.8	24.4
Male 6	Apr 2013	3	94	73.9	7.9	2.9
Male 7	Apr 2013	3	130	243.2	79.0	18.4
Male 8	Apr 2013	3	168	108.4	137.5	41.2
Male 9	Apr 2013	2	155	238.9	18.4	4.2
<b>Mean (SD)</b>		<b>3.1 (0.9)</b>	<b>123.7 (27.6)</b>	<b>258.9 (213.3)</b>	<b>68.0 (60.0)</b>	<b>15.5 (13.5)</b>
<b>Total Mean (SD)</b>		<b>3.1 (0.8)</b>	<b>100.6 (42.0)</b>	<b>209.4 (193.6)</b>	<b>91.8 (140.6)</b>	<b>24.3 (39.8)</b>



**Fig. 2** – Percentage of interfix distances in relation to the distances moved between location fixes, averaged over multiple nights for the tracked bats. Pairwise Wilcoxon rank-sum tests using Holm–Bonferroni correction provided statistically significant groupings (a-d, alpha = 0.0033) of separate distance classes.

#### 2.4.2 Roosting behavior

All individuals used communal roosts and many had solitary day roosts. All roosts used by individuals were located within native forest. Solitary day roosts were used by both sexes, but were more common in females ( $n = 8$  females,  $n = 2$  males). Only one individual (discussed below) possessed multiple solitary day roosts, all others used only a single solitary roost. Females that possessed solitary day roosts used them on average 51% of days tracked (range: 40 – 71%) while the two males used solitary roosts on average 25% of days tracked (the remaining days were spent in communal roosts by all individuals). We observed one of these males using three separate solitary day roosts, one of which has been identified as a singing roost in the preceding year. We monitored this male’s roosting behavior beyond the usual tracking period as it was the first male with a singing roost to be tracked. Over 11 consecutive days of monitoring the male spent two days in a communal roost, two days in a solitary roost (that did not serve as a singing roost), and seven consecutive days in the singing roost. A

week later a check of the transmitter revealed this male using a third solitary roost that also was not a singing roost.

Communal and solitary roosts on average were 1891.5 m (range: 107.6 – 5942.4 m) and 111.7 m (range: 31.5 – 287.4 m) from the centroids of home-range cores, respectively. These observations exclude data from the male that had multiple solitary roosts, as he spent most nights near a communal roost (107.6 m from the centroid of his home range) over a kilometer away from those roosts.

### 2.4.3 *Habitat selection*

With respect to second-order selection, the bats' home ranges contained a non-random assortment of habitat types ( $F_{1, 52} = 27.65$ ,  $P < 0.05$ ), with both native and exotic plantation forests over-represented relative to their wider availability within the study area, and open space under-represented (Table 2a; Appendix B). Mean distance ratios for native forest were significantly lower than those for exotic plantations and open space, while ratios for exotic plantations were significantly lower than open space (Table 2b).

Preference for habitat by individuals (third-order selection) was also non-random ( $\chi^2_2 = 30.36$ ,  $P < 0.05$ ). Individuals favored native forest while neither preferring nor avoiding exotic plantations and open space (Table 3a; Appendix B). Native forest was chosen over both exotic plantations and open space, but there was no difference in preference between exotic plantations and open space (Table 3b). There was no significant difference between the sexes with respect to either second- and third-order selection (all  $P$ -values  $> 0.05$ ).

**Table 2.** Second-order habitat selection (i.e., home-range composition) analyses for *Mystacina tuberculata* in 3 habitat types in the Pikiariki Ecological Area, New Zealand. A) Mean selection ratios (i.e., mean distance of random locations within home ranges to each habitat type divided by mean distance of random locations throughout study area to each habitat) and *t*-statistics when compared to a mean ratio of 1.0 (i.e., no preference) and B) significance levels from Welch's *t*-tests of between-habitat comparisons of mean selection ratios.

<b>a) Habitat Type</b>	<b>Mean Ratio (SD)</b>	<b><i>t</i><sub>17</sub></b>
Native Forest	0.30 (0.19)	-16.06***
Exotic Plantation	0.56 (0.37)	-5.08***
Open Space	1.79 (1.04)	3.25***

<b>b) Habitat Type</b>	<b>Exotic Plantation</b>	<b>Open Space</b>
Native Forest	*	***
Exotic Plantation		***

\*\*\*  $P < 0.001$ , \*  $< 0.05$

**Table 3.** Third-order habitat selection (i.e., habitat use) analyses for *Mystacina tuberculata* in 3 habitat types in the Pikiariki Ecological Area, New Zealand. A) Mean selection ratios (i.e., mean distance of location fixes for each individual to each habitat type divided by mean distance of random locations throughout that individual's home range) and univariate statistics for Wilcoxon rank-sum tests when compared to a mean ratio of 1.0 (i.e., no preference) and B) significance levels from Wilcoxon rank-sum tests of between-habitat comparisons of mean selection ratios.

<b>a) Habitat Type</b>	<b>Mean Ratio (SD)</b>	<b><i>V</i><sub>17</sub></b>
Native Forest	0.18 (0.33)	2***
Exotic Plantation	1.35 (0.96)	116
Open Space	0.95 (0.74)	68

<b>b) Habitat Type</b>	<b>Exotic Plantation</b>	<b>Open Space</b>
Native Forest	***	***
Exotic Plantation		-

\*\*\*  $P < 0.001$

## 2.5 Discussion

Our study has shown that within fragmented landscapes *Mystacina tuberculata* occupied both exotic plantations and open space, although they prefer native forest. To our knowledge our findings represent the first such demonstration of plasticity in patterns of space use in a species believed to be an obligate deep-forest bat. Furthermore, roosting behavior appears to be unaffected in this fragmented landscape, as many individuals possessed multiple roosting sites. An increased fidelity to roosting sites would be expected if the bats experienced negative effects of fragmentation. We suggest that *M. tuberculata* likely possesses morphological and/or behavioral plasticity that permits it to exploit disturbed habitats.

### 2.5.1 Home ranges and habitat selection

Distance-based analyses of habitat selection indicate that both native forests and exotic plantations are over-represented within home ranges compared to their wider availability, while open space is under-represented. However, for actual habitat-use within individual home ranges, native forest was preferred while exotic plantations and open space were neither selected nor avoided, likely because of high individual variation in foraging strategies. While all bats spent some time in native forest (they all roosted within native forest, and many predominantly occupied native forest), some individuals occupied exotic plantations or open space almost exclusively. *Mystacina tuberculata* previously has been documented within pine plantations through acoustic monitoring (Borkin and Parsons 2010), but our current study is the first to confirm extensive occupation of plantations by the species. Likewise, although *M. tuberculata* has been shown to use coastal forests and forest edges to visit flowering pohutukawa trees (*Metrosideros excelsa*) (Arkins et al. 1999), they have not been documented actively travelling outside of forests. Unfortunately, our methods do not allow us to determine how individual *M. tuberculata* spend their time once they leave their

day roost. However, given the extended periods spent within open habitats and exotic plantations by some individuals, it is likely that they are foraging in these areas at least part of the time. This suggests that *M. tuberculata* is able to exploit alternative habitats for required resources.

*Mystacina tuberculata* appear to have employed smaller home-range areas and included different habitats inside home ranges within fragmented forests. While home ranges and home-range cores in this study varied considerably in size, at the individual level they were all relatively small (range: 5 to 560 ha) when compared to individuals from a population in contiguous old-growth native forest (i.e., the Eglinton Valley, Fiordland), where mean 100% MCP area has been measured at 3,300 ha (range: 320 to 6,930 ha) (O'Donnell et al. 1999). Radio-tracked individuals within the unmodified 10, 000 ha Rangataua Forest, North Island, were observed to range across at least 8,000 ha (based on roosting data), with consecutive day roosts used by some individuals separated by 10 km (B.D. Lloyd, pers. comm.). Individual bats in the Eglinton Valley were estimated to travel on average 18.9 km per night (Christie 2006) compared to just 7.1 km in this study, in which the majority of movements (i.e., distance between consecutive fixes) were under 200 m (although it should be noted that the two studies varied in the length of time between location fixes, which can influence distance estimates of movements; Rowcliffe et al. 2012). It should be noted that although there were considerable differences in the number of location fixes attained for the individuals in this study we do not believe this has affected our measures of home-range size. Running a linear regression on home-range size (for both 100% MCP and 95% FK) against the number of location fixes for each individual indicates there is no correlation between these two metrics (i.e., increasing the number of location fixes does not lead to a larger home range size).

Space-use differences between *M. tuberculata* populations may be a result of the fragmented nature of the study area, constraining individuals to a much-smaller patch size within the ‘hostile matrix’ of pastoral land; a habitat that is generally avoided by many species of bats (e.g., Walsh and Harris 1996b; Russ and Montgomery 2002; Gehrt and Chelsvig 2003). This is unlikely, however, considering that a male in our study was tracked leaving Pikiariki nightly, travelling across pastoral land to do so. Bernard and Fenton (2003) found that savannahs in a naturally-fragmented mosaic landscape in Brazil did not inhibit mobility for the majority of species in the local bat community, and *M. tuberculata* has been observed crossing open grassland in the Eglinton Valley (O'Donnell et al. 1999).

Higher resource availability may permit individuals to occupy smaller home ranges (Mitchell and Powell 2012). Variance in home-range area has been observed in other bat species due to differences in resource availability both between- and within populations. Commuting distances for Jamaican fruit bats (*Artibeus jamaicensis*) inhabiting an area of low food abundance were found to be more than 13 times larger than those of individuals in an area of high food abundance (Morrison 1978). Similarly, mean home-range area increased by five times for a population of red fruit bats (*Stenoderma rufum*) in Puerto Rico following Hurricane Hugo, likely caused by decreased fruit availability (Gannon and Willig 1994).

Increased resource abundance does not explain the shift in habitat use by some individuals in our study, and the relatively small home-range areas we found suggest a behavioral adaptation by *M. tuberculata* to the fragmented habitat. Our results complement those of a recent study by Ancillotto et al. (2014) on a population of barbastelle bats (*Barbastella barbastellus*) living in a badlands habitat created through deforestation. Barbastelle bats, thought to be specialists due to their reliance on mature forests for roosting sites, were found roosting within rock crevices and foraging in non-forest habitats. Individuals in the badlands habitat possessed smaller home ranges than those observed for

populations inhabiting forested regions, suggesting ecological and behavioral flexibility within the species (Ancillotto et al. 2015). However, a key difference is that barbastelle bats frequently forage outside of forests (Hillen et al. 2011; Zeale et al. 2012), whereas *M. tuberculata* do not. Our results also are similar to those observed in a population of New Zealand long-tailed bats (a species that actively forages at forest edges and over shrubland; O'Donnell 2001) inhabiting a heavily managed plantation forest: home-range areas were smaller following a clear-fell event that removed older stands of trees (Borkin and Parsons 2014). Greater gliders (*Petauroides volans*) also have been observed to have reduced home-range areas with decreasing patch size within modified plantation forests in Australia (Pope et al. 2004), and some primates can reduce home-range area in regions of fragmented habitat apparently without negative consequences (see Offerman et al. 1995). These findings contrast those reported by Reiter et al. (2012) in two populations of lesser horseshoe bats (*Rhinolophus hipposideros*) in Austria – one occurring in largely contiguous forest and the other in highly fragmented forest. Home-range and home-range core areas along with nightly distances travelled were the same between the two populations, suggesting an inability for the species to adapt its foraging behavior in degraded landscapes (Reiter et al. 2012).

### 2.5.2 Roosting behavior

Native forest was preferred for both communal and solitary roosting sites by all individuals we tracked. Roosting sites are an essential resource for all bats (Kunz and Lumsden 2003; Barclay and Kurta 2007) and roost availability has been linked with population size in several species (e.g., Humphrey 1975; Brigham et al. 1997; Sedgeley and O'Donnell 1999; Lacki and Schwierjohann 2001; Parsons et al. 2003; Russo et al. 2004). Likewise, roosts are important for *M. tuberculata* life history, as solitary day roost sites were used by almost two thirds of tracked individuals, and all individuals used communal roost trees. Furthermore, solitary day

roosts were linked with nightly behavior; roosts were generally located close to the centroids of individuals' home-range cores. Therefore it is likely that further reductions of native forest (and with these the removal of suitable roost trees) will eventually lead to population decline regardless of any space use adaptations.

Roosting behavior appears to be unaffected in female *M. tuberculata* despite a decreased amount of native forest, contrary to what has been found for other species inhabiting fragmented landscapes. In a farmland mosaic in Australia, Gould's wattled bats (*C. gouldii*) and lesser long-eared bats (*Nyctophilus geoffroyi*) travelled much further from their roosting sites to their foraging areas (up to 12 km) than had been observed for either species previously, and farther than would be expected based on their flight morphology, likely due to limitations in the number of suitable roosts (Lumsden et al. 2002). A similar pattern was observed for several species in a fragmented landscape in Brazil (Bernard and Fenton 2003). In our study we did not observe this pattern for female *M. tuberculata*, as solitary roost locations were often located within 120 m of the centroids of their home-range cores. Female *M. tuberculata* also appear to retain the same plasticity of roost use in fragmented forest as seen in contiguous forest (e.g., Sedgeley 2001, 2003), with individuals switching between solitary roosts and multiple communal roosts frequently. Roost fidelity is inversely related to roost availability in many species (Lewis 1995), and thus our results suggest that either roosting sites are not limited within the forest habitat or that *M. tuberculata* is flexible in its selection of roosts (although these explanations are not mutually exclusive).

Male *M. tuberculata* displayed an unexpected degree of fidelity to communal roosts. Such fidelity is common in reproductive females, as the thermal benefits of clustering ease the energetic demands of pregnancy, lactation, and pup rearing (Altringham 2011). Males have no such demands and can roost solitarily. While sex-specific roosting strategies have

been observed in several bat species (see Ormsbee et al. 2007; Altringham 2011), this has not been observed in populations of *M. tuberculata* inhabiting contiguous forest (e.g., Lloyd 2001; Sedgeley 2001, 2003). Very few studies that examine sex-specific roosting strategies are male-focussed (Borkin and Parsons 2011) and as such it is hard to infer the importance of male roost selection for *M. tuberculata*, particularly in the context of fragmented versus unfragmented forests.

### 2.5.3 Future directions

Bats have been identified as useful environmental indicators due to the large number of ecosystem services they provide and their susceptibility to stressors (Fenton et al. 1992; Jones et al. 2009). Our findings suggest that even species that historically have been considered to be sensitive to perturbation actually may be able to tolerate at least some degree of habitat fragmentation. Although the effects of habitat degradation (including fragmentation) remain unknown for many bat species, our study joins a small but growing body of research suggesting a tolerance to anthropogenic effects for some species (e.g., Law et al. 1999; Russo et al. 2004; Ancillotto et al. 2015). However, more species-specific studies are required to determine how changing landscapes affect the behavior and population dynamics of bats on regional scales. Such studies will allow development of informed conservation strategies for species under threat from further habitat loss and fragmentation.

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**Females as mobile resources: communal roosts promote the adoption of lek breeding in a temperate bat**

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### 3.1 Abstract

Males of lek-breeding species defend clustered territories from which they display to visiting females. However, the mechanisms leading to the adoption of clustered male display sites are often unknown. In this study we examined the possibility of a resource-based lek in New Zealand's lesser short-tailed bat (*Mystacina tuberculata*) (Mammalia: Chiroptera), by assessing the placement of 'singing roosts' used by males in relation to communal roosting sites used by females. The 'resource-based lek' model posits that males settle near resources required by females to increase female encounter rates. For most bat species, where females are highly mobile and widely dispersed across landscapes while foraging, communal daytime roosts dominated by females may represent such a resource. Through use of video footage, spatial analyses of singing-roost locations, and passive integrated transponder tags we confirmed that *M. tuberculata* employs a lek mating system. We found that male singing roosts were significantly clustered in space, were defended by resident individuals, and were visited by females (who did not receive resources from males) for mating purposes.

Transponder records also indicated that some singing roosts were shared between multiple males. Spatial logistic regression indicated that singing-roost locations were associated with communal roosting sites. Communal roosts are selected based on criteria independent of the locations of singing roosts, suggesting that males responded to the location of communal roosts and not the reverse. *Mystacina tuberculata* thus provides evidence of a resource-based lek, and is only the second bat species worldwide confirmed to use a lek-mating system.

### 3.2 Introduction

In lek-breeding species males establish clustered, resource-free territories where they produce sexual displays for receptive females. Lek breeding has become one of the most-studied mating systems in behavioral ecology over the last 50 years, primarily for two reasons. First, leks provide an ideal system for the study of sexual selection in free-living animals, as mate choice is not confounded with the possession of resources and display aggregations allow easy assessment of multiple males by females (Höglund and Alatalo 1995; Morales et al. 2001). Second, the defining characteristic of leks – aggregated males – is also the most puzzling aspect of lek breeding. Often it is unknown why competing males incur the costs of increased competition and a potential reduction in individual mating success when courting females (Isvaran and St. Mary 2003), and what factors influence the selection of aggregation sites by males (Wiley 1991; Höglund and Alatalo 1995).

Lek breeding in mammals is rare, having been confirmed in only a dozen species worldwide (for a review, see Toth and Parsons 2013). Lek breeding is virtually undescribed in bats, despite the fact that they display the widest range of mating behaviors amongst mammals (Altringham 2011) and possess all of the necessary prerequisites for the evolution of leks (Toth and Parsons 2013). To date, only the hammer-headed bat (*Hypsignathus monstrosus*; Bradbury 1977a) of equatorial Africa has been confirmed to be a lek breeder. However, it is possible that the rarity of lekking in Chiroptera is simply due to a lack of widespread knowledge of bat mating systems (details of mating behavior are known for only approximately 7% of all bat species; McCracken and Wilkinson 2000), rather than any life-history characteristics that may preclude the adoption of this mating system. For example, in temperate climates ecological conditions promote large home ranges, seasonal migration, and low population densities in many bat species (Barclay and Harder 2003; Kunz and Lumsden 2003). Under these conditions males must adopt reproductive tactics that include mating with

females during hibernation (Bradbury 1977b), or establishing territories and attracting females through self-advertisement (McCracken and Wilkinson 2000). Thus, it is likely that lek-like behavior (i.e., male display clusters) has been adopted by bats in temperate regions.

Lek breeding may be further promoted in bats by the use of communal day roosts (hereafter referred to as “communal roosts”). In many temperate species, reproductive females will form large communal roosts of up to several hundred individuals that are maintained until their young reach independence (Kunz and Lumsden 2003; Kerth 2008). Communal roosting offers numerous benefits, including information sharing for foraging areas and other roosting sites (e.g., Wilkinson 1992; Kerth and Reckardt 2003), protection from predators (e.g., Fenton et al. 1994), and favorable microclimates (e.g., Kalcounis and Brigham 1998; Sedgely 2001) – a trait particularly important for reproductive females to reduce energetic costs (e.g., Kerth et al. 2001; Lausen and Barclay 2003). Roosting sites are consequently important resources for bats, and are chosen based on numerous selection criteria (for reviews, see Kunz and Lumsden 2003; Barclay and Kurta 2007). Furthermore, females with dependent offspring are likely also limited to foraging in areas close to communal roosts (Tuttle 1976; Henry et al. 2002). Thus, if males rely on self-advertisement and females remain near- and return to predictable locations in high numbers, it is reasonable to assume that males would settle around those locations.

Leks that form in areas containing resources valuable to females, or in areas where females gather for purposes other than mating, are known as “resource-based leks” (Alexander 1975). Resource-based leks are typically associated with insects (see Alexander 1975; Höglund and Alatalo 1995), with swarming males aggregating at the sites where females feed, emerge, or oviposit (Thornhill and Alcock 1983). Conversely, resource-based leks appear to be rare within vertebrates, having been described in some birds (see Jiguet et al. 2000), anurans (see Höglund and Alatalo 1995), and one species of pinniped (Soto and

Trites 2011). However, resource-based leks may not be rare within Chiroptera. Given the ecological restrictions imposed upon the mating systems of temperate bat species and the aggregating behavior of reproductive females, we would expect that: 1) lek-like behavior would be adopted by some species of temperate bat; and 2) these systems would follow a resource-based pattern, with the areas surrounding communal roosts being the preferred site for male display territories.

The lesser short-tailed bat (*Mystacina tuberculata*) of New Zealand is a useful species for testing the theory of lek placement with respect to resources required by females.

Throughout the year, but particularly in summer, *M. tuberculata* populations establish communal roosts in cavities of several trees and form some of the largest aggregations observed among cavity-roosting bats (Kunz and Lumsden 2003). One or more communal roosts also serve as maternity roosts where the females of a given population give birth and reside until the pups reach volancy (Carter and Riskin 2006). *Mystacina tuberculata* has also long been suspected to be a lek breeder (Daniel 1990); during the reproductive season (approximately February – May), male *M. tuberculata* use small tree cavities as night roosts from which they sing (hereafter referred to as “singing roosts”). The role of male singing is unknown, but it is likely to attract females for mating, and the locations of male singing roosts have been suggested to be located in areas of high female density (Winnington 1999). Given that females can travel large distances throughout the night while foraging (over 10 km; O'Donnell et al. 1999), but return in high numbers to predictable locations each morning, areas surrounding communal roosts would provide ideal locations for male settlement

The aims of our study were twofold. The first was to confirm that mating occurs in male singing roosts (*M. tuberculata* has not been observed copulating in the wild) and to provide quantitative evidence for the long-held assumption that *M. tuberculata* is a lek breeder. To achieve these objectives we used video footage, spatial analyses, and passive integrated

transponder (PIT) tags to examine three of the defining characteristics of lek breeding (Bradbury 1977a): 1) males aggregate to display to females; 2) females are free to select mates; and 3) females receive no resources from males with which they mate. Second, we tested the hypothesis that *M. tuberculata* forms a resource-based lek by determining if male singing roosts are aggregated near communal roosts, as communal roosts are predictable resources required by females.

### **3.3 Methods**

#### *3.3.1 Study site*

We conducted this study in the Pikiariki Ecological Area of the Pureora Forest Park (38°26'S, 175°39'E), central North Island, New Zealand, between November and May 2011-12 and 2012-13, and between February and April in 2013-14. Pikiariki is located within the 78,000-ha Pureora Forest Park and comprises approximately 450 ha of native, mature podocarp-hardwoods bordered by exotic pine plantations and pastoral land (Wallace 2006).

Pikiariki supports a population of approximately 700 *M. tuberculata*, with 11 communal roosts known at the time of the study (Wallace 2006). We captured (either with mist nets or harp traps) and marked individual bats with PIT-tags for identification throughout the three years of study. Tags were injected subcutaneously between the shoulder blades according to the New Zealand Department of Conservation's Standard Operating Procedure (Sedgeley et al. 2012). As of February 2014, 711 individuals (494 adults, 217 volant juveniles) had been PIT-tagged (adult sex ratio = 254:240 males/females).

We divided the study site into two zones: the 'main' site (approximately 205 ha) where the majority of communal roosts (nine of eleven) were located, and a separate 'north' site (approximately 10 ha), which contained the two remaining communal roosts. During the 2011-12 season survey lines were sited every 175 m; during 2012 new survey lines were used

for half of the forest. Half of these were placed at 100 m intervals, while the remainder maintained the original system of transects (see Appendix C). The study site (defined explicitly for use in statistical tests) was delimited by a 75 m buffer around the limits of the survey grid; 75 m was estimated to be the maximum distance over which male singing could be heard by the surveyor (see Appendix C).

### 3.3.2 *Lek criteria*

Male singing begins in the spring and peaks during late summer (Lloyd 2001), with males singing for long periods throughout the night. Male songs are audible to humans but also contain ultrasonic components, and consist of several rapidly-repeated song elements (C.A. Toth, unpublished data). Singing roosts were located primarily by walking transects of the forest using the survey lines and listening for male song. Transect surveys were performed twice monthly during the 2011-12 season, once per month during the 2012-13 season, and irregularly in the 2014 season, as these roosts were only used in video analyses. A small number of singing roosts were discovered while performing other tasks (e.g., mist-netting, radiotelemetry for other studies, etc.). Once we located a singing roost we recorded its geographic coordinates with a handheld global positioning system (GPS) unit. Heights of roost entrances were calculated using a clinometer, and the compass bearing of each entrance was recorded. Entrances to all but one roost tree were located. For more information regarding both singing and communal roosts, see Appendix C.

To determine whether male singing roosts were spatially clustered within the available habitat (i.e., site-level spacing) we performed a Clark-Evans test (Clark and Evans 1954) using the package ‘spatstat’ (Baddeley and Turner 2005) available for the statistical program *R* v3.01 (R Development Core Team 2013). We tested the extent of clustering in the spatial distribution of singing roosts versus 1,000 Monte Carlo simulations of complete

spatial randomness within the study domain. Due to the relatively low sample size for the north site this analysis was only performed on singing roosts within the main site, resulting in a single aggregation for the population (hereafter referred to as “the aggregation”). We further tested the pattern of spacing of singing roosts within the aggregation (i.e., aggregation-level spacing) to determine whether roosts were uniformly, aggregately, or randomly distributed. For example, a uniform distribution implies that the areas surrounding the singing roosts are defended by males in addition to the roosts themselves. We tested the spacing pattern within the aggregation on the main study site by delimiting the area around singing roosts with a minimum convex polygon (MCP) and then performing an ‘Average Nearest-neighbor’ analysis (Mitchell 2005) within the MCP using *ArcMap 10* (ESRI, Redlands, CA). The MCP was created using the ‘Minimum Bounding Geography’ tool in *ArcMap 10*, and was used to define the area within which to perform the average nearest neighbor analysis, as it is very sensitive to area. This analysis omitted a single singing roost from the 2011-12 season, as it was located almost a kilometer from the nearest communal roost, and therefore was not considered part of the aggregation.

It should be noted that while *M. tuberculata* colonies regularly move to new communal roosts (on average every 5.6 days; Sedgeley 2003), all communal roosts located at our main site were close to one another (the greatest distance between two communal roosts was 647 m). Given these relatively short distances we treated all singing roosts on the main site (minus the outlier discussed above) as a single aggregation (roughly 64 ha in area) that surrounded the communal roosts. Furthermore, while both males and females in our study population occasionally roost alone (Toth et al. 2015), solitary roosts likely do not influence lek placement. Communal roosts always contain hundreds of individuals on any given day, and individuals rarely spend longer than a day or two roosting solitarily before returning to their communal roost (Toth et al. 2015).

During 2014, video recordings were made at singing roosts using infrared cameras to determine: 1) if copulations occurred, and 2) if females receive resources from males. In conjunction with the cameras, automatic PIT-tag readers were mounted on roost entrances to log the identities of resident males and visiting individuals. PIT-tag antennas were fixed to roosts three days prior to filming to allow resident males to acclimate to the antenna's presence. Recordings were made in two phases: a pilot round of filming (February 19 – March 8, 2014) used 23 singing roosts to determine roosts suitable for data collection (e.g., visibility of roost cavity, PIT-tag status of resident male, etc.), and a second phase (March 27 – April 9, 2014) devoted to data collection used 12 suitable roosts chosen from the first round. Roosts were filmed in groups of three (chosen randomly without replacement) and each group was filmed for three days. Filming began approximately an hour before sunset and continued until after dawn. To assess levels of competition for singing roosts we determined the number of visits to each roost by non-resident males (identified by their PIT-tags).

### *3.3.3 Associations with communal roosts*

We used spatial logistic regression (“SLR”; Agterberg 1974; Baddeley et al. 2010) to determine whether the locations of communal roosts were statistically associated with those of male singing roosts. For this analysis the study region was overlaid with equal-area cells (see below), each of which was assigned a value of 0 (absence) or 1 (presence) depending on the occurrence of an event (in this case, the presence of one or more singing roosts). The SLR then predicted the probability of an event (i.e., singing roosts) as a function of a covariate (i.e., communal roosts) (see Baddeley et al. 2010). Although a number of environmental factors may influence males in their selection of singing roosts, we specifically wanted to examine the relationship between communal roosts and singing roosts. As such, we kept the

models as parsimonious as possible, using only the locations of communal roosts as the predictor variable. To test this model we generated 10 sets of 11 randomly-located communal roost locations (keeping two in the north site and nine in the main site) and conducted the analysis for each set of locations. A null model (no predictor variable) was also tested. Spatial logistic regression models were developed and executed using the *R* package ‘spatstat’.

We defined a study domain for the SLR models by generating the smallest rectangle that encompassed the study site MCP. Within this domain, inter-roost distance maps were generated for each set of communal roosts by dividing the domain into grid cells and assigning a distance value from the centroid of each grid cell to the nearest communal roost (see Appendix C). For this operation we selected a grid cell size of 5.64 m x 5.64 m, as this value was twice the mean location error for GPS points of communal and singing roosts, thus allowing a sufficiently large area over which to avoid placement of roosts within an incorrect cell. Singing-roost locations were then regressed against each set of distance maps, and Akaike's Information Criterion (AIC) values and Akaike weights calculated for model validation.

We performed a Rayleigh's uniformity test using the *R* package ‘CircStats’ (Lund and Agostinelli 2007) on the entrance bearings of singing roosts to determine whether the roosts were oriented to a specific compass bearing. We were particularly interested in the orientation of singing roosts with respect to the locations of communal roosts, as we thought males could be directing their songs towards emerging/returning females. To establish whether singing roosts were oriented towards communal roosts we identified the closest communal roost to each singing roost and calculated the difference between the measured entrance bearing and the ‘true’ entrance bearing (i.e., the bearing from the singing roost to the closest communal roost). We then transformed these differences into circular data (by adding 360 to negative values; e.g., a difference of -5 became a bearing of 355°), and performed a

Rayleigh test on the resulting values. Clustering of the entrance bearings around an orientation of  $0^\circ$  would imply that males select roosts that face the closest communal roost.

We also were interested in identifying any patterns in the placement of the singing roosts in relation to communal roosts. The bearings of singing roosts located within 50 m, 75 m, and 100 m of each communal roost were determined using the ‘Near’ function of *ArcMap 10* and assessed with Rayleigh’s uniformity tests. As the hearing sensitivity of *M. tuberculata* is unknown we included roosts within of 50 m and 100 m of communal roosts, because they represent distances that are well within and outside of human hearing range of male *M. tuberculata* song, respectively.

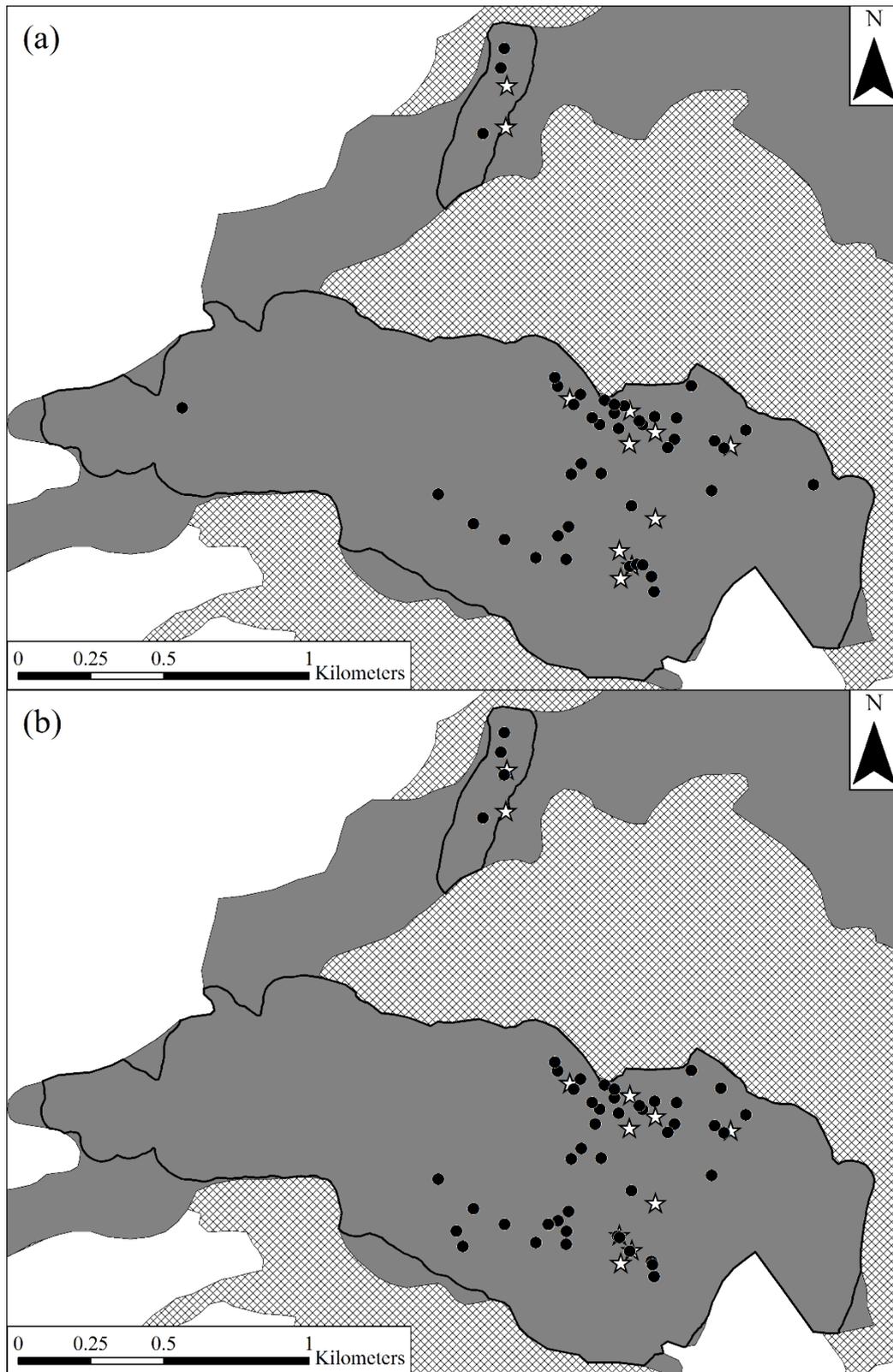
### **3.4 Results**

#### *3.4.1 Lek criteria*

We located fifty-five singing roosts in total, 43 that were active in 2011-12 (40 on the main site, 3 on the north site) and 49 in 2012-13 (45 on the main site, 4 on the north site) (Figure 1a, b). Thirty-eight roosts were active in both years. Although some males began singing in November of both years, most roosts were identified after January (38 in 2011-12, 37 in 2012-13). Approximately 414 hours of video footage were obtained at singing roosts during the data collection phase of filming in 2014 (mean = 691 minutes/roost/night, SD = 137 minutes).

Singing roosts at the main site were significantly clustered during 2011-12, 2012-13, and both years collectively (Table 1). Spacing within the aggregation itself, however, was random with distances between roosts ranging from 1.4 – 300.0 m (SD = 47.6 m) (Table 1).

Two types of singing roosts were identified through PIT-tag records: those with a single resident male ( $N = 6$ ), and those shared between multiple resident males ( $N = 6$ , range: 2 – 3 males/roost). At these ‘timeshare’ roosts resident males were never present simultaneously, although as little as 3 seconds separated the departure of one male from the



**Figure 1.** Locations of male singing roosts during (a) 2011–2012 and (b) 2012–2013 in the Pikiariki Ecological Area, along with the 11 known communal roosts used by the population. Stars = communal roosts; filled circles = singing roosts; dark gray = native forest; hatched = exotic plantations (mainly *Pinus* spp.); white = open space (mainly pastoral land and harvested forest); solid line = border of the study site. Forty-three singing roosts were identified during the 2011–2012 season and 49 during the 2012–2013 season, 38 of which were common between years. Singing roosts generally were located close to communal roosts in both years of study.

**Table 1.** Spatial patterns of male *Mystacina tuberculata* singing roosts, both within the 205-ha study site as a whole (above) and the 64-ha aggregation (below).

<b>Site-Level Spacing</b>			
<b>Year</b>	<b>Average Nearest Neighbor (m)</b>	<b>R</b>	<b>P</b>
2011-12 (N = 40)	87.65	0.43	< 0.05
2012-13 (N = 45)	54.17	0.25	< 0.05
Combined	74.14	0.41	< 0.05
<b>Within-Aggregation Spacing</b>			
	<b>Average Nearest Neighbor / Expected Nearest Neighbor (m)</b>	<b>z</b>	<b>P</b>
2011-12 (N = 39)	66.06 / 61.36	0.91	0.36
2012-13 (N = 45)	54.17 / 54.68	-0.12	0.9

Site-level spacing was determined using Clark–Evans tests, whereas aggregation-level spacing was determined with average nearest neighbor analyses. Roosts were clustered when considered in relation to the site, but randomly distributed within the aggregation itself.

arrival of another. The site fidelity of resident males within each timeshare roost remained stable throughout the observational period (i.e., the same males used the same roosts each night, as determined from the PIT-tag data).

Intrusions (i.e., non-residents approaching the roost entrance or entering the roost cavity) by males were recorded at three singing roosts, averaging 2.3 events/roost (range: 1 – 3 visits, SD = 1.5). On every occasion, resident males successfully defended their roost.

Three copulations were recorded – one in a solitary singing roost and two in a timeshare roost. Copulations in the timeshare roost occurred on consecutive nights with two different females; both mated with the same resident male. During these copulation events females were not observed receiving nuptial gifts (e.g., food items) from the resident males,

and none of the resident males used the singing roosts as day roosts following mating. During all three copulation events non-resident bats were observed visiting the singing roost while the resident male was mating. Non-residents either landed on the tree but did not approach the roost entrance, or interrupted copulation by entering the roost and subsequently being chased away by the resident male. Although it seems likely these were ‘sneaker’ males, only one was PIT-tagged – a second resident male from the timeshare roost.

In addition to singing, scent-marking was observed at all singing roosts. Males would collect urine with their hind feet to rub over their bodies, predominantly under the chin. This was often followed by rubbing their chins on the entrance to the singing roost.

Singing roosts were generally not used as day roosts by resident males – out of the 36 nights of filming, singing roosts were only used as day roosts twice (5%).

#### *3.4.2 Associations with communal roosts*

On average, singing roosts were 164.1 m (range: 8.6 – 1331.4 m, SD = 215.0 m) from the nearest communal roost. Model validation confirmed that the location of communal roosts were important in explaining the location of singing roosts, more so than any of the 10 sets of randomly generated communal roosts (Table 2).

Entrances of singing roosts on average were 8.9 m (range: 1.3 – 24.6 m, SD = 5.1 m) above ground and entrance bearings were not significantly oriented in any particular direction (mean = 170.0°, SD = 120.9°, Rayleigh:  $Z = 0.63$ ,  $P = 0.53$ ). Singing roosts also were not oriented towards the closest communal roost (mean = 72.3°, SD = 106.3°, Rayleigh:  $Z = 1.73$ ,  $P = 0.18$ ), nor were they oriented in any particular direction from the nearest communal roost at distances of 50 m ( $N = 13$ , mean = 151.9°, SD = 86°, Rayleigh:  $Z = 1.37$ ,  $P = 0.26$ ), 75 m ( $N = 34$ , mean = 310.2°, SD = 137.6°, Rayleigh:  $Z = 0.11$ ,  $P = 0.9$ ), and 100 m ( $N = 53$ , mean = 5.8°, SD = 130.8°, Rayleigh:  $Z = 0.29$ ,  $P = 0.75$ ).

**Table 2.** Outcomes of spatial logistic regression models using either communal roosts, 10 iterations of randomly distributed communal roosts, or nothing (null) as predictive variables for the position of singing roosts.

Model	$\Delta AIC$	$w_i$
Communal roosts	0	1.0
Random communal roosts (averaged)	90.6	< 0.001
Null	142.1	< 0.001

$\Delta AIC$  is the Akaike Information Criterion value scaled by  $AIC_i - AIC_{min}$ , and  $w_i$  is the Akaike weight. Model performance for the randomly-located communal roost datasets were similar and so are averaged for presentation here. Communal roosts were the best predictors of the locations of singing roosts throughout the study site; these results therefore provide evidence that communal roosts influence the location of singing roosts.

### 3.5 Discussion

Our study provides evidence that *Mystacina tuberculata* satisfies the definitional criteria for lek breeding. Males form aggregated display sites, and females are free to select males with whom to mate while receiving no resources in return. Our data also support the formation of a resource-based lek by *M. tuberculata*: the locations of singing roosts held by males were associated with the communal roosts used by the population.

*Mystacina tuberculata* is only the second bat species confirmed to use a lek-mating system, the other being *Hypsignathus monstrosus* (Bradbury 1977a). However, the two species differ widely in morphology and life history (Langevin and Barclay 1990; Carter and Riskin 2006) and the adoption of lek breeding in both likely represents a case of convergent evolution. Aggregations of male *H. monstrosus* are sited at traditional locations that are independent of female roosting- and foraging areas. By contrast, lek formation in *M. tuberculata* appears to be largely promoted by communal roosting behavior. Communal roosts are likely to be the only areas where male *M. tuberculata* encounter females in high numbers. Analyses of radiotelemetry data from Pikiariki show that females often travel large distances nightly to forage, even visiting neighboring forests, but eventually all females return to communal roosts (Toth et al. 2015). Furthermore, maternity roosts are focal points

for reproductive females as they must remain close to their offspring until they reach volancy (Tuttle 1976; Henry et al. 2002).

It is possible that communal roosts are chosen for their proximity to singing roosts, rather than the reverse. However this is unlikely because: 1) communal roosts are located in the largest and oldest trees, and are selected for specific environmental and thermal criteria (Sedgeley et al. 2003, 2006), while singing roosts are often little more than cracks in trees; 2) males roost within the communal roosts on most days and travel to their singing roosts at dusk; and 3) communal roosts are used year round, but males only sing for a few months each year. Further evidence of males responding to the location of females has been observed for *M. tuberculata* in the Eglinton Valley, South Island, where a captive population of 30 individuals (21 of whom were female) was kept in an outdoor aviary for two weeks in March 2006. During this time six males began to sing in the trees surrounding the aviary, but abruptly left once the captive bats were released (C.F.J. O'Donnell, pers. comm.).

We suggest that similar resource-based leks have been adopted in other bat species where females possess large home ranges, but return to predictable communal roosting sites in high numbers. This is likely to occur in temperate species, as ecological conditions in temperate climates promote territory establishment and self-advertising courtship displays in male bats (McCracken and Wilkinson 2000). For example, a pattern similar to that of *M. tuberculata* has been observed in common pipistrelles (*Pipistrellus pipistrellus*) in Bavaria; males hold courtship territories located near large over-winter roosts that are visited by hundreds of individuals during yearly 'invasion' events (Sachteleben and von Helversen 2006). At such sites, males display on courtship territories with a conspicuous songflight behavior and females have the ability to appraise multiple males as they move to explore over-wintering sites. Similarly, McWilliam (1990) observed a population of least long-fingered bats (*Miniopterus minor*) in coastal Kenya that may form an 'olfactory lek'. In this

case approximately 30 males (which were both the oldest and heaviest males in the population) occupied a small hollow in the roof of the colony's cave during the breeding season and displayed to females by covering themselves with urine. The hollow was located near the mouth of the cave, thus ensuring close proximity to females as they travelled to and from roosting sites sited deeper within the cave. Despite being a tropical species, McWilliam (1990) hypothesized that lek-like behavior was adopted as females migrate inland during the dry season, rendering maintenance of harems uneconomical. Matings were not observed in either *P. pipistrellus* or *Mi. minor*, however, so further work is required to fully understand the mating systems of these two species.

In addition to male clustering and display behavior, *M. tuberculata* appears to satisfy the remaining three criteria for lek breeding. Two filmed males copulated (one with multiple females over two nights), and females were not coerced into roosts, suggesting they are free to select males. Furthermore, females did not receive nuptial gifts from males. Even if singing roosts were to be used as day roosts by females (which was not observed) they are unlikely to be considered a required resource as: 1) the random orientation of their entrances suggests occupants derive no thermal benefits (bats prefer day roosts exposed to the evening sun to aid in exiting torpor; Fenton and Barclay 1980; Solick and Barclay 2006); and 2) roosting sites do not appear to be limiting in Pikiariki, as a previous study indicates most adult females possess solitary day roosts in addition to roosting communally (Toth et al. 2015). Finally, male parental care has yet to be described in bats (McCracken and Wilkinson 2000; but see Vehrencamp et al. 1977), and there is no indication it occurs in *M. tuberculata* (Carter and Riskin 2006). It should be noted that while singing roosts were significantly clustered within the available habitat, the average nearest neighbor for roosts across both years was approximately 74 m, a spacing more akin to an 'exploded lek' (Emlen and Oring 1977; Höglund and Alatalo 1995). However, given that the minimum spacing between

singing roosts was as little as 1.4 m, the level of clustering may have been limited by the amount of suitable roosts available to males. In forests with a higher number of cavities, spacing between males may approach levels typical of ‘classic’ leks.

The availability of suitable singing roosts near communal roosts may induce competition between males, given that only some males hold singing roosts. Intense male-male competition for access to territories is a common feature in some lekking species (see Höglund and Alatalo 1995), as are territorial intrusions and disruptions of copulation by non-resident males (Trail 1985). PIT-tag records for resident male *M. tuberculata* in our study show that the same males return to- and defend the same roosts each night, and demonstrate the occurrence of competition between resident males and apparent sneaker males. Males have been observed to visit and roost during the day in singing roosts, even outside of the breeding season (Toth et al. 2015) – a trait reported in many other lekking species where competition is high (Wiley 1991). What traits best predict the ability of *M. tuberculata* males to obtain and defend singing roosts remain unknown, but lekking has been shown to be costly for males of other lekking species due to reduced opportunities for forage (e.g., Nefdt and Thirgood 1997), increased numbers of agonistic interactions (e.g., Gosling et al. 1987; Apollonio et al. 1992), and higher exposure to predation (e.g., Boyko et al. 2004). Thus, ownership of singing roosts may be an honest indicator of quality (e.g., Kokko et al. 1998) in addition to a male’s sexual displays.

Beyond confirming definitional lek criteria we have avoided an in-depth analysis of male behavior at singing roosts as we believe this warrants assessment in a larger, more extensive study. However, we observed a notable – and potentially unique – behavior at singing roosts: half of the recorded roosts were occupied by multiple males. This behavior differs from a cooperative display (e.g., McDonald and Potts 1994; Krakauer 2005), as males in these “timeshare” roosts did not overlap temporally and thus are not combining displays. It

is unknown what mechanism(s) prompt males to share singing roosts – possibilities include genetically-related individuals operating in response to kin selection or unrelated, low-quality males following a ‘best of a bad job’ strategy (e.g., Kempenaers et al. 1995). Further analyses of this behavior, including determination of relatedness among resident males at timeshare roosts and a comparison of resident males in both solitary singing roosts and timeshare singing roosts, is underway.

It is possible that *M. tuberculata* is displaying a subset of resource-based lek breeding known as a ‘hotspot lek’, which posits that males settle where the probability of encountering females is highest (Lill 1976; Emlen and Oring 1977; Bradbury and Gibson 1983; Bradbury et al. 1986). Rates of female encounters for males may be higher in some areas through behavioral and ecological processes such as the clumping of non-defendable resources required by females, or from females possessing large, overlapping home ranges, where areas of overlap between females are considered a ‘hotspots’ (Bradbury and Gibson 1983; Bradbury et al. 1986). Empirical support for the hotspot model has been equivocal; while some systems demonstrate an association between male display sites and female density (e.g. Apollonio et al. 1990; Théry 1992; Westcott 1997; Ryder et al. 2006; Hingrat et al. 2008; Alonso et al. 2012), others have failed to find such associations (e.g., Wegge and Rolstad 1986; Höglund and Robertson 1990; Balmford et al. 1993; Loiselle et al. 2007; Durães et al. 2007) or only weak associations at very coarse spatial scales (e.g., Bradbury et al. 1989; Gosling and Petrie 1990; Gibson 1996; Bro-Jørgensen 2003).

Communal roosts, being point locations that all females within a population return to eventually, would constitute hotspots for males. However, our present study does not test many of the predictions of the various iterations of the hotspot model (e.g., adult sex ratio on the lek, ratio of females in estrus on the lek, resource density through the study site; see Bro-Jørgensen 2003) beyond the basic premise, as the unique life history of bats makes it difficult

to adapt predictions developed for other lekking taxa such as ungulates or gamebirds. For example, communal roosting sites are both areas of highest female space-use overlap and female density, which are the predictive locations of hotspots in the female home-range overlap model (Bradbury et al. 1986) as well as the ideal-free-distribution model (Fretwell and Lucas Jr 1970), respectively. Furthermore, it is not feasible to quantify factors such as adult sex ratio and ratio of females in estrus at *M. tuberculata* leks. Likewise, the spatial and temporal distribution of resources throughout their home ranges is not easily characterized for *M. tuberculata* as their foraging behavior is extremely flexible and dictated by marked seasonal variation (Daniel 1976, 1979; Arkins et al. 1999; Cummings et al. 2014). Thus, without further research we cannot definitively state whether or not *M. tuberculata* leks represent true hotspots.

We note that the findings of our study cannot unequivocally determine whether lek breeding is the primary mating system for this population of *M. tuberculata* or only one of many different mating systems. Multiple mating strategies can be adopted within a population depending on individual competitive ability, with males choosing a strategy that maximizes their reproductive success (Apollonio et al. 1992). For example, off-lek matings and/or displays have been observed in several species (e.g. Apollonio et al. 1992; Alatalo et al. 1996; Lanctot et al. 1997; Semple et al. 2001; Lesobre et al. 2010). Even if males in our study population adopt alternative mating strategies (as evidenced by the observation of apparent sneaker males), *M. tuberculata* – at least partially – uses a lek mating system, as males form display aggregations that females visit primarily for the purpose of fertilization.

### 3.5.1 Summary and conclusions

*Mystacina tuberculata* in the Pikiariki Ecological Area form a resource-based lek, with clustered males displaying in areas surrounding resources required by females – in this case

the resources are communal roosts. Communal roost locations are selected independently from male singing roosts, implying the display sites of males are dictated by female presence and not the reverse. Males display by singing for extended periods during the breeding season and possibly augment this behavior by scent-marking with urine. Female *M. tuberculata* are free to select mates and have not been observed receiving resources from males, thus fulfilling the general criteria of true lek-breeding – only the second bat species confirmed to use this mating system. Many aspects of the mating system of *M. tuberculata* remain unknown, however, and additional study is needed to determine what constitutes male quality (and therefore female selection of male traits), describe variation in the song characteristics of males, characterize the level of competition between males for access to singing roosts, and quantify spatial relationships between male quality and position within the aggregation.

It is likely that other bat species have adopted similar resource-based leks, given the proclivity of many (mainly temperate) bats to possess large home ranges and form large communal roosts during the breeding season. However, current knowledge of the mating systems of bats is limited, and much further work in this area is required.

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**Charming countertenors? Song output is inversely related to male size in lesser short-tailed bats (*Mystacina tuberculata*)**

## 4.1 Abstract

The use of courtship songs by males has been studied in many taxa. Such songs are often complex and include honest information on the singer's condition and/or genetic quality. One useful indicator is "size-pitch allometry", the correlation between the frequency of vocalisations and body size, as females in many species prefer males of certain sizes. Size-pitch allometry appears rare in the courtship songs of mammals, however, having only been described in one species. The lesser short-tailed bat (*Mystacina tuberculata*) provides an ideal system to test the use of size-pitch allometry in a mammal, as lekking male *M. tuberculata* appear to use song as a primary method for attracting mates. Given that males sing at night and from within roosts, male songs may contain the maximum amount of information for females, including body size, as visual information of males is limited. In this chapter I identified the songs produced by 16 male *M. tuberculata* in the Pikiariki Ecological Area based on their acoustical properties, as the singing behaviour of the species has not been studied previously. Furthermore, to test if male size influences singing behaviour and song frequency I regressed several song variables against forearm length. *Mystacina tuberculata* song types are composed of four basic elements: upsweeps, downsweeps, trills, and tones. Males produced these elements either singly, or combined them to form composite song types. In total I classified 51 distinct song types (with an average of 29 song types per male), with four (trills, upsweep-trills, trill-downsweeps, and upsweep-trill-downsweeps) comprising 69% of the song types produced. The frequency characteristics of the four most-common song types did not scale with forearm length, nor did song rate. However, both the duration of trill-downsweeps and the duty cycle of male singing bouts scaled negatively with male size. Furthermore, *M. tuberculata* potentially has one of the highest sustained song outputs yet described. The songs of *M. tuberculata* thus seem to fit the criteria of a courtship

signal, with information contained within male song on which females may be able to base mate choice.

## 4.2 Introduction

In many species, characteristics of courtship vocalisations (hereafter referred to as “songs”) function as an honest indicator of male quality, allowing for the easy assessment of male traits by females (Thorson et al. 1982; Cocroft and Ryan 1995; Marler and Slabbekoorn 2004). For example, in many songbirds the number of individual song types sung by males is an indicator of male age, as males continue to learn new song types throughout their lives (e.g. Lehongre et al. 2006). Furthermore, song output (including the length of songs, the rate of singing, and the amount of time spent singing) is an honest indicator of the condition of the singer, as singing is an energetically-expensive activity (Gil and Gahr 2002).

Body size is a trait that affects many aspects of an organism’s biology (Peters 1986), including male competitive- (Arnott and Elwood 2009) and hunting ability (Hakkarainen et al. 1996), and female selection of males of particular sizes has been well documented (e.g. Ryan and Wagner Jr 1987; Hakkarainen et al. 1996). The frequency characteristics of male songs can carry accurate information on the size of the male producing the songs (e.g. Linhart and Fuchs 2015), as the size of the vocal organs generally scale with body size (known as “size-pitch allometry”; Bradbury and Vehrencamp 1998). Accordingly, females in many species have been observed to use male courtship songs as cues for body size (e.g. Ryan 1980; Gray 1997; Galeotti et al. 2005). However, such evidence is rare in mammals, with only one study demonstrating female preference for males of certain sizes based on courtship song traits (female red deer, *Cervus elaphus*, preferentially responded to playbacks of male roars that simulated larger callers; Charlton et al. 2007).

Bats provide an interesting system to examine the honesty of mammalian courtship songs. Due to their nocturnal behaviour, bats rely heavily on information-rich acoustic cues for both navigational (Fenton 2013) and social purposes (e.g. Wilkinson and Boughman 1998; Pfalzer and Kusch 2003). In addition, ecological conditions in temperate regions

promote the use of self-advertisement courtship displays (including songs) in reproductive males (Toth and Parsons 2013; Appendix A). However, the use of courtship songs by bats is relatively understudied and the role of song as a sexually-selected signal is unknown for most species. This is likely for a number of reasons, including early recording devices not being able to detect the high-frequency songs produced by males (Bradbury and Emmons 1974), and the fact that bats rarely display courtship behaviour in captivity (Behr and von Helversen 2004). Furthermore, it is difficult to study bats *in situ* due to their nocturnality and tendency to roost in inaccessible locations, meaning it is not always possible to collect detailed information on known individuals in the context of their courtship behaviours. The few studies that have examined bat songs have shown that many species produce songs as complex as those of birds (e.g. Bradbury and Vehrencamp 1977; McWilliam 1987; Behr and von Helversen 2004; Jahelková et al. 2008; Bohn et al. 2009). To date, the only species whose song has been studied in the context of sexual selection has been the sac-winged bat (*Saccopteryx bilineata*). *Saccopteryx bilineata* is a harem-polygynous species where males produce daytime courtship songs directly at females in their harems, and augment these songs with wing-flapping and olfactory displays (Behr and von Helversen 2004). However, there is no evidence for size-pitch allometry in male songs (Davidson and Wilkinson 2004; Behr et al. 2006).

The lesser short-tailed bat (*Mystacina tuberculata*) provides an excellent system to examine the link between song and a functional morphological trait. Song appears to be the primary method of advertisement used by lekking *M. tuberculata* males, with individuals singing for upwards of 8 hours per night during the breeding season (C. Toth, pers. obs.). Males also show high fidelity to specific singing roosts (Toth et al. 2015; Chapter 3), allowing individuals to be consistently identified and recorded through passive methods (e.g. transponder tags, video cameras). In contrast to *S. bilineata*, where males defend territories

for females (Heckel and von Helversen 2002), *M. tuberculata* is a lekking species, and lek theory predicts that female selection of mates is based solely on honest male advertisements, as female choice is not confounded by territory quality, resource ownership, or paternal care (Höglund and Alatalo 1995). Given that male *M. tuberculata* must initially attract females travelling to/from communal roosts using only songs (visual appraisal of males by females would be limited, as males signal at night from within singing roosts), we might expect songs to carry the maximum amount of information on the singer, including cues of body size.

In this chapter I present an overview of the singing behaviour of male *M. tuberculata*, including an analysis of the frequency and temporal characteristics of the most-common song types produced by males and a quantification of male song output, as *M. tuberculata* singing behaviour has not been studied previously. Furthermore, I hypothesise that if lekking *M. tuberculata* use song as a primary method for attracting females, characteristics of male songs and singing behaviour should be distinguishable between individuals and function as an honest indicator of male traits. Accordingly, I have used male body size as a predictor variable for the characteristics of male songs.

## **4.3 Methods**

### *4.3.1 Field methods*

I studied *Mystacina tuberculata* in the Pikiariki Ecological Area of Pureora Forest Park (38°26'S, 175°39'E), central North Island, New Zealand, between November and May 2011–2012 and 2012–2013, and between February and April in 2013–2014. As part of a larger study (see Chapter 3), 712 individuals in this population had been captured (either using mist nets or harp traps) and marked with passive integrated transponder (PIT) tags for individual identification. After marking, individuals were weighed with a Pesola scale (0.1 g precision) and had their forearms measured with callipers as a proxy for body size. I used forearm

length rather than body mass as an indicator of body size as the mass of individual *M. tuberculata* can vary widely with time; individuals can consume between 36% – 50% of their pre-feeding body mass in a single night (Carter and Riskin 2006).

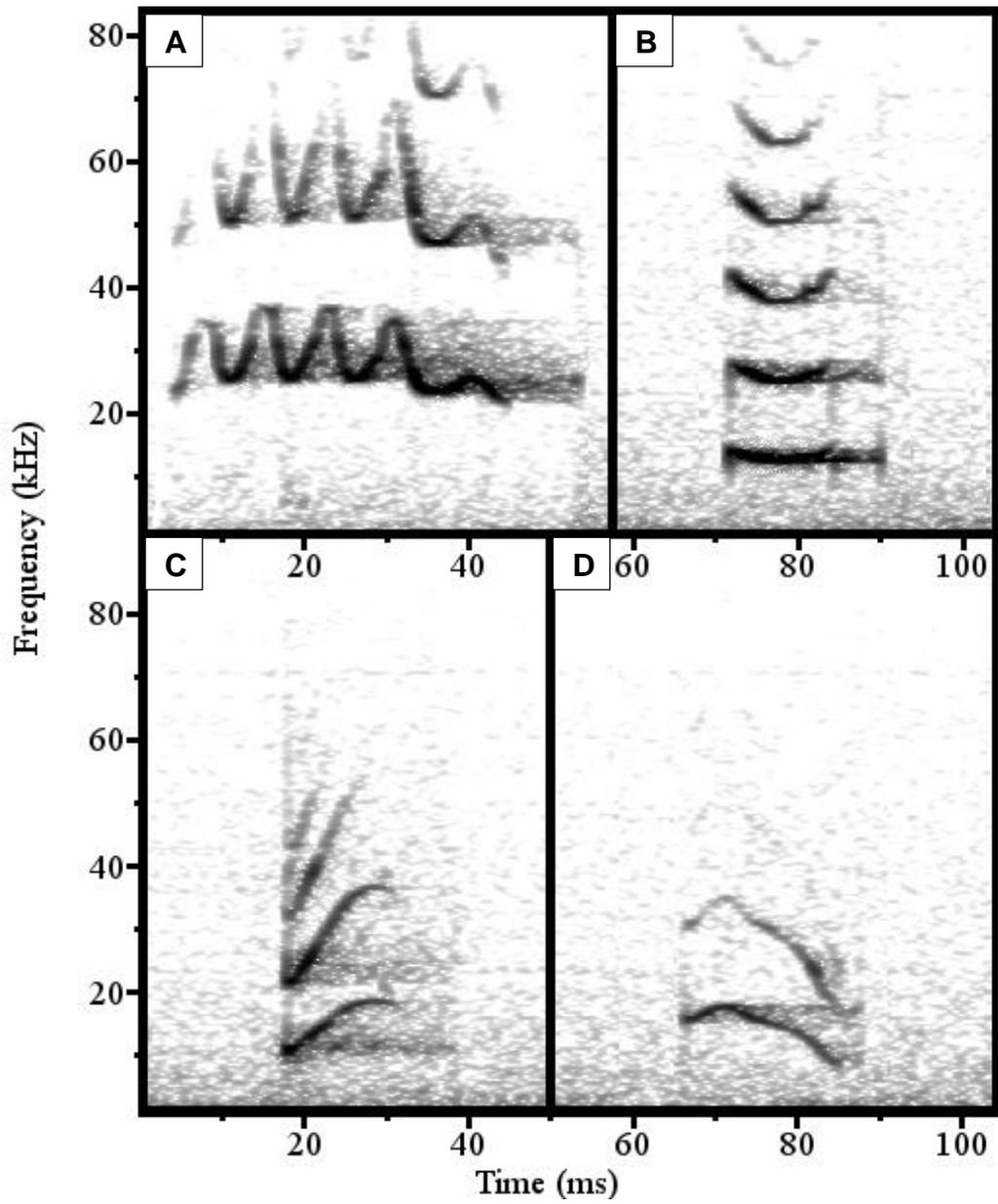
#### 4.3.2 Song recording

I recorded the songs of 16 males at 12 singing roosts between February 19 and April 5 2014. All males were recorded between 1900 and 2130 hours, and only on nights with relatively clear weather (i.e. no rain or strong winds). I recorded male songs using a D980 bat detector (Pettersson Elektronik AB, Uppsala, Sweden) linked to a Sound Devices 722 digital recorder (Sound Devices, Reedsburg, WI). Sound was recorded at a sampling rate of 192 kHz with 24-bit precision. Recordings were made within 10 m of the roost tree and generally took place just after the male arrived at dusk (although in the case of timeshare roosts other resident males had to be recorded as they arrived). The identities of recorded males were determined using a Biomark HPR Plus automatic PIT-tag reader (Biomark, Idaho, USA) mounted on the entrances of the singing roosts, and I only recorded the songs of PIT-tagged males. Males were recorded for 10 minutes of what was deemed to be continuous singing to ensure that I had recorded the male's full repertoire. Additional detailed information on the study site, population size, and singing roost selection can be found in Toth et al. (2015; Chapter 3).

#### 4.3.3 Song annotations

I used RavenPro 1.4 (Cornell Laboratory of Ornithology, Ithaca, NY) to perform the acoustic analyses of male songs. Spectrograms were generated using a 1024-sample discrete Fourier transformation and a Hann window with 95% overlap (frequency resolution 188 Hz, time resolution 0.135 ms).

Due to the high song output produced by *M. tuberculata*, annotations were only made for every other minute in each 10 min recording (i.e. first minute, third minute, fifth minute, etc.). When annotating I defined a song as a continuous vocalisation separated by at least 10 ms of silence (after Behr and von Helversen 2004). Songs were categorised based on the presence and combination of four basic elements: tones, trills, upsweeps, and downsweeps (Figure 1). A trill was defined as an element that rapidly fluctuated in frequency, while tones – although they may gradually increase or decrease in frequency – did not fluctuate (Figure 1ab). Upsweeps and downsweeps were defined as tonal elements that rapidly increased or decreased in frequency, respectively (Figure 1cd). Thus, songs could be comprised of a single element or a composite of several elements (e.g. an upswEEP immediately followed by a trill was classified as an “upswEEP-trill”). Songs were also scored on their quality: songs with complete structures (i.e. the entire songs was clearly visible) were given a score of 1, songs with incomplete structures (e.g. sometimes the high pitch components of songs were faint on spectrograms) were given a score of 2, and songs with poor structures were given a score of 3. This allowed songs to be sorted based on the requirements of later analyses. For the list of parameters measured from male songs, see Table 1.



**Figure 1** – Sample spectrograms of the four basic song elements that comprise *M. tuberculata* songs: A) trills, B) tones, C) upsweeps, and D) downsweeps. Songs may be comprised of several elements in combination, or as solitary elements.

**Table 1** – Frequency and output parameters recorded from the songs of male *Mystacina tuberculata*. Frequency parameters were measured from the fundamental harmonic of each song. Each of the frequency characteristics were measured in kHz, duration in ms, and average song rate in songs/min.

Song Parameter (Abbreviation)
Lowest frequency (LF)
Highest frequency (HF)
Peak frequency (PF) - i.e. the frequency at which the maximum power occurs
Centre frequency (CF) - i.e. the frequency that divided the song into two intervals of equal energy
Delta frequency (DF) – i.e. HF minus LF
Duration (DU)
Duty cycle – i.e. sum total of all song lengths divided by 300 s
Average song rate

#### 4.3.4 Statistical analyses

To determine if additional recordings would have revealed more song types I used the exponential function developed by Wildenthal (1965) modified by Davidson and Wilkinson (2002) for estimating repertoire size:

$$n(t) = N_{TOT} \left( 1 - e^{\frac{-t \cdot A}{N_{TOT}}} \right)$$

where  $n(t)$  is the observed number of song types,  $t$  is the observed number of songs,  $N_{TOT}$  is the estimated total repertoire size, and  $A$  is a scaling constant. To obtain  $N_{TOT}$  the model was regressed against the cumulative curve of song types and adjusted until the curve passed through the last points of data. The asymptote of the resulting curve is the estimated repertoire size (Wildenthal 1965; Davidson and Wilkinson 2002).

Prior to performing regression analyses on forearm length, I performed a principal component analysis (PCA) on the four most-common song types (i.e. those that comprised > 10% of the proportion of all observed songs), as it is likely that these would be most important for mate attraction. Thirty high-quality songs of each type were randomly selected

from each male for use in the analyses. Principal components were calculated with varimax rotation on LF, HF, CF, PF, and DF for each song type, as these parameters were largely correlated. For each of the four song types, the Kaiser-Meyer-Olkin measures of sampling adequacy were  $> 0.5$  and Bartlett's test of sphericity was significant ( $P < 0.0001$ ). I retained principal components with Eigenvalues of  $> 1.0$  and interpreted the resulting principal components (PCs) on the presence of variables with loadings  $> 0.7$ . All values were checked for normality (Shapiro-Wilk test,  $P > 0.05$ ), however DU values had to be log transformed for up-sweep-trills, trill-downsweeps, and up-sweep-trill-downsweeps.

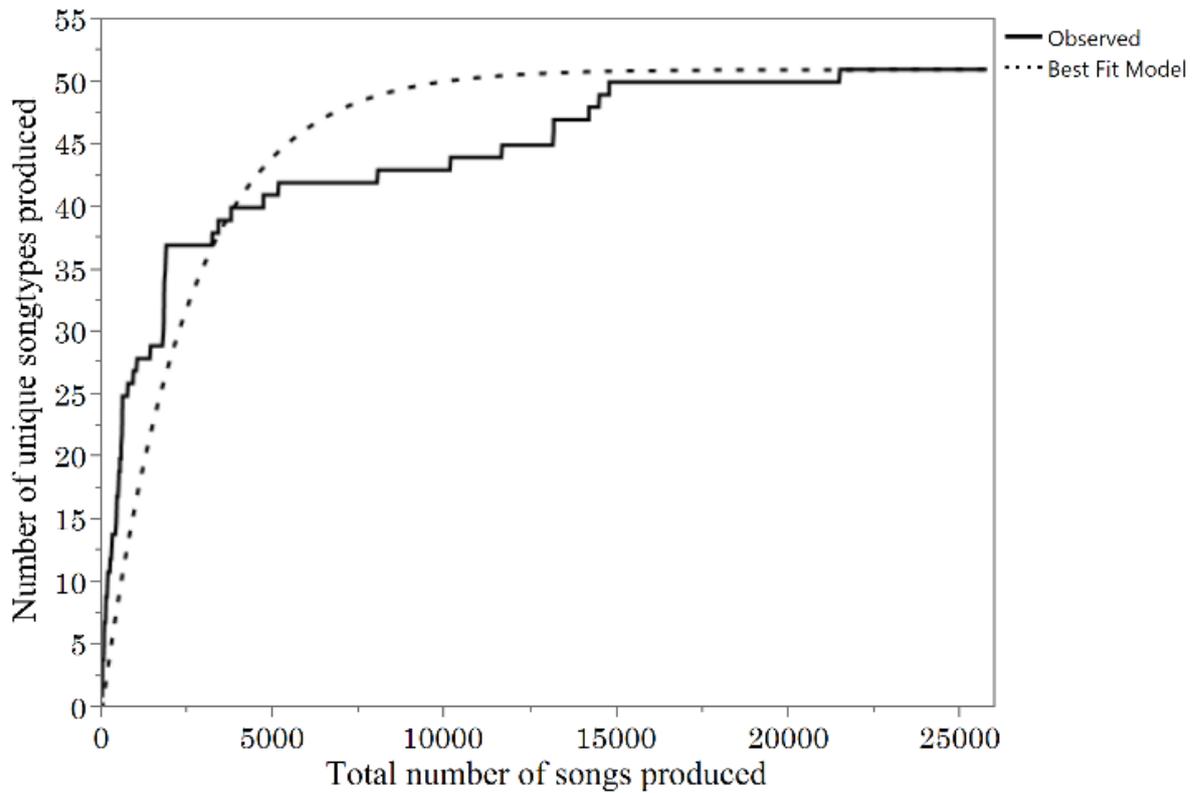
To test whether male size influenced song characteristics I used multiple linear regression models with song PCs as the dependent variables and both forearm length and recording date (a potential confounding factor) as the independent variables, with male identity as a random effect. To test the influences of male size on song output, I also performed multiple linear regressions on song duration, duty cycle, and song rate as dependent variables against forearm length and recording date.

I used the program JMP v. 11.2 (SAS Institute Inc. 2012) for statistical analyses, and report mean  $\pm$  SD. All reported  $P$  values are two tailed.

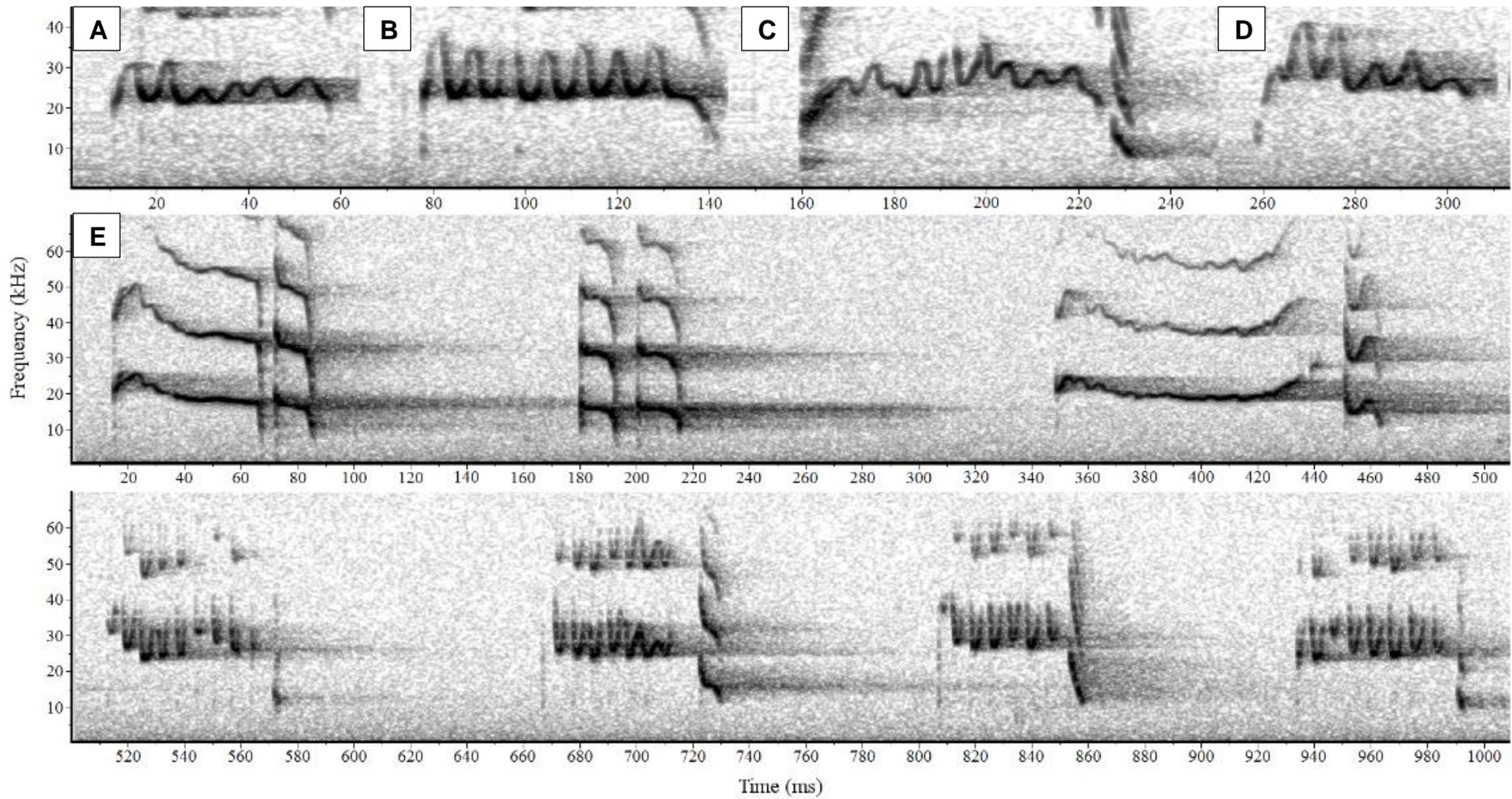
#### **4.4 Results**

In total I annotated 25,701 songs ( $1,606.4 \pm 475.1$  songs/male, range: 726 – 2,713), comprised of 51 distinct song types ( $28.6 \pm 3.9$  song types/male, range: 21 – 35). Based on a modified Wildenthal (1965) model of estimated repertoire size (Davidson and Wilkinson 2002) the observed number of song types agrees with the estimated repertoire size of the population (approximately 51; Figure 2). The four most-common song types were trills (27.1% of all songs), trill-downsweeps (14.8%), up-sweep-trill-downsweeps (13.7%), and up-sweep-trills (13.5%; Figure 3). All other song types individually comprised  $< 4\%$  of total

songs produced, including the three other basic song elements (for a list of all song types recorded, please see Appendix D). Average song rate was 321.3 songs/min ( $\pm 95.0$ , range: 145.2 – 542.6 songs/min) and average duty cycle was 0.28 ( $\pm 0.06$ , range: 0.13 – 0.38).



**Figure 2** – Estimated repertoire size in male *M. tuberculata* as shown by comparing the total number of songs analysed with the number of unique song types identified. The solid line represents the cumulative curve of unique song types identified while the dashed line represents a modified model of repertoire size estimation (Davidson and Wilkinson 2002).



**Figure 3** – Sample spectrograms of *M. tuberculata* songs, showing the four most common-song types (A – D) and an example of 1 second of continuous singing (E). A) Trill, B) trill-downsweep, C) upsweep-trill-downsweep, and D) upsweep-trill. Spectrograms were generated using a 1024-sample discrete Fourier transformation and a Hann window with 95% overlap (frequency resolution 188 Hz, time resolution 0.135 ms).

The average weight of recorded males was  $14.4 \pm 1.2$  g (range: 12.5 – 16.0 g), and average forearm length was  $41.9 \pm 0.9$  mm (range: 40.2 – 43.7 mm). Weight and forearm were not correlated (Pearson correlation:  $r_{14} = -0.12$ ,  $P = 0.66$ ). Two males were removed from analyses of certain song types – one from trill-downsweeps and one from upsweep-trill-downsweeps – as they did not produce enough high-quality songs of those types. The PCAs generated two principal components for each of the four main song types, together accounting for 93% of the variance in trills, 89% of the variance in trill-downsweeps, 81% of the variance in upsweep-trill-downsweeps, and 86% of the variance in upsweep-trills (Table 2).

Some features of male song scales with morphometric features (Table 3). Contrary to my predictions, the frequency characteristics of the four most-common song types did not vary with male size (Table 3), although some measures of song output did; the duration of trill-downsweeps was significantly, negatively related to forearm length (Table 3), as was duty cycle (Table 3; Figure4). There was no relationship between male size and song rate (Table 3).

**Table 2** – Parameters measured from the four most-common song types produced by *M. tuberculata*, along with results of PCAs that combined frequency characteristics. Sample sizes refer to total number of songs used in the PCAs.

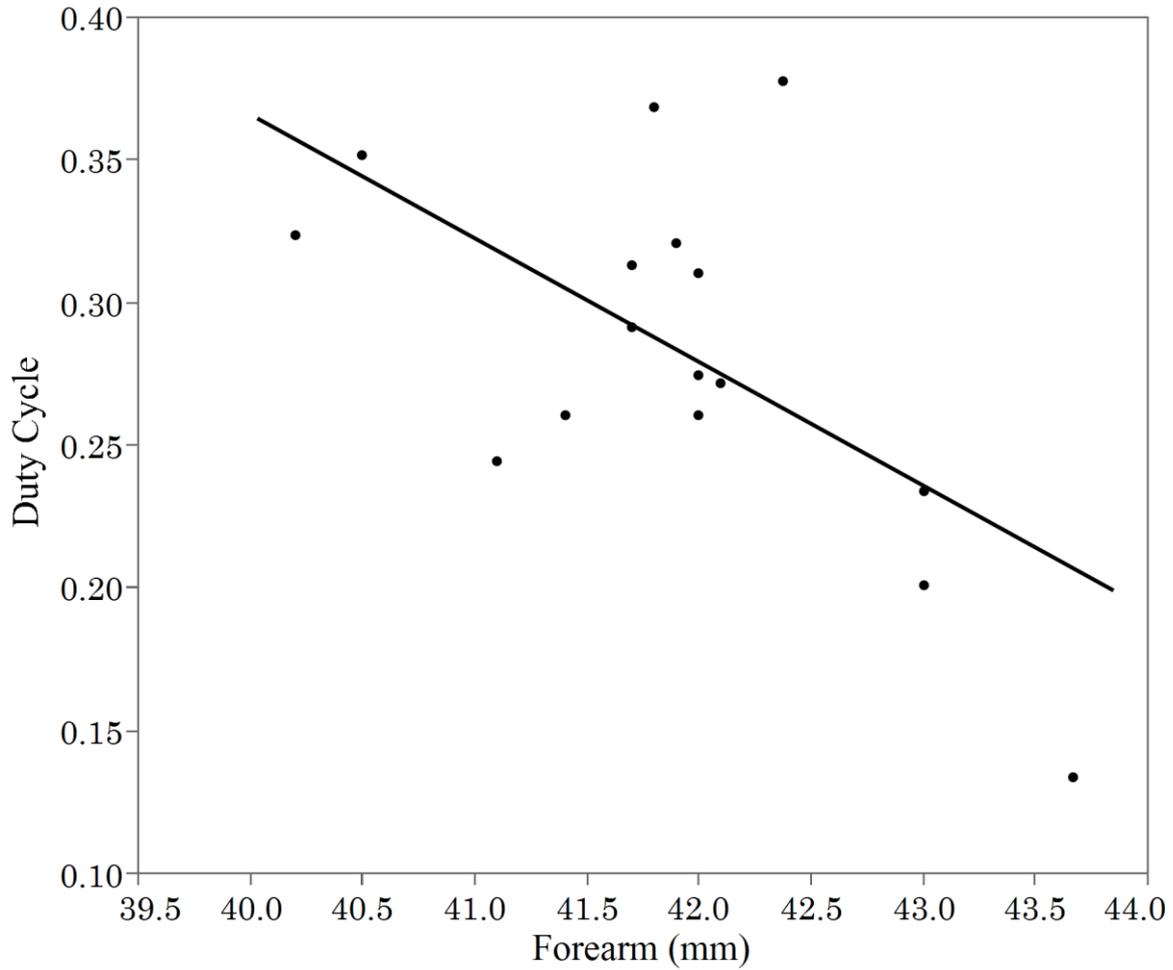
	PC1	PC2	Song Parameters Mean $\pm$ SD
<b>Trills</b> ( $n = 480$ )			
Low F (kHz)	<b>0.96</b>	-0.50	12.28 $\pm$ 5.00
High F (kHz)	0.66	<b>0.73</b>	26.23 $\pm$ 7.40
Centre F (kHz)	<b>0.91</b>	0.33	17.40 $\pm$ 5.40
Delta F (kHz)	0.017	<b>1.00</b>	13.95 $\pm$ 5.67
Peak F (kHz)	<b>0.90</b>	0.19	17.10 $\pm$ 5.67
Eigenvalue	3.44	1.20	
% Variance explained	59.4%	33.6%	
Duration (ms)			45.27 $\pm$ 19.93
<b>Trill-downsweeps</b> ( $n = 450$ )			
Low F (kHz)	<b>0.91</b>	-0.12	10.53 $\pm$ 3.94
High F (kHz)	0.62	<b>0.73</b>	29.74 $\pm$ 5.57
Centre F (kHz)	<b>0.89</b>	0.30	19.71 $\pm$ 5.08
Delta F (kHz)	-0.028	<b>1.00</b>	19.21 $\pm$ 4.55
Peak F (kHz)	<b>0.88</b>	0.20	18.22 $\pm$ 5.79
Eigenvalue	3.17	1.29	
% Variance explained	55.5%	33.6%	
Duration (ms)			62.11 $\pm$ 23.9
<b>Upsweep-trill-downsweeps</b> ( $n = 450$ )			
Low F (kHz)	-0.097	<b>0.81</b>	8.67 $\pm$ 1.83
High F (kHz)	<b>0.90</b>	0.31	30.09 $\pm$ 4.80
Centre F (kHz)	0.50	<b>0.72</b>	19.02 $\pm$ 4.40
Delta F (kHz)	<b>1.00</b>	0.006	22.24 $\pm$ 4.51
Peak F (kHz)	0.33	<b>0.78</b>	17.43 $\pm$ 5.63
Eigenvalue	2.87	1.18	
% Variance explained	43.4%	37.7%	
Duration (ms)			62.44 $\pm$ 20.22
<b>Upsweep-trills</b> ( $n = 480$ )			
Low F (kHz)	-0.12	<b>0.88</b>	9.43 $\pm$ 2.30
High F (kHz)	<b>0.89</b>	0.35	28.95 $\pm$ 5.48
Centre F (kHz)	0.54	<b>0.72</b>	18.42 $\pm$ 4.54
Delta F (kHz)	<b>0.99</b>	-0.023	19.52 $\pm$ 5.18
Peak F (kHz)	0.40	<b>0.77</b>	17.19 $\pm$ 5.51
Eigenvalue	3.04	1.24	
% Variance explained	45.0%	40.5%	
Duration (ms)			58.87 $\pm$ 22.78

Loadings >0.7 are highlighted in bold.

**Table 3** – Relationships between forearm length and various song parameters, including principal components (used to combine frequency measurements) and duration of the four main song types, as well as general song output variables (duty cycle and song rate). Frequency parameters that inform the song PCs are listed in brackets: lowest frequency (LF), highest frequency (HF), centre frequency (CF), peak frequency (PF), and delta frequency (DF). Multiple regressions were used, and parameters were regressed against male forearm length and the date each male was recorded, with male identity as a random effect.

<b>Song Parameter</b>	<b><i>x</i></b>	<b><i>b</i></b>	<b>Adjusted <i>R</i><sup>2</sup></b>	<b><i>t</i></b>	<b><i>P</i></b>
<b>Trills</b>					
PC1 (LF, CF, PF)	Forearm	-0.021	0.3	-0.12	0.9
	Date	0.014		1.21	0.24
PC2 (HF, DF)	Forearm	-0.12	0.27	-0.71	0.49
	Date	0.0057		0.51	0.62
Duration	Forearm	-0.0023	0.099	-1.23	0.24
	Date	2.1x10 <sup>-4</sup>		-1.59	0.13
<b>Trill-downsweeps</b>					
PC1 (LF, CF, PF)	Forearm	0.007	0.36	0.37	0.72
	Date	0.0059		0.56	0.58
PC2 (HF, DF)	Forearm	-0.2	0.4	-1.23	0.32
	Date	-0.0023		-0.22	0.83
Duration	Forearm	-0.063	0.4	-1.49	<b>0.029</b>
	Date	6.18x10 <sup>-4</sup>		0.43	0.67
<b>Upsweep-trill-downsweeps</b>					
PC1 (LF, CF, PF)	Forearm	0.27	0.22	1.65	0.12
	Date	0.0028		0.29	0.78
PC2 (HF, DF)	Forearm	0.15	0.16	1.09	0.3
	Date	0.011		1.33	0.21
Duration	Forearm	-0.054	0.48	-1.7	0.12
	Date	-0.0014		-0.79	0.44
<b>Upsweep-trills</b>					
PC1 (HF, DF)	Forearm	-0.27	0.26	-1.87	0.084
	Date	0.0083		0.84	0.41
PC2 (LF, CF, PF)	Forearm	0.17	0.28	1.06	0.31
	Date	0.0039		0.34	0.74
Duration	Forearm	-0.041	0.42	-1.37	0.19
	Date	-0.0025		-1.2	0.25
Duty cycle	Forearm	-0.05	0.31	-2.95	<b>0.011</b>

Song rate	Date	$-5.42 \times 10^{-4}$		-0.51	0.62
	Forearm	-18.62	-0.081	-0.59	0.57
	Date	1.37		0.68	0.51



**Figure 4** – Duty cycle of singing males against forearm length. There was a significant, negative relationship between duty cycle and male size ( $n = 16$ ,  $b = -0.05$ , adjusted  $R^2 = 0.31$ ,  $t = -2.95$ ,  $P = 0.011$ ).

## 4.5 Discussion

My results indicate that the singing behaviour of male *M. tuberculata* is a complex set of signals that may function as an honest indicator of male quality. Males possess large song type repertoires, and have prodigious song outputs that scale with body size. The songs of *M. tuberculata* are thus comparable to the songs of other non-bat species and have the potential to function as a sexually-selected signal to females.

*Mystacina tuberculata* songs are composed of four basic elements – tones, trills, upsweeps, and downsweeps – that are either produced singly, or combined with other elements. Out of 51 described song types, only four individually comprised > 10% of total songs produced: trills, upswing-trills, trill-downsweeps, and upswing-trill-downsweeps. Trills have been shown to be important for mate selection in several species of songbirds, likely because they require high levels of vocal performance to produce (see Podos et al. 2004). Additionally, trills are the most-frequent song type in the courtship songs of *S. bilineata* (Behr and von Helversen 2004), are common in the songs of Mexican free-tailed bats (*Tadarida brasiliensis*; Bohn et al. 2009), and have been recorded in the social calls of multiple European species (Pfalzer and Kusch 2003), suggesting a common function across taxa. As each of the common song types produced by *M. tuberculata* contain trill elements, it suggests that they serve a mate-attraction purpose.

None of the four of the most-common song types produced by male *M. tuberculata* displayed size-pitch allometry. While size-pitch allometry has been demonstrated in non-courtship vocalisations of mammals (Ey et al. 2007; Sell et al. 2010; including bats, Puechmaille et al. 2014), it appears to be rare in courtship vocalisations. Size-pitch allometry is thought to be rare both in small animals (Jones and Siemers 2011) and animals with high vocal performance (Patel et al. 2010), and *M. tuberculata* appears to adhere to these rules as

well. Thus the frequency of male songs may not be as an important signal to females as song output, which did vary with male size (see below).

Although male *M. tuberculata* singing bouts were dominated by four song types, individual males possessed large song repertoires. Female preferences for elaborate male song repertoires have been studied in songbirds for decades using both laboratory and field methods (e.g. Kroodsma 1976; Baker et al. 1986; Baker et al. 1987; Hiebert et al. 1989; Mountjoy and Lemon 1996; Reid et al. 2004). Repertoire size has been positively associated with offspring survival (Hasselquist et al. 1996), and there is evidence that female preference for large song repertoires predates the evolution of repertoires in males (Searcy 1992). In bats, the study of male song repertoires is still in its infancy, but repertoire size has been positively correlated with the number of females roosting on male territories in *S. bilineata* (Davidson and Wilkinson 2004). Individual *M. tuberculata* in the Pikiariki Ecological Area possessed an average of 29 song types, with a population-level repertoire of 51, which is larger than many songbirds (see Beecher and Brenowitz 2005). Thus it is likely that males with larger repertoires would be preferred as mates by females. Without further study it is unknown what accounts for repertoire-size differences in male *M. tuberculata*, whether they are “open-ended learners” and continue to accrue new song types as they age (e.g. canaries, *Serinus canaria*; Lehongre et al. 2006), or “closed-ended learners” that crystallise their repertoires after a set amount of time (e.g. song sparrows, *Melospiza melodia*; Nordby et al. 2002). However, given the size of male repertoires the former seems likely. If males continue to learn new song types throughout their lives, large repertoires could function as a reliable indicator of male age (Nottebohm and Nottebohm 1978; Mountjoy and Lemon 1995, 1996), with older males being perceived as more attractive by females (e.g. O’Loghlen and Rothstein 1995; Ward et al. 2014).

Gross song output (i.e. song rate, song duration, duty cycle) is also a trait that can reflect aspects of male quality. In this study, male *M. tuberculata* were found to have high song outputs, producing hundreds of songs per minute with high duty cycles. Additionally, I found that larger males had significantly shorter songs for trill-downsweeps (the second most-common song type) and significantly lower duty cycles than smaller males, further allowing for size discrimination by females. Song output is a useful signal for females across various taxa, as singing is an energetically-demanding signal that appears to be constrained by energetic costs in many species (see Vehrencamp 2000; Gil and Gahr 2002). In black-capped chickadees (*Poecile atricapillus*), males with higher dominance ranks begin singing earlier, sing for longer, and sing at a higher song rate during the dawn chorus (Otter et al. 1997). In blue tits (*Cyanistes caeruleus*), earlier onset of singing during the dawn chorus is correlated with increased extra-pair paternity (Poesel et al. 2006), and strophe length in great tits (*P. major*) is positively correlated with dominance rank, higher survival, and greater lifetime reproductive success (Lambrechts and Dhondt 1986). Similar results have been found in other taxa. In Gulf Coast toads (*Bufo valliceps*), females preferred males with higher call rates and longer call durations, and males with higher call rates were more likely to attain matings (Wagner Jr and Sullivan 1995). In bats, *S. bilineata* males that possess higher song rates have been found to sire more offspring (Behr et al. 2006), and males with longer calls had more females on their territories (Davidson and Wilkinson 2002, 2004). In *M. tuberculata*, given there was no significant relationship between size and song rate we might expect that smaller males – possessing longer songs and higher duty cycles – may be perceived as more attractive to females.

It is worth noting how high the song outputs of *M. tuberculata* in comparisons to other species. The Eastern whippoorwill (*Caprimulgus vociferus*) and the red-eyed vireo (*Vireo olivaceus*) are two bird species regarded as having some of the highest sustained song

outputs (Kroodsma 2005). Across one night of observation (9 hours), a single whippoorwill was recorded singing approximately 21,000 songs at a rate of 0.66 songs/sec (Kroodsma 2005). Similarly, a single red-eyed vireo has been recorded as producing 22,197 songs within a 14-hour period at a rate of 0.44 songs/sec (Kroodsma 2005). In contrast, over a five minute period *M. tuberculata* males produced over 3,200 songs on average, at a rate of approximately 5 songs/sec. Given that the average amount of time spent by males in the singing roosts is approximately 6 hours, and males vocalise for the majority of the time they are in their singing roosts (C. Toth, pers. obs.), many males are producing over 100,000 songs nightly. While it is difficult to compare the song output of birds and bats due to the differences in their vocal organs, many studies on bat song characteristics either do not report a song rate (e.g. Bohn et al. 2008) or define a song as a full set of vocalisations, instead reporting the number of these vocalisations over a set amount of time (e.g. Behr et al. 2006). However, one comparable example would be the songflight (i.e. courtship) calls of the common Pipistrelle bat (*Pipistrellus pipistrellus*), which have been recorded at 1.73 calls/s (Jones 1997). Even though songflights can last for hours (Sachteleben and von Helversen 2006), it is unlikely they reach the same outputs as *M. tuberculata*. Regardless, *M. tuberculata* likely has one of the highest sustained song outputs yet described.

Although the songs of *M. tuberculata* appear suited for mate attraction, they likely also serve a purpose in territorial defence, similar to the songs of many songbirds (Gil and Gahr 2002). In *S. bilineata*, males produce distinct bouts of singing for both territory defence and mate attraction (Davidson and Wilkinson 2004), although frequency aspects of the former have been found to be important in reproductive success (Behr et al. 2006). As Behr and von Helversen (2004) point out, vocalisations used for territorial defence should be short, repeatable, and individually distinguishable. All four of the main song types produced by *M. tuberculata* fit this description, and thus it is possible that *M. tuberculata* song also serves an

antagonistic purpose. Unfortunately my study design does not allow me to attribute a behavioural function to specific song types, and so further study is needed.

Based on the evidence presented in this study, the songs and singing behaviour of male *M. tuberculata* are likely important signals for mate attraction. However, many details of this behaviour still need to be examined. Beyond a broad classification of the song types produced by individual males I have avoided a detailed analysis of male song repertoires. Future studies examining the composition of repertoires within and between individuals, including the degree to which neighbours – or roostmates, in the case of timeshare roosts (Toth et al. 2015; Chapter 3) – share song types (e.g. Beecher et al. 2000), would be of considerable interest. Furthermore, analysis of whether males order their song types into predictable ‘phrases’ (e.g. Bohn et al. 2009), and if these phrases differ between individuals, would also be of interest. Lastly, the acoustic properties of singing roosts are currently unknown. Given the importance of singing roosts for displaying males, it may be expected that roosts are selected for particular acoustic characteristics. For example, males may use singing roosts as resonating chambers in order to increase the amplitude of their songs (e.g. Lardner and bin Lakim 2002).

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## **Smaller males have higher reproductive success in a lek-breeding bat**

## 5.1 Abstract

Bats provide a difficult study system largely due to their nocturnal habits, ability to fly, and use of inaccessible roosting sites. As a result there is relatively little information on the life histories of most bat species, particularly with regards to sexual selection. Accordingly, the use of genetics has been increasingly instrumental to inferring breeding behaviour in many bats species. The lesser short-tailed bat (*Mystacina tuberculata*) of New Zealand presents an interesting system for the use of genetic tools to study sexual selection in a bat, as it is one of only two lek-breeding bat species in the world (neither of which have been studied with regards to male reproductive success). During the breeding season, male *M. tuberculata* occupy small, clustered roosts from which they sing to females. Interestingly, some singing roosts are occupied by multiple males appearing to work in shifts (dubbed “timeshares”), the function of which is unknown. In this study I examined the breeding behaviour of *M. tuberculata* in the Pikiariki Ecological Area, central North Island, with respect to forearm length, as several aspects of male singing behaviour have previously been shown to be influenced by male size. I used video cameras in conjunction with automatic passive integrated transponder (PIT) tag readers to monitor 12 male singing roosts containing 19 PIT-tagged males. Additionally, I performed genetic analyses using 11 microsatellite loci to estimate male reproductive success and the relatedness between timeshare males. I found that not only did smaller males spend a larger proportion of the night within singing roosts than larger males, but smaller males also sired more offspring and had more relatives within the colony than larger males (indicating a higher long-term success). Furthermore, males in solitary singing roosts were smaller than timeshare males and spent a larger proportion of the night within singing roosts, however the two groups did not differ in reproductive success. These results compliment my previous work showing that smaller males have higher song outputs than larger males. However, larger males may use timesharing as an alternative

reproductive strategy to regain reproductive success that would otherwise be lost. I discuss the possibility that smaller males expend less energy than larger males, allowing them to invest more in courtship.

## 5.2 Introduction

The study of sexual selection in bats (Order: Chiroptera) has long presented a challenge. With over 1,100 species extant today, bats are one of the most-successful and speciose mammalian groups on Earth (Simmons 2005), feats aided by their ability to fly and thereby exploit a myriad of niches (Kruttsch 2000; Altringham and Senior 2005). Bats are also unrivalled in the diversity of breeding behaviours they display (Altringham 2011). However, given that bats are nocturnal, can travel large distances in short amounts of time, roost in inaccessible locations, and rarely display courtship behaviour in captivity (Behr and von Helversen 2004), studying their breeding behaviour is often difficult; at the time of the last review, details were known for less than 7% of all bat species (McCracken and Wilkinson 2000). Consequently we have little information on how sexual selection (both the use of courtship displays by males and female selection of male traits) operates in most species.

Leks – aggregations of sexually-displaying males visited by females solely for fertilisation – provide a very useful system for studying sexual selection in free-living animals. Lekking males control no resources valuable to females and do not provide parental care to offspring (Bradbury 1977). Male displays are often energetically expensive to produce, and thus represent honest indicators of quality to females (e.g. Ciuti and Apollonio 2011; Lebigre et al. 2013). As females are able to compare multiple males on leks simultaneously, and mate choice is not confounded by factors such as resource ownership or the quality of the male as a provider, female selection of indirect male benefits (i.e. “good genes”) is relatively easy to quantify (Höglund and Alatalo 1995). This is aided by the fact that females in many lek systems reach a high level of consensus with respect to mate choice, selecting a small number of males with the highest attractiveness (Bradbury et al. 1985). Consequently male reproductive success on leks is often typified by a pronounced skew (Höglund and Alatalo 1995). Thus, leks have been used as model systems for studying mate

choice in various taxa (e.g. Jiguet et al. 2000). Bats that display lek-breeding behaviour would therefore be useful for investigating the link between male courtship displays and female selection of mates, given that such information is largely unknown for the majority of species. However, despite showing a diversity of mating systems, lek breeding appears to be disproportionately rare in Chiroptera.

To date, only two species of bats have been confirmed to breed using leks: the lesser short-tailed bat (*Mystacina tuberculata*) of New Zealand (Toth et al. 2015b; Chapter 3), and the hammer-headed bat (*Hypsignathus monstrosus*; a large fruit bat) of equatorial Africa (Bradbury 1977). In *H. monstrosus*, up to 130 males will arrange themselves along stretches of river and produce loud vocalisations and wing-flapping displays for visiting females. Females appear to appraise multiple males before selecting one to mate with, and only a small fraction of males receive the majority of copulations (6% of males received 79% of observed copulations; Bradbury 1977). In *M. tuberculata*, males occupy ‘singing roosts’ nightly during the breeding season from which they sing to attract passing females. Male songs are complex signals that vary considerably between individuals; smaller males (measured by forearm length) have higher song outputs than larger males (Chapter 4). Singing roosts are aggregated around the large communal roosts used during the day by the population, likely in an effort by males to maximise the number of females they encounter (Toth et al. 2015b; Chapter 3). Some of these singing roosts – dubbed “timeshares” – are shared between multiple males, who appear to take shifts throughout the night to sing (Toth et al. 2015b; Chapter 3). While some lekking species have been shown to produce cooperative displays (i.e. multiple males displaying together to increase female visitation rates; e.g. McDonald and Potts 1994), males in timeshare roosts do not overlap temporally. Timeshare males may be pursuing a kin selection strategy (e.g. Krakauer 2005), however this

remains to be shown. Thus, the function of timeshare roosts is currently unknown as such sharing behaviour has, to my knowledge, not been observed previously.

Male reproductive success and female selection criteria have not been quantified in either *H. monstrosus* or *M. tuberculata*. Bradbury (1977) was unable to attribute male characteristics to female preferences, or quantify reproductive success beyond the number of copulations male *H. monstrosus* received. Similarly, while copulations have been observed at *M. tuberculata* singing roosts (Toth et al. 2015b; Chapter 3), these observations were not sufficient to determine what male characteristics females find attractive.

Increasingly, researchers have benefited from the use of genetic analyses when studying lekking species as it has allowed the quantification of reproductive success where such information was previously unavailable (e.g. aquatic species; Kellogg et al. 1995; Cerchio et al. 2005). Likewise, studies of bat mating systems have benefited from the use of molecular tools, and recent studies have been able to provide details on breeding behaviour that would be impossible to determine otherwise (e.g. Burland et al. 2001; Burland and Wilmer 2001; Heckel and von Helversen 2003; Behr and von Helversen 2004; Voigt et al. 2005; Puechmaille et al. 2014; Ward et al. 2014). Thus, genetic analyses of paternity appear to be well-suited for quantifying sexual selection in *M. tuberculata*, particularly since large numbers of individuals (both adults and juveniles) can be captured at communal roosts to obtain tissue samples (see Toth et al. 2015b; Chapter 3).

The aim of this chapter is to use genetic analyses to quantify male reproductive success and female selection criteria in *M. tuberculata*. I hypothesise that reproductive success will be higher in small males, as smaller males have higher song outputs than larger males (a trait that is attractive in many taxa; Vehrencamp 2000; Morrison et al. 2001; Gil and Gahr 2002). Furthermore, I also aim to elucidate the timesharing behaviour displayed by some lekking males, as the function of this strategy is currently unknown. I hypothesise that

timeshare males are related and using a kin selection strategy (e.g. Krakauer 2005). To accomplish these objectives I use video footage of singing roosts with known (i.e. marked) resident males to evaluate male singing strategies (e.g. length of time spent in the roost, number of resident males), as well as tissue samples collected from both adult males and volant juveniles to assess reproductive success and relatedness. Additionally, as genetic analyses using nuclear DNA have not been performed on *M. tuberculata* previously, my first goal is to develop microsatellite markers for use in genetic analyses.

## **5.3 Methods**

### *5.3.1 Field methods*

My study took place in the Pikiariki Ecological Area, central North Island. I captured individual *M. tuberculata* from 2012-2014 using a variety of methods (for a description of the field site and capture protocols, please see Chapters 2 and 3, respectively). I removed a small piece of wing tissue (3 mm punch biopsy from each wing's plagiopatagium) from 333 individuals for genetic analyses. Samples were taken from 175 adult males (23 caught in 2012, 112 in 2013, and 40 in 2014), 76 juvenile males (8 in 2012, 23 in 2013, and 45 in 2014), and 82 juvenile females (11 in 2012, 17 in 2013, and 54 in 2014). Although tissue samples were collected from adult females, these individuals were not genotyped as I was only interested in assigning paternity to offspring. I also recorded measurements of forearm length for each individual as a proxy of body size to use in regression analyses (see below; Chapter 4).

### *5.3.2 Video recording and male characteristics*

Twelve singing roosts were monitored using infrared cameras between 27 March and 9 April 2014. Singing roosts were filmed in groups of three for three nights per group (although one

roost experienced a camera failure and so was only filmed for two nights). I mounted automatic PIT-tag readers (Biomark HPR Plus, Biomark, Idaho, USA) on the entrances of filmed singing roosts to determine the identities of resident males and other visiting individuals (for additional information on the filming methods, please see Toth et al. 2015; Chapter 3).

For each roost I made the following observations: 1) the length of time between sunset and when the resident male first entered the singing roost (this was only recorded for the first male to arrive at the singing roost in timeshares, and recorded as zero if the resident male spent the preceding day in the singing roost); 2) the proportion of the night the resident male(s) spent within the singing roost (i.e. total time within the roost as a fraction of the total night length); and 3) the order of arrival of resident males at timeshare singing roosts. The first two values were averaged for individuals across the three days of filming. Sunset and sunrise times were obtained for Benneydale (which is approximately 15 km from Pureora Forest Park and situated at the same latitude) from the Royal Astrological Society of New Zealand (<http://rasnz.org.nz/>). Given that many aspects of male singing behaviour (i.e. song duration, and duty cycle) are related to male forearm length (Chapter 4), I used simple linear regressions to determine if arrival after sunset and time spent in roost were similarly related to forearm length.

To evaluate if the resident males in solitary singing roosts differ from those in timeshare roosts I compared the following variables between the two groups: forearm lengths, arrival time after sunset, time spent in roost by individual males, proportion of night spent within singing roosts, and average relatedness of resident males to all other genotyped individuals (see below for details). Furthermore, to estimate the relatedness of males within timeshare roosts to one another I used the program Coancestry v1.0 (Wang 2011) to generate

triadic likelihood estimator values (Wang 2007) for male dyads within four timeshare roosts (three males per roost).

### *5.3.3 Microsatellite development and genotyping*

Microsatellite markers were developed and tested for polymorphism by ecogenics GmbH (Switzerland) using tissue from 15 individuals. Size-selected fragments from genomic DNA were enriched for single-sequence repeat (SSR) content using magnetic streptavidin beads and biotin-labelled CT and GT repeat oligonucleotides. The SSR-enriched library was analysed on an Illumina MiSeq platform using the Nano 2x250 v2 format. After assembly, 1,176 contigs or singlets contained a microsatellite insert with a tetra- or a trinucleotide of at least 6 repeat units or a dinucleotide of at least 10 repeat units. Suitable primer design was possible in 252 microsatellite candidates, with 11 selected for further development.

For genetic analyses I extracted genomic DNA from tissue samples using a Gentra Puregene Core Kit (Qiagen, Valencia, CA) according to the manufacturer's instructions. Microsatellite markers were amplified using the method described by Schuelke (2000). The PCR amplification used a reaction volume of 12  $\mu$ l containing double-distilled water (6.1  $\mu$ l), 1  $\times$  buffer (1  $\mu$ l), 200  $\mu$ M dNTP mix (1  $\mu$ l), 0.04  $\mu$ M M13 tailed locus-specific forward primer (0.2  $\mu$ l), 0.16  $\mu$ M locus-specific reverse primer (0.8  $\mu$ l), 0.16  $\mu$ M universal M13 primer with its 5'-end labelled with one of four fluorescent dyes (6-FAM, VIC, NED, and PET; 0.16  $\mu$ l), 1 – 5 ng/ $\mu$ l genomic DNA (2  $\mu$ l), and 0.5 units of HotStarTaq (Qiagen; 0.1  $\mu$ l). The cycling protocol was 95° C for 15 min, 30 cycles of 30 s at 95° C, 45 s at 56° C (i.e. annealing temperature), and 45 s at 72° C. This was followed by 8 cycles of 30 s at 95° C, 45 s at 53° C and 45 s at 72° C, and an elongation phase of 30 min at 72° C. For sizing, the final products were multiplexed into two aliquots: 1) 0.1  $\mu$ l Mystub\_3075c, 0.1  $\mu$ l Mystub\_1707c, 0.2  $\mu$ l Mystub\_334c, 0.1  $\mu$ l Mystub\_3324c, 0.2  $\mu$ l Mystub\_624c, 0.2  $\mu$ l Mystub\_5594c, and

0.1 µl distilled water; 2) 0.2 µl Mystub\_667c, 0.2 µl Mystub\_525c, 0.1 µl Mystub\_2982c, 0.1 µl Mystub\_2432c, 0.1 µl Mystub\_4251c, and 0.3 µl distilled water. Each of the aliquots were mixed with 10 µl HiDi formamide and 0.4 µl internal size standard (GeneScan 600 LIZ ladder, Applied Biosystems, Foster City, CA). Aliquots were then denatured at 95° C for 5 min and then kept at 4° C until ready for sizing. PCR products were sized on a GeneScan 3100 (Applied Biosystems) with Geneious v8.1 (Applied Biosystems) used to assign genotypes.

The descriptive statistics and the test for Hardy–Weinberg Equilibrium (HWE) and linkage disequilibrium were inferred using Genepop v4.2 (Rousset 2008). The number of alleles per locus ranged from 5 (Mystub\_3324c) to 20 (Mystub\_2982c), with an average of 13.27 (Table 1). The observed heterozygosity ( $H_o$ ) ranged between 0.62 (Mystub\_3075c) and 0.86 (Mystub\_4251c) with an average of 0.78, while the expected heterozygosity ( $H_E$ ) ranged from 0.7 (Mystub\_33245c) to 0.92 (Mystub\_5594c) with an average of 0.82. Four loci (Mystub\_334c, Mystub\_525c, Mystub\_3075c, and Mystub\_5594c) showed a significant deviation from HWE after Bonferroni correction. Linkage disequilibrium was detected between loci Mystub\_334c/Mystub\_624c, Mystub\_3707c/Mystub\_667c, Mystub\_334c/Mystub\_667c, Mystub\_624c/Mystub\_667c, Mystub\_334c/Mystub\_525c, Mystub\_5594c/Mystub\_2983c, Mystub\_3707c/Mystub\_2432c, Mystub\_3324c/Mystub\_2432c, and Mystub\_525c/Mystub\_2432c after sequential Bonferroni correction (Table 1). The presence of null alleles was tested using Micro-Checker v2.2 (van Oosterhout et al. 2004) and detected in loci Mystub\_334c, Mystub\_2982c, Mystub\_3075c, and Mystub\_5594c (Table 1).

**Table 1** – Characterisation of 11 microsatellite loci for *Mystacina tuberculata*, allelic size range, number of alleles, and observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity assessed in 333 individuals from the Pikiariki Ecological Area.

Locus		Primer sequences 5' – 3'	Repeat Type <sup>a</sup>	Size bp <sup>b</sup>	No. of alleles	$H_O$	$H_E$
Mystub_0334c*†	F	TCAAGAATGTCTGTGTGTGCC	(AC) <sub>15</sub>	78 – 102	19	0.8	0.91
	R	TATCCCTGAAGCCCCCTTTC					
Mystub_0525c*	F	GTGTGTACGGGAAAAGGCTC	(AC) <sub>12</sub>	201 – 220	14	0.82	0.85
	R	TCTCTGGTTTTAGGTGTGGAC					
Mystub_0624c	F	TCCTGCGTACTAGTGAGACTG	(TG) <sub>13</sub>	132 – 152	8	0.69	0.72
	R	TGATTCAAAGGCAGACAACCC					
Mystub_0667c	F	GTGCCTCTTGGAGAACAAGG	(TG) <sub>15</sub>	199 – 219	9	0.8	0.79
	R	TTGCAAAGGTTATAGGGAACAC					
Mystub_1707c	F	TGCACTGAAAGTAAACACAGC	(TC) <sub>17</sub>	157 – 187	13	0.8	0.82
	R	AGGACATTAGAGGCTGAAGGAG					
Mystub_2432c	F	CGAAGCTGAGAAAGCCAGTC	(AG) <sub>12</sub>	98 – 120	10	0.83	0.82
	R	TGGTAAAGCTGGAAGTAATGTCTC					
Mystub_2982c†	F	AAGCACCCTACCTGTTCCC	(GT) <sub>13</sub>	198 – 219	20	0.78	0.85
	R	CTGCGCTGAGTTCAAGCTG					
Mystub_3075c*†	F	ACTCCATATGTGGCAATTTATAATAGG	(AC) <sub>13</sub>	85 – 103	19	0.62	0.82
	R	TGAGCTAGACTGCCCTTTCC					
Mystub_3324c	F	AGGAGGCCTGTAGAATGTGG	(AC) <sub>12</sub>	115 – 125	5	0.73	0.7
	R	AGCATGTTTGTAAAAGAGCTGG					
Mystub_4251c	F	GATGGGGTGGCTTAAACAGC	(AC) <sub>15</sub>	196 – 230	13	0.86	0.85
	R	GAAGCAGATCTCTGTGCGTG					
Mystub_5594c*†	F	AAGTTGATGGAAACAAGGTCAG	(GT) <sub>12</sub>	192 – 228	16	0.8	0.92
	R	TGTGATGCAGTGCCTAAACC					

<sup>a</sup> Based on genomic DNA sequence analysed on an Illumina MiSeq platform

<sup>b</sup> Based on the fragment analysis of 333 individuals on a GeneScan 3100

\* Significant departure from Hardy-Weinberg Equilibrium after Bonferroni correction

† Significant evidence of null allele

#### 5.3.4 *Reproductive success analyses*

I used the software Colony v2.0 (Jones and Wang 2010) to evaluate paternal and sibling relationships, as well as estimate the amount of inbreeding within the population. Colony uses a maximum-likelihood method to allocate individuals into family groups, including fathers/offspring, full siblings, and half siblings. Sample from all years were pooled for runs. All adult males were included as potential fathers, and juvenile males caught in 2012 were also included as potential fathers for juveniles caught in 2014. Although it has been demonstrated that males in some bat species can breed in their first year (e.g. Cryan et al. 2012) this is likely an exception, and so I excluded juvenile males caught in 2012 as the potential fathers for juveniles caught in 2013. For my primary run in Colony, which used a full-likelihood method on a “very long” setting, males were set as polygamous while females were set as monogamous (females generally give birth to just a single pup per year; Carter and Riskin 2006), inbreeding was set as absent, allele frequencies were calculated, sibship scaling was not included, and sibling size prior was set as ‘weak’. A second run using the same settings but with inbreeding included was also carried out to attain an estimate of inbreeding for the population.

Given the low number of loci available for analyses I also used an alternative method to estimate male reproductive success in addition to number of offspring. Following the methods of Puechmaille et al. (2014) I used Coancestry to estimate the average relatedness (via the triadic likelihood estimator) of known singing males to all other genotyped individuals. The reasoning behind this method is that more-successful males will sire more offspring on average and have more relatives within the population, resulting in a higher average relatedness.

To determine factors that may influence male reproductive success I used simple linear regressions to examine the relationship between average relatedness and the following

predictor variables: forearm length (given the allometric scaling of song characteristics; Chapter 4), song rate (which does not scale with forearm; Chapter 4), song repertoire size (Chapter 4), and arrival time after sunset at the singing roost. The regression of forearm length included 20 individuals known to be singing males, however arrival after dusk only included 14 individuals (six males from timeshare roosts were excluded as they were never the first to arrive to the singing roost following sunset). Finally, song rate and repertoire size only included the 16 males for whom I had song recordings (Chapter 4). For males to which offspring could be assigned, I also performed a regression of forearm length vs. number of offspring.

Statistical analyses were performed in the program JMP v. 11.2 (SAS Institute Inc. 2012), and I report mean  $\pm$  SD. Variables in analyses were all assessed for normality (Shapiro-Wilk test,  $P > 0.05$ ), and non-parametric tests used where appropriate. All reported  $P$  values are two tailed.

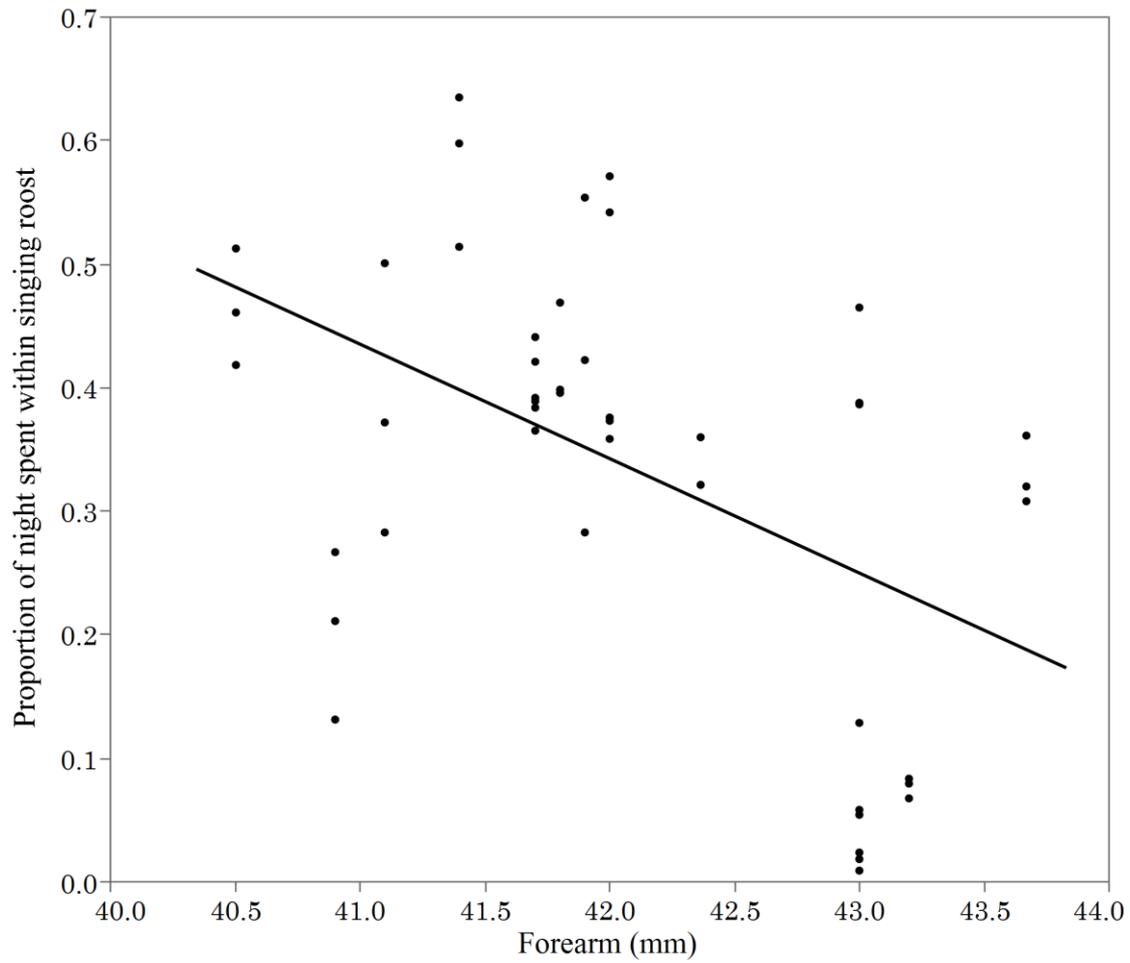
## **5.4 Results**

### *5.4.1 Video recording and male characteristics*

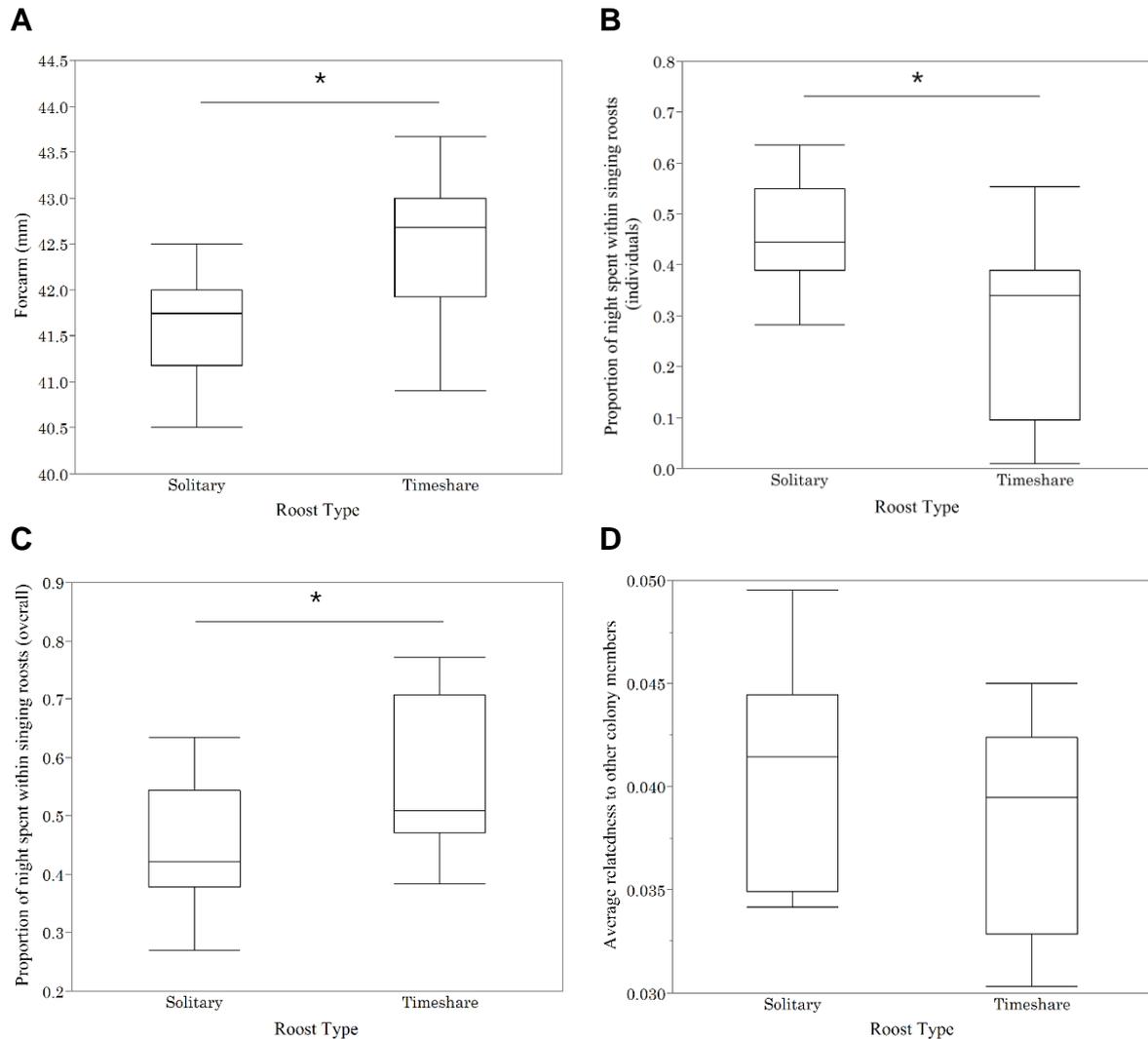
The 12 investigated singing roosts were populated by at least 22 resident males during the filming period: seven males in solitary roosts and at least 15 males in five timeshare roosts (12 tagged males and at least three untagged males). An additional solitary male was included in some analyses to boost sample sizes; this male was identified as a singing male during a pilot trial (see Toth et al. 2015b; Chapter 3), but was not included in the filming period for logistic reasons. Males arrived on average 43 minutes after sunset (range: 0 – 96 minutes,  $SD = 18.23$ ,  $n = 36$ ), but there was no relationship between male size and arrival time ( $b = 4.06$ , adjusted  $R^2 = -0.0021$ ,  $F_{1,36} = 0.93$ ,  $P = 0.34$ ). The proportion of the night males spent in roosts ranged between 0.0099 – 0.63 ( $0.34 \pm 0.17$ ,  $n = 46$ ), and smaller males spent a

significantly larger proportion of time within singing roosts than larger males ( $b = -0.093$ , adjusted  $R^2 = 0.23$ ,  $F_{1,46} = 14.16$ ,  $P = 0.0005$ ; Figure 1).

There was a clear statistical difference between males occupying solitary and timeshare roosts in terms of morphology and behaviour, but not in reproductive success. Males in solitary singing roosts were significantly smaller than males in timeshare roosts (solitary:  $41.50 \pm 0.55$  mm,  $n = 7$ ; timeshare:  $42.43 \pm 0.93$  mm,  $n = 12$ ;  $t$ -test:  $t = 3.21$ ,  $P = 0.0054$ ; Figure 2a), and individually spent a significantly larger proportion of the night in singing roosts than timeshare males (solitary:  $0.46 \pm 0.1$ ,  $n = 14$ ; timeshare:  $0.28 \pm 0.16$ ,  $n = 32$ ;  $t$ -test:  $t = -4.6$ ,  $P < 0.0001$ ; Figure 2b). However, timeshare roosts were occupied for a longer proportion of the night overall (solitary:  $0.45 \pm 0.11$ ,  $n = 17$ ; timeshare:  $0.56 \pm 0.12$ ,  $n = 18$ ;  $t$ -test:  $t = 2.87$ ,  $P = 0.0072$ ; Figure 2c). Males in solitary roosts arrived to their singing roosts earlier after sunset on average, although the relationship was not significant (solitary:  $37.0 \pm 18.3$  minutes,  $n = 17$ ; timeshare:  $48.7 \pm 16.7$  minutes,  $n = 18$ ;  $t$ -test:  $t = 1.98$ ,  $P = 0.057$ ). Average relatedness of males in singing roosts to others in the population did not differ significantly between the two groups (solitary:  $0.038 \pm 0.008$ ,  $n = 8$ ; timeshare:  $0.038 \pm 0.0039$ ,  $n = 12$ ;  $t$ -test:  $t = -0.27$ ,  $P = 0.61$ ; Figure 2d).



**Figure 1** – The proportion of night resident males spent within known singing roosts (expressed as a fraction of total night length) against forearm length. There was a significant negative relationship between the proportion of night spent within the singing roost and male size ( $n = 46$ ;  $b = -0.093$ , adjusted  $R^2 = 0.23$ ,  $F_{1,46} = 14.16$ ,  $P = 0.0005$ ).



**Figure 2** – Morphological, behavioural, and reproductive comparisons for resident male *M. tuberculata* in solitary singing roosts vs. those in timeshare singing roosts. **A**) Males in solitary singing roosts were significantly smaller than males in timeshare roosts (solitary:  $41.50 \pm 0.55$  mm,  $n = 7$ ; timeshare:  $42.43 \pm 0.93$  mm,  $n = 12$ ;  $t$ -test:  $t = 3.21$ ,  $P = 0.0054$ ); **B**) individual males in solitary singing roosts spent a significantly larger proportion of the night in their singing roosts than timeshare males (solitary:  $0.46 \pm 0.1$ ,  $n = 14$ ; timeshare:  $0.28 \pm 0.16$ ,  $n = 32$ ;  $t$ -test:  $t = -4.6$ ,  $P < 0.0001$ ); **C**) however, timeshare roosts were occupied for a larger proportion of the night than solitary singing roosts overall (solitary:  $0.45 \pm 0.11$ ,  $n = 17$ ; timeshare:  $0.56 \pm 0.12$ ,  $n = 18$ ;  $t$ -test:  $t = 2.87$ ,  $P = 0.0072$ ); and **D**) males in both roost types did not differ in their level of reproductive success, based on their average relatedness (triadic likelihood estimator values) to all other genotyped individuals (a higher average relatedness value means an individual has more relatives within the colony, indicating higher reproductive success; solitary:  $0.038 \pm 0.008$ ,  $n = 8$ ; timeshare:  $0.038 \pm 0.0039$ ,  $n = 12$ ;  $t$ -test:  $t = -0.27$ ,  $P = 0.61$ ).

No consistent pattern in relatedness existed for males sharing singing roosts ( $0.078 \pm 0.13$ , range: 0 – 0.32, Table 2). Based on the range and amount of overlap of relatedness scores, it is not possible to predict the relationship between timeshare males with accuracy. In one roost all three individuals were unrelated, in two others some individuals were unrelated while others were distantly related, and in the fourth all individuals were somewhat closely related to one another (Table 2). Interestingly, one individual moved between two singing roosts during the filming period, but was only distantly related to one individual in one of those roosts, and unrelated to all others. To further infer the relationship between timeshare individuals I used Coancestry to calculate the triadic likelihood estimator values for known familial connections (i.e. full siblings, half siblings, and father/offspring) generated by Colony. Fifteen dyads with probability ratings of  $> 0.75$  were used for full siblings, 85 dyads with probability scores of 1.0 were used for half siblings, and all 24 father/offspring dyads were used (see below). However, relatedness values varied widely and overlapped by a wide margin for known relationships: full siblings possessed triadic likelihood scores between 0.26 – 0.66 ( $0.39 \pm 0.11$ ), half siblings possessed scores between 0.017 – 0.52 ( $0.2 \pm 0.11$ ), and father/offspring dyads possessed scores between 0.5 – 0.85 ( $0.53 \pm 0.081$ ).

#### 5.4.2 Reproductive success analyses

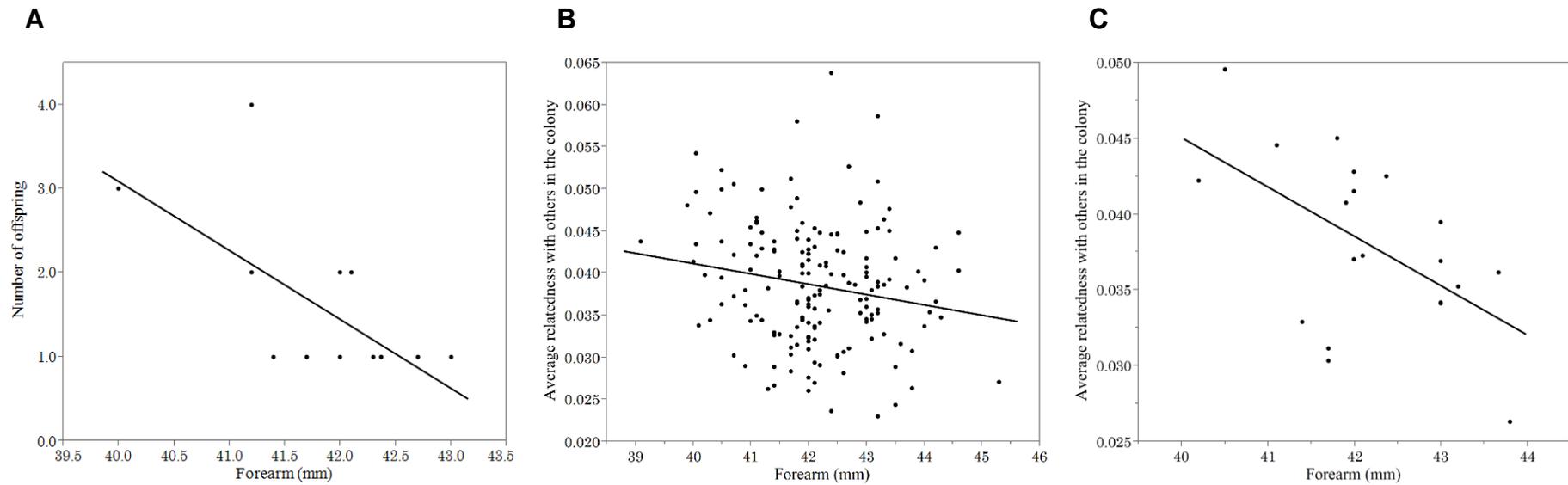
There was a moderate skew in reproductive success for males. Paternity could be assigned for just 24 juveniles (two from 2012, seven from 2013, and 15 from 2014) to 15 males ( $1.6 \pm 0.91$  offspring/male, range: 1 – 4), four of which were known to be singing males. None of the males were juveniles first caught in 2012. Among those 15 males, there was a significant negative relationship between number of offspring and forearm length (Spearman rank correlation:  $\rho = -0.64$ ,  $P = 0.0072$ ; Figure 3a). However, there was no significant difference in forearm length between males that fathered offspring and those that did not (paternity

**Table 2** – Relatedness estimates (using triadic likelihood estimators) of male dyads within four timeshare singing roosts. Zero represents completely-unrelated individuals while 1 represents clones. Timeshare roosts were composed of unrelated individuals (singing roost 12), a mix of unrelated and distantly-related individuals (singing roosts 36 and 48), and relatively closely-related individuals (singing roost 58). Males are identified by their PIT-tag numbers.

<b>Male Dyads</b>		<b>Relatedness Score</b>
<b>Singing Roost 12</b>		
356799541	356559297	0
167879784	356559297	0
167879784	356799541	0
<b>Singing Roost 36</b>		
356549813	167788152	0.03
356549813	356551179	0.0077
356551179	167788152	0
<b>Singing Roost 48</b>		
190977468	356743055	0.026
356551179	190977468	0
356551179	356743055	0
<b>Singing Roost 58</b>		
356766438	356563881	0.23
356766438	356565178	0.32
356565178	356563881	0.32

assigned:  $41.8 \pm 0.73$  mm, range: 40.0 – 43.0 mm,  $n = 15$ ; no paternity assigned:  $42.2 \pm 1.08$  mm, range: 39.1 – 45.3,  $n = 160$ ; Wilcoxon rank-sum:  $W = 1478$ ,  $P = 0.25$ ). Maximum-likelihood configuration estimates indicated that in addition to the 15 known males, there were 186 inferred parents for the 178 juveniles (the sex of the parents could not be inferred by the software). The average inbreeding coefficient for the genotyped individuals was 0.066.

There was a significant, negative relationship between forearm length and average relatedness in all adult males ( $b = -0.0012$ , adjusted  $R^2 = 0.034$ ,  $F_{1,175} = 6.09$ ,  $P = 0.015$ ; Figure 3b), although the predictive ability of the model was low. However, when limited to known singing males the relationship was much stronger ( $b = -0.0032$ , adjusted  $R^2 = 0.27$ ,  $F_{1,20} = 7.92$ ,  $P = 0.012$ ; Figure 3c). However there was no relationship between average relatedness and arrival after sunset at singing roosts ( $b = -1.54 \times 10^{-5}$ , adjusted  $R^2 = -0.81$ ,  $F_{1,14} = 0.026$ ,  $P = 0.88$ ), repertoire size ( $b = -0.00044$ , adjusted  $R^2 = 0.011$ ,  $F_{1,16} = 1.17$ ,  $P = 0.30$ ), or song rate ( $b = -7.64 \times 10^{-6}$ , adjusted  $R^2 = -0.052$ ,  $F_{1,16} = 0.26$ ,  $P = 0.62$ ).



**Figure 3** – Morphological predictors of reproductive success (estimated by number of offspring and average relatedness to all other colony members, a proxy for reproductive success) for male *Mystacina tuberculata*. A) Number of offspring against forearm length for males with known paternity ( $n = 15$ ; Spearman rank correlation:  $\rho = -0.64$ ,  $P = 0.0072$ ); B) average relatedness (triadic likelihood estimator values) of all genotyped adult males to all other genotyped individuals against forearm length ( $n = 175$ ;  $b = -0.0012$ , adjusted  $R^2 = 0.034$ ,  $F_{1,175} = 6.09$ ,  $P = 0.015$ ); and C) average relatedness of known singing males to all other genotyped individuals within the colony against forearm length, ( $n = 20$ ;  $b = -0.0032$ , adjusted  $R^2 = 0.27$ ,  $F_{1,20} = 7.92$ ,  $P = 0.012$ ).

Thirty four full-sibling dyads were identified by Colony, although only 17 had a probability rating of  $> 0.5$ . Of those 17 dyads, 10 featured juveniles from different years; five from 2012/2014 and five from 2013/2014. Two hundred and seventy half-sibling dyads were also inferred, 166 of which had a probability of  $> 0.5$ . Of those 166 dyads, 89 were multiyear; 22 from 2012/2014, 10 from 2012/2013, and 57 from 2013/2014.

## 5.5 Discussion

Male reproductive success scales negatively with body size in male *M. tuberculata*. Smaller males not only sired more offspring than larger males during the years of my study, but also had more relatives within the colony, indicating a higher long-term success. I found that smaller males spent a longer proportion of the night within their singing roosts than larger males which suggests – along with previous findings of higher song outputs in smaller males (Chapter 4) – that the amount a male signals is attractive to females.

My results are the first to quantify male reproductive success with respect to male displays in a lek-breeding bat. Although Bradbury (1977) was able to demonstrate a skew in the number of copulations attained by male *H. monstrosus* at calling sites, he was unable to attribute particular qualities to their success, or quantify the reproductive success achieved by individuals. In *M. tuberculata*, smaller males have significantly higher song outputs than larger males (Chapter 4), and spend a significantly larger proportion of the night in the singing roost (this chapter). Given that smaller males also fathered more offspring and had higher average relatedness than large males, it suggests that females find one or more of the preceding traits attractive. Selection for small males appears to be relatively rare in lekking species, as large males are often able to outcompete smaller males for territories and access to females. For example, in Uganda kob (*Kobus kob thomasi*), larger males hold the most-popular territories and have higher reproductive success than smaller males (Balmford et al.

1992). Similarly, in a population of American bullfrogs (*Lithobates catesbeianus*) from central Michigan, larger (and therefore older) males occupied preferred territories near the centre of the male aggregation, while smaller males were forced to the periphery (Emlen 1976). Furthermore, larger males arrived to breeding ponds earlier than smaller males, were more successful at establishing territories, were more efficient at moving between choruses, and were active for a longer proportion of the breeding period (Emlen 1976).

Increased reproductive success for smaller males has been demonstrated in bats previously. In *Saccopteryx bilineata*, individual males defend harems of females to whom they perform aerial wing-flapping displays. Voigt et al. (2005) performed parentage analyses on 209 juveniles from a population of *S. bilineata* in Costa Rica and found that small males sired more offspring than large males, both within harems and within the colony as a whole. The authors reasoned that smaller males, possessing higher manoeuvrability and suffering reduced energetic costs from flying, had a competitive advantage over large males with respect to harem defence and aerial courtship displays (Voigt et al. 2005). Similar results have also been found in raptors (Hakkarainen and Korpimäki 1991; Hakkarainen et al. 1996; Massemin et al. 2000). Likewise, my results suggest that smaller males possess greater energy reserves than larger males. Singing has been shown to be an energetically-expensive signal (Gil and Gahr 2002), and thus the higher song outputs and longer roost occupancy of smaller males suggests they are able to expend more energy on these activities. Furthermore, males in solitary singing roosts were significantly smaller than those in timeshares (discussed below). Studies of other lekking species has shown that possessing a lek territory results in increased fights (Gosling et al. 1987; Apollonio et al. 1992) and reduced foraging opportunities (Nefdt and Thirgood 1997). Thus it is possible that smaller males may be able to better mitigate the energetic costs of solitary ownership of a singing roost.

Smaller male *M. tuberculata* may be better suited to save energy in three (not mutually exclusive) ways. First, the act of singing may itself be more expensive for larger males. For example, in two chorusing frog species – *Litoria chloris* and *L. xanthomera* – smaller males were found to be more successful than larger males, which was attributed to smaller males calling for longer than larger males (Morrison et al. 2001). It is unknown at this time if the spectral properties of male songs could account for the observed differences in song output between males. A second possibility is that a smaller body size translates into a greater flying- and foraging efficiency (e.g. Hakkarainen and Korpimäki 1991). For example, in kestrels (*Falco tinunculus*), smaller males expend less energy during hunting and have greater hunting success than large males (they are more manoeuvrable and better at catching agile prey; Hakkarainen et al. 1996), and females paired with smaller males produce larger clutches and more fledglings than those paired with larger males (Massemin et al. 2000). The wing morphology of *M. tuberculata* suggests the species has evolved a high manoeuvrability, likely for traversing and foraging within cluttered forest habitats and taking flight from the ground (Jones et al. 2003). Manoeuvrability is inversely related to body size in bats (Norberg and Rayner 1987, but see Barclay and Brigham 1991), and the energetic costs of flight is higher in large individuals (e.g. Voigt 2000; Stockwell 2001). Thus, by saving energy while flying and foraging, smaller males are able to expend more on courtship. Lastly, larger males may suffer from a greater number of parasites, thereby reducing their overall condition. Reduced efficacy of male sexual signals has been linked to a parasite load in a number of species (e.g. Hamilton and Zuk 1982; McGraw and Hill 2000; MacDougall-Shackleton et al. 2002). For example, mite load is correlated with a lower song output in barn swallows (*Hirundo rustica*), likely as a result of anaemia caused by the parasites (Møller 1991). *Mystacina tuberculata* hosts a variety of ectoparasites (see Carter and Riskin 2006), as well as internal parasites (Duignan et al. 2003). However, a link between body size and parasite

load has yet to be demonstrated. Unfortunately, without further study it is unknown if any of the above possibilities account for the variations between singing males.

While I found evidence for a moderate skew in mating success (an estimated 15 males fathering 24 juveniles), there was not the pronounced skew typical of some lekking species (see Bradbury et al. 1985; Wiley 1991). There are two possible explanations for this. Firstly, reproductive skew appears to be inversely related to lek size (e.g. Alatalo et al. 1992); as the number of males that females need to compare increases, it likely becomes progressively more difficult for females to select between them (Höglund and Alatalo 1995; Johnstone and Earn 1999). In the Pikiariki Ecological Area there may be over 100 singing males in any given year (Toth et al. 2015b; Chapter 3), and thus comparison between males is likely difficult for females, resulting in a relaxed skew. Secondly, given the length of the breeding season (females mate during the spring or summer, but do not give birth until the following year; Carter and Riskin 2006) it is unlikely that many males can completely secure their reproductive success over such a long period of time, particularly when alternative tactics such as sneaking (Toth et al. 2015b; Chapter 3) are present. The lack of unanimity in female choice may also account for the relatively low level of inbreeding that was estimated, despite the population inhabiting a relatively isolated forest (Toth et al. 2015a; Chapter 2).

Inbreeding avoidance may be further aided by the use of scent marking by singing males (Toth et al. 2015b; Chapter 3), as urine can carry detailed information about individuals, including relatedness (Hurst et al. 2001; Sherborne et al. 2007; Hurst 2009).

It should be noted that the relationship between average relatedness and male size, while significant, was quite weak when considering all 175 genotyped adult males. This is likely because the model included not only singing males, but also males that are in their first year of adulthood and have not had a chance to breed yet, as well as males that pursue alternative strategies such as sneaking. When considering only males known to employ

singing as a method of courtship, the relationship between average relatedness and size became much stronger, highlighting the importance between male size and female selection. Furthermore, it should be noted that while average relatedness to other colony members is a useful proxy for long-term reproductive success, the same relationship between body size and average relatedness would ideally be tested in adult females in addition to adult males (see Puechmaille et al. 2014). As females can only have one pup per year (Carter and Riskin 2006), a much weaker relationship (if any) between average relatedness and forearm length would be expected, and provide stronger evidence that the observed relationship is indeed due to female selection and not some other process. Unfortunately I was unable to test this relationship in this study due to time constraints.

There were several important morphological and behavioural differences between males that occupied solitary singing roosts and those that occupied timeshare singing roosts. Males in solitary singing roosts were significantly smaller than those in timeshare roosts and individually spent a larger proportion of the night within their respective singing roosts. However, timeshare roosts were occupied for a larger proportion of the night overall than solitary singing roosts, and the two groups did not differ in reproductive success (as estimated by average relatedness to colony members). As suggested above, the size difference between the two groups may indicate a competitive advantage possessed by smaller males, allowing them to claim sole ownership of a singing roost. Timesharing may therefore represent an alternative strategy used by larger males that would otherwise be unable to defend a roost on their own, and/or unable to sustain singing for as long as smaller males. Furthermore, as the two groups did not differ in estimated reproductive success it suggests that timesharing may also allow larger males to recover matings (and may also explain why there is no sexual size dimorphism in this population; C.A. Toth, unpublished data). How timesharing allows males to recoup reproductive success is unknown. It is possible that passing females are more likely

to hear the songs of timeshare males, as timeshare roosts were occupied for a larger proportion of the night. Although the songs of individual males may be less likely to be heard, the roost members – as a whole – may encounter more females.

Interestingly, I found no apparent pattern in the relatedness of timeshare males; one roost consisted of completely unrelated individuals, two roosts were a mix of unrelated and distantly-related individuals, and another consisted of relatively closely-related individuals (although how closely related the individuals were could not be inferred with much accuracy). This is further complicated by the fact that one timeshare male was a resident of two separate roosts during the course of my study. Thus, timeshare roosts do not necessarily represent a pure kin-selection strategy. Instead, timeshare males may be pursuing a strategy similar to those of lekking long-tailed manakins (*Chiroxiphia linear*), wherein multiple unrelated males produce cooperative dances and song duets to attract females (McDonald 1989). In the manakin system, up to 13 males form multiyear partnerships in which an alpha and beta pair provide the bulk of displays, although the alpha male attains approximately 99% of the matings. Furthermore, males within partnerships are not related, and thus gain no kinship benefits from the alpha male's success (McDonald and Potts 1994). Instead, beta males are able to inherit the alpha status when their partnered alpha dies, as well as the alpha's previous mates (females display high fidelity to male territories between years; McDonald and Potts 1994). While the *M. tuberculata* system differs in the fact that males in timeshare roosts do not combine displays (other than producing a higher total song output), a system of inheritance may be used by resident males, perhaps with more "senior" males occupying more-desirable time slots during the night (e.g. right after sunset, when females are travelling from the communal roost to their foraging areas).

The results of this study are somewhat limited by the small number of loci available for analyses. For example, as discussed above, I was unable to infer the familial relationship

(e.g. cousins, half siblings, etc.) between timeshare males with any accuracy. When considering known fathers and offspring, full siblings, and half siblings, the relatedness values ranged widely and overlapped by a large margin. Similarly, the large number of half siblings inferred by Colony may be indicative of the low number of loci used, and the fact that not all loci were independent (i.e. significant evidence of linkage disequilibrium between some pairs). Ideally, future studies will build on the findings of this study by using a larger number of loci with greater variability.

Although my study has been able to identify male traits that female *M. tuberculata* likely find attractive, several new questions have emerged from this system that would benefit from future studies. For example, lengthier observations of roost memberships, in conjunction with male-removal experiments, would be useful in determining how timeshare roosts operate (e.g. whether or not an inheritance system is in place). Furthermore, such observations may also provide information on whether dominance hierarchies exist within timeshare roosts and how they are manifested (e.g. Hartzler 1970). Playback experiments would also be valuable, both to determine what song traits females find attractive (e.g. by manipulating the frequency characteristics and output of songs) and the function of individual song types produced by males (e.g. Bohn et al. 2013). Finally, the use of PIT-tags for identification will facilitate long-term assessments of male reproductive success in this species, as it is not clear what function male age plays in female mate choice. Age has been shown to be positively correlated with male reproductive success in other long-lived mammalian species (e.g. Willis et al. 2012; Ward et al. 2014). Bats are the longest-lived mammals (corrected for body size; Austad and Fischer 1991), and thus it might be expected that older males have an advantage over younger males in *M. tuberculata*. With further work, *M. tuberculata* has the potential to become one of the most prominent species for studying sexual selection in bats.

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# 6

## **Summary, management implications, and conclusions**

## 6.1 Summary

In this thesis I have provided an overview of the mating behaviour of the lesser short-tailed bat (*Mystacina tuberculata*). *Mystacina tuberculata* in the Pikiariki Ecological Area breeds using leks: males occupy clustered singing roosts during the breeding season that females visit for mating purposes. The females receive no resources from the males they mate with, and do not use the singing roosts as day roosts. Prior to this study there were little-to-no details on the breeding behaviour of *M. tuberculata* and I have contributed significantly to our understanding of its ecology and behaviour. *Mystacina tuberculata* has been confirmed as only the second lek-breeding bat in the world (and one of the few vertebrates to display resource-based lek breeding), have one of the highest recorded song outputs of any animal yet described, and display a courtship behaviour that is potentially unique to both lek-breeding species and bat species as a whole (timesharing).

### 6.1.1 Determinants of lek breeding in *Mystacina tuberculata* (Chapters 2 – 3)

The home ranges and roosting behaviour of females provides some indication as to why lek breeding has been adopted by males. My radiotelemetry studies show that females in Pikiariki have large (> 500 ha) home ranges and change roosts frequently – moving between several communal roosts, as well as spending a high proportion of days tracked (> 50% in some cases) in solitary roosts. These characteristics likely make it either impossible or uneconomical for males to form harems (Clutton-Brock 1989; McCracken and Wilkinson 2000), and resources defence is likely not feasible due the ephemeral nature of their food sources (e.g. Cummings et al. 2014).

Spatial regression analyses indicate that singing roosts are aggregated around the large communal roosts used by the population. While individual females may change roosts often, the areas surrounding communal roosts likely have the highest consistent densities of

females anywhere within the population's home range. Thus, males appear to be aggregating in areas where females are known to occur in high numbers to maximise female encounter rates. This behaviour represents a type of lek breeding known as "resource-based leks", which appears to be rare in vertebrates (see Toth et al. 2015b; Chapter 3). Furthermore, large female home ranges and high-density communal roosts are characteristics shared by many temperate bat species (Barclay and Harder 2003; Kunz and Lumsden 2003), and so it is unlikely that the unique evolutionary history of *M. tuberculata* is responsible for the adoption of lek breeding. Instead, it is plausible that many temperate bat species display resource-based lekking behaviour, but they have not been identified or confirmed due to the general lack of knowledge of bat mating systems as a whole (McCracken and Wilkinson 2000).

#### *6.1.2 Male singing behaviour (Chapter 3 – 4)*

Through the use of video cameras and automatic PIT-tag readers I was able to observe several male reproductive strategies. In addition to solitary males in singing roosts, almost half of the observed singing roosts were shared between multiple (2 – 5) males that apparently worked in shifts. I have referred to these roosts as "timeshares". Additionally, several "sneaker" males were detected at singing roosts. Sneakers were observed trying to disrupt copulations between resident singing males and females, although none were successful.

Male songs and singing behaviour are complex signals that carry honest information about the singer's quality. Songs are composed of four basic elements (trills, tones, upsweeps, and downsweeps) that are produced either singly, or combined to form composite song types. Although males possess large song type repertoires (up to 35 song types per male), singing bouts were largely dominated by four main song types: trills, upswing-trills, downswing-trills, and upswing-trill-downsweeps. Males have high song outputs – producing

thousands of individual songs within the span of a few minutes. It is possible that *M. tuberculata* has the highest song output of any animal yet described (see Kroodsma 2005 for a comparison to songbirds). Song output also scales with body size: smaller males have longer song durations (for trill-downsweeps), have higher duty cycles, and spend a larger proportion of the night within their singing roosts (likely translating into a longer time spent singing) than larger males. Interestingly, timeshare males were significantly larger than males in solitary singing roosts, and individually spent a smaller proportion of the night within their singing roosts.

### *6.1.3 Male strategies and female mate choice (Chapter 5)*

I found evidence of a moderate skew in reproductive success, with 15 males fathering 24 offspring. This relaxed skew (compared to other lekking species; Bradbury et al. 1985) may be a result of the large number of males displaying within the aggregation, making it difficult for females to choose between them (Höglund and Alatalo 1995). Among the males that fathered offspring, females appear to prefer smaller males as mates. I found that smaller males sired more offspring than larger males, and also had more relatives within the colony, indicating a higher long-term reproductive success. Thus it is possible that females find the higher song outputs of small males attractive. Smaller males may possess greater energy reserves than larger males, possibly by expending less energy during flight (e.g. Hakkarainen and Korpimäki 1991; Hakkarainen et al. 1996) and singing (potentially due to the frequency characteristics of their songs; e.g. Morrison et al. 2001). These greater energy reserves may allow small males to invest more energy into courtship.

I found that timeshare males were larger than solitary males, but their average relatedness was not significantly different from solitary males. This suggests that: 1) solitary males may be better able to defend solitary singing roosts (given their higher energy

reserves), and 2) timeshare males use roost sharing as an alternative reproductive strategy to boost mating success. Timeshare males may be able to recoup reproductive success because timeshare roosts were occupied for a significantly larger proportion of the night than solitary roosts, indicating a higher overall song output. Thus, females may be more likely to hear the songs from timeshare roosts, although less likely to hear individual males.

Interestingly, there was no pattern of relatedness between timeshare males. This suggests that timeshare males do not gain kinship benefits. Instead, there may be some hierarchical organisation that includes an inheritance system at work (perhaps for ideal singing times within the roost; see McDonald and Potts 1994). This behaviour requires further study.

#### 6.1.4 *Mystacina tuberculata* as a model species

The breeding behaviour of bats is chronically understudied (McCracken and Wilkinson 2000; Altringham and Senior 2005; Altringham 2011), despite there being over 1,100 known species with a large diversity of forms (Simmons 2005). As I have outlined throughout this thesis, this lack of information is largely due to the difficulty in studying bats, particularly with regards to known individuals in a courtship setting. However, I believe this thesis has demonstrated that *M. tuberculata* may be a model species to study sexual selection in a bat, much as several lekking grouse (e.g. Alatalo et al. 1992; Alatalo et al. 1996) and cervid species (e.g. Pemberton and Balmford 1987; Carranza et al. 1995) have served as model organisms for birds and ungulates, respectively. Firstly, the species is non-migratory, and several populations (such as Pikiariki) are easily accessible. Consequently, populations can be monitored throughout the year in relative comfort (in comparison to some tropical species; e.g. Bradbury 1977). Secondly, *M. tuberculata* can be caught in large numbers at predictable locations (i.e. communal roosts), permitting the easy collection of tissue samples and

morphometrics. Thirdly, individuals can be marked with PIT-tags, allowing for passive, long-term identification at communal roosts and singing roosts. And finally, male singing roosts are easily identifiable, largely persistent across years, and can be monitored remotely. This is in contrast to species such as *Pipistrellus* spp. that produce songflights that can last for hours and cover large areas (e.g. Sachteleben and von Helversen 2006; Jahelková and Horáček 2011), or swarming species where it is difficult to observe courtship behaviours (e.g. Thomas et al. 1979).

There are some limitations to studying *M. tuberculata* breeding behaviour. For one, the breeding season of the species is long, with males beginning to sing in September or November and continuing into May (Carter and Riskin 2006). Any feasible methods for observing male courtship behaviour are therefore going to be snapshots of a much longer season (although courtship appears to peak in February; Toth et al. 2015b; Chapter 3). Likewise, given the large number of singing roosts active in any given year it is likely not possible to: 1) monitor all singing roosts, but rather a small subset of them; and 2) capture and PIT-tag all singing males (although with a long enough study this may become feasible). Moreover, females mate sometime in summer but do not give birth until the following year by delaying either fertilisation, implantation, or development (Lloyd 2001). This potentially provides males with alternative reproductive tactics ample opportunity to regain reproductive success, thereby obscuring trends that would otherwise be apparent from female selection of lekking males (although this is not necessarily uncommon in lekking species; e.g. Apollonio et al. 1992; Alatalo et al. 1996; Lanctot et al. 1997; Semple et al. 2001; Hingrat et al. 2008).

#### 6.1.5 Future directions

While this thesis has provided a useful overview of the *M. tuberculata* mating system as a whole, it has also raised several additional questions that would benefit from future studies.

Many of these questions are discussed within the preceding chapters, but I will highlight three of the more important/interesting ones here.

As mentioned above, beyond a basic description of timeshare male characteristics and singing behaviour, none of the mechanisms of how timeshare roosts form or operate are known. Timesharing will likely require a long-term study with experimental characteristics (e.g. male-removal experiments) to provide a thorough description of the strategy. However, timesharing is potentially a unique strategy among both lek-breeding species and bat species as a whole, and thus future studies into this system would be of great interest to a wide range of researchers.

While I was not able to identify any patterns in the way singing roosts were oriented (e.g. towards the closest communal roost; Toth et al. 2015b; Chapter 3), it is unknown what – if any – selection criteria are used by males when establishing singing roosts. Although singing roosts may serve little function beyond protection from predators such as morepork (*Ninox novaeseelandiae*), a detailed survey of singing roost characteristics, including the acoustic properties of known singing roosts vs. unused cavities, as well as a survey of unused cavities both within- and outside of the main aggregation could identify characteristics preferred by males (for similar studies on day roosts, see Sedgeley and O'Donnell 1999; Sedgeley 2001, 2003, 2006). Such work could be important for future population translocations (discussed below), as it would allow potential translocation sites to be surveyed for suitable singing roosts.

While I was able to provide an overview of the singing behaviour of *M. tuberculata*, it was, by necessity, very basic in extent. Male songs are structurally complex and future studies describing not only the composition and diversity of male song repertoires (e.g. song type sharing between neighbours/roost mates; Beecher et al. 2000), but also the pattern of song types produced in singing bouts (e.g. Bohn et al. 2009; Bohn et al. 2013), would be of

interest. Furthermore, investigations into whether or not male songs qualify as something akin to language (e.g. Jansen et al. 2012) could highlight the complexity of bat social calls, particularly in a field usually dominated by a limited number of taxa, such as songbirds and primates (e.g. Kondo and Watanabe 2009).

## **6.2 Management Implications**

*Mystacina tuberculata* faces several threats to survival, including habitat loss (Dwyer 1962; although this is likely not a contemporary threat; O'Donnell et al. 2010), predation from introduced pests (Dwyer 1962; Lloyd 2001; O'Donnell et al. 2010; Scrimgeour et al. 2012; O'Donnell et al. 2013), and competition with introduced pests for food sources (Daniel 1976; O'Donnell et al. 2010; O'Donnell et al. 2013). As such, the species is of conservation concern, and is listed as Nationally Endangered and Declining across its range (O'Donnell et al. 2013). However, information on breeding behaviour can provide pertinent cues for the development of effective management strategies, particularly with respect to lek-breeding species (e.g. Jiguet et al. 2000; Storch 2007). Therefore I will use the results of my thesis to suggest some strategies that may be useful for future conservation efforts for *M. tuberculata*. Each of these recommendations is particularly well suited for future translocation efforts to reintroduce the species to forests and offshore islands within its historic home range (e.g. Ruffell and Parsons 2009), and so they are framed in that context.

Although the selection of specific roost characteristics has been demonstrated for *M. tuberculata* previously (e.g. Sedgeley 2003; 2006), my work in Chapter 2 (Toth et al. 2015a) further reinforces the requirement of old growth native forest as suitable roosting habitat. While I found that *M. tuberculata* in Pikiariki could tolerate some level of habitat fragmentation by adopting both open space and exotic plantations into their home ranges, all roosting sites (communal, solitary, and singing) were only found in native forest (Toth et al.

2015a; Chapter 2). Future translocation efforts should therefore not only assess the number of potential communal and solitary roosts at proposed release sites (e.g. Ruffell et al. 2007), but also for potential singing roosts. As discussed above, future research should identify characteristics (e.g. thermal, acoustic) preferred by males for singing roosts to ensure available cavities provide males with appropriate courtship spaces.

Male singing presents a potentially challenging obstacle for successful mating in future translocations. My results in Chapter 4 demonstrate the complexity of male songs, both in terms of repertoire size and frequency range. The songs of *M. tuberculata* are thus comparable to those of songbirds in many respects (Marler and Slabbekoorn 2004). In many species of birds and mammals that produce complex vocalisations it has been shown that young individuals need to hear the songs of tutors (i.e. adults) to learn new song types and ensure their songs have ‘correct’ frequency characteristics (Janik and Slater 1997; Gil and Gahr 2002; Marler and Slabbekoorn 2004). Evidence also indicates that young female songbirds use the songs of adult males to develop future mate choice preferences (e.g. Riebel 2000). Furthermore, there is evidence that similar mechanisms also occur in bat species that produce complex songs (Knornschild et al. 2010). Future translocation efforts for *M. tuberculata* will likely use juveniles born in captivity to minimise the chance of homing once introduced to their new location (see Ruffell and Parsons 2009). Therefore, these juveniles will likely require the songs of adult males recorded from their source population (to ensure incorrect song dialect does not create barriers to reproduction; Baker and Mewaldt 1978; Slabbekoorn and Smith 2002) to be played for them during maturation. This will ensure normal song development in males, as well as the development of useful song-trait preferences in females. Furthermore, when translocated males begin singing I suggest that their songs be compared to those of non-translocated males to ensure that founder effects (due to the relatively small number of individuals translocated) have not affected the

frequency and temporal characteristics of their songs, as well as their repertoires (e.g. Baker and Jenkins 1987).

Translocated populations may eventually be at risk from inbreeding depression due to lek breeding. Lek breeding is likely promoted in *M. tuberculata* by the high female densities created by communal roosting (Toth et al. 2015b; Chapter 3). Thus, as translocated populations will initially have a low number of individuals, it is unlikely that they will use a lek mating system (male territories may be used instead; Clutton-Brock 1989). However, as these populations grow over time, they will likely shift back to using leks. Male reproductive skew in these new leks may be much more pronounced than what was observed in Pikiariki (Chapter 5), as females will be better able to compare the traits of multiple males. This produces the possibility of a small number of attractive males fathering the majority of offspring over several generations (given that bats are long lived and reproduce relatively slowly; Austad and Fischer 1991). Ordinarily this may be mitigated via gene flow from neighbouring populations (e.g. McDonald 2003), however long-distance dispersal has not been documented in *M. tuberculata* (Lloyd 2003) and is unlikely to occur given translocations will likely be to offshore islands (Ruffell and Parsons 2009). Although the scent-marking behaviour of males may aid in inbreeding avoidance (Chapter 5), I suggest that all pups born in translocated populations be tested for paternity. This will determine if additional individuals need to be released into the population to simulate gene flow that would otherwise occur naturally.

### **6.3 Concluding Remarks**

In this thesis I have highlighted the complex mating behaviours demonstrated by *M. tuberculata*, as well as the species' usefulness as a model to study sexual selection in Chiroptera. Through the combination of passive marking, radiotelemetry, spatial analyses,

remote monitoring, acoustic analyses, and genetic analyses I have been able to describe multiple unique behaviours and characteristics. Some of these findings will be of use to future conservation efforts for the species. It is my hope that my work will be used as a springboard for further research elucidating many of the behaviours described in this thesis, as well as serve as motivation for new studies investigating the breeding behaviour – lekking or otherwise – of bats.

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## Is lek breeding rare in bats?

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## A.1 Abstract

Bats (Mammalia: Chiroptera) display a degree of niche variation that is unparalleled among mammals. One mating system that is underrepresented in the Chiroptera is lek breeding, which is characterised by aggregations of sexually-displaying males that are visited by receptive females who appraise male displays and actively choose mates, yet receive no direct benefits such as assistance in parenting. Leks are thought to form when males can defend neither resources nor females, making it more economical to establish small breeding territories and self-advertise through sexual displays. Lekking is rare in mammals, and it has been suggested that a lack in the mobility required by females to economically seek out aggregations of sexually-displaying males may explain this rarity. Bats, like birds, do not suffer reduced mobility and yet out of over a thousand described species, only one has been confirmed to breed in leks. We examine the rarity of lekking in bats by providing an overview on the current state of knowledge of their mating systems and discuss the ecological and social determinants for the observed trends, contrasted with the prerequisites of lek-breeding behaviour. We use the breeding behaviour of New Zealand's lesser short-tailed bat (*Mystacina tuberculata*), which is believed to be a lek breeder, as a case study for the examination of potential lekking behaviour in bats, and highlight the importance of such research for the development of effective conservation strategies.

## A.2 Introduction

Lek breeding has been referred to as one of the most bizarre mating systems (Wiley, 1991), with males aggregating and establishing resource-free territories (“leks”) and producing sexual displays for visiting females. Females visit leks solely to appraise male displays and select mates, receiving no direct benefits in the process. For these reasons lekking species have long been used by evolutionary biologists for studying sexual selection in free-living animals, as mate choice can be investigated independently from the influence of resources and the clustering of males ensures that multiple males can be assessed by females (Höglund & Alatalo, 1995; Morales, Jiguet & Arroyo, 2001). Female selection is typified by an often extreme skew in male reproductive success, with a small proportion of males receiving the majority of copulations (e.g. Bradbury & Gibson, 1983; Bradbury, Vehrencamp & Gibson, 1985; Alatalo *et al.*, 1992; but see Höglund & Alatalo, 1995; Johnstone & Earn, 1999).

Lekking is generally defined by four characteristics: 1) males aggregate to display within a specific area of their habitat, 2) females gain no direct benefits from males when mating (if females gain benefits from mate choice, they can only be indirect genetic benefits), 3) males provide no parental care to offspring, and 4) females are free to select the males they mate with (Bradbury, 1977a, 1981). Leks may be further split into two broad categories: “classic” leks involve males clustered within sight of one another, typically within a particular part of the suitable display habitat (Bradbury, 1981); or “exploded” leks wherein males are separated by large distances and aggregations may only be determined statistically (Bradbury, 1981; Foster, 1983). There is no clear level of distinction between the two categories and it is important to remember when considering the criteria of mating systems that one is dealing with continuums rather than discrete categories (Bradbury, 1981).

Despite being intensively studied for over 50 years leks remain one of the least-understood mating systems, particularly with respect to their evolution. In spite of this, five

ecological and physiological prerequisites are thought to be necessary for lek formation (Höglund & Alatalo, 1995): 1) males are emancipated from parental care, 2) resources used by females are indefensible, 3) fertilisation is internal (or there is no association between the chosen male and the site of oviposition in species with external fertilisation), 4) high mobility allows females to accept the cost for searching for male aggregations (and for males to avoid predation attempts while displaying), and 5) females have the ability to discriminate between males. Under these conditions lek breeding has independently evolved a number of times in both vertebrates and invertebrates.

Within invertebrates, lekking is almost exclusively found in insects (particularly in highly volant groups such as swarm-forming Diptera: e.g. Spieth, 1978), but has also been described in fiddler crabs (*Uca* spp.: Croll & McClintock, 2000) (see Höglund & Alatalo, 1995). Among vertebrates, lekking appears to be most common in birds with the most recent review listing 148 known lek-breeding species (see Jiguet, Arroyo & Bretagnolle, 2000). Lekking behaviour has also been documented in other vertebrate taxa including amphibians (e.g. Hedlund & Robertson, 1989), fish (e.g. Clavijo, 1983) and reptiles (e.g. Wikelski, Carbone & Trillmich, 1996). In mammals, lek breeding appears to be comparatively rare compared to birds, with just over a dozen confirmed species, most of which are ungulates and pinnipeds (Table 1). While many mammals share most of the prerequisites for lek breeding, such as the absence of male parental care (Woodroffe & Vincent, 1994), the evolution of leks is likely constrained by relatively low mobility (compared to birds), apparently limiting it to predominantly large, free-roaming species.

Bats appear to satisfy all the prerequisites of lek breeding as they are one group of mammals that should not be limited by mobility, and yet lek breeding is virtually undescribed in the Order. In this paper we discuss reasons for the apparent rarity with respect to the

**Table 1.** Mammals with reported lek- or lek-like breeding behaviour.

Taxa	Common Name	Source	Notes
<b>Pteropodidae</b>			
<i>Hypsignathus monstrosus</i>	Hammer-headed bat	Bradbury, 1977a	Classic lek.
<b>Ursidae</b>			
<i>Ursos arctos</i>	Brown bear	Steyaert <i>et al.</i> , 2012	Some populations use lek-like “mating areas”.
<b>Dasyuridae</b>			
<i>Antechinus stuartii</i>	Brown antechinus	Lazenby-Cohen & Cockburn, 1988	Has since been refuted; likely to be scramble polygyny (Fisher <i>et al.</i> , 2011).
<b>Procyonidae</b>			
<i>Nasua narica</i>	White-nosed coati	Booth-Binczik, Binczik & Labisky, 2004	Described as a “mobile lek” as male aggregations follow female bands.
<b>Caviidae</b>			
<i>Galea spixii</i>	Spix's yellow-toothed cavy	Lacher, 1981	Unconfirmed. Likely a “lek-like male-dominance polygyny” (see Emlen & Oring, 1977), but would require genetic studies to confirm (T.E. Lacher Jr., pers. comm.).
<b>Dugongidae</b>			
<i>Dugong dugon</i>	Dugong	Anderson, 1997	Classic lek.
<b>Otariidae</b>			
<i>Otaria flavescens</i>	South American sea lion	Soto & Trites, 2011	Classic lek.
<i>Zalophus californianus</i>	California sea lion	Robertson <i>et al.</i> , 2008	Described as a “modified lek” as male display grounds become enveloped by females and pups during the whelping period (Boness, 1991).
<i>Z. wollebaeki</i>	Galapagos sea lion	Kunc & Wolf, 2008	Male behaviour resembles a lek, but likely a resource defence as females rest within male territories.
<i>Phocarctos hookeri</i>	New Zealand sea lion	Boness, 1991	Originally described as a “modified lek” but has since been reported as a harem defence polygyny (Gales, 2009).
<b>Phocidae</b>			
<i>Phoca vitulina richardii</i>	Pacific harbour seal	Hayes <i>et al.</i> , 2004	Classic lek.
<b>Odobenidae</b>			
<i>Odobenus rosmarus divergens</i>	Pacific walrus	Fay, Ray & Kibal'chich, 1984	Mating behaviour resembles a lek, but has characteristics of harem defence. Höglund & Alatalo (1995) suggest lek breeding is unlikely.

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<b>Cervidae</b>			
<i>Dama dama</i>	Fallow deer	Pemberton & Balmford, 1987	Classic lek.
<i>Cervus nippon</i>	Sika deer	Balmford <i>et al.</i> , 1993	Classic lek.
<i>C. elaphus</i>	Red deer	Carranza, Garcia-Muñoz & Vargas, 1995	Experimentally induced via food supplementation.
<i>Rangifer tarandus</i>	Reindeer	Leader-Williams, 1988	Höglund & Alatalo (1995) suggest lek breeding is unlikely.
<b>Bovidae</b>			
<i>Antilope cervicapra</i>	Blackbuck	Isvaran & Jhala, 2000	Classic lek.
<i>Kobus kob kob</i>	Buffon's kob	Wanzie, 1988	Classic lek.
<i>K. kob leucotis</i>	White-eared kob	Fryxell, 1987	Classic lek.
<i>K. kob thomasi</i>	Uganda kob	Buechner & Schloeth, 1965	Classic lek.
<i>K. leche</i>	Lechwe	Schuster, 1976	Classic lek.
<i>Connochaetes taurinus</i>	Blue wildebeest	Estes, 1968	Male territories are likely too large to be classified as a classic lek (Höglund & Alatalo, 1995).
<i>Damaliscus korrigum</i>	Topi	Gosling, Petrie & Rainy, 1987	Classic lek.
<i>Pantholops hodgsonii</i>	Chiru	Buzzard <i>et al.</i> , 2008	Classic lek.
<i>Procapra przewalskii</i>	Przewalski's gazelle	You & Jiang, 2005	Classic lek.
<b>Balaenopteridae</b>			
<i>Megaptera novaeangliae</i>	Humpback whale	Clapham, 1996	Described as a "floating lek" as there are no clearly-defined male territories and males travel freely.

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ecological determinants of bat mating systems while also highlighting the limited knowledge we have of these mating systems as a call for further research.

### **A.3 Bat Mating Systems**

Bats are among the most successful mammals on the planet; the evolution of flight and echolocation are thought to have contributed to rapid diversification since the Eocene (Altringham & Senior, 2005), with an estimated 1116 species extant today (Simmons, 2005). Flight has allowed bats to exploit a range of roost sites and roosting behaviours and develop a wide range of feeding habits, resulting in the greatest niche differentiation of any mammalian Order (Kruttsch, 2000; Altringham & Senior, 2005). This has resulted in the evolution of numerous reproductive strategies to meet their various seasonal, ecological and social requirements. As such, bats likely show the greatest range of reproductive behaviours of all mammals (Altringham, 2011).

Most mammals (>90%) use some form of polygynous mating system (Clutton-Brock, 1989) and bats appear to follow this general pattern. Harem polygyny (one male roosting with multiple females) is likely the most common mating system, but there are a range of others including a surprising number of species that use facultative monogamy (24% of species listed by McCracken & Wilkinson, 2000), which is rare in mammals (Clutton-Brock, 1989). Also reported are species that use resource defence polygyny (e.g. Bradbury & Vehrencamp, 1977), swarming (e.g. Furmankiewicz & Altringham, 2006), and mating territories (e.g. Gerell & Lundberg, 1985) (for a review, see McCracken & Wilkinson, 2000; Altringham, 2011).

To date, the hammer-headed bat (*Hypsignathus monstrosus*) of equatorial Africa is the only species of bat confirmed to form classic leks (Bradbury, 1977a). Hammer-headed bats are the largest in continental Africa and display one of the most marked examples of

sexual dimorphism among mammals; males are nearly twice as heavy as females and the larynx is nearly three times larger in males than females, occupying half of their body cavity (Bradbury, 1977a; Langevin & Barclay, 1990). The large larynxes of males produce the vocal displays used in courtship, consisting of loud, low-frequency honking. During the breeding season upwards of 130 males will arrange themselves along stretches of river (spaced approximately 10 m apart) and vocalise rapidly while wing-flapping. Females fly through these aggregations and hover in front of males in quick succession before selecting a male to copulate with. There appears to be high stereotypy in female selection of males with 6% of males receiving 79% of observed copulations in one year of study (Bradbury, 1977a).

Further descriptions of lek-like behaviour (i.e. male display clusters) in bats are rare, and either do not represent classic lek mating or remain to be confirmed as such. To date, only seven bat species (other than *H. monstrosus*) have been observed with lek-like characteristics in their breeding behaviour (Table 2). The least long-fingered bat (*Miniopterus minor*) represents perhaps the best case of unconfirmed classic lek breeding in bats. A population in coastal Kenya was observed across two years by McWilliam (1990), and an aggregation of 5 – 19 males was described occupying a “mating dome” (a small erosion hollow in the roof of the colony’s cave) during the breeding season. These males were both older and heavier than males outside the mating dome, and residency in the dome across three breeding seasons was limited to approximately 30 males (out of a population of over 300 males), suggesting intense competition between males to retain their positions within it. Display behaviour in the dome appeared to be primarily olfactory, with males covering themselves in urine resulting in a pungent odour (McWilliam, 1988). While McWilliam (1990) argued that the male display behaviour in the mating dome suggested a lek mating system, no copulations were ever observed at this display site. Lek breeding therefore cannot

**Table 2.** Bat species where lek-like breeding characteristics have been suggested in literature. \* = Assumed but either not reported or tested.

	Lekking Criteria				Likely Mating System	Additional Explanation	Source
	Absence of ♂ Parental Care	♂ Clumping (# males per aggregation)	No Resources Obtained by ♀♀	♀ Selection of ♂♂			
<b>Pteropodidae</b>							
<i>Epomops franqueti</i>	✓*	✓ <sup>1</sup>	✓	✓*	Exploded lek	<sup>1</sup> Male calling territories are fairly large (0.6 – 0.9 ha). Copulations not observed but females show similar appraisal behaviour as female <i>Hypsignathus monstrosus</i> .	Bradbury, 1977a, 1981
<i>Epomophorus wahlbergi</i>	✓*	? <sup>2</sup>	?	?	Resource defence polygyny?	<sup>2</sup> Males call from perches estimated to be approximately 50 m apart. Size of aggregations not reported. Likely does not lek (Bradbury, 1977a).	Wickler & Seibt, 1976
<b>Vespertilionidae</b>							
<i>Pipistrellus pipistrellus</i>	✓	✓ <sup>3</sup>	?	?	Mating territories or resource defence polygyny	<sup>3</sup> Males hold large (1.2 – 10 ha) courtship territories located near communal roosts. Copulations were not observed, and it is unknown if females gain access to male day roosts.	Sachteleben & von Helversen, 2006
<i>P. nathusii</i>	✓	✓ (2 – 3)	✗	?	Variable	Male aggregations are very small in size, and many males do not form aggregations but appear to adopt resource defence polygyny, among other strategies.	Jahelková & Horáček, 2011
<b>Miniopteridae</b>							
<i>Miniopterus minor</i>	✓	✓ (5 – 19)	✓	?	Unknown	Copulations not observed at male aggregations.	McWilliam, 1990
<b>Phyllostomidae</b>							
<i>Erophylla sezekorni</i>	✓	✓ (2 – 9)	✗	✓	Resource defence polygyny	Females roost within the male display sites.	Murray & Fleming, 2008
<b>Mystacinidae</b>							
<i>Mystacina tuberculata</i>	✓	✓ (~39)	?	?	Unknown	Currently undergoing study.	C.A. Toth, unpubl. Data

be confirmed since male aggregations and display behaviour do not necessarily translate into a female preference for those males, and mating could be a random scramble.

Franquet's epauletted fruit bat (*Epomops franqueti*), which occurs sympatrically with *H. monstrosus*, is another species with lek-like breeding behaviour. Male *E. franqueti* establish territories of 100 – 200 m in diameter and produce whistle-like calls from four or five perches situated within the territories (Bradbury, 1977a). Like *H. monstrosus*, female *E. franqueti* visit male territories and hover in front of calling males to appraise them, even engaging in vocal duets with males (although copulations were not observed) (Bradbury 1977a). The relatively large size of male territories means *E. franqueti* are not classic lek breeders, but would be consistent with exploded leks (Bradbury, 1981).

#### **A.4 Why is Lek Breeding Rare Among Bats?**

In mammals, polygynous mating systems appear to be largely influenced by four characteristics: 1) parental care required for offspring survival, 2) female home range size, 3) female group size and stability, and 4) the density and distribution of females (Clutton-Brock, 1989; Clutton-Brock, Deutsch & Nefdt, 1993). If male assistance is required for offspring survival, obligate monogamy will result. If female home ranges are small enough, males commonly defend territories encompassing one or more female territories. If female groups are small and have stable membership, males individually defend these groups (or multiple males may defend female groups if they are large). If neither females nor their home ranges can be defended by males, males will defend mating territories within female home ranges. In areas of low female density these territories will be relatively large and spaced far apart, but in areas of high density male territories will be relatively small and clustered, giving rise to leks and similar mating systems (Emlen & Oring, 1977). Additional theoretical (Bradbury, Gibson & Tsai, 1986) and empirical (e.g. Bradbury *et al.*, 1989) work has highlighted the

importance of factors such as female home range size in further determining the attributes of resulting leks, such as the dispersion of male territories.

With respect to bats, the determinants of mating systems are poorly studied but are thought to operate on the same basic assumptions listed above (Altringham, 2011). Male parental care is largely absent in bats (but see Vehrencamp, Stiles & Bradbury, 1977) and high female mobility promotes polygyny and promiscuity (McCracken & Wilkinson, 2000). Additionally, the roosting behaviour of bats is a unique characteristic that further influences their reproductive strategies (see Kunz & Lumsden, 2003); some species roost solitarily while others form the largest aggregations of mammals on earth, numbering in the millions (e.g. Davis, Herreid & Short, 1962). Roosting structures are as varied as abandoned bird, ant, and termite nests; exposed tree limbs; 'tents' constructed from leaves; anthropogenic structures such as bridges, tombs, mines, and buildings; caves; or cavities in trees. These can serve as sites for mating, hibernating, rearing offspring, and protection from predators and the elements (see Kunz & Lumsden, 2003; Altringham, 2011). Thus, the influence roosting behaviour has on the evolution of bat mating systems is significant. For example during the breeding season *Pipistrellus nanus* in Malawi roost in clumps of rolled banana leaves, forming mixed-sex groups of one male and several females (Happold & Happold, 1996). These roosts persist for only one to three days before the leaf rolls open requiring both males and females to relocate. Female group membership changes frequently and individual females roost with several males in quick succession. Banana leaves are not limiting within the habitat, and territorial competition between males is not observed. Thus, the abundance of resources (roosts), the fluidity of female groups, and the protracted breeding season (approximately three months) has likely resulted in the evolution of a promiscuous mating system rather than a harem defence which might be favoured with less ephemeral roosting sites (Happold & Happold, 1996).

Given the importance of roosting behaviour, bat researchers must reconcile several factors to elucidate the ecological determinants of mating systems. Moreover, additional features of bat life histories may facilitate or hinder the evolution of particular mating strategies. Corrected for body size, bats are the longest-lived mammals, averaging three times longer lifespans than non-flying eutherians (Austad & Fischer, 1991); several species have been recorded with lifespans of over 30 years (Barclay & Harder, 2003). Additionally, many species of bat show female philopatry with females remaining in the area in which they were born and males dispersing (Burland & Wilmer, 2001). The combination of these characteristics promotes social systems involving female groups inhabiting the same roost (Kerth, 2008). Based on the work of Clutton-Brock (1989), we would expect harem mating systems to be common under such conditions and this appears to be the case with bats, as harem polygyny is a common mating system in the Order (McCracken & Wilkinson, 2000). It should be noted, however, that not all harem-forming bats have stable female group composition (McCracken & Wilkinson, 2000) and one – *Saccopteryx bilineata* – exhibits female dispersal rather than male dispersal (Bradbury & Vehremcamp, 1976), and so the lack of these features does not necessarily preclude the evolution of harems.

Some clues to help explain the adoption of male display clusters in bats can come from the comparison of closely-related species that differ in their reproductive strategies, such as *M. minor* (discussed above) and *M. australis*. *Miniopterus australis* exhibits a harem polygyny system with individual males defending unstable groups of up to six females (Medway, 1971). An important difference in the life histories of the two species is their roosting behaviour; female *M. minor* migrate seasonally, leaving little opportunity for males to monopolise them (McWilliam, 1990). For female *M. australis*, the required roosting sites in small erosion domes in cave roofs are limiting and they must remain in these sites annually (Medway, 1971), thus promoting the formation of harems by males (McWilliam, 1990).

Climate also plays a large role in the evolution of bat mating systems and may provide insight on where leks are likely to evolve. In temperate regions ecological factors promote large home ranges, seasonal migration, and low population densities (Barclay & Harder, 2003; Kunz & Lumsden, 2003), all of which restrict the formation of harems. In some species males may completely avoid mate attraction by simply copulating with hibernating females (Bradbury, 1977b). In other cases, the conditions imposed by temperate climates require males to establish territories and attract females through self-advertisement, resulting in mating systems such as resource (i.e. roost) defence, mating territories, or lek mating systems. Thus it is surprising that so few lek-breeding bat species have been documented in temperate regions, likely due in part to the lack of studies which assess behaviours associated with leks.

#### **A.5 *Mystacina tuberculata***

Currently we are investigating the possibility of lek breeding in the temperate New Zealand lesser short-tailed bat (*Mystacina tuberculata*), as their life history and ecology make them a good candidate species for the evolution of a lek mating system. *Mystacina tuberculata* are medium-sized (10 – 20 g), tree-roosting bats associated with large (>1000 ha), old-growth native forests across New Zealand. From September to May males individually occupy and defend small cracks and holes in trees and sing from within the cavity, presumably to attract passing females. These songs are audible to humans (although they contain ultrasonic components), and contain several song elements including trills, tonal notes, and modulated harmonics (C.A. Toth, unpubl. data). Male ‘singing roosts’ have been reported to be clustered in space leading to the suggestion that *M. tuberculata* employ a lek mating system (Daniel, 1990). However, the breeding behaviour of *M. tuberculata* has never been formally investigated and so this remains unconfirmed.

*Mystacina tuberculata* colonies are some of the largest among cavity-roosting bats (Kunz & Lumsden, 2003), with the largest communal roost trees containing upwards of 6000 individuals (Lloyd, 2001). In addition to high population densities, females possess large home ranges. Individuals radio-tracked from a population in the Eglington Valley in Fiordland ranged the entire length of the valley (26.5 km), covering an area of over 130 km<sup>2</sup>, with individual home ranges covering between 3.2 to 69.3 km<sup>2</sup> (O'Donnell *et al.*, 1999). Preliminary data from a population of *M. tuberculata* in the Pikiariki Ecological Area in the central North Island further suggests that males may have little opportunity to monopolise females despite the occurrence of large communal roosts. Of nine adult females we radio-tracked across the summer of 2011-12, eight had solitary day roosts in which they roosted an average of 57% of days tracked (range: 20 – 100%) (C.A. Toth, unpubl. data). The combination of high female densities, large home ranges, and frequent roost changes provide an excellent environment for the evolution of leks.

Additional work in Pikiariki has also begun to describe male courtship behaviour. During the summer months of 2011-12 there was an increase in male singing following the female birthing period (December – January), with most males singing between February and March. Male singing roosts were aggregated in space, with most located within an area of 0.59 km<sup>2</sup>. However further study will be required to reveal the level of female choice via female visits to male roosts and male reproductive success (through paternity analyses), and whether females gain access to male singing roosts as day roosts (i.e. resources). If lek breeding can be confirmed in *M. tuberculata* it will be the first temperate bat conclusively demonstrated to use this mating system, allowing the appropriate ecological conditions necessary for the evolution of lek breeding in bats to be determined.

## A.6 Conservation Implications and the Need for Research

Despite a lack of direct evidence, the numbers of lek breeding temperate bat species may be relatively high. Cryan (2008) has hypothesised that the high numbers of bats killed by wind turbines each year are a consequence of behaviours associated with lek breeding. Many of the species killed in North America and Europe are tree- or foliage-roosting, with peaks in fatalities coming in late summer and autumn. Cryan (2008) reasons that some bats could be mistaking turbines for the tallest and most mature trees in the forest, which would serve as ideal landmarks (and thus display sites) for lekking bats mating on migration. Fatalities of two species killed by wind turbines – *Lasiurus borealis* and *L. cinereus* – are largely adult males (Arnett *et al.*, 2008), suggesting display aggregations (although the trend may also be due to separate habitat use by males and females, as sexual segregation is common in bats; Altringham and Senior, 2005).

The swarming behaviour of many temperate bats may also represent lek-like breeding. Swarming behaviour typically takes place in late summer to autumn (but has also been reported in spring; Furmankiewicz, 2008), with large groups briefly visiting potential hibernacula (caves and mines; e.g. Parsons *et al.*, 2003). Swarms can contain thousands of individuals from several species and mating is known to occur during these events (e.g. Rivers, Butlin & Altringham, 2006). Mating in swarms appears to be superficially random (e.g. Thomas, Fenton & Barclay, 1979), however genetic evidence in the little brown bat (*Myotis lucifugus*) has shown that fertilizations are actually skewed towards certain males or male lineages (although this pattern could be caused by males mating during hibernation) (Watt & Fenton, 1995). Such large aggregations of mating individuals provide the opportunity for lek-like behaviour (Altringham, 2011).

In tropical species, nightly calling behaviour similar to that observed in *H. monstrosus* and *E. franqueti* has been reported in closely-related species (e.g. Wickler & Seibt, 1976;

Boulay & Robbins, 1984; McCracken & Wilkinson, 2000), although there are no detailed studies describing male spacing or female choice. Thus it is likely that several other epomophorine bats display lek-like breeding behaviour analogous to the gradients of lekking behaviour observed within several families of birds (J.W. Bradbury, pers. comm.), ranging from classic leks to exploded leks to more widely-spaced mating territories (Jiguet *et al.*, 2000). This remains to be shown, however, given the absence of detailed research.

The above examples bring us to an important point about the current state of knowledge of bat mating systems. The last comprehensive review on breeding behaviour was compiled by McCracken & Wilkinson (2000), and at that time information of reproductive behaviours was known for less than 7% of all species. The nocturnal habits of bats and the difficulty in reaching their roosts make it challenging to study their social interactions, particularly reproduction. The numbers of lekking bat species may be relatively high with respect to other mammals (or perhaps even to birds), but this will remain unknown without further research. Modern molecular techniques are a useful tool that could be used to overcome the difficulty in directly observing copulations that has hindered past studies (e.g. McWilliam 1990), although the effort required in gaining such data may still be prohibitive for some species.

Leks not only offer interesting research opportunities for behavioural ecologists, but also present unique conservation considerations for species at risk. Determining the mating system of a species implicitly requires an understanding of sexually mature male and female distributions, male display site requirements, and female mate selection criteria – all of which provide information necessary for conservation (Morales *et al.*, 2001). As of 2002, almost a quarter of known bat species were considered threatened due to factors such as habitat loss, persecution, and roost site disturbance (Mickleburgh, Hutson & Racey, 2002). In the intervening time white-nose syndrome has decimated populations of bats across eastern

North America (Blehert *et al.*, 2009). For potential lek breeding species, such as *M. tuberculata* (which is considered Critically Endangered across its range; O'Donnell *et al.*, 2010) and other yet-described lekking bats, conservation strategies must take this distinct mating system into account. Important factors such as male display site requirements, traditional display grounds, and resource distributions must all be considered when designing holistic rescue policies.

### **A.7 Summary and Conclusions**

The evolutionary origins of leks and the ecological determinants of bat mating systems are both poorly understood, and so reconciling the two is difficult without further research. It appears as though the evolution of lek breeding may be limited in bats (at least in tropical species) by life history characteristics that promote the use of harem-defence by males. Because ecological constraints in temperate regions restrict the evolution of harems, males must instead focus on self-advertisement, potentially leading to the use of leks under the ideal conditions (e.g. high population densities with large home ranges, as observed in *Mystacina tuberculata*). However, as Höglund & Alatalo (1995) note, given the degree to which species differ in their habitat use, ecology, and life history, it should not be surprising if leks form under several different conditions. This is particularly likely in an Order as successful and diverse as Chiroptera.

Any inferences on the adoption of lekking behaviour in bats are hamstrung, however, by the unfortunate lack of knowledge on bat reproduction, and we hope this article highlights the need for further research. Contrasted with work on birds, for example, studies of bats have lagged in both the use of genetic tools to determine levels of polygyny and of experimentation to clarify causal factors influencing mating systems (McCracken &

Wilkinson, 2000). Further research will not only provide benefits for the understanding of mating systems, but will aid in the conservation of the many species of bats at risk.

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# **B**

## **Supporting information for Chapter 2**

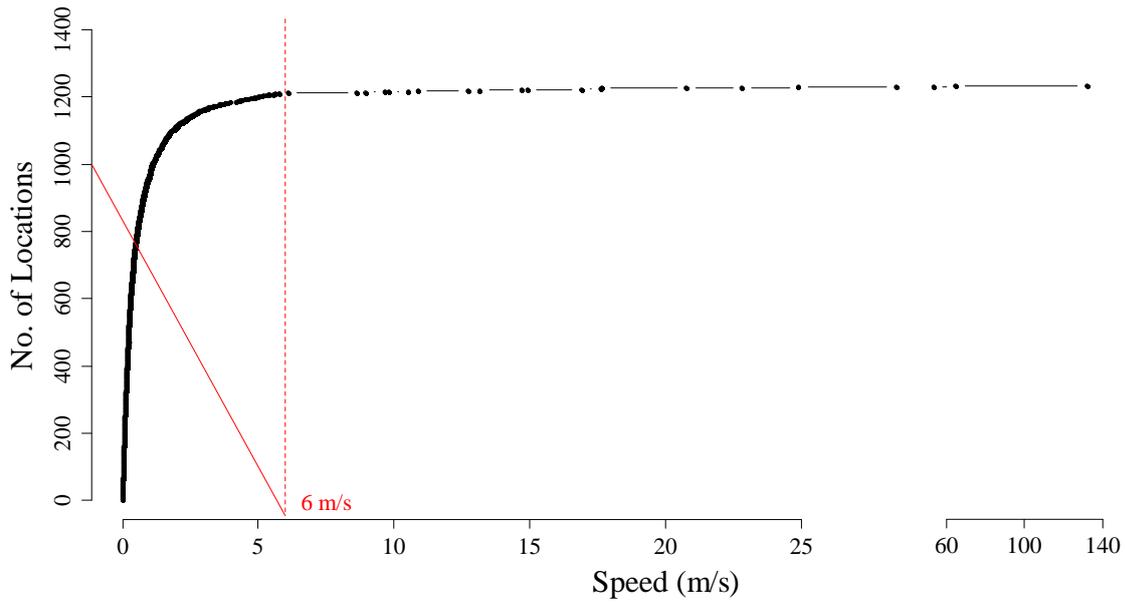
## **B.1 Screening and Error Quantification for Radiotelemetry Data**

Telemetry data were first screened for probable errors using a speed filter (Patterson et al. 2010). The speed travelled between consecutive location estimates was calculated following the 2011-12 field season for the dataset and the cumulative frequency distribution of these speeds plotted (Fig. 1). The inter-fix speed at which the asymptote was reached provides an unbiased estimate of a threshold value above which the bats rarely travelled. The observed threshold velocity of 6 m/s was then used as the maximum plausible velocity for the bats moving between locations. Thus, any pair of location estimates for which this speed was surpassed was excluded from subsequent analyses.

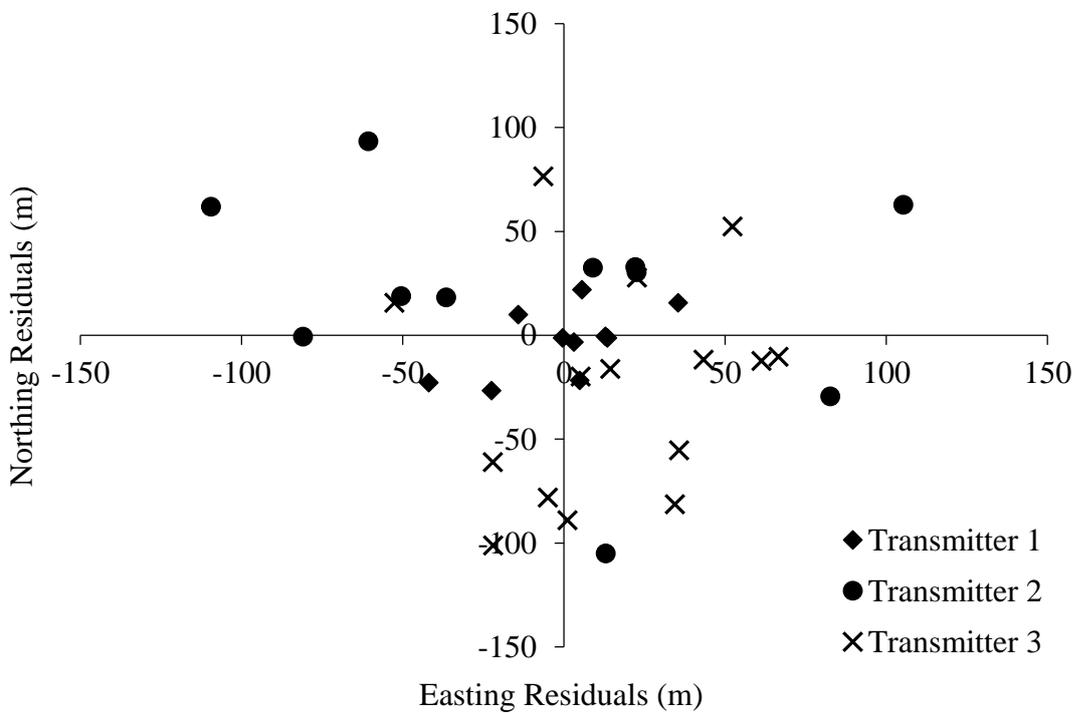
‘Biological reasoning’ was used for filtering points to control for temporal autocorrelation, which occurs when observations closer in time are more correlated than distant observations (Aarts et al. 2008). The data were subdivided so that all fixes were at least 10 minutes apart. Ten minutes was deemed appropriate as this is sufficient time for the bats to traverse their entire range length at a speed of 6 m/s. This reasoning assumes spatial and temporal independence necessary for statistical analysis, as a bat could theoretically move anywhere within its range during this time.

To estimate the location error of the observed locations, we took position fixes of stationary transmitters (beacons) placed at known locations. Quantifying location error permits calculation of the circular error probable (CEP) of the biangulation procedure. The 50% CEP is a measure of accuracy giving the radius of the circle centered on the transmitter within which 50% of the location estimates fall. The CEP distance can then be used as an estimate of potential error in spatial analyses. Three test beacons were used: one was placed close to the ground in the forest and the remaining two were bats with transmitters located in their day roosts. At least 10 biangulation estimates were taken for each transmitter at varying distances and compass bearings. This procedure allowed for investigation into the range of

the receivers and to find if the error increased with a weaker signal. Location estimates were then compared with the actual beacon locations. The residual distances of the estimates were plotted and visually assessed for obvious directionality in the error (Fig. 2). After confirming that the data were normally distributed (Shapiro-Wilks test,  $W = 0.96$ ,  $P = 0.13$ ,  $n = 36$ ), 50% CEPs were calculated using the program DNR GPS 6.0.0.15. The mean 50% CEP of the three beacons was  $54.7 \pm 19.1$  m ( $\bar{x} \pm SE$ ).

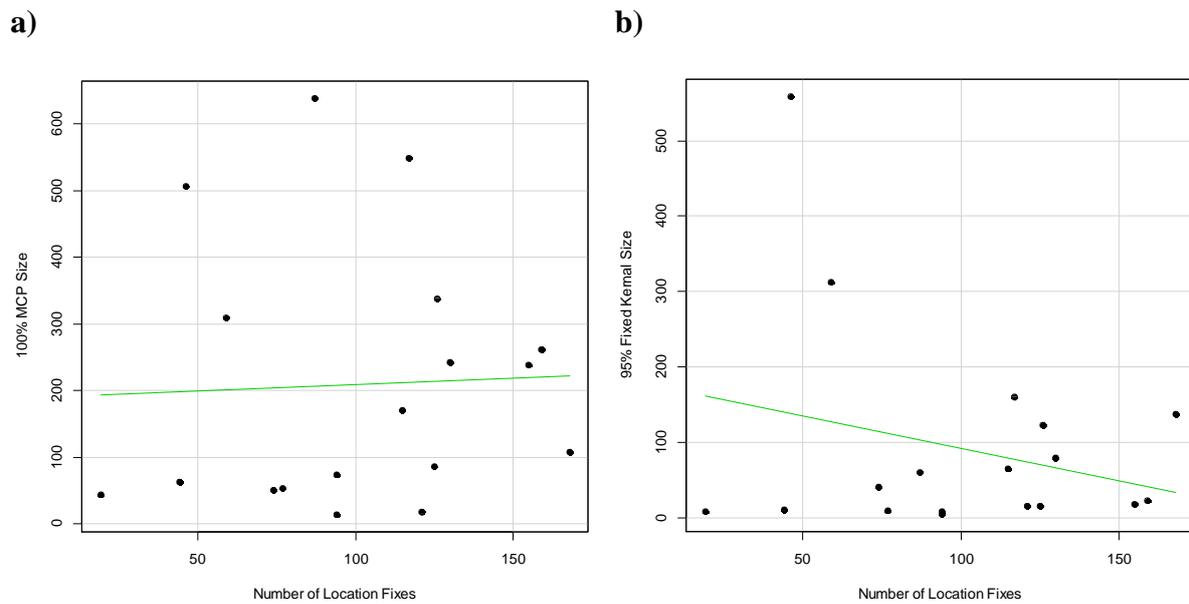


**FIG. 1.** Cumulative frequency distribution of the number of location fixes plotted against inter-fix speeds. The red line denotes the 6 m/s speed at which the number of fixes approached the asymptote. This value was used as the maximum probable speed of the bats; consecutive fixes whose speed was  $> 6$  m/s were removed before further analysis. This procedure excluded 19 location fixes.



**FIG. 2.** Residual error of telemetry location estimates compared against known locations of each transmitter. The plot shows no strong directionality in error patterns, other than a slight northwards trend for transmitter 2 and a slight opposite trend for transmitter 3.

## B.2 Number of Telemetry Location Fixes vs. Home Range Size (area in hectares)



**FIG 3.** Scatterplots with least-squares lines showing the relationship between the number of telemetry location fixes attained for individuals versus their resulting a) 100% MCP size, and b) 95% FK size. No significant correlation was detected between these variables.

### B.3 Second- and Third-Order Habitat Selection Values for Individual *Mystacina tuberculata*

**TABLE 1.** Second- and third-order distance ratios of habitat selection for adult male and female *Mystacina tuberculata* in a fragmented habitat. Second-order habitat selection compares the habitats that occur within an individual's home range to the availability of those habitats within the wider landscape, while third-order selection refers to the use of habitats within an individual's home range. Values < 1.0 indicate preference for a habitat, while values > 1.0 indicate avoidance.

	Second-order			Third-order		
	Native Forest	Exotic Plantation	Open Space	Native Forest	Exotic Plantation	Open Space
Female 1	0.052	0.63	0.46	0	0.94	3.08
Female 2	0.34	0.46	2.14	0.47	1.2	1.25
Female 3	0.42	0.67	1.27	0.32	1.16	0.45
Female 4	0.58	0.18	3.7	0.00018	2.55	1.1
Female 5	0.28	0.17	0.59	0.17	0.63	1.99
Female 6	0.59	0.1	3.22	0.062	4.4	0.56
Female 7	0.19	0.52	2.13	0.022	2.04	0.4
Female 8	0.21	0.28	2.5	0.037	1.81	0.85
Female 9	0	1.14	3.22	0	1.17	1.1
Male 1	0.17	0.56	1.89	0.033	1.5	0.46
Male 2	0.19	0.81	0.46	0.016	0.41	1.69
Male 3	0.2	0.59	1.08	0	1.3	0.49
Male 4	0.05	0.93	0.45	0.0026	1.46	0.35
Male 5	0.35	0.48	1.52	0.011	1.49	0.47
Male 6	0.38	0.47	1.59	1.04	0.53	0.34
Male 7	0.52	0.22	1.97	0.98	0.16	0.69
Male 8	0.56	1.54	1.06	0.052	0.84	0.25
Male 9	0.28	0.32	3.07	0.0039	0.81	1.57

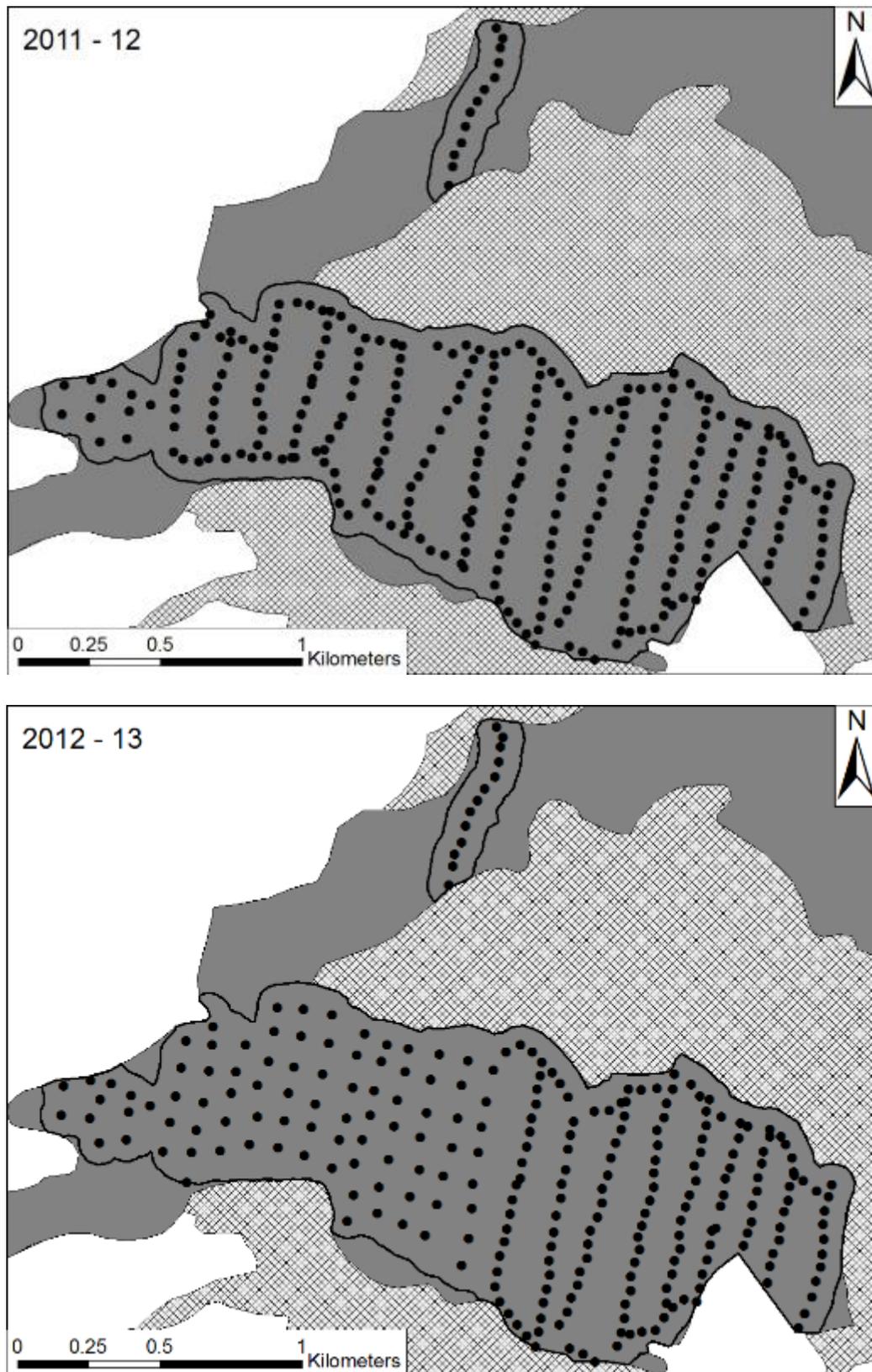
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# C

## **Supporting information for Chapter 3**

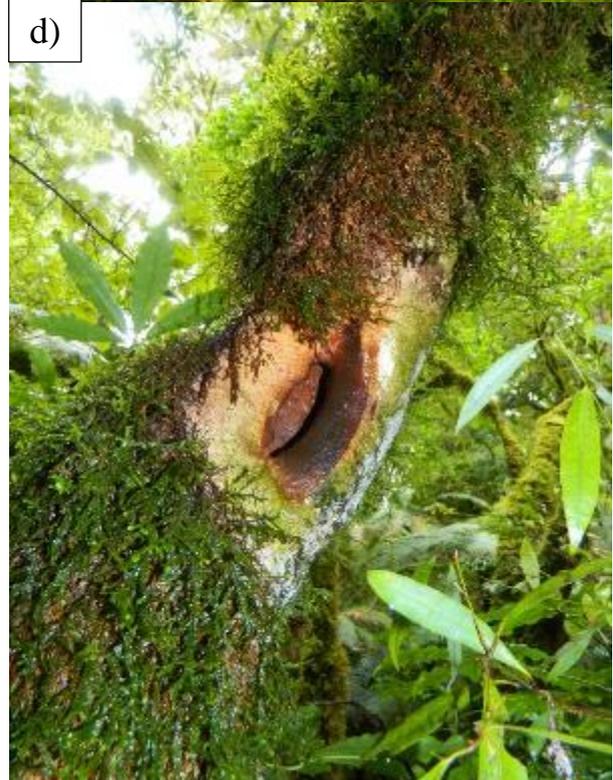
### C.1 Study Site and Bait Station (Grid) Locations in Pikiariki



**Figure 1.** Maps of the study site within the Pikiariki Ecological Area. The black dots represent bait station locations that formed the survey grid used for walking transects in the first two years of study. In the 2011-12 season most bait stations were arranged in lines spaced approximately 150 m apart with bait stations every 50 m.

In the 2012-13 season new bait stations were placed in half of Pikiariki with both stations and lines spaced 100 m apart. The study site was divided into the smaller “north” site and the “main” site to the south. Dark grey represents native forest, hatched areas represent exotic plantations, and white represents open space (pastoral land and harvested forest). The black border represents the theoretical limit that male singing could be detected by researchers (75 m from each bait station) within native forest and denotes the area of the field site used in spatial analyses. Although the location of bait stations changed between the years, the border of the field site remained constant for ease of analyses.

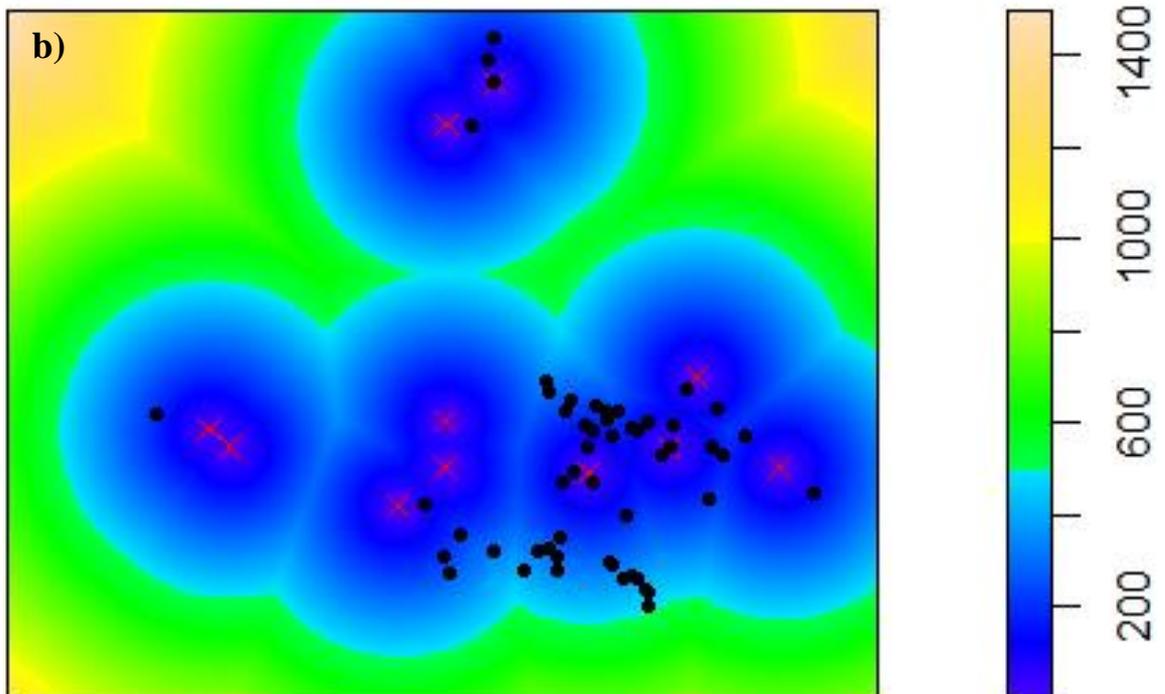
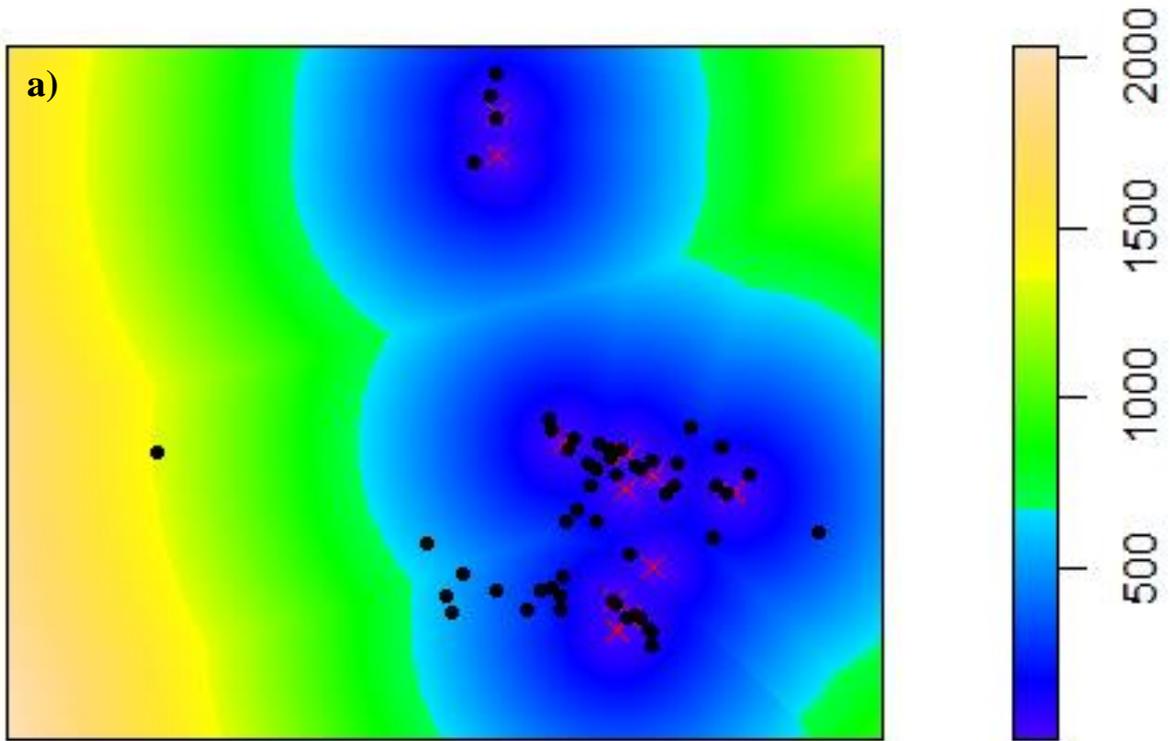
## C.2 Examples of Singing- and Communal Roosts in the Pikiariki Ecological Area

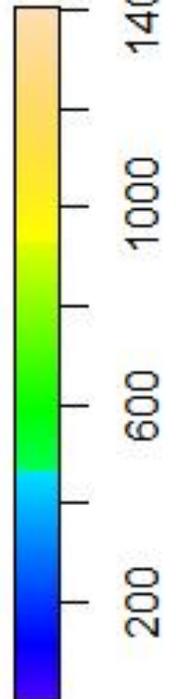
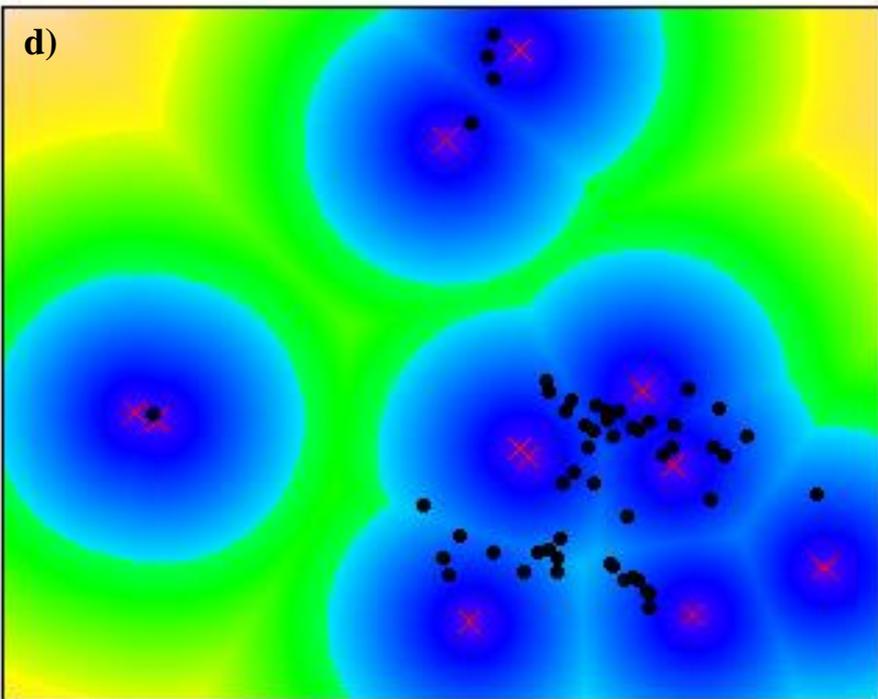
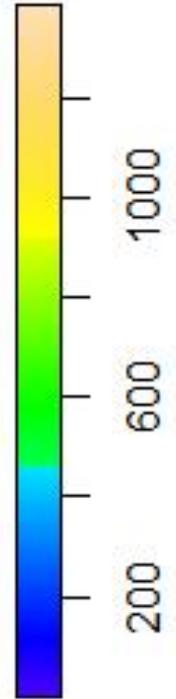
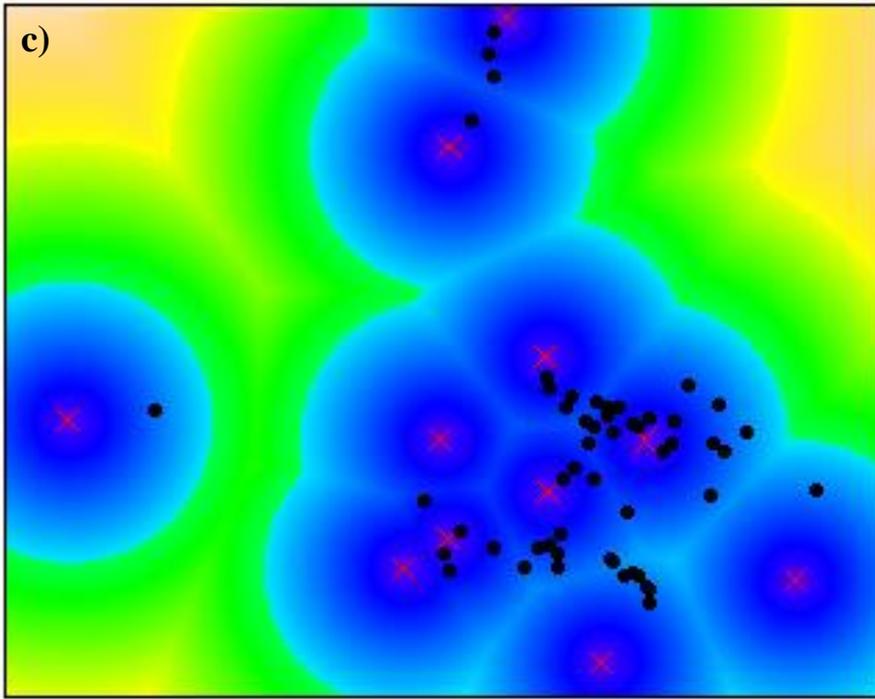


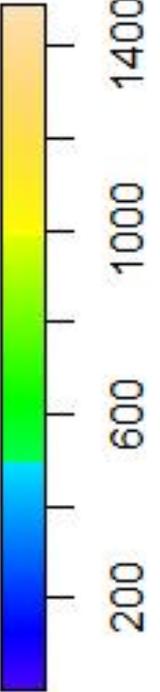
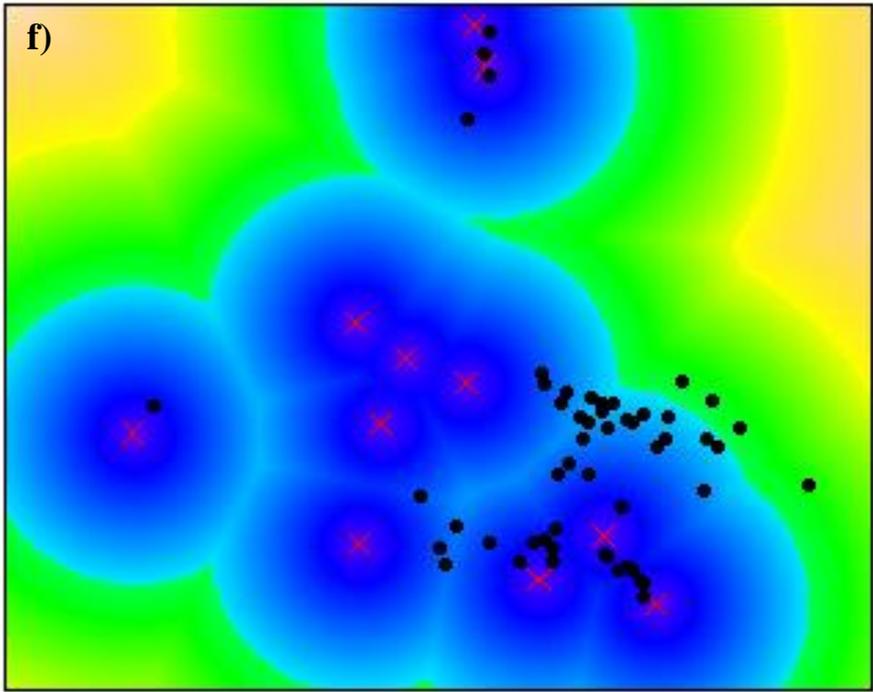
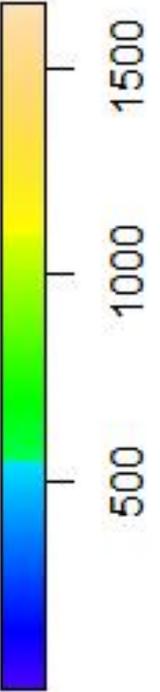
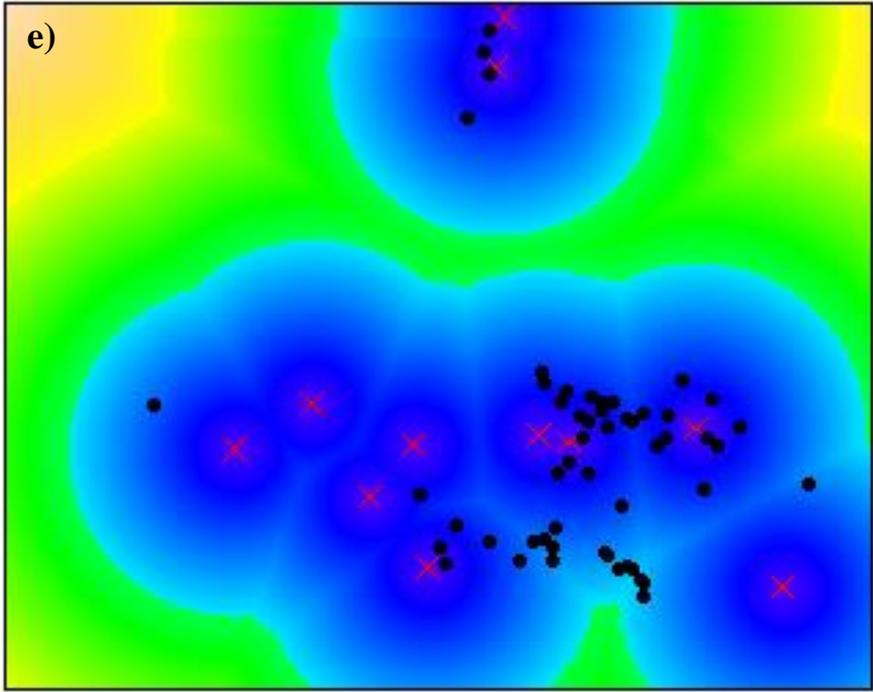


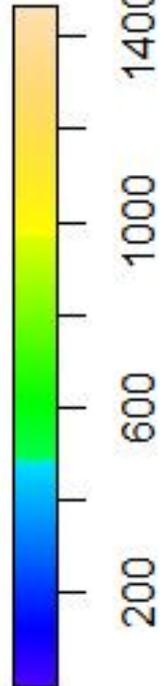
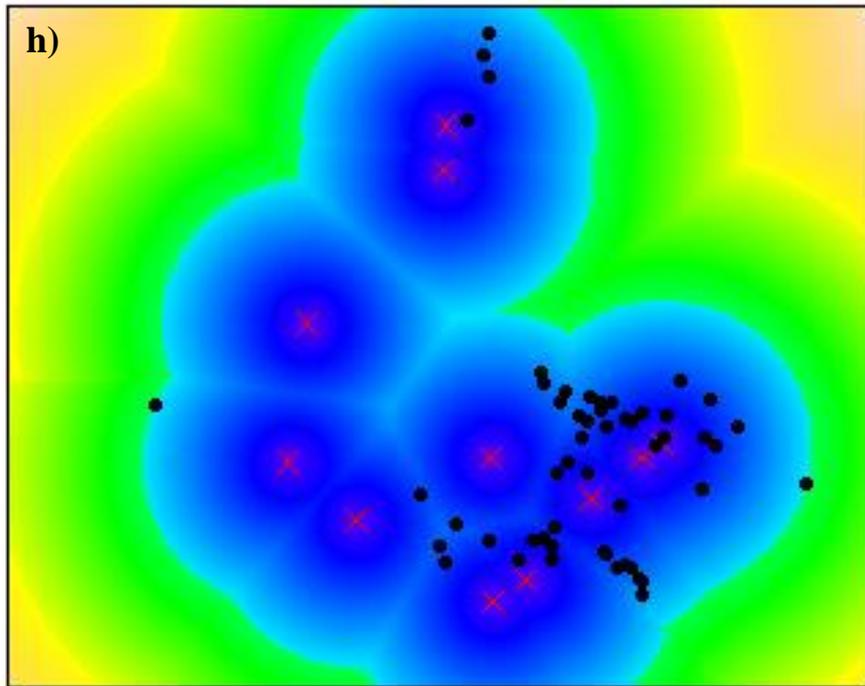
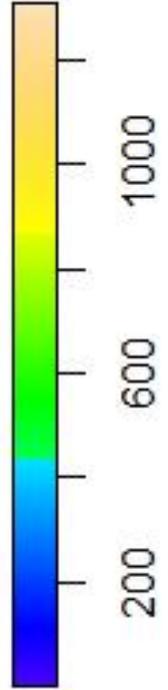
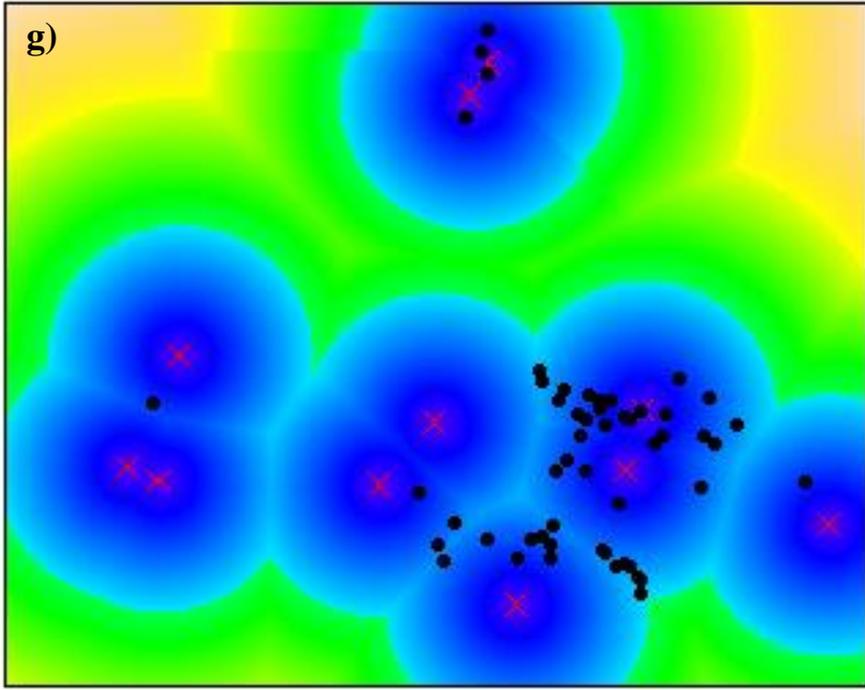
**Figure 2.** Examples of singing roosts (a – d) and communal roosts (e – f) used by *Mystacina tuberculata* in the Pikiariki Ecological Area. Singing roosts used by males are generally small cracks or hollows in trees of varying sizes. Communal roosts used by the population are among the oldest and largest trees in the forest.

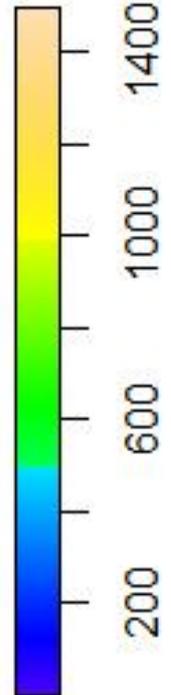
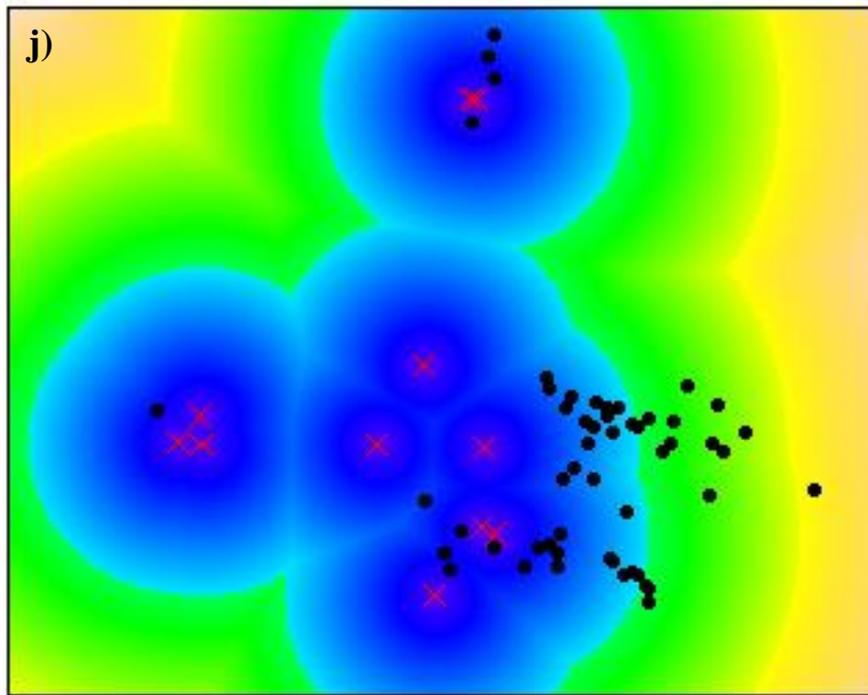
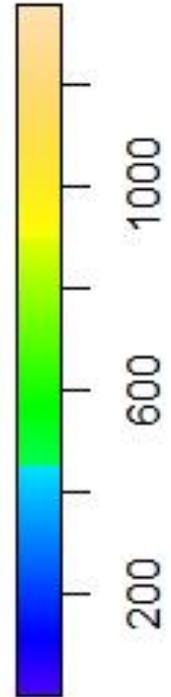
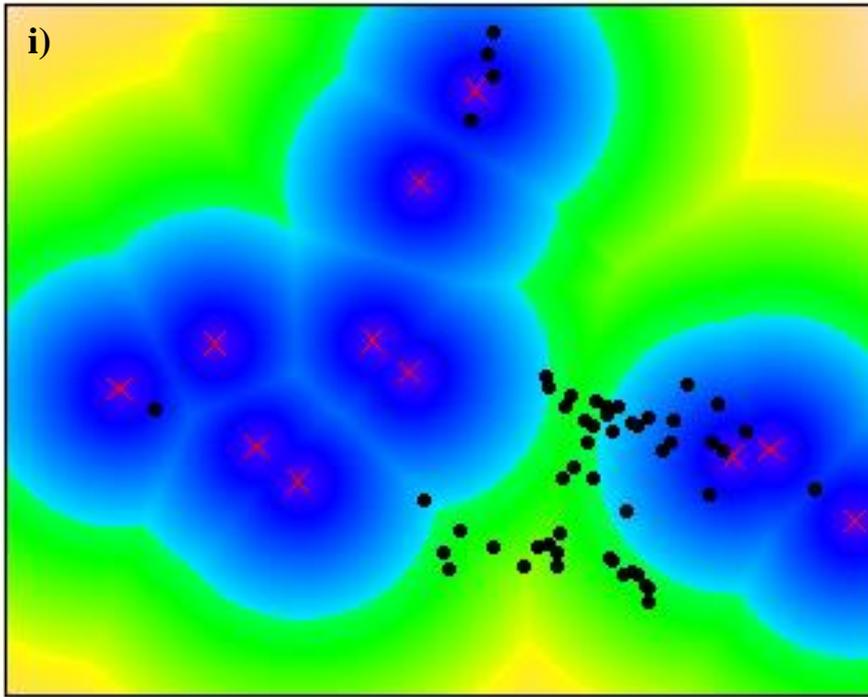
### C.3 Distance Maps for Actual and Random Communal Roosts

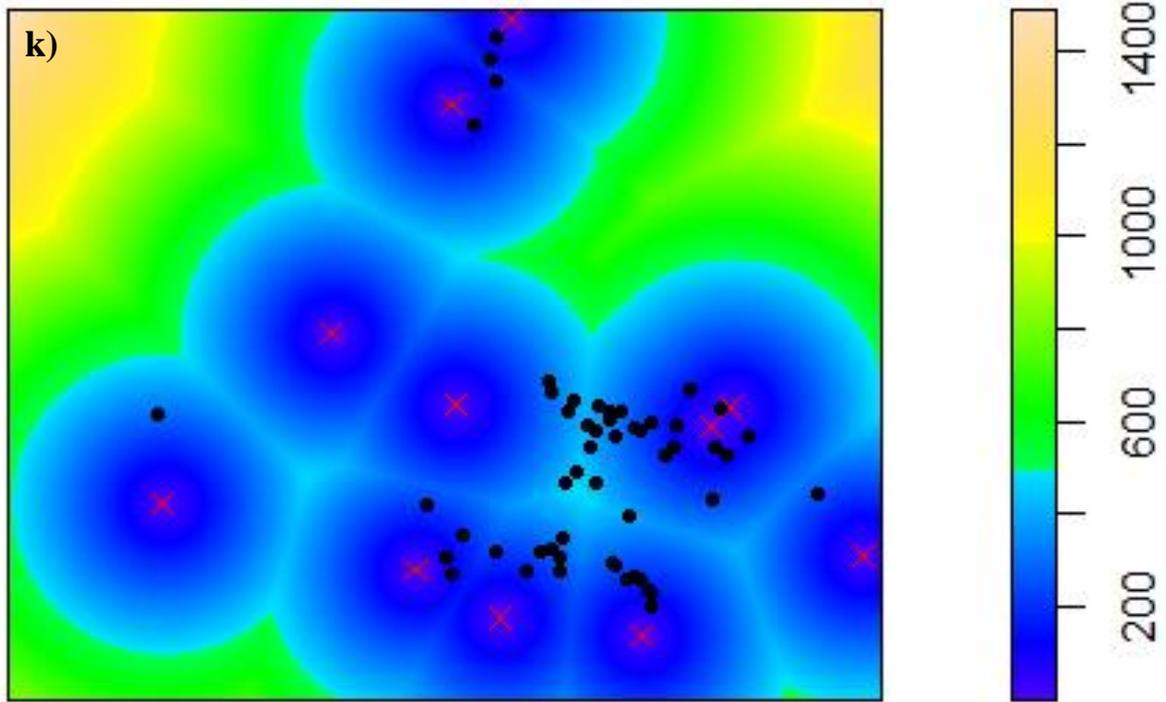












**Figure 3.** Distance maps for 11 actual (a) and randomly-placed (b – k) communal roosts within the study site for use in spatial logistic regression models on singing roost locations. Communal roost locations are marked with red X's, while singing roost locations are marked with black circles. Pixels (5.64 m x 5.64 m) are color-coded by their distance in meters from the closest communal roost.

# D

## Supporting information for Chapter 4

**Table 1** – Complete listing of song types recorded in the singing bouts of 16 male *M. tuberculata*, along with number of instances each was recorded.

<b>Song Type</b>	<b>Total Number Produced</b>
Trill	6,956
Trill-downsweep	3,791
Upsweep-trill-downsweep	3,517
Upsweep-trill	3,460
Tone-trill	914
Tone-upsweep-trill-downsweep	696
Trill-tone	616
Tone-upsweep-trill	589
Tone	544
Upsweep-tone	449
Tone-trill-downsweep	412
Downsweep-tone	408
Upsweep-trill-tone	334
Upsweep-tone-downsweep	310
Trill-upsweep	294
Downsweep-trill	223
Tone-downsweep	215
Downsweep-trill-downsweep	163
Downsweep-trill-tone	153
Upsweep	148
Trill-tone-downsweep	131
Upsweep-tone-trill	107
Upsweep-trill-upsweep	103
Upsweep-trill-tone-downsweep	102
Tone-upsweep	86
Downsweep	66
Tone-trill-tone	60
Trill-downsweep-tone	50
Downsweep-tone-trill	46
Downsweep-tone-downsweep	34
Trill-tone-trill	34
Upsweep-trill-downsweep-tone	28
Tone-upsweep-tone-downsweep	21
Tone-trill-upsweep	19
Upsweep-tone-upsweep	17
Tone-trill-tone-downsweep	13
Upsweep-tone-trill-downsweep	11
Tone-upsweep-trill-tone	11
Downsweep-trill-upsweep	10
Tone-upsweep-tone	8
Downsweep-trill-tone-downsweep	7
Upsweep-trill-tone-trill	6
Trill-tone-upsweep	4

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Downsweep-tone-upswEEP	3
Downsweep-trill-downsweep-tone	3
Tone-upswEEP-trill-upswEEP	3
Downsweep-tone-trill-downsweep	2
Upsweep-tone-trill-tone	2
Tone-upswEEP-trill-tone-downsweep	1
Trill-tone-trill-downsweep	1
Downsweep-trill-tone-trill	1
Unidentifiable structure	519
<b>Total</b>	<b>25,701</b>

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# E

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