THE EFFECTIVENESS OF THE MULTI-Spatial SCALE APPROACH TO FOREST MANAGEMENT: A CASE STUDY OF TASMANIAN BATS

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

University of Tasmania
Cooperative Research Centre for Forestry
March 2014
“To hold a little microbat in your hand, its body the size of the end of your thumb, is nothing but astounding” - Richards and Hall (2012)
DECLARATIONS BY THE AUTHOR

Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Lisa Cawthen
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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australia codes on animal experimentation. Animal ethics permits were obtained from the University of Tasmania Animal Ethics Committee for all aspects of the project where experiments involved live animals (Permit: A10640).

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STATEMENT OF CO-AUTHORSHIP AND THESIS CONTRIBUTIONS

This thesis comprises a series of manuscripts (chapters) prepared for publication. For the purpose of this thesis, manuscript abstracts have been removed and references collated.

The following people and organizations contributed to the manuscripts prepared as part of this thesis:

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Published papers forming part of this thesis:


Published papers that include data collected as part of this thesis but are not included in this thesis:


Author statement and contributions

Author roles
The candidate contributed ideas, designed and undertook the majority of all fieldwork, conducted the analyses and wrote the manuscripts.

Stewart Nicol, Sarah Munks and Bradley Law contributed ideas and edited the manuscripts.
Susan Jones and Tamara Kabat contributed ideas, data collected from previous work and edited chapter 4.

We the undersigned agree with the above stated, “proportion of work undertaken” for each of the above chapters contributing to this thesis:

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Supervisors

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Bat researchers

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Abstract

**Abstract**

Sustainable forest management is increasingly being recognised as a key component of biodiversity conservation, as much of the world’s terrestrial biodiversity is dependent on forests. Understanding the effectiveness of approaches to forest management and how they are implemented on-ground in practice is crucial for the ongoing improvement of forest management strategies for biodiversity conservation. This is especially so in Tasmania’s dry Eucalypt forests where a range of land management practices, such as timber harvesting, have altered the type, amount and spatial arrangement of mature forest available to fauna. Using Tasmania’s hollow-roosting bats as a case study, the overall aim of this thesis is to gather information that can be used to assess the effectiveness of a multi-spatial scale approach to forest management, as applied on the ground in Tasmania. In particular this thesis aims to determine how effectively retained forest habitat provides suitable habitat for hollow-using bats, facilitates recolonisation of harvested areas and thus maintains bat populations in timber production landscapes.

Effectiveness monitoring for biodiversity conservation can be hampered by a lack of basic information on the species studied, as was the case in Tasmania. In order to understand the effectiveness of forest management strategies I first had to develop an accurate method for identifying bat calls recorded during bat call surveys. Bat call surveys were used to assess the spatial and temporal variation in bat activity, species richness and assemblages across and between landscapes. I then had to establish baseline data on the basic life history and activity patterns of Tasmanian bats to understand how temporal variation in bat activity is related to changes in the timing and patterns of reproduction. The findings of these studies fill a significant gap in our understanding of Tasmania’s bats. Notably, the discovery of the white-striped freetail bat in Tasmania during these studies highlights the importance of collecting such data and monitoring bat communities. Importantly the information derived from these
Abstract

studies provided the necessary information for using radio-telemetry and bat call surveys to investigate the effectiveness of forest management strategies for bats.

The main findings of this thesis were that no single forest retention measure was preferred by all bats or catered for all their habitat requirements (e.g. food, shelter and breeding sites). This is because species and individuals varied in their habitat requirements. Such differences are likely underpinned by variations in their social, physiological and ecological needs. The effectiveness of different forest retention measures for bats also varied between landscapes. In landscapes where mature forest was rare or lost, small patches (<1ha) and large strips (50ha) were used more extensively by bats than in landscapes where mature forest was more abundant. Not all species formed maternal colonies in such patches and strips, instead preferring large patches (>350ha) to breed. All species, however, did show a preference for roost areas, though not always roost sites, in parts of the landscape with the highest availability of hollow-bearing trees.

The findings of this thesis indicate that Tasmania’s current forest management strategies are effective at providing suitable habitat for bats, facilitating recolonisation of harvested areas and maintaining bat species in the landscape. They also support the multi-spatial scale approach to forest management as applied on the ground in Tasmania as a viable and effective way of conserving bats in Tasmania’s timber production forests. A ‘one-size-fits-all approach’ is unlikely to cater for the habitat requirements of all bats. These findings have important implications for the continued improvement of forest management strategies in human-modified landscapes and demonstrate that native forest management can be an important part of any biodiversity conservation strategy, provided that habitat is retained into the future at a variety of spatial scales and taking into consideration the broader landscape.
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CHAPTER 1: GENERAL INTRODUCTION

Kellevie – An example of timber production landscape in south-eastern Tasmania.
Biodiversity in changing forest landscapes

The maintenance of biodiversity is crucial for ecosystem functionality, and its loss has dire consequences for the stability, productivity and sustainability of natural resources (Foley et al. 2005; Hooper et al. 2005; Loreau et al. 2001). One of the major threats to the world’s biodiversity is the loss and modification of forest habitat, as forests support approximately 65 percent of known terrestrial biodiversity (World Commission on Forests and Sustainable Development 1999). Over the last century, forests have been cleared, modified and fragmented at an unprecedented rate as a result of the rapid expansion of urban, agricultural and pastoral areas, conversion of native forests to plantation and increases in timber harvesting to meet the growing needs of the human population (Foley et al. 2005). This has resulted in the decline and loss of many species, contributing to what has been described as a 21st century catastrophic extinction crisis (Novacek & Cleland 2001).

The mechanisms leading to the loss of fauna diversity are complex (Turner 1996). In the short term, many species can persist and take advantage of newly created habitat in areas where forest has been lost, modified or fragmented (e.g. Azevedo-Ramos et al. 2006). Some species, however, particularly those with restricted distributions, can go extinct immediately if the entire extent of habitat on which they depend is lost (Kuussaari et al. 2009). For those species that do persist, reduced dispersal ability, increased predation risk and competition, reduced availability of foraging, breeding and shelter sites and increases in the number of invasive species, diseases and parasite can have medium to long-term effects on populations (Ford et al. 2001; Kuussaari et al. 2009). These include altered sex ratios (Martin & Handasyde 2007) and social systems (Banks et al. 2007; Banks et al. 2005), increased mortality rates (Keyser et al. 1998), genetic isolation effects (Stephens et al. 2012b) and reduced breeding success (Burke & Nol 1998; Robinson et al. 1995). Such effects put species at risk of latent decline and extinction in the medium to long-term.
The loss of species sensitive to forest loss, modification and fragmentation can result in changes to forest community composition towards species that are more tolerant of forest loss and fragmentation (Barlow et al. 2006; Castelletta et al. 2005). Though only a few species may be lost as a result of disturbance to forest habitat, their loss can have a domino effect on the persistence of remaining flora and fauna. This is because many species play an important role in the persistence of other species and the functioning of forest ecosystems (e.g. insectivores, pollinators and seed dispersers) (Jones et al. 2009). These are the same ecosystems upon which humans depend upon for their needs. Therefore though biodiversity conservation is often considered to be detrimental to the utilisation of forests for human needs, it is in fact essential as biodiversity plays an important part in maintaining healthy stable forest ecosystems and regeneration post-disturbance (Burton et al. 1992). The challenge is how to achieve a balance between forest utilisation for human needs and biodiversity conservation.

**CONSERVING FOREST BIODIVERSITY: A MULTI-SPATIAL SCALE APPROACH**

It is well recognised that protected areas alone will not conserve the world’s biodiversity. This is because a large proportion of the world’s forests are unprotected and important habitat for many species occurs outside of protected areas. Protected areas are also not necessarily managed for their biodiversity benefits nor will they necessarily be protected indefinitely (FAO 2010; Lindenmayer et al. 2012; Mascia & Pailler 2011; Munks et al. 2009). Sustainable forest management in multi-use landscapes outside of protected areas (the matrix) is therefore promoted as a key component of any biodiversity conservation strategy (Lindenmayer et al. 2000; Saunders et al. 1993).

Many forest management agencies recognise this and incorporate measures for the conservation of biodiversity into forest management strategies (Munks et al. 2009; Polasky et al. 2005; Sergio & Pedrini 2007). In many cases however, there is little information on the habitat requirements of species to inform the development of such strategies. As a consequence, these strategies are often based on approaches used in other regions or accepted
Chapter 1: General introduction

sustainable forest management principles developed using ecological theory (Lindenmayer et al. 2006; Schulte et al. 2006).

The multi-spatial scale approach (also known as the matrix management approach) is often used by forest management agencies to guide the development of forest management strategies (Lindenmayer & Franklin 2002; Schulte et al. 2006). This approach aims to maintain forest habitat across a range of spatial scales in formal reserves and off-reserve areas guided by a series of principles supported by ecological theory (Lindenmayer et al. 2006). These principles aim to achieve biodiversity conservation through the maintenance of forest stand structural complexity, landscape heterogeneity and connectivity, integrity of aquatic ecosystems and an understanding of natural disturbance regimes to guide human disturbance regimes (Lindenmayer et al. 2006). This is generally achieved by developing forest management strategies that retain forest habitat at multiple spatial scales and configurations ranging from an individual tree, small patch and large strip to large patches in and surrounding disturbed areas (Munks et al. 2009; Whitford & Stone 2004).

Lindenmayer and Franklin (2002) identify four reasons why this multi-spatial scale approach is desirable: forest-dependent species occur at a range of spatial scales and have different spatial requirements; species may respond to a range of environment factors that impact at different spatial scales; there is interdependence between different scales (i.e. the influence of landscape context); and a multi-scaled approach is more likely to provide a heterogeneous landscape that is important for many species. Another advantage of this approach is that in the absence of empirical information on the habitat requirements of fauna, retaining forest habitat at multiple spatial scales across a landscape “spreads the risk “ by increasing the likelihood of a strategy or strategies being effective if a single strategy is not (Lindenmayer et al. 2006). The effectiveness of the multi-spatial scale approach in achieving biodiversity conservation is however poorly understood (Felton et al. 2010; Munks et al. 2009). Such research is an important part
of adaptive forest management, a principle that underpins many forest management systems around the world (Lindenmayer & Franklin 2002).

**USING BATS TO MONITOR THE EFFECTIVENESS OF FOREST MANAGEMENT STRATEGIES**

Jones et al. (2009) promotes bats as good bioindicators. This is because they exhibit taxonomic stability, population trends can be monitored, short- and long-term effects on populations can be measured and they are distributed widely around the world. Bats provide several ecosystem services (e.g. pollination and insect control) and so changes in their activity and abundance can also reflect the health of plant populations and insect communities (Duchamp et al. 2010; Jones et al. 2009; Kunz et al. 2011).

Bats are likely to be good indicators of the effectiveness of forest management strategies because most species depend on forests for foraging, socialising, mating, breeding or roosting habitat (Lacki et al. 2007). A range of studies have demonstrated that bats respond to forest loss, modification and fragmentation through changes in species richness, community structure, activity and roost site selection (Barclay & Kurta 2007). For example, changes to forest structure (i.e. the conversion of mature forest to regrowth) can have profound impacts on the ability of bats to manoeuvre and forage in regrowth forests resulting in reduced bat activity (Jung et al. 2012). Similarly a decline in the availability of hollow-bearing trees in the landscape is considered to have a detrimental influence on bat populations because of the dependence of many species on this resource for roost and breeding sites (Barclay & Kurta 2007), though no studies have clearly demonstrated this. Given these responses by bats, it is likely that bats will respond to mitigation measures such as the retention of forest patches in areas where forest has been lost, modified and fragmented.

The response of bats to forest management strategies is likely to vary between species. Species exhibit marked variation in their habitat use patterns depending on their traits such as wing morphology and echolocation call structure. Collectively such traits are referred to as
ecomorphology. Both wing morphology and echolocation call structure contribute to a bat’s ability to manoeuvre, navigate and capture prey (Saunders & Barclay 1992). Large species with long wings and low frequency calls generally select open areas and edges for foraging because they cannot manoeuvre easily through cluttered habitat (e.g. *Austronomus australis*). In contrast, small species with broad wings and high frequency calls (e.g. *Nyctophilus* spp.) generally select for more cluttered habitat such as the forest interior because they are more manoeuvrable in such environments (Hanspach et al. 2012). As a consequence ecomorphology can be used to make predictions of bat habitat use patterns around the world (Brigham et al. 1997; Ethier & Fahrig 2011; Hanspach et al. 2012) and may be an important consideration when understanding the effectiveness of forest management strategies for bats.

Figure 1. Examples of bat species with two distinct ecomorphologies. A) An open air specialist with long narrow wings and a low frequency echolocation call (*Austronomus australis*) and B) a clutter specialist (*Nyctophilus bifax*) with short broad wings and a high frequency echolocation call. Photos by Michael Pennay.

**RESEARCH CONTEXT: TASMANIAN FOREST MANAGEMENT STRATEGIES**

Prior to early European settlement it is estimated that 70% of Tasmania’s landmass was covered in forest. Over the last 260 years, clearing for agriculture, timber production, urbanization and plantation development has reduced the state’s forest cover to 49.5%. Of the remaining forest, over half is unreserved and potentially available for timber harvesting and
other human land use practices (Forest Practices Authority 2007) (Figure 2). As a consequence, off-reserve forest management for biodiversity conservation is crucially important, particularly as the formal reserve system is not representative in terms of forest type and region (Forest Practices Authority 2007). For example, many hollow-using species occur in the eastern half of the state in dry forests subject to human land use. The formal reserve network is, however, biased towards the western half of the state, making off-reserve management important for the conservation of many species (Koch et al. 2008b). This includes species such as the Swift Parrot, a species whose habitat lies mostly outside of the formal reserve system (Allchin et al. 2013; Munks et al. 2004).

![Figure 2. Tasmania’s formal reserve network and Eucalypt forest cover from Munks et al. (2009).](image-url)
In off-reserve areas in Tasmania, forests are utilised for a range of human land use practices which combined with natural disturbances (e.g. fire) have created landscapes comprised of a mosaic of mature forest, regrowth forest, native and non-native eucalypt and pine plantations, agricultural pastures and urban areas (Forest Practices Authority 2012). In off-reserve areas where timber production occurs, forests can be modified in a variety of ways depending on the silvicultural methods used. The type of silvicultural methods used to harvest forest depend on the forest type (Forest Practices Board 2000). Methods include a variety of partial harvesting techniques in dry forest (e.g. advanced growth or seed tree retention) and clear-fell burn and sow or aggregated/variable retention in wet forest (Neyland 2010; Wilkinson 1994)(Figure 3).

Figure 3. A visual comparison of the structure of Eucalypt (A) unharvested dry Eucalyptus forest and (B) partially harvested dry Eucalyptus forest (C) clear felled wet Eucalyptus forest and (D) aggregated/variable retention wet Eucalyptus forest.
Forest management strategies in off-reserve areas are delivered via the Tasmanian Forest Practices System (Forest Practices Board 2000; Munks et al. 2009). Through this system which is guided by the multi-spatial scale approach to forest management, habitat is retained on private and public forest at a range of spatial scales and configurations ranging from large patches and strips (e.g. informal reserves, visual landscape reserves, cultural heritage reserves, threatened species reserves, wildlife habitat strips) to small patches forest (e.g. wildlife habitat clumps) and narrow strips (e.g. streamside and roadside reserves)(Taylor 1991). Individual trees are also sometimes retained as part of a particular silvicultural method (i.e. partial harvest).

There are, however, gaps in our understanding of the effectiveness of these forest retention measures for fauna. Broad scale research has demonstrated that retaining forest habitat in timber production landscapes can maintain species diversity and richness (Flynn et al. 2011a; Wardlaw et al. 2012), though not necessarily species assemblages (Flynn et al. 2011a). Similar findings have been demonstrated when examining the effectiveness of specific forest retention measures such as wildlife habitat strips (Grove & Yaxley 2005; Grove; MacDonald et al. 2005; MacDonald et al. 2002). Finer-scale studies have demonstrated that though forest retention measures are used by some species as foraging, commuting and shelter habitat they are not necessarily used by all species similarly over time and space (Baker et al. 2009; Cawthen & Munks 2011; Cawthen et al. 2012; Haseler & Taylor 1993; Koch et al. 2009a; Koch et al. 2009b; Law & Law 2011; Lefort & Grove 2009; Stephens et al. 2012a; Wapstra & Taylor 1998). This is not surprising given the differences in the habitat requirements, range and dispersal abilities of different species. To make informed strategic decisions relating to forest management, managers need to understand which forest retention measures best meet the habitat requirements of different species and how much forest needs to be retained to maintain species in the landscape, for the short and long-term.
Figure 4. Examples of types of retained forest in partially harvested dry sclerophyll timber production landscapes.

Figure 5. An aerial view of a timber production landscape in south-east Tasmania (Source: Google Earth).
Chapter 1: General introduction

TASMANIA’S BAT COMMUNITY

Tasmania’s bat community consists of species entirely dependent on hollow-bearing trees for roost and breeding sites in forested areas (Koch et al. 2008b). Eight of Australia’s 67 micro-bat species are resident to Tasmania. This includes one bat species that is endemic to Tasmania, the Tasmanian long-eared bat. Vagrant mega-bats also arrive in Tasmania periodically (Figure 6) and it is possible that other bat species that are vagrant have gone undetected. Compared to mainland Australia, Tasmania has a low diversity of bats - all are micro-bats, from a single family (Vespertilionidae), are insectivorous and use tree hollows (Churchill 2009; Driessen et al. 2011). Tasmanian bats do, however, vary in their ecomorphology and as a consequence are likely to vary in their response to different forest retention measures (Table 1). Prior to the implementation of Tasmania’s current forest management strategies, Taylor and Savva (1988) concluded that if large areas of Tasmania’s forest were converted to regrowth forest, there would be a severe shortage of roosts and bat populations would probably decline. This was because their preliminary work indicated that although bats were found foraging in regrowth forest, none roosted there, instead selecting roosts in the mature forest surrounding the harvested area.

Information on the life history and ecology of Tasmanian bats is needed to inform the collection and interpretation of data required to answer questions about the effectiveness of forest management strategies. Such information is, however, limited because there have been few systematic studies on Tasmanian bats. For example, it was only recently discovered that Tasmania has an endemic bat species - the Tasmanian long-eared bat (*Nyctophilus sherrini*) (Churchill 2009; Parnaby 2009). This species was believed to be the Gould’s long-eared bat (*Nyctophilus gouldii*) and later to be the greater long-eared bat (*Nyctophilus timoriensis*) until a review by Parnaby (2009) determined that it was a unique species. Other studies have focused on Tasmanian bat distribution and natural history (Inada 2010; O’Neill 1983; Schulz & Kristensen 1996; Taylor et al. 1987; Taylor & O’Neill 1985), reproduction (Kincade 1999), roost use (Taylor & Savva 1988; Woinarski 1986), flight behaviour (O’Neill & Taylor 1986), diet (O’Neill
& Taylor 1989), activity patterns (Inada 2006, 2010; Taylor & Savva 1990), echolocation calls (Fueser 1997; Inada 2006, 2010; Rhodes 1996) and thermal energetics (Dixon & Rose 2003), but these studies have all been limited in scope and have had small sample sizes.

Figure 6. Tasmania’s eight resident bats (A-H) and one vagrant bat (I) A = little forest bat (Vespedelus vulturnus), B = southern forest bat (Vespadelus regulus), C = large forest bat (Vespadelus darlingtoni), D = eastern falsistrelle (Falsistrellus tasmaniensis), E = Tasmanian long-eared bat (Nyctophilus sherrini), F = lesser long-eared bat (Nyctophilus geoffroyi), G = chocolate wattled bat (Chalinolobus morio), H = Gould’s wattled bat (Chalinolobus gouldii) and I = grey-headed flying fox (Pteropus poliocephalus).
Table 1. Ecomorphology and ecological traits of Tasmanian insectivorous bats (Hanspach et al. 2012; O’Neill & Taylor 1986; Rhodes 1996; Threlfall et al. 2011).

<table>
<thead>
<tr>
<th>Species</th>
<th>Flight behaviour</th>
<th>Echolocation frequency</th>
<th>Foraging strata</th>
<th>Foraging area</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chalinolobus gouldii</em></td>
<td>Fast-flying, low manoeuvrability</td>
<td>Low</td>
<td>Canopy</td>
<td>Open area / edge</td>
</tr>
<tr>
<td><em>Chalinolobus morio</em></td>
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<td>High</td>
<td>Mid-canopy</td>
<td>Edge</td>
</tr>
<tr>
<td><em>Falsistrellus tasmaniensis</em></td>
<td>Fast-flying, low manoeuvrability</td>
<td>Low</td>
<td>Canopy</td>
<td>Edge</td>
</tr>
<tr>
<td><em>Nyctophilus geoffroyi</em></td>
<td>Slow-flying, high manoeuvrability</td>
<td>Linear</td>
<td>Ground - Understory</td>
<td>Clutter</td>
</tr>
<tr>
<td><em>Nyctophilus sherrini</em></td>
<td>Slow-flying, high manoeuvrability</td>
<td>Linear</td>
<td>Ground - Understory</td>
<td>Clutter</td>
</tr>
<tr>
<td><em>Vespadelus darlingtoni</em></td>
<td>Fast-flying, low manoeuvrability</td>
<td>Medium</td>
<td>Mid-canopy</td>
<td>Edge</td>
</tr>
<tr>
<td><em>Vespadelus regulus</em></td>
<td>Fast-flying, high manoeuvrability</td>
<td>Medium</td>
<td>Above understory</td>
<td>Edge</td>
</tr>
<tr>
<td><em>Vespadelus vulturnus</em></td>
<td>Fast-flying, high manoeuvrability</td>
<td>High</td>
<td>Above understory</td>
<td>Edge</td>
</tr>
</tbody>
</table>
Research objectives and thesis structure

**RESEARCH OBJECTIVES AND THESIS STRUCTURE**

The overall aim of this thesis is to assess the effectiveness of the multi-scale approach to forest management at providing suitable habitat for bats, enabling recolonisation of harvested areas by bats and maintaining Tasmanian bats in timber production landscapes.

This thesis is structured into a series of chapters written in the form of scientific manuscripts aimed at collectively addressing this overall aim.

**Chapter 2** describes the development of an effective approach for identifying bat call sequences collected during bat call surveys. This chapter includes descriptions of the variation in Tasmanian bat echolocation calls, compares different approaches to bat call sequence identification and provides a quantitative assessment of the effectiveness of the bat call identification approach used in the collection of data for chapters 3, 5 and 6.

**Chapter 3** presents and discusses the first evidence of a new bat species record for Tasmania, the bat call sequences of the white-striped freetail bat, recorded during data collection for chapters 5 and 6. These findings showcase the power of bat call surveys and the effectiveness of the approach for bat call identification described in chapter 2 for detecting new bat species.

**Chapter 4** examines the annual reproductive and activity cycles of Tasmanian bats and discusses how these cycles vary compared to lower latitude bat populations. The findings of this chapter inform the development and interpretation of results in chapters 5 and 6.
Chapter 5 investigates differences in roost site selection and behaviour of three Tasmanian bat species during the breeding season in two timber production landscapes. The aim of this chapter is to investigate how differences in the type, amount and spatial arrangement of mature forest influences the extent of bat roost use in retained forest patches in timber production landscapes.

Chapter 6 investigates bat activity, species assemblages and species richness in different types of retained forest patches in timber production landscapes. The aim of this chapter is to determine the importance of different types of retained forest patches for bats and how this varies temporally and spatially in timber production landscapes.

Chapter 7 synthesises the main findings of this thesis and discusses how they have contributed to expanding our knowledge of Tasmanian bats and evaluating the effectiveness of the multi-scale approach to forest management for bats. By collectively examining the main findings of chapters 5 and 6 this chapter finishes with recommendations for forest management.

Appendices provide additional information on Tasmanian bats prepared during the development of this thesis.
CHAPTER 2: THE EFFECTIVENESS OF DIFFERENT APPROACHES FOR THE DEVELOPMENT OF A BAT CALL IDENTIFICATION KEY FOR USE IN AUTOMATED SOFTWARE: A TASMANIAN CASE STUDY

A sonogram of a chocolate wattled bat (Chalinolobus morio) call sequence
INTRODUCTION

Insectivorous bats use echolocation calls to create a three-dimensional acoustic image for detecting prey and navigating throughout their environment. Bat echolocation calls vary between species, leading to their recording as a method to identify bat species assemblages, richness and activity patterns around the world (Kalcounis et al. 1999; Law et al. 1998; Wickramasinghe et al. 2003). Such survey methods are particularly useful in areas where species cannot be effectively detected through capture methods alone (e.g. species adapted to flying in open spaces - Duffy et al. 2000; Mills et al. 1996), where capture methods are not practical (e.g. wind farm monitoring at height - Johnson et al. 2004) or for long-term monitoring (e.g. species declines - Brooks 2011). One of the greatest challenges of undertaking bat call surveys is determining the most accurate and efficient approach to bat call identification.

The two most commonly used approaches to bat call identification are manual identification (O'Farrell et al. 1999) and statistical identification using multivariate statistics and machine learning algorithms (Britzke et al. 2011). Manual identification enables subjective bat call identification based on the users’ experience, but it is time consuming when dealing with large data sets, users cannot calculate a probability of accurate identification and identifications from different observers may not be directly comparable within or between studies (Parsons & Szewczac 2009). In contrast, statistical identification does not rely on the users’ prior experience, it is faster, and users can calculate a probability of identification enabling direct comparisons between users (Adams et al. 2010). Both approaches do, however, require a bat reference call library to make identifications of unknown calls (Parsons & Szewczac 2009).

Various studies have compared the success of different approaches to bat call identification in an effort to inform users of the most accurate and efficient approach. These studies have primarily focused on comparing statistical techniques (e.g. Armitage & Ober 2011; Biscardi et al. 2004; Britzke et al. 2011; Gannon et al. 2004; Preatoni et al. 2005; Redgwell et al. 2009), for example, comparing multivariate statistical techniques such as discriminant
function analysis with relatively modern approaches to classification problems such as machine learning techniques (Parsons & Szewczac 2009). These studies have found that machine learning techniques, such as neural networks, outperform the traditional approaches such as discriminant function analysis in most (e.g. Armitage & Ober 2011; Britzke et al. 2011), but not all cases (Preatoni et al. 2005). Statistical techniques such as random forests have also shown great promise as an alternative approach to neural networks, but few studies have reported on the accuracy of this approach (Armitage & Ober 2011).

Despite advances in statistical techniques for the identification of bat calls, there are several limitations of currently used approaches, such as negating a large proportion of the associated bat reference call library in an effort to avoid pseudo replication (Parsons & Jones 2000), a lack of ‘species-groups/complexes’ or ‘unknown/unidentified call’ categories to minimise the likelihood of misidentification of poor quality calls, complicated outputs (Adams et al. 2010) and an inability to quantify bat call parameters that describe call shape, which is an important parameter in manual identification using sonograms (O'Farrell et al. 1999).

A third and relatively new approach which overcomes many of the limitations of using manual identification and statistical techniques is using specialised computer software programs for bat call identification. Automated acoustical identification programs use either a pre-defined bat call classification key (AnaScheme: Adams et al. 2010) or use inbuilt classification algorithms to identify bat calls (SonoBat 2012; SoundID 2012; Wildlife acoustics Inc. 2013). Only one study has compared acoustical identification programs Sonobat and Song Scope with statistical techniques at correctly identifying the calls of five bat species from North America. Both programs were outperformed by the statistical technique ENN (Evolutionary Neural Network) by 35% and 25% respectively in relation to overall correct classification rates. Song scope did, however, perform as well as ENN for some species (Mirzaei et al. 2011). Despite this study, automated acoustical identification programs have several advantages over manual and statistical approaches, such as the ability to process large data sets, to use an entire reference call library encompassing the full
range of bat calls, identify poor quality ‘fragmented’ call sequences as unknowns, identify bat calls that overlap between species to a species group (also known as a complex) and to provide a measurable degree of accuracy independent of the users prior knowledge (Adams et al. 2010).

AnaScheme is an automated bat call identification software program (Gibson & Lumsden 2003) that has shown a great deal of promise in terms of accuracy and efficiency (Adams et al. 2010; Hanspach et al. 2012; Law & Law 2011; Lumsden & Bennett 2005; Threlfall et al. 2012b). AnaScheme has been developed using the Anabat bat recording system and has the ability to measure a range of bat call parameters that describe both call frequency and shape (Adams et al. 2010). However, because it uses pre-defined classification keys rather than inbuilt classification algorithms, more studies are required to develop methods for classifying calls and building identification keys. Research is also required to optimise how programs accurately and efficiently identify bat calls at a continental (e.g. Walters et al. 2012) and/or regional scale (e.g. Adams et al. 2010). Continental scale bat call identification techniques are new and allow objective, consistent and comparable species identifications across regions (e.g. Walters et al. 2012). In contrast, regional based keys make a trade-off between improved identification rates by taking into consideration different species assemblages present in a given region and the ability to readily compare the results of studies from different regions, where different keys will often yield different species’ detectability.

The island of Tasmania, 240 kilometres off the south-eastern coast of mainland Australia is home to eight of Australia’s 67 echolocating bat species - the lesser long-eared bat (Nyctophilus geoffroyi), Gould’s wattled bat (Chalinolobus gouldi), chocolate wattled bat (Chalinolobus morio), eastern falsistrelle (Falsistrellus tasmaniensis), little forest bat (Vespadelus vulturnus), southern forest bat (Vespadelus regulus), large forest bat (Vespadelus darlingtoni) and the endemic Tasmanian long-eared bat (Nyctophilus sherrini). Management issues potentially threatening Tasmania’s bats such as habitat loss, wind farms and disease require monitoring bat populations, although there are no existing monitoring programs (Driessen et al. 2011) except carcass monitoring at wind farms (Hull & Cawthen
Chapter 2: Bat call identification

2013). This may be in part a result of the difficulty in surveying bats through bat capture techniques alone. Bat call surveys are a potentially an efficient and accurate method for surveying Tasmania’s bats. Several studies have described Tasmanian bat calls (Fueser 1997; Inada 2006, 2010; Rhodes 1996) and two bat call identification keys have been developed at an island and regional scale, but both keys excluded species not captured and had small sample sizes (Inada 2010; Law & Law 2011).

The overall aim of this study was to develop an accurate and efficient approach for identification of Tasmanian bat calls for monitoring bats for management and conservation projects. This was achieved through: (1) understanding the interspecific variation in Tasmanian bat calls, (2) comparing the correct identification rates of three statistical techniques at identifying bat call sequences, (3) using the most appropriate statistical technique to create a bat call identification key for manual and AnaScheme identification and (4) using an independent set of calls not included in key development to evaluate the accuracy of AnaScheme as a tool for bat call identification.

**METHODS**

*Data collection*

Between October 2009 and March 2012 Tasmania’s eight bat species were captured using harp traps (2 bank, Faunatech, AUS) and mist nets (Ecotone, PL) set in gaps and along forest trails and outside known roosts in eucalypt forests and woodlands throughout 17 locations in Tasmania, ranging from the north-west to south-east. Harp traps were set in the late afternoon and checked after sunset, and before sunrise the following day. Mist nets were set at sunset and checked every 10 minutes for up to four hours after sunset. Upon capture all bats were identified to species using field guides (Churchill 2009; Taylor et al. 1987). Animals were weighed, sexed, aged and reproductive condition assessed following the methods outlined in Churchill (2009).

Bat call sequences, as described in Figure 7 and illustrated in Appendix 3, were recorded using Anabat SD1-2s and Anabat IIs connected to zero crossings analysis interface modules
(ZCAIM) (Titley Electronics, Australia). A ‘bat call’ was defined as an individual pulse of sound produced by a bat and a ‘bat call sequence’ was defined as a series of calls produced by a bat contained with a 15 second Anabat file (Adams et al. 2010).

To maximise the intra-specific variation in the reference call library, calls were collected in a variety of situations and, but where logistically possible, calls were recorded in open spaces such as small forest clearings and roadside edges where all bats (including clutter tolerant bats) had been observed flying. This approach provided two main advantages. Firstly, by recording calls in open spaces with a forest edge, a variety of different call types were recorded as the bats navigated in the open and closed areas of vegetation (e.g. clutter and open space calls). Secondly, this approach allowed us to extend the visual identification of bats in flight, enabling a larger number of bat reference calls to be recorded. The majority of calls were recorded from bats released from the hand post-capture and to a lesser extent upon release from rehabilitation and as individuals emerged from known roosts. Call sequences were recorded directly to a compact flash memory card in a time-date file and then downloaded onto a laptop for analysis. A small proportion of bat call sequences were used from bat call collections during previous work, which were recorded using Anabat IIs attached to ZCAIMS (Inada 2006, 2010; Law & Law 2010).

**Bat call analysis**

Bat call sequence files were initially processed by AnaScheme software (Gibson and Lumsden 2003) to extract call parameters (Table 2). AnaScheme reads bat call sequence files from Anabat bat detectors, displaying the sequences on a time-frequency graph (sonogram), fitting a model to the calls and allowing the user to extract parameters that describe the numerical features of the call for selected call models within the bat call sequence (Adams et al. 2010) (Figure 7). Not all reference calls recorded were included in analysis, as when bats emerge from roosts and are released post-capture they generally produced a steep ‘release/stress/excitement’ call of short duration and high bandwidth (Figure 7). Such calls were not characteristic of the calls produced by free-flying bats and were therefore omitted from the bat reference call library. Weak calls with poor call feature
representation, calls with poor model fit ($R^2<0.9$) to the data points, feeding buzzes, social calls, calls known to be made by other species and noise mistakenly modelled as calls were omitted from the analysis in an effort to reduce misidentification rates. In total, 20 bat call parameters considered meaningful for identification of calls (not sequences), the exclusion of noise (that is non bat calls) and poor quality calls were extracted from selected reference calls (Table 2).

Table 2. Description of bat call parameters extracted or derived from one or more parameters used to describe bat calls using the program AnaScheme as defined in Adams et al (2010).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model quality</td>
<td>Goodness of fit ($R^2$) of data points to call model</td>
</tr>
<tr>
<td>Number of points</td>
<td>Number of data points in a call</td>
</tr>
<tr>
<td>Duration</td>
<td>Time between the start and end data points of a call</td>
</tr>
<tr>
<td>Model curvature</td>
<td>Degree of curvature in the call model</td>
</tr>
<tr>
<td>Start frequency</td>
<td>Frequency of the first data point</td>
</tr>
<tr>
<td>End frequency</td>
<td>Frequency of the last data point</td>
</tr>
<tr>
<td>Minimum frequency</td>
<td>Frequency of the lowest frequency data point</td>
</tr>
<tr>
<td>Maximum frequency</td>
<td>Frequency of the highest frequency data point</td>
</tr>
<tr>
<td>Model frequency</td>
<td>Frequency of the call model at the time of the last data point (intercept in</td>
</tr>
<tr>
<td>Mean model curvature</td>
<td>Mean value of model curvature for all modelled calls in a sequence</td>
</tr>
<tr>
<td>Model average frequency</td>
<td>Average frequency, derived from the area under the call model</td>
</tr>
<tr>
<td>Model slope</td>
<td>Slope of the model; model slope = frequency / ((time^{\text{model curvature}}) − \text{model frequency})</td>
</tr>
<tr>
<td>Model end slope</td>
<td>Linear slope of the last half of the call model (halfway split based on time)</td>
</tr>
<tr>
<td>Model start slope</td>
<td>Linear slope of the first half of the call model (halfway split based on time)</td>
</tr>
<tr>
<td>Bandwidth a</td>
<td>Maximum frequency – minimum frequency of a call</td>
</tr>
<tr>
<td>CurvatureXModel start slope a</td>
<td>Model curvature x model start slope of a call</td>
</tr>
<tr>
<td>Start – End slope a</td>
<td>Model start slope – model end slope of a call</td>
</tr>
<tr>
<td>Start X End slope a</td>
<td>Model start slope x model end slope of a call</td>
</tr>
<tr>
<td>Tail a</td>
<td>End frequency – model frequency of a call</td>
</tr>
<tr>
<td>Tail 2 a</td>
<td>End frequency – minimum frequency of a call</td>
</tr>
</tbody>
</table>

* Data derived from two calls extracted from AnaScheme.
Chapter 2: Bat call identification

Three statistical techniques: discriminant function analysis, classification tree and random forests were compared to assess accuracy (bat call sequence misidentification) and detection (correction identification) ability of each approach and for later comparison with AnaScheme. Traditionally, discriminant function analysis has been used to identify bat calls and determine what bat call parameters are important for species identification (i.e. Parsons 1997), but more recently, classification trees (Adams et al. 2010) and random forests analysis (Armitage & Ober 2011) have been used. All three techniques vary in output, assumptions and ability to handle multi-species datasets, as detailed below.

Discriminant function analysis generates a linear combination of variables that maximises the probability of correctly assigning observations (i.e. bat calls) to their pre-determined groups (i.e. species) (Quinn & Keough 2002). This approach, however, has several limitations: it may not be appropriate for suites of groups (i.e. species) using large data sets (Gannon et al. 2004), assumes data is normally distributed, and is not able to handle highly correlated variables resulting in the exclusion of some bat call parameters that may be useful for identification (e.g. Armitage & Ober 2011). Alternative approaches such as classification tree and random forests may be more appropriate for multi-species datasets and correlated bat call parameters.

Classification trees and random forests are tree-based statistical techniques that use a non-parametric approach for conducting classification analyses by recursive partitioning. Unlike discriminant function analysis, they are very efficient at selecting from large numbers of predictor variables (Lunetta et al. 2004). Classification trees create a tree by recursively partitioning the observations (i.e. bat calls) into subgroups based on categorical responses (i.e. species). At each node of the tree, the explanatory variable (i.e. bat call parameter) giving the most homogenous sub-groups (i.e. species) is selected. In this study, classification trees were constructed using the ‘rpart’ package in R (De’ath & Fabricius 2000). Initially a large tree was constructed to include all bat calls and cross-validation using the “1-SE rule” to determine the optimal tree size (Maindonald & Braun 2007).
Chapter 2: Bat call identification

Random forests, an extension of classification tree analysis, is a machine learning technique that uses multiple classification trees to increase classification accuracy and stability, reduce the effects of bias and correlation among variables compared to classification trees (Cutler et al. 2007). Random forests grows multiple trees on a bootstrap sample of the observations (i.e. bat calls) and randomly selects potential predictors to determine the best split at each node on each tree. Those observations left out of the analysis (OOB) are used to estimate prediction error. Importantly, because each tree is grown from a different bootstrap sample, there is a different set of OOBs for each tree. The correct classification for each observation (i.e. bat call) is determined by the class with the most votes. Random Forests is also useful for measuring variable importance, as it provides an objective method of measuring variable importance (Cutler et al. 2007). For the purpose of this study, variable importance was measured by calculating importance scores using the mean decrease in accuracy measure for each parameter (Lunetta et al. 2004). The mean decrease in accuracy measure calculates the average decrease in prediction accuracies in the OOB portions of the data from the permuting values of the variables. The larger the mean decrease in accuracy value, the more important the variable. Although this technique does not produce a tree or model of any kind, it is useful to determine variable importance when little is known about variable interactions (Lunetta et al. 2004), so may be well suited for bat calls. All statistical techniques were performed in the statistical program R using the ‘MASS’, ‘mvpart’ and ‘rpart’ packages (R Development Core Team 2006).

The development of a bat call identification key

A bat call identification key was developed following the methodology outlined in Adams et al. (2010), which involved creating sub-sets of bat reference calls by manually selecting species calls that overlapped in model frequency. For each sub-set of bat reference calls, a bat call identification key was created using classification tree analysis as described previously. The results from random forests were used to assist in variable selection (Figure 9). The classification tree was pruned at a node when >90% of calls were assigned to a single species. If <90% of calls were assigned to one or more species, a species complex was formed. The final bat call identification key was constructed using Python programming.
Chapter 2: Bat call identification

ActivePython V2.2.1-222 by combining the bat call classification trees for each frequency-based sub-set of the reference call library. Additional classification trees were included in the key to exclude poor quality calls and noise (Appendix 2).

The following conditions were set in AnaScheme for testing the bat call identification key: call identifications were only made if model quality > 0.9, more than 50% of calls in a sequence were identified to the same species, at least 3 calls in total had to be identified to the same species. A sequence that could not be identified to species, using the species identification data for each call and the above conditions was classified as unknown. Further information on AnaScheme is available in Adams et al. (2010).

The accuracy and detection ability of the key was tested using reference call sequences not included in the development of the bat call identification key by running the initial key in AnaScheme and calculating the proportion of call sequences correctly identified (detection) and misidentified (accuracy). The results of this first test were used to refine the key to decrease misidentifications and where possible increase correct identifications. The refined key was then re-tested on the original test set and a set of calls of free-flying bats that were manually identified.

RESULTS

A total of 12,004 high quality bat calls from 537 call sequences were recorded from 446 individual bats. Sample sizes varied markedly, ranging from 147 to 3916 calls and 8 to 153 sequences per species (Table 3). Variation in the number of bat calls recorded resulted from a combination of low capture rates for several species (i.e. C. gouldii, F. tasmaniensis and N. sherrini) and post-release flight behaviour of circling around the area of release, which enabled a higher proportion of calls to be recorded per sequence (i.e. C. morio). Sonograms of bat reference calls are in Appendix 1.
Chapter 2: Bat call identification

An exploratory examination of the reference call collection showed extensive overlap in bat call parameters that described call frequency and shape, such as model frequency and model end slope. This was particularly evident for the two Nyctophilus spp., and for the three Vespadelus spp. and C. morio (Figure 2; Table 4). Although the two Nyctophilus spp. exhibited the broadest range of bat call frequencies they were easily distinguishable as a genus from all other species using the call parameter model end slope. Model end slope and other parameters describing call shape could not readily distinguish all the calls of C. morio and the three Vepsadelus spp. C. gouldii and F. tasmaniensis could be readily distinguished using the call parameters model frequency and model end slope.

Figure 7. Reference, feeding and social calls. (A) A reference call sequence showing stress and approach calls (B) details of an individual call showing the fit of the model (solid line) to the call data (dots) and selected parameters used for identification (C) shows sequences of feeding and social calls, which were excluded from the reference call library.
Using cross-validation to evaluate each statistical technique’s ability to correctly identify bat calls, random forests and classification trees performed better overall than discriminant function analysis (81% vs 79% vs 69%, respectively). Both random forests and classification trees varied markedly at correctly identifying particular bat species, with classification trees outperforming random forests for four of the eight bat species (Table 5).

Species whose calls overlapped extensively with other species in call frequency and shape were the most commonly misidentified (Table 5). *N. sherrini* calls were misidentified as *N. geoffroyi*. The three *Vespadelus* spp. and *C. morio* also exhibited relatively high misclassification rates, particularly *V. regulus* which was misidentified as *V. darlingtoni* and to a lesser extent *C. morio* and *V. vulturnus*. *C. gouldii*, *F. tasmaniensis* and *N. geoffroyi* exhibited the lowest misidentification rates of all bat species.

Overall, random forests was the most accurate statistical technique for bat call identification, the mean decrease in accuracy measure in random forests was used to evaluate the importance of each bat call parameter for each species’ call identification (Figure 9). The most important parameters for bat call classification were: model frequency, model end slope, minimum frequency, tail, end frequency and start X end slope. The relative importance of each bat call parameter for accurate species identification, however, varied between species. For example, model frequency was the most important bat call parameter for identifying *C. gouldii*, whereas model end slope was most important bat call parameter for identifying *N. sherrini*. 
Table 3. Details of bat reference calls collected for the development of a Tasmanian bat reference call identification key (n=12,004 bat calls; n=446 bats)

<table>
<thead>
<tr>
<th>Name</th>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Individuals</th>
<th>Locations</th>
<th>Sequences</th>
<th>Calls</th>
<th>Situation b</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chalinolobus gouldii</em></td>
<td>Gould’s Wattled bat</td>
<td>5</td>
<td>5</td>
<td>8</td>
<td>147</td>
<td>a</td>
<td></td>
</tr>
<tr>
<td><em>Chalinolobus morio</em></td>
<td>Chocolate Wattled bat</td>
<td>43</td>
<td>9</td>
<td>110</td>
<td>3916</td>
<td>a,b</td>
<td></td>
</tr>
<tr>
<td><em>Falsistrellus tasmaniensis</em></td>
<td>Eastern Falsistrelle</td>
<td>7</td>
<td>3</td>
<td>18</td>
<td>565</td>
<td>a,b,c</td>
<td></td>
</tr>
<tr>
<td><em>Nyctophilus geoffroyi</em></td>
<td>Lesser Long-eared bat</td>
<td>71</td>
<td>6</td>
<td>74</td>
<td>2012</td>
<td>a,b</td>
<td></td>
</tr>
<tr>
<td><em>Nyctophilus sherrini</em></td>
<td>Tasmanian Long-eared bat</td>
<td>18</td>
<td>4</td>
<td>21</td>
<td>367</td>
<td>a,b</td>
<td></td>
</tr>
<tr>
<td><em>Vespadelus vulturnus</em></td>
<td>Little Forest bat</td>
<td>82</td>
<td>9</td>
<td>53</td>
<td>1181</td>
<td>a,c</td>
<td></td>
</tr>
<tr>
<td><em>Vespadelus regulus</em></td>
<td>Southern Forest bat</td>
<td>141</td>
<td>12</td>
<td>100</td>
<td>1087</td>
<td>a,b</td>
<td></td>
</tr>
<tr>
<td><em>Vespadelus darlingtoni</em></td>
<td>Large Forest bat</td>
<td>80</td>
<td>11</td>
<td>153</td>
<td>2730</td>
<td>a,b</td>
<td></td>
</tr>
</tbody>
</table>

aExcludes individuals recorded at roosts as this is impossible to estimate. bSituation abbreviations: a= Recorded as bat was released post-capture, b= Recorded at known roost site, c= Upon release of rescued and / or rehabilitated bat.
Chapter 2: Bat call identification

Figure 8. The distribution of model frequency (left) and model end slope (right) values of Tasmanian bat reference calls (n=12,004 bat calls; n=446 bats).

Figure 9. Bat call parameter importance for identification measured using the MeanDecreaseAccuracy calculation in the random forests package. Higher values indicate greater importance of the call parameter to the predictive accuracy of bat call identification.
Five frequency-based sub-sets of the bat call reference collection were created based on model frequency groupings (63.2-51.3 kHz, 51.3-44.kHz, 41.5-44 kHz, 41.5-39.6kHz & 39.6-21.14kHz). Classification trees were run on each bat reference call sub-set and combined in Python to create a bat call identification key. When tested on the training reference call data set, the initial key had an overall correct identification rate of 75% and a misclassification rate of 4% resulting in an overall accuracy rate of call identification of 96%. Correct identification rates for species and species complexes ranged from 80 – 100% (Table 5).

Refinement of the initial key resulted in an increased correct identification rate of 13%, but no change in the misclassification rate and therefore overall accuracy rate (Table 5). For specific species, key refinement decreased misidentification rates for *N. geoffroyi*, but increased misidentification rates for *C. morio* by 2%. Tests of the refined key on the ability of the key to identify non-reference calls showed an 18% decrease in correct identification rates, a 2% decrease in misidentification rates and a 2% increase in overall accuracy rates resulting in correct identification rates ranging from 94 – 100% (Table 5).

**DISCUSSION**

This study was undertaken to develop the most accurate and efficient approach for identification of Tasmanian bat calls to facilitate surveying and monitoring for management and conservation purposes. The driver for this study was a need for bat call surveys to test the accuracy of bat call identification methods with independent reference call collections and using good sample sizes, particularly in novel regions where species may exhibit shifts in their call parameters. Unlike previous studies which have focused on comparing manual or statistical approaches of bat call identification, this study provides insights into a relatively new approach - bat call identification software (at the level of the bat call sequence) - with more traditional statistical approaches at identifying bat calls to species and species groups. Such studies are becoming increasingly important for the effective processing, in terms of accuracy and time, of large datasets which are now being collected as part of systematic studies and monitoring programs.
Similar to their mainland conspecifics, Tasmanian bats exhibited interspecific variation in echolocation calls, enabling calls to be identified to species (Milne 2002; Pennay et al. 2004). The level of inter-specific variation in echolocation calls was similar to that described in previous unpublished research on Tasmanian bat calls. The large number of bat calls recorded in this study also rectified the species identification issues of previous studies where either particular species were missing from datasets or reference calls were collected from bats not identified in the hand (Fueser 1997; Inada 2006, 2010; Law & Law 2011; Rhodes 1996).

It would be useful from a methodological and evolutionary biology perspective to compare bat calls from Tasmania with conspecifics on mainland Australia, and between different regions of Tasmania. Several studies have highlighted geographic variation in bat echolocation calls throughout species ranges in Australasia (Armstrong & Coles 2007; Law et al. 2002; Leary & Pennay 2011; Reinhold et al. 2001). In this study, comparison of geographic variation in bat calls between Tasmanian and mainland bats was confounded by issues of methodology, a lack of published descriptions of bat calls, and, when published, variations in bat call parameters used to describe bat calls (De Oliveira et al. 1999; Jones & Corben 1993; Law et al. 2002; Leary & Pennay 2011; Reinhold et al. 2001; Scanlon & Petit 2008).

Tasmanian bat species exhibit similar overlaps in bat call parameters to their mainland conspecifics (Pennay et al. 2004). Species such as *N. geoffroyi* and *N. sherrini* overlapped considerably in call parameters in Tasmania. Such overlap is well recognised on mainland Australia in the *Nyctophilus* genus and prevents the reliable identification of *Nyctophilus* to species level throughout its range using Anabats (Bullen & McKenzie 2001; Hanspach et al. 2012; Lumsden & Bennett 2005).
Table 4. A summary of the important bat call parameters for the identification of Tasmanian bats, detailing the mean ± standard deviation and (range) of adult morphological and call features (n=12,004 calls; n=446 individuals).

<table>
<thead>
<tr>
<th>Species</th>
<th>Bat call parameters</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Model frequency (kHz)</td>
<td>Minimum frequency (kHz)</td>
<td>End frequency (kHz)</td>
<td>Model slope</td>
<td>Model end slope</td>
<td>Start X Model end slope 2</td>
<td>Tail</td>
</tr>
<tr>
<td>C. gouldii</td>
<td>32 ±2 (24 - 35)</td>
<td>31±2 (26 – 35)</td>
<td>31±2 (26 – 36)</td>
<td>0.6±0.8 (0.0 – 4.0)</td>
<td>-0.95±0.80 (-4.02 - -0.04)</td>
<td>3.80±4.52 (0.11 – 22.4)</td>
<td>-1.32±1.13 (-5.06 – 0.9)</td>
</tr>
<tr>
<td>C. morio</td>
<td>47±2 (41 - 60)</td>
<td>46±2 (26 – 60)</td>
<td>46±2 (32 – 60)</td>
<td>1.1±2.4 (0.00 – 25.7)</td>
<td>-1.68±2.36 (-25.7 – -0.02)</td>
<td>18.44±47.95 (0.07 – 661.3)</td>
<td>-0.97±1.08 (-10.81 – 6.3)</td>
</tr>
<tr>
<td>F. tasmaniensis</td>
<td>36±2 (32 - 41)</td>
<td>35±2 (26 – 41)</td>
<td>35±2 (30 – 41)</td>
<td>0.1±0.2 (0.0 – 4.3)</td>
<td>-0.40±0.28 (-5.3 – -0.02)</td>
<td>1.59±3.0 (0.07 – 51.5)</td>
<td>-0.75±0.88 (-7.1 – 3.2)</td>
</tr>
<tr>
<td>N. geoffroyi</td>
<td>39±4 (24 - 59)</td>
<td>39±5 (22 – 59)</td>
<td>39±5 (23 – 59)</td>
<td>5.3±1.2 (-0.1 – 28.4)</td>
<td>-5.66±3.62 (-28.3 – -0.07)</td>
<td>61.13±80.64 (0.20 – 804.4)</td>
<td>-0.64±1.13 (-7.96 – 4.0)</td>
</tr>
<tr>
<td>N. sherrini</td>
<td>41±6 (29 – 63)</td>
<td>41±6 (29 – 63)</td>
<td>41±6 (29 – 63)</td>
<td>9.1±6.9 (0.1 – 29.6)</td>
<td>-8.93±6.14 (-29.5 – -0.06)</td>
<td>138.38±169.58 (0.27 – 873.5)</td>
<td>-0.28±0.99 (-3.59 – 4.0)</td>
</tr>
<tr>
<td>V. darlingtoni</td>
<td>43±1 (40- 51)</td>
<td>43±1 (35 – 47)</td>
<td>43±1 (37 – 47)</td>
<td>0.2±0.6 (0.0 – 15.6)</td>
<td>-0.39±0.56 (-8.9 – 0.00)</td>
<td>2.30±8.33 (0.00 – 89.5)</td>
<td>-0.20±0.42 (-4.48 – 3.5)</td>
</tr>
<tr>
<td>V. regulus</td>
<td>44±1 (41 - 52)</td>
<td>44±1 (40 – 51)</td>
<td>44±1 (40 – 51)</td>
<td>0.3±0.9 (0.0 – 16.4)</td>
<td>-0.78±0.56 (-12.2 – -0.04)</td>
<td>7.24±13.16 (0.17 – 250.94)</td>
<td>-0.50±0.63 (-2.88 – 2.2)</td>
</tr>
<tr>
<td>V. vulturnus</td>
<td>48±1 (43 - 52)</td>
<td>47±1 (41 – 51)</td>
<td>47±1 (41 – 51)</td>
<td>0.3±0.6 (0.0 – 7.2)</td>
<td>-0.56±0.50 (-5.3 – -0.01)</td>
<td>3.12±3.73 (0.00 – 53.1)</td>
<td>-0.10±0.40 (-4.93 – 1.7)</td>
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</tbody>
</table>
Table 5. A comparison of the % of calls correctly identified (detection rates) and overall mean identification rates of three statistical techniques (random forests, classifications trees and discriminant function analysis) for the classification of bat calls (pulses) to species level using selected bat reference calls recorded from eight sympatric bat species from Tasmania, Australia. All calls were recorded using the Anabat bat detector system.

<table>
<thead>
<tr>
<th>Species</th>
<th>Cgou</th>
<th>Cmor</th>
<th>Ftas</th>
<th>Ngeo</th>
<th>Nshe</th>
<th>Vdar</th>
<th>Vreg</th>
<th>Vvul</th>
<th>Mean% correctID</th>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. gouldii</td>
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<td>9</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.93</td>
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<td>0</td>
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<td>6</td>
<td>88</td>
<td>94</td>
<td>167</td>
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<td>1</td>
<td>9</td>
<td>0</td>
<td>0</td>
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<td>5</td>
<td>1884</td>
<td>60</td>
<td>11</td>
<td>2</td>
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<td>0</td>
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<td>% correct ID</td>
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<td>0.88</td>
<td>0.96</td>
<td>0.86</td>
<td>0.63</td>
<td>0.82</td>
<td>0.60</td>
<td>0.80</td>
<td>0.81</td>
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<tr>
<td>CTrees</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>C. gouldii</td>
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<td>6</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<td>0.86</td>
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<tr>
<td>C. morio</td>
<td>0</td>
<td>3551</td>
<td>0</td>
<td>27</td>
<td>6</td>
<td>81</td>
<td>129</td>
<td>146</td>
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<td>F. tamaniensis</td>
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<td>0</td>
<td>542</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td></td>
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<td>N. geoffroyi</td>
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<td>40</td>
<td>6</td>
<td>1919</td>
<td>237</td>
<td>25</td>
<td>6</td>
<td>1</td>
<td></td>
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<td>N. sherrini</td>
<td>2</td>
<td>5</td>
<td>0</td>
<td>37</td>
<td>120</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
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<tr>
<td>V. darlingtoni</td>
<td>0</td>
<td>77</td>
<td>10</td>
<td>8</td>
<td>1</td>
<td>2486</td>
<td>321</td>
<td>10</td>
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<tr>
<td>V. regulus</td>
<td>0</td>
<td>88</td>
<td>1</td>
<td>6</td>
<td>1</td>
<td>114</td>
<td>559</td>
<td>20</td>
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<tr>
<td>V. vulturnus</td>
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<td>155</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>21</td>
<td>32</td>
<td>1004</td>
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<td>% correct ID</td>
<td>0.86</td>
<td>0.90</td>
<td>0.95</td>
<td>0.96</td>
<td>0.32</td>
<td>0.91</td>
<td>0.53</td>
<td>0.85</td>
<td>0.79</td>
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<tr>
<td>DFA</td>
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<td></td>
<td></td>
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<tr>
<td>C. gouldii</td>
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<td>0</td>
<td>5</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.65</td>
</tr>
<tr>
<td>C. morio</td>
<td>0</td>
<td>3434</td>
<td>1</td>
<td>16</td>
<td>27</td>
<td>146</td>
<td>150</td>
<td>142</td>
<td></td>
</tr>
<tr>
<td>F. tamaniensis</td>
<td>16</td>
<td>0</td>
<td>470</td>
<td>13</td>
<td>0</td>
<td>66</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>N. geoffroyi</td>
<td>52</td>
<td>53</td>
<td>3</td>
<td>1697</td>
<td>186</td>
<td>6</td>
<td>10</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>N. sherrini</td>
<td>2</td>
<td>6</td>
<td>0</td>
<td>264</td>
<td>91</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>V. darlingtoni</td>
<td>0</td>
<td>136</td>
<td>26</td>
<td>14</td>
<td>4</td>
<td>2356</td>
<td>170</td>
<td>21</td>
<td></td>
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<tr>
<td>V. regulus</td>
<td>0</td>
<td>184</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>521</td>
<td>358</td>
<td>21</td>
<td></td>
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<tr>
<td>V. vulturnus</td>
<td>0</td>
<td>408</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>38</td>
<td>53</td>
<td>681</td>
<td></td>
</tr>
<tr>
<td>% correct ID</td>
<td>0.65</td>
<td>0.81</td>
<td>0.93</td>
<td>0.84</td>
<td>0.29</td>
<td>0.75</td>
<td>0.48</td>
<td>0.79</td>
<td>0.69</td>
</tr>
</tbody>
</table>
### Table 6. Identification rates of the 8 species of Tasmanian bats using automated bat call identification software  AnaScheme. n=number of call sequences, C= correct; I =incorrect; UID = those unidentified / unknowns; AC = Level of accuracy (100% - I%).

<table>
<thead>
<tr>
<th>Species</th>
<th>Initial key test on training calls</th>
<th>Key test on training calls 2</th>
<th>Key test on non-reference calls</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>C</td>
<td>I</td>
</tr>
<tr>
<td>C. gouldii</td>
<td>2</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>C. morio</td>
<td>228</td>
<td>87</td>
<td>1</td>
</tr>
<tr>
<td>F. tasmaniensis</td>
<td>3</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>N. geoffroyi</td>
<td>144</td>
<td>71</td>
<td>4</td>
</tr>
<tr>
<td>N. sherrini</td>
<td>51</td>
<td>23</td>
<td>4</td>
</tr>
<tr>
<td>V. darlington</td>
<td>2</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>V. regulus</td>
<td>4</td>
<td>60</td>
<td>20</td>
</tr>
<tr>
<td>V. vulturnus</td>
<td>6</td>
<td>83</td>
<td>0</td>
</tr>
<tr>
<td>Mean proportion</td>
<td>75</td>
<td>4</td>
<td>21</td>
</tr>
</tbody>
</table>

All bat call sequences of *N. geoffroyi* and *N. sherrini* were identified as *Nyctophilus* spp. All other species were identified to a combination of species and species complexes:  
- C. morio-V. vulturnus  
- V. darlingtoni-regulus  
- V. regulus-vulturnus  
- C. morio-Vespadelus sp.
Similarly, the three *Vespadelus* species in Tasmania (*V. vulturnus*, *V. regulus* and *V. darlingtoni*) exhibited broad frequency ranges in their calls, overlapping extensively in frequencies. Such overlap is similar to that observed in south-eastern Australia, where *V. darlingtoni* and *V. regulus* can call between 40 – 48 kHz and *V. vulturnus* between 43 - 53 kHz depending on region (Law et al. 2002). Law et al. (2002) investigated call frequency shifts in *Vespadelus* throughout New South Wales and found that all three species exhibited shifts in call frequency throughout their range. It is unclear what mechanisms are behind such shifts. Understanding shifts in bat call frequencies could increase our ability to identify species in particular regions where species may shift their call frequency in response to the presence of other species (Law et al. 2002). Future work in Tasmania should aim to quantitatively compare bat call variation throughout the island and if present, aim to use regional specific reference call libraries and identification keys to potentially increase accuracy rates.

The three statistical techniques evaluated in this study showed considerable variation in their ability to correctly identify Tasmanian bat calls. Overall random forests outperformed classification tree and discriminant function analysis at identifying bat calls (mean correct identification - 81% vs 79% vs 69% respectively). Identification rates were within 3% of each other for random forests and classification tree analysis, with classification trees outperforming random forests for identifying certain bat species calls. Several comparative studies have demonstrated that machine learning techniques such as neural networks and random forests perform better than discriminant function analysis at correctly identifying bat calls (Armitage & Ober 2011; Britzke et al. 2011; Parsons & Jones 2000; Redgwell et al. 2009). A review of the literature shows, however, that correct identification rates for bat calls vary markedly within and between species. For example, neural networks: 62% to 100% (Armitage & Ober 2011; Britzke et al. 2011; Jennings et al. 2008; Parsons 2001; Parsons & Jones 2000; Preatoni et al. 2005; Redgwell et al. 2009), random forests: 70% to 96% (Armitage & Ober 2011), discriminant function analysis - 71 - 87% (Armitage & Ober 2011; Parsons & Jones 2000; Preatoni et al. 2005), support vector machines (SVM): 87 - 96% (Armitage & Ober 2011; Redgwell et al. 2009),
adaptive regression splines 93% (Britzke et al. 2011) and classification trees: 56% to 95% (Adams et al. 2010; Herr et al. 1997; Preatoni et al. 2005).

It is important to recognise that when selecting an approach to bat call identification on the basis of accuracy rates, rates will vary depending on the type, number and degree of call overlap of species, quality of calls recorded, call recording technique, sample size of reference calls, subjective approach used to categorise calls, the software used to measure call parameters and the call parameters measured (Britzke et al. 2011; Herr et al. 1997; O'Farrell et al. 1999). For example, Parsons et al. (2001) reported a correct identification rate of 97% using artificial neural networks, whereas Preatoni et al. (2005) reported a much lower correct identification rate of 64%. The variation in accuracy rates between these studies is likely to be in part because Parsons et al. (2001) was classifying the calls of the only two extant echolocating bat species in New Zealand, which are considered to be readily identifiable from their calls. In contrast, Preatoni et al (2005) was classifying the calls of 20 bat species from Europe that overlap extensively in call parameters.

The selection of statistical technique depends on the type of output the user requires. Although random forest was the most accurate statistical technique for bat call identification and provided a means of rating call parameter importance for identification purposes, its output was not as easily interpretable as classification tree analysis, which produced a diagrammatic and coded tree. The benefit of classification tree output is that it can be used as a manual bat call identification tool and can be easily coded for use in automated bat call identification software - AnaScheme (Adams et al. 2010). In contrast, random forest is a more effective technique at determining the most important call parameters for bat call identification and can be used when building classification trees to improve accuracy rates.

AnaScheme shows considerable promise for accurate bat call identification, with an overall correct identification rate of 98% achieved in this study, outperforming the statistical
techniques of random forests, classification tree and discriminant function analysis. Only 2% of calls were misidentified. Unlike the statistical techniques tested, AnaScheme was able to classify poor quality calls as unknowns, which reduced the number of calls correctly identified to 70%, but greatly reduced misclassification rates to 2% of calls – much lower than statistical techniques. Calculating and minimising the misclassification rates of bat call identification approaches is important, particularly when detecting rare or threatened species where misidentification could have implications for research and management.

Like statistical techniques, the accuracy rate of bat call identification keys used in AnaScheme to identify bat calls varied across regions and species, with misclassification rates ranging from 0 to 0.7% of calls (Adams et al. 2010; Law & Chidel 2006; Lumsden & Bennett 2005). In Victoria, Lumsden and Bennett (2005) achieved an overall correct identification rate of 72% (range 32-100%) whereas in New South Wales Law and Chidel (2002) achieved 63% overall (range 33-100%) and Adams et al. (2010) 75.4% overall (range 20-100%). Misclassification rates of bat calls will depend largely on the particular assemblages of bats present in a region and the degree of overlap in their calls.

AnaScheme is one of few automated sound identification programs developed, but is unique in that it has been specifically designed for bat calls recorded using zero-cross analysis and frequency-division recorders such as Anabats (Adams et al. 2010). Other automated sound identification programs use full-spectrum call recordings from time-expansion recorders such as the Petterson D240X and EM3 include SonoBat, Song Scope and SoundID (Boucher et al. 2012; SonoBat 2012; SoundID 2012) and more recently Kaleidoscope which can use calls recorded in any format (Wildlife acoustics Inc. 2013). SonoBat is the only other automated sound identification program specifically designed for identifying bat calls. It uses a hierarchical decision algorithm-based approach that uses amplitude and time-frequency parameters of reference calls from across North American to identify bat calls. It shares many similar parameters to AnaScheme in that user-defined call quality can be assessed and poor quality
calls, noise and non-bat calls can be ignored to reduce misclassification rates. SonoBat classifies sequences to species and species complexes by generating a mean sequence decision of the calls identified in the sequence and provides a reportable level of identification probability (Kennedy 2011; SonoBat 2012). Like AnaScheme, manual identification is sometimes required for low frequency bat calls which can be confused with bird and insect noises or for bat species which are poorly represented in reference call libraries (Kennedy 2011). The main limitation of SonoBat however is that currently it only identifies the calls of North American bat species (Pennay 2012; SonoBat 2012).

Song Scope and Sound ID were originally developed for bird call identification (Agranat 2009; Boucher et al. 2012) and have only recently been applied to bat call identification (Boucher 2012; Pennay 2012). Like AnaScheme, Song Scope and Sound ID are not limited by region and can be used anywhere where reference calls have been collected. Unlike AnaScheme, Song Scope uses a classification algorithm approach that identifies call sequences based on specific patterns of interest (Syllables) rather than individual calls (Wildlife acoustics Inc. 2012). In contrast, SoundID uses a Geometric distance similarity measure approach to call identification. The limitations of both programs for bat call identification remain unknown.

Comparisons of the effectiveness of automated bat call identification programs at identifying bat calls are hampered by a lack of reporting on accuracy and detection rates for each program. Mirzaei et al. (2011) conducted the only study to compare automated bat call identifications – SonoBat and Song Scope – with four statistical techniques. That study reported that identification rates of five species of bat in North America varied markedly between species and identification method. Overall, Song Scope outperformed Sonobat for three of the five species with accuracy rates ranging from 25 to 100% and an overall accuracy rate of ~65 and 75%, respectively. In another study using 12 species, SonoBat was reported to have identification rates of 47.1% to species and 52.9% to species complexes (Kennedy 2011). Identification and misidentification rates of Song Scope are reported for birds and frogs (Brown et al. 2009; Hardin...
Waddle et al. 2009), but there is no reported data available for bats. Currently SoundID is being trialled on bats with no reported misclassification and identification rates available as yet (Boucher 2012).

Irrespective of the approach used for bat call identification, the user is limited by the intra-specific variability accounted for in the bat reference call library used. In this study, more bat reference calls for those species that overlapped in bat call parameters, such as Vespadelus spp. could possibly have decreased species misclassification rates and the ability to identify to species level. Other detecting systems, such as full spectrum detectors, may also record greater detail about calls enabling more accurate identification, but this has yet to be demonstrated for the species in this study (Parsons & Szewczac 2009). This study included multiple known sources of call variation in the reference call library, such as different body conditions, sexes, social groups and environments (woodland vs temperate rain forest) (Jones & Siemers 2011), which may have reduced classification rates when tested on known calls. It should have, however, increased the applicability of classification rates for unknown calls recorded in a variety of situations for which the key was developed (Britzke et al. 2011).

**MANAGEMENT IMPLICATIONS**

Bat call surveys are widely used and recognised as an invaluable technique for surveying bats for wildlife management and conservation, despite their inherent limitations. This is particularly so for those species not readily captured and for long-term studies and situations where trapping is impractical. Using the approach described here, users of bat detectors can make an informed decision on how to identify bat calls using empirical evidence of the accuracy rates of three statistical techniques and automated bat call identification program Anascheme. The future of bat call surveys as a technique for surveying echolocating bats lies in the continued improvement in bat call recording technology and particularly bat call classification techniques, targeting species that are currently considered to be problematic.
CHAPTER 3: WHITE-STRIPED FREETAIL BAT IN TASMANIA: RESIDENT, VAGRANT OR CLIMATE CHANGE MIGRANT?

A white-striped freetail bat (*Austronomus australis*) in Victoria, Australia.
INTRODUCTION

Australia has a diverse range of bat species distributed from the tropics to temperate regions. These bats belong to eight extant families, several of which occur in temperate south-eastern Australia (Churchill 2009). Tasmania, Australia’s largest island, off the south-east coast of the mainland, is home to only one of these families: the Vespertilionidae (Driessen et al. 2011). Vespertilionidae, ‘the evening bats’ is the largest family of bats in Australia, and one of the most widely dispersed groups of mammals in the world (Hall & Woodside 1989). It is surprising, however, that no other bat families occur on the island.

Tasmania has a cool temperate climate and this may explain the absence of other bat families. Resident Vesperptilionids are known to use prolonged torpor bouts (hibernation) to conserve energy in the colder months (Churchill 2009). Other bat families such as Molossidae ‘the freetail bats’, however, rarely use prolonged torpor bouts (Allison 1989; Arlettaz et al. 2000; Cory Toussaint et al. 2010) which may be limiting their southern distribution in Australia and explain their absence from Tasmania. A lack of systematic surveys of the distribution of bats throughout Australia could mean that some bat species and families may be more widespread than previously thought.

This paper describes the confirmed recording from bat call surveys of a ninth microbat species in Tasmania, the white-striped freetail bat (Austronomus australis), from the Molossidae. Bat call surveys have been used as an effective tool for expanding our understanding of the distribution of many microbat species from around the world, including Australia. I discuss three hypotheses: that it is (1) an undetected resident, (2) a vagrant, or (3) a species expanding or shifting its range.

METHODS

Bat call surveys were carried out using Anabat bat detectors (Model: II, SD1 and 2, Titley, Ballina, Australia) throughout Tasmania between December 2009 and January 2012 as part of a concurrent study on Tasmanian bats (Cawthen et al. unpubl. data), community night-
Chapter 3: White-striped freetail bat in Tasmania

walks and mammal surveys in which I was involved. Sampling effort and methodology was not consistent across surveys, as a combination of passive and active bat call survey approaches were used depending on the objectives of the survey. Surveys varied in duration from hours (i.e. community night walks) to weeks (i.e. concurrent study). Sampling was also strongly biased to the south-eastern region of Tasmania in eucalypt forests and woodlands in timber-production landscapes because this was where the concurrent study was being undertaken.

The files recorded by the Anabats were identified as containing bat call sequences (a series of calls produced by a bat contained within a 15 second Anabat file) that were then identified to species and species complexes (i.e. Nyctophilus spp.) using the automated bat call identification software AnaScheme (Adams et al. 2010). AnaScheme used a pre-defined echolocation call key for Tasmanian bats developed by Cawthen and Law (in prep) that included a sub-key for low frequency calls between 10 and 15 kHz in the known range of A. australis (Churchill 2009). This subkey was included because of the possibility of A. australis occurring in Tasmania based on previous unconfirmed reports in the 1980s (Martin Schulz, pers. comm.). The following specifications were set in AnaScheme: identifications were made only when a minimum of 50% of bat calls within a sequence were identified to the same species or species complex and only sequences with a minimum of three calls were identified to a species or species complex. If neither of these specifications were met, the sequence was identified as an unknown.

RESULTS

In total, 386,476 files were analysed in AnaScheme. Of the files recorded, six were identified as belonging to A. australis. I visually confirmed that these files contained calls of A. australis by viewing files as sonograms (time frequency graphs) in AnaScheme. A. australis produces a constant-frequency search-phase echolocation call that ranges from 11 to 13 kHz and is much lower than any other bat call in Australia (Churchill 2009) (Figure 10 & Table 7). To confirm these identifications, three bat experts familiar with the calls of A. australis (Brad Law, Michael Pennay and Greg Richards) were consulted and all confirmed that at least
some of these call sequences, those of high call quality, were that of *A. australis*. Most call sequences (five of the six) were recorded at Woodsdale (Figure 11), a region containing a mosaic of pasture, forest, woodland and plantation and where forest patches in timber-production landscapes were being surveyed weekly.

![Figure 10](image.jpg)

**Figure 10.** An example of the echolocation calls identified as that of a White striped freetail bat (*Austronomus australis*) in Tasmania recorded on 26/2/2010 at 21:55 hrs at Woodsdale, south-east Tasmania.

**Table 7.** Details of bat calls identified as White-striped freetail (*Austronomus australis*) from Tasmania. N=Number of calls in sequence, Fc = Characteristic frequency

<table>
<thead>
<tr>
<th>Date</th>
<th>Time</th>
<th>Location</th>
<th>N</th>
<th>Fc range (KHz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>26/02/2010</td>
<td>2057</td>
<td>Woodsdale</td>
<td>3</td>
<td>8.62 – 9.61</td>
</tr>
<tr>
<td>26/02/2010</td>
<td>2155</td>
<td>Woodsdale</td>
<td>29</td>
<td>9.48 – 11.43</td>
</tr>
<tr>
<td>25/03/2010</td>
<td>0212</td>
<td>Woodsdale</td>
<td>37</td>
<td>11.96 – 15.54</td>
</tr>
<tr>
<td>26/03/2010</td>
<td>0016</td>
<td>Woodsdale</td>
<td>8</td>
<td>11.12 – 16.50</td>
</tr>
<tr>
<td>28/04/2010</td>
<td>1846</td>
<td>Woodsdale</td>
<td>5</td>
<td>9.15 – 9.60</td>
</tr>
<tr>
<td>27/12/2011</td>
<td>0440</td>
<td>Binalong Bay</td>
<td>2</td>
<td>12.94-13.29</td>
</tr>
</tbody>
</table>
DISCUSSION

The White-striped freetail bat (*Austronomus australis* formerly *Tadarida australis*) is a mainland Australian endemic (Ammerman et al. 2012; Churchill 2009). The *A. Australis* call recordings presented in this paper provide the first confirmed record of this species in Tasmania. I discuss three hypotheses that may explain this new species record for Tasmania.

**Hypothesis 1: Undetected resident**

One possible hypothesis that is unlikely to be true given the evidence is that *A. australis* is a long-term member of the Tasmanian bat community but has previously been overlooked in Tasmania. This could be because people have been unfamiliar with its audible echolocation call, a regular metallic “ting...ting...ting...” (Churchill 2009), there have been no systematic bat call surveys undertaken (Driessen et al. 2011) and this species can be difficult to capture when present (Hourigan et al. 2008). Unconfirmed observations of this species have been
made in Tasmania previously by Martin Schulz, a researcher familiar with this species. In the 1980s he heard an audible call that he identified as *A. australis* and spotlighted a bat that resembled *A. australis* on the north coast of Tasmania and Flinders Island.

If this species were an undetected resident it is unlikely that it would have been overlooked during the numerous bat call surveys in areas of suitable habitat that have been conducted since the 1990s (see Driessen *et al.* 2010 for a review), particularly by Feuser (now Rhodes) (1997) who later studied this species on mainland Australia (Rhodes 2006). Carcasses of this species are also regularly found during wind farm mortality surveys on mainland Australia, yet no carcasses of this species have been recorded in mortality surveys at wind farms in north-west Tasmania (Hull & Cawthen 2013) suggesting that it is not a resident or if it is, it is not widespread or abundant.

**Hypothesis 2: Vagrant**

A more likely hypothesis given the evidence that *A. australis* has not been recorded in many parts of Tasmania in the 1990s is that this species is a periodic vagrant. Vagrant bats have been recorded previously, with flying foxes arriving periodically to mainland Tasmania and the Bass Strait Islands since the 1940s (Driessen *et al.* 2011). Though no micro-bats have been recorded as vagrants in Tasmania, micro-bats are known to be vagrants to islands throughout the world (Hutson *et al.* 2001) so it is entirely possible that they do arrive in Tasmania from time to time.

*Austronomus australis* can fly long distances (at least 50km in a night) (Rhodes 2006) and has been observed on several occasions flying over open water. For example, at Port Phillip Bay in southern Victoria, *A. australis* is frequently observed foraging over beaches and inshore waters, including hunting for insects, over 2km from the nearest land (Martin Schultz, pers.). In New South Wales, an individual *A. australis* was observed flying 6 km off Wollongong during the day (28/03/1999, SOSSA. 1999) and on two separate occasions, an individual was observed again during the day 46 km ESE of Sydney heads, over Browns Sea.
Mount (26/10/11 & 14/10/12, Dave James, pers. comm.). *Austronomus australis* has also been observed flying off the coast of Western Australia, 150 km south of Esperance, where a group of 14 individuals were observed to land at 2am on the radar mast of a shark fishing boat (Terry Reardon, unpublished data). Given these observations, this species is capable of flying between mainland Australia and mainland Tasmania, especially via the Bass Strait Islands.

During the same period that *A. australis* was recorded in Tasmania, flying foxes were also reported on mainland Tasmania and the Bass Strait Islands. These reports resulted in four specimens being collected, two of which were identified as the Grey-headed flying fox (*Pteropus poliocephalus*) (Driessen 2010). At the same time Grey-headed flying foxes also arrived in South Australia outside their normal range (Churchill 2009; Cox 2010). It is unlikely that these events are unrelated. There are several possible explanations to the arrival of these bats in Tasmania including strong wind fronts blowing bats southward, individuals becoming lost during migrations, or accidentally being introduced by humans in freight (O'Donnel 2009). Severe storms in 2010 that caused flooding, strong winds and extreme daily temperatures on mainland Australia may have caused both *A. australis* and *P. poliocephalus* to go outside of their normal range in search of suitable habitat, take advantage of favourable conditions outside of their range, become disorientated and or arrive assisted by strong northerly winds. The accidental introduction of these species to Tasmania in freight also cannot be ruled out but is unlikely given the number of flying foxes recorded.

**Hypothesis 3: Range extension / shift**

A hypothesis that cannot be overlooked is that *A. australis* is undergoing a range extension or shift into Tasmania. A range expansion of *A. australis* into Tasmania could occur in one of two ways: vagrant bats find suitable habitat in Tasmania and persist, or an overall movement of the population southward occurs increasing the probability of vagrants reaching Tasmania and establishing a breeding or seasonal population.
The historic absence of *A. australis* from Tasmania may be because this species cannot physiologically withstand Tasmania’s cool temperate climate or because climatic conditions make habitat (i.e. maternity roosts) unsuitable. If this were true and temperatures in Tasmania increase this species may be able to expand its southern distribution into Tasmania and to persist using a combination of short torpor bouts, seasonal migration or reduced activity during the cooler months to survive. This could be beneficial for the species if temperatures do not rise in its northern distribution. Temperature increases in its northern distribution could result in a range shift of this species because it is highly sensitive to high temperatures as a result of its inability to dissipate physiological heat during high-speed flight (Bullen & McKenzie 2005).

Increasing temperatures as a result of climate change has been implicated as a main driver of changes to the known ranges of many bat species around the world (Hughes et al. 2012; Humphries et al. 2002; Lundy et al. 2010; Richards et al. 2012). In Australia, several researchers have attributed range extensions of mega and micro-bats to climate change. Between 2005 and 2012, Bullen and Ford (2012) observed southwards range extensions of two micro-bat species – the Finlayson’s Cave Bat (*Vespadelus finlaysoni*) and Hill’s Sheath-tailed bat (*Taphozous hilli*). They suggested that this southwards range expansion was evidence of the effect of climate change making conditions more favourable for these species at the southern edge of their range (Bullen & Ford 2012). Similarly, Richards et al. (2012) suggest that the Grey-headed and Black Flying foxes and Little bent-wing bat have shifted their range southwards in response to climate change. However, as Roberts et al. (2011) point out, without quantitative analysis, climate change cannot be inferred as the primary driver of species range shifts.

**CONCLUSION**

Without previous systematic surveys of Tasmanian bats and their distribution it will remain unknown whether *A. australis* is a resident, a vagrant, or is expanding/shifting its range into Tasmania. The evidence suggests that it is unlikely that this species is a long-term resident and is highly likely that it is a vagrant that periodically arrives in Tasmania. Large-scale bat
monitoring programs such as Climate Watch’s *Tadarida australis* monitoring program (ClimateWatch 2012) could provide evidence to support or refute whether this species is expanding or shifting its range into Tasmania and whether climate change is driving this. Voucher specimens, video and photographs are also required to further verify this species in Tasmania. Understanding whether bat communities are changing is critical given the range of threats that species are under and the important functional role bats play in the environment.
CHAPTER 4: THE REPRODUCTIVE AND ACTIVITY CYCLE OF TASMANIAN BATS: IMPLICATIONS FOR BAT MONITORING

A juvenile chocolate wattled bat (*Chalinolobus morio*)
Chapter 4: The reproductive and activity cycle of Tasmanian bats

**INTRODUCTION**

Understanding the reproductive patterns of bats is essential to their conservation and management (Cryan et al. 2012), yet relatively little is known about the timing and patterns of reproduction of many bat species. This is despite bats being one of the most widespread, diverse and abundant vertebrate groups on the planet (Hutson et al. 2001; Mickleburgh et al. 2002). Such information is crucial when undertaking bat monitoring, as the timing and patterns of reproduction are associated with changes in bat activity (Daniel et al. 2010; Mackie & Racey 2007; Russ et al. 2003; Rydell 1993), social behaviour (Behr & Von Helversen 2004) and roost site selection (Lumsden et al. 2002b; Patriquin et al. 2010). When life history information is lacking from a given region, many researchers use information on the reproductive and activity cycles of conspecifics in other regions or closely related species (Churchill 2009). However information on the reproduction of bats is not readily transferable from one region to another because of latitudinal variation in the timing and patterns of reproduction.

Throughout the world insectivorous bats exhibit a diverse range of reproductive patterns (Racey & Entwistle 2000). Variation in the timing of reproductive patterns amongst bats are linked to environmental factors and the influence these have on resource availability, particularly food supplies (Greiner et al. 2011a). Bats are believed to time their reproductive cycle so that the most energetically demanding reproductive stages, such as lactation and weaning of young, coincide with optimal resource availability (Heideman 2000).

Environmental factors such as photoperiod, temperature and rainfall have all been directly or indirectly associated with variation in the timing and patterns of reproductive stages in bats (Greiner et al. 2011a; Greiner et al. 2011b).

For wide-ranging bat species, the timing and patterns of reproductive stages are known to vary throughout their range as environmental factors vary with latitude (Racey & Entwistle 2000). In temperate regions, environmental factors vary markedly between winter and summer, affecting the availability of food resources (Racey & Entwistle 2000). As a
consequence, temperate insectivorous bats exhibit a seasonal monoestrous breeding pattern because of the necessity for most species to hibernate during periods of low food availability and high energetic costs, such as winter (Bernard & Tsita 1995; Turbill & Geiser 2008). In tropical and sub-tropical regions, less pronounced seasonality in environmental conditions enables bats to remain active year round (Milne et al. 2005) resulting in a range of breeding patterns ranging from seasonal monoestry and polyoestry through to multimodal polyoestry (Happold & Happold 1990). Many Australian insectivorous bat species range from the tropics to temperate regions (Churchill 2009), but there are no published studies on how the timing and patterns of reproduction and activity vary across their range.

Tasmania represents the highest latitude bat population in Australia (located at 43° South). Like bat species around the world, Tasmania’s bats are faced with impacts from human activities such as habitat loss and mortality from wind farms (Hull & Cawthen 2013; Taylor & Savva 1988), yet little is understood about the reproductive and activity patterns of Tasmanian bats to inform conservation and management. Two of Tasmania’s eight bat species: the Gould’s wattled bat (*Chalinolobus gouldii*) and the lesser long-eared bat (*Nyctophilus geoffroyi*) are widespread throughout Australia, ranging from southern Tasmania to the northern tropics of Australia. For these species, the timing of reproductive stages, such as lactation has been reported to be later with increasing latitude (Churchill 2009). Of the chocolate wattled bat (*Chalinolobus morio*), eastern falsistrelle (*Falsistrellus tasmaniensis*), little forest bat (*Vespadelus vulturnus*), southern forest bat (*Vespadelus regulus*) and large forest bat (*Vespadelus darlingtoni*) species, little is known of the variation in their reproductive patterns throughout their range. There is no information on the timing and patterns of reproduction in Tasmania’s endemic long-eared bat (*Nyctophilus sherrini*) which could be crucial for the conservation of this species.

It is expected, given Tasmania’s island maritime climate and high latitude, that Tasmanian bats would alter the timing of reproductive stages from their mainland conspecifics because of environmental differences between populations. Based on limited data, several studies have documented variations in Tasmanian bat reproduction and physiology compared to
Chapter 4: The reproductive and activity cycle of Tasmanian bats

mainland conspecifics. Taylor et al. (1987) reported that Tasmanian bats tend to be larger than their mainland conspecifics which may in part mitigate against the effects of environmental extremes in temperature (Racey & Entwistle 2000). Kincade et al. (1999; 2000) reported that some Tasmanian bats exhibited a shift in the timing of reproductive stages compared to their mainland conspecifics, and that duration of lactation was shorter in Tasmanian bats. Expanding on the work of Kincade et al. (1999; 2000), Dixon and Rose (2003) reported that Nyctophilus geoffroyi exhibited physiological differences between Tasmania and mainland Australia, such as lower basal metabolic rates and a 10°C downward shift in the ambient temperature at which torpor is utilised. Dixon (2000) also reported that Tasmanian Nyctophilus geoffroyi produce fewer offspring than their mainland conspecifics as a potential adaptation to relatively low resource availability compared to mainland populations.

The overall aim of this study was to provide the basic reproductive and activity data on Tasmanian bat species necessary for the undertaking of bat monitoring programs for management and conservation. The specific aims of this study were to describe the reproductive cycle of Tasmanian bat species including the timing and patterns of reproductive stages, to examine whether Australian bat species exhibit latitudinal variation in their reproductive patterns, and to determine the relationship between the reproductive and activity cycle of bats and discuss the implications for bat monitoring.

METHODS

The timing and patterns of reproductive stages in Tasmanian bats was investigated by using data collected from the external physical examination of bats and hormone profiles. Both physical examination and hormone profiles have been used successfully to determine the reproductive stages of bats in previous studies of Australian insectivorous bats (Hosken 1997; Lloyd et al. 2001; Phillips & Inwards 1985).
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External physical examination of bats

Data collected in the field were supplemented with data collected from museum specimens (in particular collection notes of the physical examination of specimens stored in ethanol at time of collection - (Tasmanian Museum and Art Gallery, Queen Victoria Museum and Art Gallery), published research (Green 1965, 1966; Green 1988; Green & Rainbird 1984; Tyson 1981) and unpublished theses (Dixon 2000; O’Neill 1984). Data were collected from bats throughout mainland Tasmania.

The majority of field data were collected over two periods: October 1998 to April 1999 and October 2009 to December 2011 during two separate studies (1998 – 1999 Kincade; 2009-2011 Cawthen). Both studies captured bats in the field using standard two banded harp traps (Faunatech, Australia). The later study (2009-2011 Cawthen) also used four shelve nylon and monofilament mist nets (Mesh – 20x20mm, Ecotone, Poland) set in open spaces in the forest and outside known roosts. Upon capture all bats were identified to species using a combination of field guides (Churchill 2009; Parnaby 1999; Taylor et al. 1987). Forearm length, weight and descriptions of the sex, reproductive stage and relative age of each animal (adult, sub-adult, juvenile) were also recorded.

For females, there are four stages of reproduction that can be assessed by external physical examination: non-reproductive (nipples regressed or absent); pregnant (palpable foetus in abdomen); lactating (nipple enlarged, area surrounding the nipple hairless with milk production evident); and post-lactating (nipples prominent but fur regrowing and no milk production evident). For males, six stages of reproduction were assessed by external physical examination and categorised as: 0 (testis not enlarged: non-reproductive); 1 to 3 (testis enlarged, testis increasing in size from 1 to 4mm: sperm production); 4 (peak testicular development, testis increasing in size from 4 to 7mm, epididymis distended: sperm production and storage); and 5 (testis regressed with distended epididymis: sperm storage). These reproductive classifications were adapted from Phillips and Inwards (1985) and Churchill (2009).
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_Hormone profiles_

Concentrations of reproductive hormones (progesterone and testosterone) were measured in blood samples taken from live bats in the field between 1998 and 1999 by Kincade (2000). Blood samples were taken from the brachial vein of the wing and through piercing small peripheral veins running through the propogial (elbow joint) and uropatatalig (tail) membranes. To enable blood sampling of live bats, bats were held in a restraining device (Kabat & Kincade 2000). The blood sampling location on each bat was swabbed using 70% ethanol to disinfect and to increase blood vessel dilation. Heat from a lamp was also used to increase blood flow. The vein was punctured using a 25 gauge needle and blood collected into a heparinised capillary tube (sample size: 10 to 100µl). In the lab, plasma was separated by centrifugation and stored at -20 °C.

Plasma progesterone and testosterone concentrations were determined using standard radioimmunoassay techniques after extraction via column chromatography as described by Jones and Rose (1992). These were conducted by Kincade (2000). Due to very low volumes of plasma from the bats, the assays could not be validated specifically for bat plasma. However, the hormone assays have been validated for both reptilian and mammalian species, and there was no reason to believe that the validations would not hold for bat plasma. Where possible, 50µl samples of plasma were assayed to optimise assay precision. However, in the majority of cases, this was not possible and so the assay results were adjusted accordingly. When plasma samples were less than 20 µl, samples from two to three animals of the same species, judged to be of similar reproductive condition and collected within the same two week period were pooled.

_Bat activity_

Bat call surveys were conducted throughout south-eastern and northern Tasmania as part of a concurrent study (chapter 6). Bat activity, the total number of bat call sequences recorded per night comprised a range of bat calls indicating searching, feeding, commuting and socialising activities.
Bat call surveys were undertaken during four sampling periods between December 2009 and 2010 using Anabat detectors (models SD1 and SD 11, Titley Electronics, Ballina, Australia). Each sampling period coincided with assumed periods in the annual cycle of bats: the maternity season (Summer: December – February); mating/post lactation season (Autumn: March – May); non-reproductive/overwintering season (Winter: June – August); and pregnancy/post hibernation (Spring: Sep – Nov).

At each site, Anabat detectors were set in waterproof PVC boxes. A microphone extension cable ran from the PVC box up a 1.5 metre stake to the microphone attachment. The microphone attachment was angled up at 45° pointed into vegetation gaps of the habitat element being surveyed and enclosed in a PVC elbow for weatherproofing. Detectors were calibrated against each other using a bat chirp board (Nevada Bat Technology, Las Vegas, USA) to ensure microphone sensitivity was equal across detectors. Most studies record only for the night (Hanspach et al. 2012) but bats can be observed flying during the day when disturbed from roosts (Webala et al. 2010) so bat call surveys were conducted over a 24-hour period.

Once files containing bat call sequences were downloaded, calls recorded on days where detectors failed (drained batteries) were excluded. Although it is common to also exclude or avoid sampling on nights based on poor weather conditions (Hanspach et al. 2012; Threlfall et al. 2011) because of the correlation between bat activity and temperature (De Oliveira et al. 1999), this was not done in this study. Instead, environmental variables of daily rainfall and minimum and maximum temperature from nearby weather stations were incorporated into the analysis.

The number of bat call sequences recorded per night was averaged across all sites as a measure of mean monthly bat activity. A detailed analysis of variation in bat activity between sites is available in Chapter 6. Bat call sequences were recorded onto a compact
flash memory card as individual files for analysis in the bat call identification program AnaScheme (Adams et al. 2010) following the methods outlined in Chapter 1.

Environmental data

Two environmental factors were examined: mean monthly minimum temperature and day length. Both temperature and day length have previously been associated with variations in the reproductive patterns of bats (Racey & Entwistle 2000). Data were extracted from the Bureau of Meteorology from the Australian Reference Climate Station (Levedale weather station – within a range of 8 - 20km of each site). Day length was calculated as the time between sunrise and sunset.

Statistical analysis

One-way analysis of variance (ANOVA) was used to test for significant variations in plasma reproductive hormone concentrations between reproductive stages within species. Fishers LSD post hoc tests were used to identify significant groups within treatments. For combined data (not normally distributed), a Kruskal-Wallis one way analysis of variance on ranks with Dunn’s pairwise multiple comparison was used to examine significant difference in plasma hormone concentrations between reproductive stages and months. All data analysis was undertaken in the statistical program R (R Development Core Team 2011).

RESULTS

Timing and patterns of reproductive stages

In total, 823 records were obtained from field and historical data collected between 1938 and 2011 (female = 383, male = 411, unsexed juveniles = 29). Of these, 657 were collected from field data between: 1998-1999 (n=246) and 2009 to 2011 (n=443), all other data were collected from museum specimens (n=91) and previous studies (n=50). By species, 201 records were from *V. regulus*, 159 from *V. vulturnus*, 200 from *V. darlingtoni*, 99 from *C.*
morio, 13 from C. gouldii, 16 from F. tasmaniensis, 116 from N. geoffroyi and 19 from N. sherrini. The uneven sample sizes reflect relative capture rates of bats in the field.

An overview of the timing over which different reproductive stages occur for all bat species in Tasmania is provided in Figure 12. The earliest pregnancies were recorded in October (n=4), with 95% of pregnancies detected between November and January (n=77). Lactating females were recorded between late October and February, but as late as March (n=2), with 94% of lactating females recorded between December and February (n=115). Non-volant and volant juveniles were recorded between November and April (n=50). Testicular growth began in December (n=16) and peaked between January and March (n=28). Testicular regression and enlargement of the epididymis was recorded between January and May (n=14). During March, 68% of all males showed testicular regression and enlargement of the epididymis. Non-reproductive males and females were recorded throughout the year.

**Bat activity**

In total, 33,722 bat call sequences (passes) were recorded during 1,388 nights of bat call surveys between December 2009 and 2010. Three types of bat calls were distinguished: search phase, foraging and social calls (as described in chapter 2). Search phase and foraging calls were recorded throughout the year but social calls only occurred during autumn and early spring.

Overall, mean monthly bat activity was lowest and least variable between May and September during periods of low mean minimum temperature and short day length. Bat activity steadily increased from October onwards, peaking in January, when mean minimum temperatures were highest (Figure 12).
**Variation in the timing of reproductive stages of females**

An examination of the variation in the timing of reproductive stages between species showed that the smallest bat species (<7 grams) - *V. vulturnus, V. regulus and V. darlingtoni* were pregnant earlier (between October and December) than larger bat species, (>7 grams) - *N. geoffroyi* and *C. morio* (November – January)(Figure 13). Females of the species *N. sherrini* and *F. tasmaniensis*, were pregnant in December and lactating between January and February. No data was obtained on the reproductive condition of other bat species.

Insufficient data were collected to enable investigation of variations in the timing of birth so duration of lactation could not be estimated. However trapping at one site did reveal interspecific variation in the timing of birth between two bat species. During January 2011, *N. geoffroyi* juveniles were fully furred and learning to fly at the same time a *C. morio* unfurred young was observed. These observations support the data collected on bat reproductive condition of these two species (Figure 13).

![Reproductive stage diagram](image)

**Figure 12.** The relationship between periods of bat reproductive stages, mean bat activity ± standard error (○), day length (–) and mean minimum temperature (○) throughout the year in Tasmania, Australia.
Chapter 4: The reproductive and activity cycle of Tasmanian bats

Figure 13. A comparison of the periods over which different female reproductive stages can occur for eight insectivorous bat species in Tasmania, Australia. Fa (Forearm length) and weight measurements represent averages.

Hormone profiles

Plasma progesterone concentrations were measured in *V. darlingtoni*, *V. regulus* and *C. morio*. Samples of different species were pooled because of low sample sizes. Plasma progesterone concentrations were significantly higher in pregnant bats compared to those recorded in non-reproductive and lactating bats (Kruskal-Wallis test, $H=22.8$, df=3 $P=<0.001$). Pregnant bats also showed the greatest variance in plasma progesterone concentrations. For example the lowest concentrations of plasma progesterone were recorded for two non-reproductive and one pregnant bat (0.03, 0.31 and 0.41 ng ml$^{-1}$ respectively). Plasma progesterone concentrations were highest in November (Figure 15) coinciding with the timing of pregnancy in these species (Figure 13).

Plasma testosterone concentrations were measured in male *V. darlingtoni* and *C. morio*. Plasma testosterone concentrations varied within and between reproductive stages (Figure 14). For *V. darlingtoni*, significantly higher plasma testosterone concentrations were recorded during testicular regression and epididymis distension (stage 5) compared to all other reproductive stages (Mean=37.7±5.2 ng ml$^{-1}$; Range = 21.2-50.2 ng ml$^{-1}$; ANOVA: $F_{5,41}=3.55$, $P=<0.01$) and the lowest for bats with little and no testicular growth (stage 0-1,
0.7 to 1.1 ng ml\(^{-1}\)). However, for \textit{V. darlingtoni}, the highest testosterone concentrations of 64.9 and 77.6 ng ml\(^{-1}\) were recorded from bats with early testicular growth (stage 3 and 2 respectively) rather than peak testis size (stage 4). Similarly, for \textit{C. morio}, the highest testosterone concentrations were recorded from bats with no testicular development (stage 0) and testicular development (stage 2) at 39.2 and 32.8 ng ml\(^{-1}\) respectively.

An examination of plasma testosterone concentrations across months was also undertaken because plasma testosterone may also be associated with mating behaviours such as social calls (Figure 15). Samples of different species were pooled because of low sample sizes. Plasma testosterone concentrations were significantly higher in February and March compared to November to January (Kruskal-Wallis test: \(H=37.045, df =4, P=<0.001\)) coinciding with the recording of social calls (Figure 12).

**DISCUSSION**

Tasmanian bat species exhibited seasonal patterns of reproduction typical of hibernating temperate insectivorous bats worldwide (Racey & Entwistle 2000). Females were pregnant in late spring and summer with lactation finishing in early autumn prior to periods of what is presumed to be prolonged torpor (hibernation). Males produced and stored sperm during summer and early autumn, coinciding with the end of lactation and juveniles becoming volant. This pattern of reproduction, known as seasonal monoestry, also occurs in bats throughout mainland Australia (Hosken 1997; Hosken et al. 1998; Hosken et al. 1996; Kitchener 1975; Kitchener & Coster 1981; Kitchener & Halse 1978; Lumsden & Bennett 1995; Phillips & Inwards 1985; Phillips et al. 1985; Tidemann 1993; Young & Ford 2000) and in other temperate bats throughout the world (Northern: Krutzsch & Nellis 2006; Southern: Le Grange et al. 2011).

There was a strong association between the reproductive stages of bats (assessed through physical examination) and concentrations of reproductive hormones. This relationship was strongest in females, which showed increased concentrations of plasma progesterone during pregnancy. This is not surprising, as progesterone is a reproductive hormone involved
in the maintenance of pregnancy and has been used in previous studies to assess the reproductive stages of female bats (Lloyd et al. 2001).

**Figure 14.** Mean female plasma progesterone concentrations (left) for pooled samples from *C. morio, V. darlingtoni* and *V. regulus* and mean male plasma testosterone concentrations for pooled samples from *V. darlingtoni* and *C. morio* by reproductive stage.

**Figure 15.** Mean female plasma progesterone concentrations (left) for pooled samples from *C. morio, V. darlingtoni* and *V. regulus* and mean male plasma testosterone concentrations for pooled samples from *V. darlingtoni* and *C. morio* by months sampled.

Plasma progesterone concentrations varied between reproductive stages, but also varied greatly between individuals, particularly those that were pregnant. Fluctuations in an
individual’s plasma progesterone concentrations during pregnancy are well documented (Buchanan & Young Lai 1988; Currie et al. 1988; Hosken et al. 1996; Mason et al. 2010; van Aarde et al. 1994; Van der Merwe & Van Aarde 1989) with concentrations remaining low during early pregnancy, and peaking prior to birth, followed by a decline (Badwaik & Rasweiler 2000). The range of plasma progesterone concentrations recorded for pregnant bats in this study is likely to be in part explained by the different stages of pregnancy which could not be determined by physical examination alone, as well as differences between species. These results support work by Mason et al. (2010) that demonstrated plasma progesterone concentration is not an accurate measure of the stage of pregnancy or determining whether an individual is pregnant, but can be used as a good indicator of the timing of pregnancy within a population (e.g. Greiner et al. 2011b) or in the case of this study, a bat community, if samples from different species are pooled.

The stages of female reproduction in Tasmanian bats were closely associated with mean monthly minimum temperature and day length. Environmental factors, such as temperature can produce ideal conditions that increase resource availability, such as insects (Greiner et al. 2011b). The availability of resources, coupled with changes to day length, are likely cues to females to ovulate and fertilise eggs, so that young are born during periods of optimal resource availability and low energetic demand of thermoregulation (Racey & Entwistle 2000). As a consequence peaks in bat activity recorded during bat monitoring are likely to correspond with the timing of lactation and the dispersal of young in summer. Bat activity in temperate regions is generally seasonal and associated with environmental factors and the timing of female reproductive stages (Milne et al. 2005; Russ et al. 2003; Wang et al. 2010). Declines in bat activity are generally associated with low temperatures and day lengths during winter when temperatures and insect availability are low and the energetic demands of thermoregulation are high (Lumsden & Bennett 2005; Sanderson & Kirkley 1998).

The association between the timing of male hormone surges, changes in reproductive stages, bat activity and environmental factors were less pronounced than for females. This may in part be because sperm production is not as energetically demanding as pregnancy and lactation, and consequently is not timed to coincide with optimal resource availability.
Chapter 4: The reproductive and activity cycle of Tasmanian bats

(Racey & Entwistle 2000). Alternatively, the role of testosterone non-reproductive behaviours such as aggression may have influenced results (Harris 1999). This would in part explain why plasma testosterone varied greatly between reproductive stages in males. In contrast, plasma testosterone concentrations did show a trend to peak in autumn, coinciding with the end of lactation, sperm storage and social calls produced by bats. Elevated plasma testosterone concentrations have been recorded in other bat species during the period of sperm storage and mating (Greiner et al. 2011a; Lloyd et al. 2001). In temperate regions, mating in bats takes place when day lengths become short (Greiner et al. 2011b) and may be influenced by female availability (Pfeiffer & Mayer 2012). The findings of this study suggest bats mate in autumn, though mating was not directly observed.

An unexpected observation in this study was the association between the timing of mating and the number of social calls. The social calls encoded in bat echolocation call sequences likely play a crucial role in bat social communication, but there function is still largely unknown (Knörnschild et al. 2012). A study by Russ et al.(2003) did, however, find that bats produce social calls year round, with peaks during mating. During mating, male bats produce territorial and courtship songs to attract a mate (Behr & Von Helversen 2004; Georgiakakis & Russo 2012) and use social calls to discriminate between sexes of conspecifics (Knörnschild et al. 2012). Such calls have not been studied in Australia, but the social calls recorded in this study are similar in attributes to those recorded elsewhere (Behr & Von Helversen 2004). Though unexplored in bats, this findings of this study suggest peaks in plasma testosterone may play a role in initiating mating behaviours, such as social calls, in bats (Greiner et al. 2011a). This is a novel area of research that requires further investigation.

Other factors such as morphology can also influence the timing of reproductive stages in closely related bat species. Variation in the timing of reproductive stages, such as birth, are known to vary with bat body size, as this influences gestation length (Altringham 2011). Bergmann’s rule states that body size increases with decreasing temperatures (Meiri & Dayan 2003), and as a consequence bats are predicted to be larger in Tasmania’s cool high latitude climate compared to the warmer mainland. Where data for comparison is available
Bergmann’s rule holds true. For example, *N. geoffroyi* in Northern Australia ranges in forearm length from 30.6 to 38.6mm, in Victoria: 32.0 to 41.7mm and in Tasmania: 37.4 to 42.3mm (Churchill 2009). Furthermore within Tasmania, bat species (*Vespadelus* spp. <7 grams) were recorded as palpably pregnant and lactating earlier than larger bat species (*Nyctophilus* spp., *Chalinolobus* spp. & *F. tasmaniensis* >7 grams). Tasmanian bats are generally larger than their mainland conspecifics as predicted by Bergmann’s rule (Bogdanowicz 1990). This may in part explain the variation in the timing of reproductive stages in Tasmanian bats compared to their mainland conspecifics. Similar patterns have also been found in ringtail possums in Tasmania (Munks 1995).

It is therefore important when undertaking bat monitoring programs not to assume life history data, such as the timing of reproductive stages from one region to another, because this may lead to the misinterpretation of data. It is well recognised that temperature, day length and thus resource availability vary with latitude and therefore so does the reproductive cycle of bats (Bernard & Tsita 1995; Happold & Happold 1990). In comparison with mainland conspecifics for which data was available, Tasmanian bat species exhibited latitudinal variation in the timing of reproductive stages, such as pregnancy and lactation (Hosken 1997; Tidemann 1993; Van Dyck & Strahan 2008). For example, in Western Australia (31°S), *N. geoffroyi* and *C. morio* lactate between September and October (Hosken 1997; Kitchener & Coster 1981), whereas in Tasmania (42°S) the majority of individuals do not lactate until at least one month later between November and February. Such variations in the timing and also the duration of reproductive stages with latitude are not confined to bats - Echidnas (Morrow et al. 2009), mice (Dark et al. 1983) and even humans (Moos & Randall 1995) vary in the timing and patterns of reproduction with latitude.

Kincade et al. (2000) reported the duration of lactation was shorter in Tasmanian bats compared to their mainland conspecifics and that this may be in response to environmental factors. In other Tasmanian fauna, such as the echidna (Morrow et al. 2009) and ringtail possum (Munks 1995), the duration of reproductive stages, such as lactation, also varies with latitude. However, examination of data in this study, including data from Kincade et al. (2000) reveals that Tasmanian bats can be found lactating up to one month later than their
lower latitude mainland conspecifics, though as in mainland Australia, this varies yearly with environmental conditions. Without knowledge of birth dates and understanding the growth rates of Tasmanian bats it still remains unclear whether lactation is shorter compared to mainland conspecifics, as birth dates may vary between populations. Similar patterns have been observed in South Africa where as little as an 8° latitudinal difference has been associated with variation in the timing of reproductive stages (Le Grange et al. 2011).

In summary, these findings indicate that like bat communities elsewhere, the reproductive and activity cycle of Tasmanian bats is strongly associated with the environment and the energetic demands of reproduction. Variation in the timing of reproductive stages between species is strongly associated with morphology, with larger bats breeding later than smaller bats. Both environmental factors and morphology are likely to be major factors responsible for the shift in the timing of reproduction with latitude. Future research into the annual reproductive and activity cycles of bats throughout their range would provide further insights into how reproductive stages shift in respond to changing environments.

IMPLICATIONS FOR BAT MONITORING

Understanding the relationship between the reproductive and activity cycle of bats, and how this varies with latitude is an important component of their conservation and management. Much information can be gained from bat activity data and this study highlighted the fact that though little is understood about bat social calls, the type, timing and number of social calls recorded potentially provide a simple indirect method for assessing the timing of bat mating during monitoring studies. The data set used for this study was however limited, and data was not always collected during the same year or to the same extent, making yearly comparisons in the timing of reproductive stages impossible. When bat monitoring, consideration should be given to the possibility that bats may breed outside of the periods outlined in this study.

Such information can be used to inform management actions across a species range, such as the timing of land management practices outside of key periods such as pregnancy and
lactation. Understanding the timing of reproductive and activity cycles of bats is also important for monitoring programs and selecting the optimal time for surveying bats and understanding how habitat requirements vary seasonally. If the timing of reproductive stages and environmental factors are not accounted for, results of bat monitoring data are likely to be erroneous.
CHAPTER 5: THE IMPORTANCE OF MATURE FOREST IN BAT ROOST SITE SELECTION IN TWO CONTRASTING TIMBER PRODUCTION LANDSCAPES

A Tasmanian long-eared bat (*Nyctophilus sherrini*) with a radio-transmitter attached
INTRODUCTION

Mature forest containing hollow-bearing trees provides an important resource for a diverse range of fauna around the world (Lohmus & Remm 2005; McComb & Noble 1982; Munks et al. 2004; Webb & Shine 1997). A reduction in the availability of hollow-bearing trees could have severe consequences for the conservation of many hollow-using fauna, particularly those that depend upon tree hollows as a place to den, nest and roost (Gibbons & Lindenmayer 2002). This is because a decline in the availability of hollow-bearing trees can affect population demographics (e.g. Martin & Handasyde 2007), mating systems (e.g. Banks et al. 2013) genetic diversity (e.g. Campbell et al. 2009) and abundance (e.g. Newton 1994; Rhind 2004; Tyndale-Biscoe & Smith 1969) thereby affecting the ability of a species to persist in landscapes where mature forest is already rare, has been lost, or is highly fragmented (i.e. urban, agricultural and timber production landscapes).

The importance of maintaining a ‘hollow resource’ in the landscape is well recognised by forest managers and consequently strategies for the retention and regeneration of hollow-bearing trees in areas where mature forest is, or will be lost or modified, have been developed around the world (Loyn & Kennedy 2009; Mazurek 2004; Munks et al. 2009; Parnaby et al. 2012; Pattanavibool & Edge 1996). One of the greatest challenges for forest managers, however, is how to make informed strategic decisions related to the management of mature forest in relation to the type, amount and spatial arrangement of mature forest that should be retained for biodiversity conservation (Munks et al. 2009; Parnaby et al. 2012; Whitford & Stone 2004). This is particularly challenging because there is relatively little information available on the effectiveness of current management strategies for mature forest retention and the mature habitat requirements of many species.

The effective management of mature forest in the landscape is an important part of the conservation of hollow-using bats (Parnaby et al. 2012). This is because many bat species rely on mature forest elements, such as hollow-bearing trees, as roost sites. Roost sites are not only important for shelter sites, but also for hibernation, socialising, mating and raising
young (Kunz & Lumsden 2003). Roost site preferences vary depending on their social, energetic and thermoregulatory needs, which can vary between species, sex, reproductive condition and seasonally (Boland et al. 2009; Lumsden et al. 2002a; Perry & Thill 2007; Ruczynski & Bogdanowicz 2008; Sedgeley 2003). Bats also exhibit both specificity and flexibility in their roosting preferences (Lumsden & Bennett 2006). This may explain why several studies have found that the type and location of roosts used by bats varies between landscapes (Law & Anderson 2000; Miles et al. 2006; Waldien et al. 2000). Such variation in roost site preferences may be a result of bats balancing their specific and flexible roost site requirements with their other needs. By understanding the roost site preferences of bats in different landscapes, an understanding of the importance of different roost site attributes to bats can be ascertained to inform forest management.

Declines in bat species world-wide have been attributed at least in part to the loss and modification of mature forest containing suitable hollow-bearing trees (Pierson & Racey 1998). It is speculated that the anticipated future loss of hollow-bearing trees, combined with threats from timber harvesting, fire and drought stress, could mean that all bat species that are dependent on hollow-bearing trees will become threatened (Parnaby et al. 2012). Tasmania, is home to eight species of insectivorous bats (Family: Vespertilionidae) (Driessen et al. 2011), including one endemic bat – the Tasmanian long-eared bat (Nyctophilus sherrini) (Parnaby 2009). The retention of suitable types, amounts and spatial arrangements of mature forest habitat is an important part of conserving Tasmania’s bats (Taylor & Savva 1988) because of their dependence on hollow-bearing trees as roost sites (Koch et al. 2008b). Management of the maintenance of mature forest for hollow-using fauna on private and public land have been developed and are delivered via Tasmanian Forest Practices Code (Forest Practices Board 2000; Munks et al. 2009; Taylor 1991). In the absence of information on the habitat requirements of many hollow-using species, these management strategies have been developed based on the multi-spatial scale approach to forest management for biodiversity conservation developed using ecological theory (Lindenmayer & Franklin 2002). These management strategies include the retention of mature forest at the landscape and stand scale in the form of small and large patches and strips (Baker & Read 2011; Forest Practices Board 2000; Munks et al. 2009; Taylor 1991).
Chapter 5: Bat roost site selection

The overall objective of this study was to investigate the roosting preferences of Tasmania’s bats in two different timber production landscapes. In particular this study wanted to investigate the importance of the type, amount and spatial arrangement of mature forest in timber production forests for bat roosting habitat.

METHODS

Study area

The study was carried out in dry Eucalypt forests in south-eastern Tasmania. Dry Eucalypt forests constitute 45% of Tasmania’s forest cover (Forest Practices Authority 2012) and have a long history of human land use practices such as timber harvesting, plantation development and agriculture over the last 200 years (Munks et al. 2007). In this region, two ‘landscapes’ were selected (‘Kellevie’ and ‘Woodsdale’). Each comprised of two partially harvested forest stands surrounded by different types, amounts and spatial arrangements of mature forest (Figure 17). The Kellevie landscape contained two regenerating forest stands (Coupe: MM002A & 4A) in which 51.2ha were harvested in 1997 (2A) and 69ha in 2004 (4A). The Woodsdale landscape contained a 153ha forest stand regenerating after harvest in 1998 (Coupe: SW049A). Both landscapes had different types of mature forest patches retained in and on the edge of the harvested area. Both landscapes were also known to have trees used by hollow-using fauna (Cawthen & Munks 2011). In addition, roost sites were found in the Woodsdale landscape during a previous study prior to the harvesting of SW049a (Taylor & Savva 1988). Each harvested forest stand was dominated by dry sclerophyll forest and woodland (Eucalyptus obliqua and Eucalyptus pulchella-globulus-viminalis) with wet sclerophyll forest in gullies (Eucalyptus obliqua) (Forest Practices Authority. 2005).

Forest management strategies for the retention of mature forest implemented at each landscape included:

- Individual trees – one hollow-bearing tree retained in the harvested area as part of the silvicultural prescriptions (Wilkinson 1994)
Chapter 5: Bat roost site selection

- Small patches – a small patch ‘wildlife habitat clump’ containing two to three hollow-bearing trees surrounded by ‘recruitment’ trees retained in the harvested area (mean size = 0.1ha)
- Narrow strips – a narrow linear strip ‘roadside reserve’ retained on the edge of a harvested area and adjacent road (mean size =3ha, 5-15 m wide)
- Large strips – a large linear strip ‘wildlife habitat strip’ retained on the edge of a harvested area between two harvested forests (mean size = 15ha, 100 m wide)
- Large patches – a large area of forest retained immediately outside the harvested area (mean size = 370ha) (Forest Practices Board 2000)

The type, amount and spatial arrangement of mature forest habitat surrounding each harvested forest stand was assessed using a mature habitat spatial layer (Forest Practices Authority. 2011) (Figure 17). The spatial layer was developed by using aerial photographs to remotely assess mature habitat availability (Forest Practices Authority. 2011; Koch & Baker 2011) as one of five types: none, negligible, low, medium and high. Areas cleared of vegetation and water bodies were classed as none and so were predicted to have no hollow-bearing trees. Areas identified as non-forest, plantation or as regrowth forest with no mature eucalypt cover were classed as negligible and so were predicted to have negligible densities of hollow-bearing trees. Areas containing less than 20% mature eucalypt crown cover were classed as low and so were predicted to have low densities of hollow-bearing trees. Areas containing between 20 and 40% mature eucalypt crown cover were classed as medium and so were predicted to have medium densities of hollow-bearing trees. Areas with more than 40% mature eucalypt crown cover was classed as high and predicted to have high densities of hollow-bearing trees (Forest Practices Authority. 2011).

The proportion of each mature habitat availability class in each landscape (‘Kellevie’ and ‘Woodsdale’) was calculated at one, three and five kilometre radii from the centre of each landscape using ArcGIS 9.1. This approach illustrated variations in the type, amount and spatial arrangement of mature habitat in each landscape (Figure 16). A five kilometre maximum area was used as ‘the landscape’ because this was the maximum distance over
which Tasmanian bat species are known to travel between roost and foraging areas (Taylor & Savva 1988). Retrospectively this was the maximum area over which bats roosted.

Using this method to characterise mature forest habitat in the landscape, the Kellevie landscape was found to have a relatively high proportion of mature forest habitat directly surrounding the harvested area comprising of a high density of hollow-bearing trees. In contrast, the Woodsdale landscape had a relatively low proportion of mature habitat directly surrounding the harvested area (Figure 16).

**Figure 16. A comparison of the type, amount and spatial arrangement of mature habitat surrounding two harvested stands – Kellevie and Woodsdale in south-east Tasmania.**
Chapter 5: Bat roost site selection

Figure 17. The type, amount and spatial arrangement of mature habitat and day roosts of lactating and non-reproductive C. morio, N. geoffroyi and N. sherrini in two timber production landscapes - Kellevie (left) and Woodsdale (right) in south-east Tasmania.

Bat capture

Between January and February 2011, bats were captured in two-bank harp traps (Austbat Research equipment Faunatech, AUS) and two types of mist nets - monofilament (M-20) and nylon (716) (Ecotone, PL). Traps and mist nets were set in gaps and along forest trails within and on the edge of the harvested forest stand (including retained patches). Harp traps were set in the late afternoon and checked after sunset and before sunrise the following day. Mist nets were set at sunset and checked every 10 minutes for up to four hours after sunset. Only species of which lactating females were captured were radio-tracked. Trapping was undertaken intermittently throughout the study until all transmitters
were deployed. Two male *F. tasmaniensis* were also radio-tracked but the results are not reported here as no lactating females were located.

Upon capture all bats were identified to species using field guides (Churchill 2009; Taylor et al. 1987). Bats were checked for a pre-existing microchip and if the bat weighed more than 9 grams and was not chipped, an ISO FDX-B transponder chip (Passive implantable transponder (PIT) tag) was implanted subcutaneously between the shoulder blades for individual identification (Biomark, 12.50mm x 2.07mm, wt=0.102g). Bats were weighed, sexed, aged and reproductive condition assessed following the methods outlined in Churchill (2009).

**Radio-telemetry**

Radio-transmitters (Model LB-2N, Holohil Systems Ltd, Ontario, Canada) weighing between 0.32 and 0.42 g and with a battery life of 9 to 21 days were glued onto the skin between the shoulder blades of bats using Urobond IV skin adhesive. Transmitter mass was between 3 and 5% of body mass to minimise potential effects on flight ecology (Aldridge & Brigham 1988).

Bats were radio-tracked by car and then on foot to their roosts by ‘homing’ in on the radio transmitter signal between dawn and dusk each day using a hand-held receiver and yagi antennae. Where possible, the location of each bat within the roost was determined by inspecting the roost (e.g. in a basal cavity), roost watching at dusk or by detaching the antennae from the receiver and locating the precise position of the transmitter to the nearest ± 0.50 m. Bats were tracked until transmitters fell off or the batteries expired. Roosts were watched before sunset for 30 to 90 minutes to determine colony size and for roost site confirmation. One to five observers were positioned at a roost so that the potential roost location (e.g. a hollow or fissure) was silhouetted against the setting sun. As bats sometimes returned to the colony whilst other bats were emerging, a conservative
estimate of colony size was used (the number of bats emerged minus the number of bats entering during the emergence).

Roosts were classified into roost types depending on number and reproductive condition of the bats occupying the roost. Roosts were classified as follows:

- Maternal solitary roost - a roost that contained one lactating bat.
- Maternal colonial roost – a roost that contained more than one lactating bat.
- Non-maternal solitary roost – a roost used by a non-reproductive bat.

**Roost site attribute assessments**

Attributes of the type and location of roost sites used by bats were measured and compared to document differences in roost sites between species and sites. Attributes measured were selected based on the results of previous studies (i.e. Webala et al. 2011) or were factors thought to potentially influence the roost site suitability. These attributes were measured using a combination of field collected and spatial data (Table 8). It was not possible to collect all attributes for all roosts as a bat’s exact location in the roost tree could not always be determined. Most roost-use studies compare the attributes of used roosts with those that are available (e.g. Threlfall et al. 2013), but in this study comparisons of only used roost sites were made because of the errors associated with assessing tree hollow occurrence and abundance (Koch 2008).
Chapter 5: Bat roost site selection

Table 8. Attributes measured for roost sites at the tree, surrounding patch, stand and landscape scale in south-east Tasmania.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree species</td>
<td>Identified from bark, capsule and leaf characteristics using EucaFlip (Wiltshire &amp; Potts 2007)</td>
</tr>
<tr>
<td>Tree DBH (cm)</td>
<td>Measured using a DBH (diameter at breast height) tape at approximately 1.3 metres from the bottom of the tree on the upper slope.</td>
</tr>
<tr>
<td>Roost entrance height (m)</td>
<td>Calculated by measuring the distance from an observer to the roost tree and the angle from the observer to the roost entrance using a clinometer.</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>Calculated by measuring the distance from an observer to the roost tree and the angle from the observer to the top of the roost tree using a clinometer.</td>
</tr>
<tr>
<td>Tree decay stage</td>
<td>Categorised from a stage of 1 (no decay, healthy tree, no dead wood in the crown) to 8 (heavily decayed, no crown) (Whitford 2002).</td>
</tr>
<tr>
<td>Tree burn damage</td>
<td>A measure of the intensity of damage done by fire to the tree: (1) no indication of fire damage; (2) some charcoal on bark; (3) burnt bark and scarring; (4) severely burnt, forming a bridge.</td>
</tr>
<tr>
<td>Tree crown class</td>
<td>Tree dominance was classified by assessing the height of the tree relative to those surrounding it: (1) dominant (emergent); (2) co-dominant; (3) subdominant or suppressed</td>
</tr>
<tr>
<td>Tree connectivity</td>
<td>The quantity of vegetation in close proximity to the tree foliage based on (Lindenmayer et al. 1996). One point is scored for each 3 m vertical section of a hollow-bearing tree where surrounding vegetation was &lt; 10 cm from the tree, on either side of the tree. A cumulative score is calculated.</td>
</tr>
<tr>
<td>Canopy cover</td>
<td>Canopy cover was estimated from hemispherical photographs taken using a fish eye lens and calculated using Gap Light Analyser version 2.0.</td>
</tr>
<tr>
<td>Basal area (patch density)</td>
<td>The cross-sectional area, in square metres, of all trees with wood greater than 10mm DBH sampled in a 10m radius around the roost tree</td>
</tr>
</tbody>
</table>
### Chapter 5: Bat roost site selection

<table>
<thead>
<tr>
<th><strong>Patch Stem density</strong></th>
<th>The number of trees with wood greater than 10mm DBH sampled in a 10m radius around the roost tree</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Patch hollow-bearing tree density</strong></td>
<td>The number of trees with a visible cavity with wood greater than 10mm DBH sampled in a 10m radius around the roost tree</td>
</tr>
<tr>
<td><strong>Patch size (ha)</strong></td>
<td>The area of the mature forest patch that the roost site was located in. If roost site not located in mature forest value equals 0. Measured using ArcGIS and georeferenced aerial images.</td>
</tr>
<tr>
<td><strong>Stand height (m)</strong></td>
<td>Median tree canopy height for the forest stand the roost tree was located in. Estimated from photo interpretation data.</td>
</tr>
<tr>
<td><strong>Stand disturbance history</strong></td>
<td>Forest classified according to the presence and significance of aged eucalypt regeneration elements as indicators of past disturbance</td>
</tr>
<tr>
<td><strong>Site slope (degrees)</strong></td>
<td>Measured using a clinometer where the roost tree was situated.</td>
</tr>
<tr>
<td><strong>Site elevation (m)</strong></td>
<td>Elevation of roost site. Estimated from spatial data (DPIPWE Contours_10m)</td>
</tr>
<tr>
<td><strong>Distance to cleared land (km)</strong></td>
<td>Calculated using ArcGIS as the distance between roost site and the nearest edge of cleared land and land converted to plantation or pasture.</td>
</tr>
<tr>
<td><strong>Distance to water source (m)</strong></td>
<td>Calculated using ArcGIS as the distance between roost site and the nearest water source</td>
</tr>
<tr>
<td><strong>Distance to regrowth forest (m)</strong></td>
<td>Calculated using ArcGIS as the distance between roost site and the nearest edge of regrowth forest</td>
</tr>
<tr>
<td><strong>Distance to roads (m)</strong></td>
<td>Calculated using ArcGIS as the distance between roost site and the nearest road or track</td>
</tr>
</tbody>
</table>
**Statistical analyses**

The attributes describing differences in the type and location of roost sites at Kellevie and Woodsdale were analysed separately because of the different groups of species studied at each landscape. MDS (multidimensional scaling) plots were used to determine whether sex and reproductive condition or roost type influenced roost site selection and samples were grouped accordingly for analysis. Since many roost site attributes measured were collinear, a machine learning approach using random forest was used to select the most important roost site attributes for comparison between species and landscapes (Breiman 2001). To test whether variation in roost site selection and movements was significant between groups, a randomization student t-test was used. For roost site attributes, selection was assessed by comparing inter-specific variation in the attributes of roosts within a site and intra-specific variation in the attributes of roosts between sites. This approach was used rather than the traditional approach of comparing ‘used’ with ‘available’ roosts because of the intrinsic issues associated with identifying ‘available’ trees that contain hollows from the ground (Koch, 2008 #902) and because no asymptotic relationship between the number of roosts located and the number of days bats were tracked had been reached, indicating that if radio-tracking were to have continued, roosts that were potentially selected as ‘available’ may have been used.

To determine whether bats were selecting roost site locations in relation to mature habitat type (i.e. the availability of hollow-bearing trees), roost site selection was analysed at two different spatial scales – the landscape and the finer local scale. Landscape habitat selection was a comparison of the availability of types of mature forest habitat throughout the area where bats were roosting with the proportion available in the landscape. Finer local scale habitat selection was a comparison of the proportion of roost sites located in each mature habitat type compared with their availability in the area over which bats were roosting. As the total area of the landscape used by each species and group varied, and the total area of the landscape used for each group was unknown due to the relatively small duration of the study, finer scale habitat selection provided a conservative estimate of the surrounding
landscape that influenced roost-site selection. A bat’s roosting range was calculated using 100% minimum convex polygon analysis under the condition that at least three roost site locations were recorded. A buffer of 100 metres at bat roost site locations was used to avoid potential incorrect classifications of bat roost site habitat as photo interpretation was mapped to 100m at these sites. Habitat selection was analysed using Fisher’s Exact Test. All statistical analyses were carried out using the statistical program R (R Development Core Team 2011).

RESULTS

Bats radio-tracked

All eight Tasmanian bat species were captured at Kellevie but at Woodsdale only *N. geoffroyi*, *C. morio*, *V. darlingtoni*, *V. regulus* and *V. vulturnus* were captured. This was despite lactating *N. sherrini* being captured at Woodsdale in the 1980s (Taylor & Savva 1988) and a male *N. sherrini* being captured the previous spring. A total of 24 individuals from three bat species were radio-tracked between January and February 2011 (Table 9). Individuals were radio-tracked for a mean 10±3 days (3-20 days) with transmitters dropping off bats at roost sites (inside and outside) as well as in forest and along tracks. All three species demonstrated site fidelity, with four of the lactating individuals radio-tracked being recaptures from the previous summer (Kellevie: 2 *N. sherrini*, Woodsdale: 1 *N. geoffroyi* and 1 *C. morio*).

Table 9. Details of the 24 bats radio-tracked at two timber production landscapes – Kellevie and Woodsdale, in south-east Tasmania.

<table>
<thead>
<tr>
<th>Species</th>
<th>Kellevie</th>
<th>Woodsdale</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Lactating</td>
<td>Non-reproductive</td>
</tr>
<tr>
<td><em>Chalinolobus morio</em></td>
<td>1♀</td>
<td>1 ♀ 1♂</td>
</tr>
<tr>
<td><em>Nyctophilus geoffroyi</em></td>
<td>-</td>
<td>1♂</td>
</tr>
<tr>
<td><em>Nyctophilus sherrini</em></td>
<td>4♀</td>
<td>2 ♀ 3♂</td>
</tr>
</tbody>
</table>
Chapter 5: Bat roost site selection

Composition of roosts

A total of 120 bat roosting locations at 76 individual roost sites were located (C. morio = 29, N. geoffroyi = 23 & N. sherrini = 24 roosts). Radio-tracked lactating individuals of the same species were found to roost in the same maternal colony. For N. sherrini, lactating individuals never roosted alone. In contrast, lactating C. morio and N. geoffroyi individuals roosted in maternal colonies which fluctuated in size as individuals also roosted occasionally singly. In contrast, non-reproductive C. morio, N. geoffroyi and N. sherrini (including males) roosted by themselves but occasionally roosted with maternal colonies, demonstrating that maternal colonies were not exclusively composed of lactating females with young and further explaining why colony sizes fluctuated. All species exhibited roost switching every one to two days and roost re-use during the study.

At Kellevie, the C. morio maternal colony comprised a maximum of 185 individuals (mean = 88±70) including at least one non-reproductive female. In contrast, the N. sherrini maternal colony comprised a maximum of 47 individuals (mean = 32±19) including non-reproductive males and females. A non-reproductive male N. geoffroyi was also found with a colony of 58 individuals of unknown sex and reproductive condition. At Woodsdale, the C. morio maternal colony contained 341+ individuals (118±115). In contrast, the N. geoffroyi maternal colony comprised a maximum of 49 individuals (29.5±40.3). The maximum size of the C. morio maternal colony could not be established because on the night where 340 individuals were counted the full emergence could not be observed due to low light. There was only one observation of two non-reproductive males roosting together – two N. sherrini.

Types of roosts

All observed roosts were in cavities (hollows, fissures or under bark) of standing Eucalyptus trees. All maternal colonies except one were located in a large trunk, branch or basal hollow with an entrance width or height greater than 10cm (up to 1m in height). The exception was a N. geoffroyi maternal roost under the lifted bark of an E. obliqua. In contrast, non-maternal roosts were in smaller entrance sized cavities (<10cm). All species
demonstrated a preference for particular types of cavities (Figure 18). For *N. geoffroyi* the majority of roosts were in fire scarred basal hollows surrounded by dead wood. In contrast, *C. morio* and *N. sherrini* roosts were primarily in large trunk and branch hollows. Six *C. morio* roosts were also located in fire scarred basal hollows, including one maternal colony. Roost sites under bark and in fissures were the least frequently used. Four roosts were located under bark used by *N. geoffroyi* and *N. sherrini*. Three roosts were also located in fissures used by *C. morio* and *N. sherrini*. Fissures were only used by individuals roosting solitarily and on a single occasion.

Roosts were in native *Eucalyptus obliqua* and *Eucalyptus pulchella*, and to a lesser extent *Eucalyptus amygdalina, Eucalyptus viminalis* and *Eucalyptus globulus*. All roost trees showed signs of decay, had burn damage and low connectivity with adjacent trees. There was no significant difference in roost tree and entrance height, decay stage, burn damage and connectivity between species and landscapes (Table 10) although bats did roost in trees of a range of heights and decay stages. Roost tree dbh however did vary between species and landscapes. At Kellevie, *N. sherrini* roosted in significantly larger dbh trees than *C. morio*. The use of roost trees with a large dbh was not consistent across landscapes, as *C. morio* roosted in significantly larger dbh trees at Woodsdale compared to Kellevie, though trees of similar dbh were available (Table 10).
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Figure 18. The proportion of roosts used by different species categorised according to cavity type.

Roost site locations

Roosts were located in all types of retained forest patches. However, the type of retained patch used varied between landscape, species and roost type (maternal or non-reproductive) (Figure 19). For maternal roosts (colonial and solitary) comparisons of roost site location between sites and species are detailed in Table 10. Few non-maternal roosts were located for each species, so sample sizes are low and data is provided in text for descriptive purposes only.

At Kellelie, 98% of roost sites were located in a large mature forest patch and strip surrounding the harvested areas (Figure 17 & Figure 18). All maternal colonies were located in large mature forest patch whereas the large strip was used only for solitary maternal and non-reproductive roost sites. No roost sites were located in small patches and only a single roost site was located in an individual tree retained in the harvested area. This roost site was used by a *N. geoffroyi* on a single occasion. Although *C. morio* and *N. sherrini* roosted in
Chapter 5: Bat roost site selection

the same forest patches, there were marked differences in roost site location in relation to stand and landscape attributes (Table 10). All *N. sherrini* roosts were located down slope from the harvested area and for maternal roosts, all were located in a small patch of intermittent dry/wet *Eucalyptus obliqua* forest adjacent to a *Pinus radiata* plantation (Figure 17). In contrast, maternal and non-maternal *C. morio* roosts were located on the upper slopes and ridges adjacent to the harvest area (Figure 17).

At Woodsdale, 72% of roost sites were located in a large mature forest patch and strip surrounding the harvested areas (Figure 17 & Figure 19). Consistent with observations from Kellevie, maternal colonies of *C. morio* were only found in large mature forest patches, whereas maternal colonies of *N. geoffroyi* were located in a range of smaller patches and strips. In contrast to Kellevie, a higher proportion of roosts were used in the harvested area, with 28% of roost sites located in individual trees and small patches. At both sites, no roosts were located in paddocks or plantations which were devoid of native trees with cavities.

Bat roost sites also varied in surrounding attributes at the patch, stand and landscape scale between species within each landscape (Table 10). At Kellevie, *N. sherrini* roosts were on significantly steeper slopes at lower elevations compared to *C. morio* roosts. *N. sherrini* roosts were also significantly closer to cleared land being adjacent a *Pinus radiata* plantation and grazing property. At Woodsdale, *C. morio* roosts were surrounded by a significantly greater stem density, were located in significantly larger patches with greater stand height, and hollow-bearing tree availability, and were in less disturbed forest stands compared to *N. geoffroyi* roosts. *Chalinolobus morio* roost sites were also located significantly closer to cleared land, in an adjacent pasture, compared to *N. geoffroyi* roosts. *N. geoffroyi* roosts were also located significantly closer to water and regrowth forest. *Chalinolobus morio* roosted shared similar patch attributes at Kellevie and Woodsdale, but stand and landscape attributes such as the abundance of hollows in the surrounding landscape, distance to cleared land and regrowth forest significantly varied between Woodsdale and Kellevie (Table 10).
Figure 19. The proportion of roost sites located in different types of retained forest patches in two timber production landscapes: A) Kellevie and B) Woodsdale.
### Table 10. A comparison of tree, patch, stand and landscape attributes of maternal roost sites selected by lactating *C. morio*, *N. geoffroyi* and *N. sherrini* at two sites – Woodsdale and Kellevie, in dry sclerophyll forests of south-east Tasmania, Australia, between January – February 2011.

Significant results shown in bold.

<table>
<thead>
<tr>
<th>Roost site attributes</th>
<th>Woodsdale species comparison</th>
<th>Kellevie species comparison</th>
<th><em>C. morio</em> site comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± S.D</td>
<td>Test statistic</td>
<td>Mean ± S.D</td>
</tr>
<tr>
<td><em>C. morio</em> (n= 15)</td>
<td>N. geo (n=19 )</td>
<td>t</td>
<td>P</td>
</tr>
<tr>
<td>DBH (cm)</td>
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<td>Roost entrance height (m)</td>
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<tr>
<td>Tree height (m)</td>
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<td>Decay stage</td>
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<td>Burn damage</td>
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<td>Stand height (m)</td>
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<td>Distance to water source (m)</td>
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<td>Distance to regrowth forest (m)</td>
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<td>4.96</td>
</tr>
<tr>
<td>Distance to roads (m)</td>
<td>210±159</td>
<td>202±139</td>
<td>0.14</td>
</tr>
</tbody>
</table>

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**Chapter 5: Bat roost site selection**

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85
Roost site habitat selection in relation to mature habitat availability at the landscape and finer local scale

Bats varied in the area over which they roosted depending on the species, reproductive condition, sex and landscape. Given the low sample sizes, however, for non-maternal roost site locations, the relationship between roost site location and mature habitat availability was analysed for maternal roosts only (Figure 20 & Figure 21). Non-maternal habitat selection data is provided for descriptive purposes only.

At the landscape scale, maternal colonies of *N. sherrini* and *N. geoffroyi* roosted over relatively small areas (4.4 & 18.6 ha respectively) compared to maternal colonies of *C. morio* (Kellevie: 29.3ha & Woodsdale: 286ha). All species, however, selected maternal roosting areas in parts of the landscape containing a greater proportion of low, medium and high mature habitat than expected if they were randomly selecting habitat in the landscape (Fisher’s exact test, P=<0.0001) (Figure 20). This is not surprising as mature habitat containing negligible densities of hollow-bearing trees and areas of no mature habitat (i.e. paddocks, plantation, 100% young regrowth forest) are presumed to be devoid of suitable hollow-bearing trees as roost site (Forest Practices Authority. 2011).

All species displayed preferences for roosting in different mature habitat classes. At Woodsdale, *C. morio* displayed a preference for roosting in areas of mature habitat with a low density of hollows despite a greater proportion of the landscape containing mature habitat with a medium to high density of hollows and similar at Kellevie a greater proportion of *C. morio* roosts were located in mature forest with a low density of hollows than would be expected based on availability (Figure 20). There was also evidence to suggest that habitat selection varied between maternal and non-maternal roosts, and for maternal roosts, whether the roost was solitary or colonial. For example all of non-maternal *C. morio* roosts at Woodsdale were in areas of low mature habitat. In contrast, all of the area used by maternal colonies were in areas of high mature habitat.
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Figure 20. A comparison of the landscape scale habitat selection by sympatric bat species in relation to mature habitat availability.

At the finer local scale, selection of roost site locations in relation to low, medium or high densities of hollow-bearing trees varied between species and landscape. Both *N. sherrini* and *N. geoffroyi* displayed no finer local scale roost site selection in relation to mature habitat availability with areas of low, medium and high mature habitat used in proportion to availability (Fisher’s Exact Test, *P*=0.5348 & 0.3922 respectively). At both Kellevie and Woodsdale *C. morio* exhibited finer local scale roost site selection but this was significantly different between sites (Fisher’s Exact Test, *P*<0.0001). At Kellevie, *C. morio* selected roost sites in areas of medium mature habitat (Fisher’s Exact Test, *P*<0.005) and used areas of high and low mature habitat less than expected. In contrast, at Woodsdale, *C. morio* selected roost sites in areas of high mature habitat (Fisher’s Exact Test, *P*<0.005), avoided areas of medium mature habitat and used areas of low mature habitat in proportion to availability. These results suggest that the availability of mature habitat, containing hollow-bearing trees is just one factor influencing roost selection in the study areas.
Figure 21. A comparison of the finer local scale habitat selection by sympatric bat species in relation to mature habitat availability.

** Movements between roost sites  

The distance travelled between consecutive roosts varied between landscapes, species and reproductive condition (Figure 22 & Figure 23). At Woodsdale, lactating *C. morio* travelled significantly greater distances between consecutive roosts than lactating *N. geoffroyi* (t = 4.3997, P = 0.0005). Similarly at Kellevie, lactating *C. morio* travelled significantly greater distances between consecutive roosts than lactating *N. sherrini* (t = 3.16, P = 0.009). Within species, *N. sherrini* lactating females travelled significantly less between consecutive roosts than non-reproductive male and females (t = -2.55, P = 0.018). Between sites, lactating *C. morio* travelled greater distances between consecutive roosts at Woodsdale where there was less mature habitat available in the landscape compared to Kellevie, but on average there was no significant difference (t = -1.93, P = 0.067). It is important to note, however,
Chapter 5: Bat roost site selection

that the sample sizes for roost movements are very low, so this data should be interpreted with caution.

![Figure 22](image1.png)

**Figure 22.** A comparison of the distance between consecutive roosts at two sites (left) - Kellevie; (right) – Woodsdale for lactating female *C. morio* (n=22), *N. sherrini* (n=33) and *N. geoffroyi* (n=11).

![Figure 23](image2.png)

**Figure 23.** Comparison of distance between consecutive roosts for lactating and non-reproductive *Nyctophilus sherrini* at Kellevie.

**Roost sharing and co-use**

Roost sharing with other species of hollow-using fauna (including other bat species) was observed. At Kellevie, a male *N. sherrini* and *C. morio* were found roosting in the same tree. At Woodsdale, maternal colonies of *C. morio* were observed on two occasions to
simultaneously share a cavity with Tasmanian common brushtail possums (*Trichosurus vulpecula fuliginosus*) (two and three individuals), and share a roost tree with a Tasmanian common brushtail possum on a third occasion. A southern boobook (*Ninox novaeseelandiae*) was also observed foraging successfully on an emerging maternal *C. morio* colony during radio-tracking (Appendix 3). A maternal colony of *N. geoffroyi* was also observed simultaneously sharing a basal cavity with a dusky woodswallow (*Artamus cyanopterus*). Three *N. geoffroyi* and one *C. morio* maternal colony roosts were found in the same tree as recorded brushtail possum dens known from a previous study (Cawthen & Munks 2011).

**DISCUSSION**

This is the first study to examine how the type, amount and spatial arrangement of mature habitat in the landscape influences bat roost site selection and behaviour in timber production landscapes. It is also one of only a handful of studies to document differences in maternal roost site preferences by Australian micro-bats. A key finding of this study was that *C. morio*, *N. sherrini* and *N. geoffroyi* roosted in forested areas of the landscape that had the highest availability of hollow-bearing trees. At finer spatial scales however, species exhibited marked variation in their roost site preferences and did not necessarily select roost sites in stands or patches of forest that had the highest availability of hollow-bearing trees. The findings have important implications for understanding variation in bat roost site selection between species and landscapes.

The selection to roost in parts of the landscape with a highest availability of hollow-bearing trees most likely relates to social and energetic advantages of roosting in areas where roost sites are more abundant (Lumsden & Bennett 2006). Several studies have also found that at various spatial scales bats select to roost in similar areas of the landscape (Perry et al. 2007, 2008; Threlfall et al. 2013). It is not surprising however that in a forested landscape the availability of hollow-bearing trees is not a strong factor in roost site selection at finer spatial scales because, as a highly mobile taxon, bats can readily access roost sites throughout the landscape if they are available. Instead, finer spatial scale roost site preferences likely reflects other roost site requirements that meet the social,
thermoregulatory and energetic needs of bats, and levels of competition and predation risk (Lumsden & Bennett 2006).

At the finer spatial scales bats roosted in the cavities of Eucalypt trees with signs of senescence (i.e. dead branch in crown) and burn damage. These findings are consistent with the attributes of bat roost sites in hollow-bearing trees throughout Australia (Goldingay 2009). Inter-specific variation in bat roost site selection was however evident. Notably that the particular type of cavity used by bats varied between species. N. geoffroyi showed a preference for basal cavities with burn damage whereas N. sherrini and C. morio preferred trunk and branch cavities. Previous work has shown that N. geoffroyi frequently breeds under the bark of dead trees (Lumsden & Bennett 2006), therefore the lack of dead trees with exfoliating bark in the landscape (Cawthen pers comm) could explain the use of basal cavities for breeding in this study. Basal cavities with burn damage may share similar thermoregulatory advances as exfoliating bark on dead trees for bat roost sites. Maternal colonies all exhibited a preference for roosting in large hollows (entrance size >10 cm) rather than the small hollows (entrance<2cm) which were used more often by solitary individuals. Maternal colonies are likely to select large hollows because they accommodate more bats (Goldingay 2009). Larger colony sizes are likely to provide either a social, physiological or ecological advantage over roosting in small groups or individually. Bats also exhibited marked inter-specific variation at the patch, stand and landscape scale in other roost site attributes. These included tree size (dbh), the density of stems surrounding the tree (forest structure), patch size, stand height, the number of visible hollows nearby and the amount of disturbance surrounding roosts. Differences in roost site attributes between species and roost types(Carter & Feldhamer 2005; Carver & Ashley 2008; Lumsden et al. 2002a; Sedgeley 2003; Webala et al. 2010) demonstrate that bats have species-specific habitat requirements that can vary depending on whether they are breeding or non-breeding.

The importance of particular bat roost site attributes to a particular species cannot be fully understood without comparing roost site preferences across landscapes. Few studies however have done this (Law & Anderson 2000). Such studies are important because they
provide insight into those roost site attributes that are flexible (i.e. vary and are less important) and those that are specific (i.e. consistent and more important) (Lumsden & Bennett 2006). In this current study it was not possible to do this for all species. For maternal colonies of *C. morio* however it was evident that these bats exhibited a strong preference for roost sites in large patches of undisturbed mature forest (>287ha in size) despite an availability of smaller patches containing large hollows that were used by other bat species and the common brushtail possum (*Trichosurus vulpecula*) (Cawthen & Munks 2011).

Attributes such as tree size (dbh), hollow abundance in the patch and the distance of the roost to regrowth forest and cleared areas were considered to be flexible roost site attributes because these varied between landscapes.

Understanding the specific and flexible roost site requirements of bats can help explain why in a particular landscape, bats did not use retained forest patches. For example, in a landscape (‘Kellevie’) where the extent of mature forest was greater and directly surrounding the harvested area (60% of the landscape containing low to high mature habitat density within 1km), maternal colonies and non-reproductive individuals of *C. morio* and *N. sherrini* roosted in large patches of mature forest (>360ha in size). Individual trees, small patches and a large strip of mature forest retained in the harvested area were not used as roost sites. In a landscape (‘Woodsdale’) where the extent of mature forest was less and little mature forest was retained directly surrounding the harvested area (20% of the landscape containing low to high mature habitat density within 1km) maternal colonies of *C. morio* roosted in the broader landscape in a nearby large patch of mature forest, whereas non-reproductive and lactating individuals of *C. morio* and maternal colonies of *N. geoffroyi* roosted in patches retained in the harvested area in form of individual trees, small patches and narrow and large strips.

In Australia’s *Eucalyptus* forest and woodlands, bats generally show a preference for roosting in large patches of mature forest and, not surprisingly, avoiding regrowth and young forest where no mature forest elements have been retained (Lunney et al. 1985; Lunney et al. 1988; Taylor & Savva 1988). In harvested areas where mature forest habitat has been retained however, bats have been found to use individual trees and narrow strips.
(Webala et al. 2010) and in some cases, young non-eucalypt trees in harvested areas when no mature forest is available in the surrounding landscape (Law & Anderson 2000). In the beech and conifer forests of Europe and North America, bats also use retained habitat in harvested forest including cut tree stumps (Russo et al. 2010; Waldien et al. 2000). These studies demonstrate that retaining habitat in disturbed area can be an effective management strategy for maintaining bats in landscapes and facilitating recolonisation of disturbed areas, particularly in landscapes where mature forest is rare or has been lost.

It remains unclear however how limiting mature forest is for bats. In this study breeding bat populations were maintained in landscapes with relatively low and high amounts of mature forest, but the distance travelled between consecutive roosts varied between landscapes. Lumsden and Bennett (2006) proposed that if habitat availability is uniformly distributed, there would be no benefit for a bat to expend energy commuting large distances between resources. Therefore if bats do travel large distances between roosts sites, it may reflect differences in habitat availability (Lumsden & Bennett 2006) and in particular roost availability (Barclay & Kurta 2007). Though sample sizes were small and pseudoreplicated, the substantially greater distances travelled by C. morio between consecutive roosts in a landscape with less mature forest may indicate that there is a scarcity or degree of limitation of suitable roosts in that landscape (Barclay & Kurta 2007) or alternatively that C. morio has a more efficient flight style than N. geoffroyi, allowing C. morio to travel greater distances more efficiently between resources.

Similarly maternal colony size may provide insight into the size of the breeding population being supported in each landscape (Borkin et al. 2011; Law & Anderson 2000). As all lactating females of the same species tracked in this study roosted in the same maternal colony, it is likely that maternal colony size reflects the local breeding population size. If maximum maternal colony size of C. morio is an indicator of population size, it is clear that variation exists between study sites (Woodsdale: 341; Kellevie 182), with the largest population observed at Woodsdale where mature habitat availability was lowest and the spatial arrangement of roost sites in the landscape less uniform. Without information on
population sizes prior to declines in mature habitat availability in each landscape it is impossible to determine what factors are influencing bat colonies.

**MANAGEMENT IMPLICATIONS**

This study has important implications for understanding the effectiveness of different approaches for managing mature forest habitat for bats. These findings suggest that the degree to which bats use different retained forest patches for roosting varies depending on the type, amount and spatial configuration of mature forest in the surrounding landscape. It is becoming well recognised by forest managers that understanding habitat use patterns at finer spatial scales cannot be fully understand without considering the landscape (Mazerolle & Villard 1999). Studies that have compared bat roost site selection between sites have demonstrated similar results to this study (Kroll et al. 2012a; Law & Anderson 2000; Miles et al. 2006; Waldien et al. 2000). The management of bats and their habitat requires an understanding of the variation in habitat requirements of sympatric species in any given region and how this varies spatially and temporally. As demonstrated by this study, while bats can have specific habitat requirements (e.g. hollow-bearing trees as roost sites), requirements can also be flexible and vary throughout a region depending on the attributes of the habitat that is available (e.g. tree diameter). Furthermore, habitat requirements can vary between individuals within a population and during different times of year (e.g. Law & Anderson 2000).

The findings of this study indicate that a ‘one-size-fits-all’ approach to managing a landscape for hollow-using bats is likely to be inappropriate (Perry et al. 2008) and that the retention of a mosaic of mature forest patches throughout timber production forest is needed to meet the spatial and temporal habitat requirements of bats. Large patches of mature forest containing a high availability of hollow-bearing trees should, however, be a priority when retaining habitat for bats to ensure breeding habitat is retained in the landscape. Other retention measures such as small and large strips and patches are also important, particularly in landscapes where mature forest is limited, because they facilitate recolonisation of forested areas regenerating after harvest. Importantly forest managers should consider the type, amount and spatial arrangement of existing mature forest in the
Chapter 5: Bat roost site selection

landscape when deciding on the type, amount and spatial configuration of mature forest to retain in a harvested area in order to provide bats and other fauna with sufficient habitat in the long-term.
CHAPTER 6: BAT ACTIVITY, SPECIES ASSEMBLAGES AND RICHNESS IN TIMBER PRODUCTION LANDSCAPES: HOW EFFECTIVE ARE FOREST RETENTION MEASURES?

A partially harvested forest with a small patch (wildlife habitat clump) retained for biodiversity
Chapter 6: Bat activity and species composition

INTRODUCTION

Forest management for biodiversity conservation is crucial as forests support a high proportion of the world’s known terrestrial biodiversity (World Commission on Forests and Sustainable Development 1999). Protected areas alone will not necessarily conserve this biodiversity because much of the world’s forests are unprotected, important habitat for many species occurs outside of protected areas and because these areas are not necessarily managed for their biodiversity benefits or will they necessarily be protected indefinitely (FAO 2010; Lindenmayer et al. 2012; Mascia & Pailler 2011; Munks et al. 2009). Many forest managers recognise this and incorporate measures for the conservation of biodiversity into off-reserve forest management strategies (Munks et al. 2009; Polasky et al. 2005; Sergio & Pedrini 2007). In many cases however, there is little information on the habitat requirements of species to inform the development of such forest management strategies. As a consequence, these strategies are often based on accepted sustainable forest management principles developed using ecological theory (Lindenmayer et al. 2006; Schulte et al. 2006).

One approach is to manage biodiversity in multi-use landscapes that are not designated primarily for conservation (the matrix) by maintaining habitat across a range of spatial scales and configurations ranging from the individual tree to large reserve. This approach, known as multi-spatial scale approach to forest management is based on the principles of: the maintenance of connectivity across a landscape; the maintenance of landscape heterogeneity; the maintenance of structure complexity and plant species diversity within managed stands; and the maintenance of integrity of aquatic ecosystems (Lindenmayer & Franklin 2002). The multi-spatial scale approach is considered an effective strategy for managing habitat for fauna because it has the greatest probability of: meeting the diverse habitat requirements of species; facilitating dispersal through the landscape; and enhancing recolonisation of disturbed areas (Whitford & Stone 2004). It is also a risk-spreading approach that is essential in the instance that any single strategy is found to be ineffective (Lindenmayer & Franklin 2002).
A key component of the multi-spatial scale approach is to collect new data to fill gaps in existing knowledge and to use this information through adaptive management to facilitate the continual improvement of strategies (Lindenmayer & Franklin 2002). Effectiveness monitoring of strategies is an essential part of adaptive management and a fundamental part of ecological sustainable forestry and the ‘social license to operate’ that is increasingly required by forest certification schemes (Forest Stewardship Council. 1996; Lindenmayer & Franklin 2002). While many studies have examined the effectiveness of a particular forest management strategy for a species or fauna group (e.g. riparian strips: Lloyd et al. 2006), there has been little research into the effectiveness of the multi-spatial scale approach to forest management in a particular matrix (Munks et al. 2004).

Another challenge for forest managers is that in many regions the value of the matrix to biodiversity is changing with increases in the conversion of mature and older-aged regrowth forest to young regrowth or plantation (FAO 2010). This is of particular concern for fauna species dependent on mature forest elements, such as hollow-bearing trees, because it takes a considerable amount of time for such elements to form in young regrowth forest – at least 100 years (Koch et al. 2008a; Whitford 2002). If insufficient amounts, spatial scales and configurations of mature forest are retained in a landscape (matrix and designated protected areas), it could have severe ramifications for biodiversity. Recognising this, a key question being asked by forest managers is what amount and spatial configuration of mature forest is needed to be retained in the landscape to maintain biodiversity? (Munks et al. 2009; Parnaby et al. 2012; Whitford & Stone 2004).

With so many species potentially influenced by ineffective forest management strategies it is an almost impossible task to determine the effectiveness of forest management strategies for all species (Koch et al. 2012). One fauna group that may provide useful insights into the effectiveness of forest management strategies is insectivorous bats. Insectivorous bats depend on forests for commuting, foraging and socializing habitat (Lacki et al. 2007) and many species depend on hollow-bearing trees for roost and breeding sites (Kroll et al. ...
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2012b). As they are highly mobile, they are likely to respond to changes at the broader landscape scale, such as the availability of hollow-bearing trees (Lucan et al. 2009; Webala et al. 2010; Zahn 1999). They are also likely to respond to changes at the finer local scale because they are sensitive to changes in forest structure (i.e. conversion of mature forest to regrowth or plantation) because it influences their manoeuvrability and ability to forage and access roosts in a particular area (Jung et al. 2012).

Tasmania is home to eight resident bat species, all of which are widespread, insectivorous and dependent on hollow-bearing trees for roost and breeding sites (Koch et al. 2008b). Tasmania has a large forest estate, with half of Tasmania’s land mass forested and unlike other regions of the world, a relatively large proportion of this, just under half, is protected as part of a formal reserve system (FAO 2010; Forest Practices Authority 2012). This reserve system is, however, biased towards the south-west region of the main island, contains both formal and informal protected areas, is not representative for all forest communities and for several hollow-using species (including threatened species) it does not cater for their habitat needs (Forest Practices Authority 2012; Munks et al. 2009). Forest managers recognise this and in the matrix outside of the formal reserve system a number of forest management strategies are applied following the principles of the multi-spatial scaled approach to forest management (Munks et al. 2009). These include the retention of mature forest habitat at the landscape and stand scale in the form of large reserves, narrow and large strips, streamside reserves, aggregates and clumps (Baker & Read 2011; Forest Practices Board 2000; Munks et al. 2009; Taylor 1991). There have been many studies investigating the effectiveness of particular forest management strategies using a variety of measures and ‘snap shots’ in time (Baker et al. 2009; Cawthen & Munks 2011; Cawthen et al. 2012; Koch et al. 2009a; Law & Law 2011; Lefort & Grove 2009; MacDonald et al. 2005; Munks et al. 2004; Stephens et al. 2012a; Wapstra & Taylor 1998). However little is understood about the effectiveness of Tasmania’s forest management strategies and the influence of the surrounding matrix (Wardlaw et al. 2012), as well as how effectiveness varies temporally as the ecological, physiological and social habitat requirements of bats change (Lumsden & Bennett 2006).
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The overall aim of this study was to investigate whether bats use forest retention measures developed using the multi-spatial scale approach to forest management and what factors influence use. To do this the following questions were asked: (1) how do bats vary in their use of different types of retained mature forest patches?; (2) what temporal, spatial and climatic factors influence the use of different types of retained mature forest patches?; and (3) how can the amount and configuration of retained mature forest patches most effectively maintain bat species in Tasmania’s timber production landscapes?

METHODS

Study area and experimental design

The study was carried out in dry Eucalypt obliqua forests of eastern Tasmania, which constitute 45% of Tasmania’s forest cover (Forest Practices Authority 2012). In this region, twelve ‘landscapes’ were selected. These landscapes ranged from areas with little mature forest to areas with a large amount of mature forest. Ten of these landscapes were areas surrounding 10 partially harvested forest stands, and two were areas surrounding unharvested forest stands. Each harvested forest stand was on average 81.5 ha in size. Each landscape varied in the amount and type of human and natural disturbance and contained a mix of agricultural, plantation and native timber forest stands. Details of each landscape is provided in Table 12.

The type and amount of mature forest in each landscape was measured at two scales - 1km from the centre of the forest stand (directly surrounding) and within 5km of the forest stand (in the broader landscape) (Table 12; Figure 24). The amount of mature habitat for each landscape (1km and 5km) surrounding each forest stand was estimated using a mature habitat spatial layer (Forest Practices Authority. 2011). This spatial layer was developed using aerial photographs to remotely allocate mature habitat availability to one of five classes and also provides a measure for the relative abundance of hollow-bearing trees in the landscape (Forest Practices Authority. 2011; Koch & Baker 2011): None - cleared areas and water bodies; Negligible - non-forest, plantation or regrowth forest with no mature
eucalypt cover; Low = <20% crown mature eucalypt crown cover; Medium = 20-40% crown mature eucalypt crown cover; and High = >40% mature eucalypt crown cover.

Within each landscape, habitat elements were surveyed in the harvested and control stand and in the immediate area surrounding the stand. These habitat elements were selected to represent the range of different forest retention measures applied during the harvest operations that retain mature forest. N denotes number of anabats used at each retention habitat element across the study. These were:

- **Individual trees** – a hollow-bearing tree retained in the harvested area as part of the silvicultural prescriptions (n=7)
- **Small patches** – a small patch ‘wildlife habitat clump’ containing two to three hollow-bearing trees surrounded by ’recruitment’ trees retained in the harvested area (mean size = 0.1ha, n= 9)
- **Narrow strips** – a narrow linear strip ‘roadside reserve’ retained on the edge of a harvested area and adjacent road (mean size =3ha, 5-15 m wide, n=6)
- **Large strips** – a large linear strip ‘wildlife habitat strip’ retained on the edge of a harvested area between two harvested forests (mean size = 15ha, 100 m wide, n= 6)
- **Large patches (harvested edge)** – a large area of forest retained immediately outside the harvested area (mean size = 370ha, n = 11)
- **Large patches (reserve)** - a large area of forest retained in a formal reserve (mean size = 761ha, n=10)
- **No retained habitat** – an area where no forest retention measures had been applied (within 50 metres of any retained forest) inside the harvested area (n=12)

Note that not all forest retention measures were applied within each harvested area, so sample sizes vary between landscapes, as denoted by ‘n’.

**Bat call surveys**

Bat call surveys were conducted at each habitat element within each landscape to assess bat activity, species richness and species assemblages. Bat activity, the total number of bat
call sequences recorded per night comprised a range of bat calls indicating searching, feeding, commuting and socialising activities. Relatively high activity at one habitat element is likely to indicate more intensive use and importance of that forest retention measure, while low levels in another habitat element may indicate that a forest retention measure is avoided and of low importance (Law and Law 2011).

Figure 24. Left - Study landscape locations in south-east and northern Tasmania and the distribution of forest throughout Tasmania. Top right – partially harvested dry forest stand. Bottom right – unharvested dry forest stand.

Bat call surveys were undertaken during four sampling periods between December 2009 and 2010 using Anabat detectors (models SD1 and SD 11, Titley Electronics, Ballina, Australia). Each sampling period coincided with periods in the annual cycle of bats: the maternity season (Summer: December – February); mating/post lactation season (Autumn: March – May); non-reproductive/overwintering season (Winter: June – August); and pregnancy/post hibernation (Spring: Sep – Nov). Sampling throughout the year, rather than
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during periods of known heightened bat activity (i.e. the maternity season) provided data on whether the importance of habitat elements to bats varied temporally. Each landscape was sampled for between five and 12 days per sampling period. Variation in the number of samples per landscape per sampling period was a result of poor weather conditions hampering access to sites or when batteries failed prematurely.

At each habitat element, Anabat detectors were set in waterproof PVC boxes. A microphone extension cable ran from the PVC box up a 1.5 metre stake to the microphone attachment. The microphone attachment was angled up at $45^\circ$ pointed into vegetation gaps of the habitat element being surveyed and enclosed in a PVC elbow for weatherproofing. Detectors were calibrated against each other using a bat chirp board (Nevada Bat Technology, Las Vegas, USA) to ensure microphone sensitivity was equal across detectors. Most studies record only for the night (Hanspach et al. 2012) but bats can be observed flying during the day when disturbed from roosts (Webala et al. 2010) so bat call surveys were conducted over a 24-hour period.

Once files containing bat call sequences were downloaded, calls recorded on days where detectors failed (drained batteries) were excluded. Although it is common to also exclude or avoid sampling on nights based on poor weather conditions (Hanspach et al. 2012; Threlfall et al. 2011) because of the correlation between bat activity and temperature (De Oliveira et al. 1999), this was not done in this study. Instead, environmental variables of daily rainfall and minimum and maximum temperature from nearby weather stations were incorporated into the analysis.

**Bat call identification**

Bat activity was assessed at two scales - the community (overall bat activity) and the individual/group (species/species complex). Bat call sequences were identified by the program AnaScheme using a pre-defined Tasmanian bat call key as described in Chapter 2. AnaScheme automatically calculated the total number of bat call sequences recorded per 24
hour period (overall bat activity) and identified bat call sequences to species or species complexes (individual/group bat activity). Not all species could be accurately identified (e.g. *Nyctophilus sherrini*) so they were identified to a species complex (e.g. *Nyctophilus* spp.). This was also the case for *Chalinolobus morio* and *Vespadelus vulturnus* and a sub-set of the calls from *Vespadelus darlingtoni* and *Vespadelus regulus*, and *V. vulturnus* and *V. regulus*. Species that were considered especially problematic to identify were double-checked by manual identification of sonograms (e.g. *Nyctophilus* spp. whose calls can be misidentified as feeding calls of other species).

The following options were set within AnaScheme. Identifications were only made when a minimum of 50% of bat calls within a sequence were identified to the same species/species complex and only sequences with a minimum of three calls were identified to a species/species complex. If neither of these specifications were met, the sequence was identified as an unknown. Species richness was estimated by calculating the number of species whereas bat taxa richness calculated the number of species and species complexes.

Based on the above call analysis, four responses at each habitat element for each night were surveyed: (1) overall bat activity, the number of files containing sequences irrespective of identification (including unknowns); (2) species/species complex activity, the number of sequences identified to a specific species/species complex (excluding unknowns), (3) species richness, the number of species identified (excluding unknowns) and (4) species/species complex richness, the number of species/species complexes identified (excluding unknowns).

**Habitat variables**

A total of 22 variables describing spatial, temporal and climatic factors were measured (Table 11). Seven variables measured the composition of the landscape surrounding each habitat elements (the matrix) at a range of scales. The scales used were 500m, 1km, 3km and 5km radii. These variables were chosen because they can be readily assessed by forest managers when determining the type and amount of forest retention measures that should
be applied in a given area and because 5 km reflects the maximum distances Tasmanian bats are known to travel between foraging and roosting areas (Taylor & Savva 1988).
Table 11. A description of the variables measured at each bat call survey location (habitat element).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description / source of information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landscape</td>
<td>Classified as one of 12 sites where sub-sites (habitat-elements) were located (10 harvested, 2 unharvested reserves). This variable accounts for variation between sites that cannot be attributed to the variables assessed.</td>
</tr>
<tr>
<td>Habitat elements</td>
<td>48 habitat sub-sites were located in one of the following forest retention measures: Large patch (reserve site), large patch edge (harvested site), large strip, narrow strip, small patch, individual tree and no retained habitat.</td>
</tr>
<tr>
<td>Harvest year</td>
<td>Determined from the Timber Harvesting Plan for a harvested forest (Forestry Tasmania, unpublished data, Vanessa Thompson, pers. Comm.). This was a surrogate for age of forest regeneration.</td>
</tr>
<tr>
<td>Harvest area</td>
<td>Determined from the Timber Harvesting Plan for a harvested forest (Forestry Tasmania, unpubl. Data, Vanessa Thompson, pers. Comm.).</td>
</tr>
<tr>
<td>Easting</td>
<td>Derived from the easting grid-coordinates for each sub-site (GDA94) measured by a hand-held GPS.</td>
</tr>
<tr>
<td>Northing</td>
<td>Derived from the northing grid-coordinates for each sub-site (GDA94) measured by a hand-held GPS.</td>
</tr>
<tr>
<td>Season</td>
<td>Season categorises the time of year the survey was conducted in relation to the reproductive cycle of bats: overwinter (June-August), pregnancy (September – November), lactation (December – February) and mating (March – May) from data collected &amp; discussed in Chapter 4.</td>
</tr>
<tr>
<td>Month</td>
<td>January to December</td>
</tr>
<tr>
<td>Minimum daily temperature</td>
<td>Bureau of Meteorology website for the nearest weather station from site.</td>
</tr>
<tr>
<td>Maximum daily temperature</td>
<td>Bureau of Meteorology website for the nearest weather station from site.</td>
</tr>
<tr>
<td>Variable</td>
<td>Description</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Daily rainfall</td>
<td>Bureau of Meteorology website for the nearest weather station from site.</td>
</tr>
<tr>
<td>Elevation</td>
<td>Extracted from the position of each sub-site from a Tasmanian digital elevation spatial layer (DEM) using ArcGis.</td>
</tr>
<tr>
<td>Geology</td>
<td>Extracted from the position of each sub-site from the digital 1:250,000 geology map of Tasmania.</td>
</tr>
<tr>
<td>Distance to nearest watercourse</td>
<td>Measured as the distance of a sub-site to the nearest mapped watercourse (metres) using the state-wide digital map layers of hydrology from DPIPWE. Measured using ArcGis.</td>
</tr>
<tr>
<td>Distance to nearest road</td>
<td>Measured as the distance of a sub-site to the nearest mapped track or road (metres) using the state-wide digital map layers of roads from DPIPWE and Forestry Tasmania. Measured using ArcGis.</td>
</tr>
<tr>
<td>Mature habitat availability</td>
<td>Amount of mature habitat classified as medium to high in the landscape using the Mature Habitat Availability spatial layer.</td>
</tr>
<tr>
<td>Forest cover</td>
<td>Estimated from the Forest Class spatial layer from Forestry Tasmania (Stone 1998).</td>
</tr>
<tr>
<td>Cleared land</td>
<td>The amount of cleared land in the landscape using the Mature Habitat Availability spatial layer (Forest Practices Authority. 2011).</td>
</tr>
<tr>
<td>Road density</td>
<td>Generated using ArcGIS to measure the total length of roads and tracks within the circular area of different radii surrounding each sub-site.</td>
</tr>
<tr>
<td>Water course density</td>
<td>Generated using ArcGIS to measure the total length of water courses within the circular area of different radii surrounding each sub-site.</td>
</tr>
<tr>
<td>Total edge density</td>
<td>The length of edge including road and water course in the landscape using the above.</td>
</tr>
<tr>
<td>Landscape heterogeneity</td>
<td>Number of land cover types calculating using the TasVeg_2_0 spatial layer from the List, State of Tasmania.</td>
</tr>
</tbody>
</table>
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Statistical analysis

Temporal, spatial and environmental variables that influence bat activity and species richness habitat elements in the different forest retention measures were assessed using a Classification and Regression Trees (CARTs) approach (De'ath & Fabricius 2000). Regression tree models included all variables listed in Table 11. The most appropriate regression tree was refined via a cross validation approach using size and deviance explained by additional branches being assessed via the cost-complexity parameter k. Bat activity and species richness data were transformed \( \log(x+1) \) & \( \log(x + 0.01) \) transformed to improve model performance. Analyses were carried out using the ‘tree’ package in R. To examine correlations between climatic variables and bat activity, a spearman’s rank correlation was used. To examine differences the use of habitat elements by different bat taxa, an ANOVA of ranks using Dunn’s method for a pair-wise multiple comparison was performed for the most commonly occurring bat taxa in the study. All analysis was undertaken in R (R Development Core Team 2011).
Table 12. Description of the 12 landscapes used in this study including location, forest type, harvest history, environmental data and habitat context. *a = Large patch (wildlife habitat strip), b = small patch (wildlife habitat clump), c = small strip (streamside reserve), d = small strip (roadside reserve), e = large patch edge (informal/formal reserve surrounding coupe boundary), f = large patch edge (landscape management zone).

<table>
<thead>
<tr>
<th>Landscape name</th>
<th>Location (GDA94)</th>
<th>Harvest year</th>
<th>Harvest area (Ha)</th>
<th>Habitat elements (Forest retention measures)*a</th>
<th>Amount of habitat (ha) within a 1km radius (1257ha area of the site)</th>
<th>% Mature high-med 1km</th>
<th>% Mature med-high 5km</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW Informal reserve</td>
<td>554498, 5292366</td>
<td>n/a</td>
<td>Reserve - 652</td>
<td>N/a</td>
<td>262</td>
<td>100</td>
<td>47</td>
</tr>
<tr>
<td>MM Informal reserve</td>
<td>551500, 5273500</td>
<td>1997 &amp; 2004</td>
<td>Reserve - 870</td>
<td>n/a</td>
<td>283.3</td>
<td>90</td>
<td>37</td>
</tr>
<tr>
<td>MM002a &amp; 4a</td>
<td>562475, 5295454</td>
<td>2005</td>
<td>108</td>
<td>a,b,c,d,e</td>
<td>175</td>
<td>66</td>
<td>64</td>
</tr>
<tr>
<td>SW059C</td>
<td>552557, 5300151</td>
<td>2001</td>
<td>73.4 &amp; 23</td>
<td>a,b,c,e</td>
<td>137</td>
<td>45</td>
<td>27</td>
</tr>
<tr>
<td>SW060A</td>
<td>552041, 5302384</td>
<td>2003</td>
<td>65.2</td>
<td>a,b,e</td>
<td>81</td>
<td>43</td>
<td>49</td>
</tr>
<tr>
<td>WT013D</td>
<td>567644, 5272176</td>
<td>2008</td>
<td>39 &amp; 9</td>
<td>a,b,c,e</td>
<td>77</td>
<td>37</td>
<td>19</td>
</tr>
<tr>
<td>CL354A</td>
<td>479917, 5392767</td>
<td>2007</td>
<td>46.2</td>
<td>b,c,d,e</td>
<td>22</td>
<td>22</td>
<td>19</td>
</tr>
<tr>
<td>FT012G</td>
<td>573342, 5241931</td>
<td>2008</td>
<td>72</td>
<td>a,b,f</td>
<td>5</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>CL362X</td>
<td>485936, 5389727</td>
<td>2004</td>
<td>35.6 &amp; 10.6</td>
<td>a,c,e,f</td>
<td>1</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>BU132A</td>
<td>445795, 5407112</td>
<td>2008</td>
<td>50.3</td>
<td>b,c,d</td>
<td>17</td>
<td>10</td>
<td>24</td>
</tr>
<tr>
<td>FT016C</td>
<td>570046, 5239630</td>
<td>2007</td>
<td>35.6 &amp; 10.6</td>
<td>a,c,e,f</td>
<td>1</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>SW049A</td>
<td>552488, 5293966</td>
<td>1998</td>
<td>153</td>
<td>a,b,d</td>
<td>19</td>
<td>7</td>
<td>37</td>
</tr>
</tbody>
</table>
RESULTS

Bat assemblages and activity across all sites

In total, 33,722 bat call sequences were recorded across during 1,388 bat call survey nights. No bat activity was recorded during the day. On average, 24 bat call sequences were recorded per night but this varied greatly, ranging from 0 to 894 calls per night at any one habitat element. The number of nights where no bat calls were recorded was high (63% of survey nights), with 83% of the habitat-elements having at least one night where no bat calls recorded. A large proportion of nights where no bat calls were recorded were during the winter, when bat calls were not recorded on 40% of nights. Of the remaining nights when no bat calls were recorded, 28% in spring, 24% in autumn and 8% in summer. Three climatic variables were examined to determine their relationship with bat activity. Bat activity was poorly correlated with daily rainfall (Spearman’s rank correlation = 0.10), with 57% of days where no calls were recorded having 0 mm of rain and 77% with <2 mm of rainfall. Nights with no bat calls were more closely related to minimum nightly temperature, with 85% nights with no bat calls recording a minimum nightly temperature of 10 °C. Bat activity was more strongly correlated with minimum nightly temperature (Spearman’s rank correlation = 0.29), but the strongest correlation was between bat activity and maximum daily temperature (Spearman’s rank correlation = 0.37).

Of the call sequences recorded, 54% could be identified accurately to species or species complex with the remainder identified as unknowns. The high proportion of calls identified as unknown reflects the conservative approach employed for bat call identification, as the key used was designed not to mis-identify calls and effect estimates of species richness. The majority of call sequences were identified to species, with 21% identified to a species complex. The most commonly recorded species was *Vespdelus darlingtoni*, accounting for 33% of call sequences identified. The least commonly recorded species were *Vespdelus regulus* and *Vespdelus vulturnus*, accounting for only 0.14% of calls combined. This may be because the
call parameters of these species overlapped with other *Vespadelus* spp. and *Chalinolobus morio*. For this reason, the bat activity of these species may be more accurately understood at the species complex level.

All bat species and species complexes except *V. darlingtoni-V. regulus*, *V. vulturnus* and *V. regulus* were recorded at all landscapes. Not every species and species complexes were recorded at every habitat element (Table 13).

**Table 13.** Percentage of landscapes (n=12) and habitat elements (n=48) where bat species were recorded using bat call surveys and the mean ± standard deviation and range of bat activity recorded per night (n=18,047).

<table>
<thead>
<tr>
<th>Bat taxon</th>
<th>Number of call sequences</th>
<th>% landscapes</th>
<th>% habitat elements</th>
<th>Mean ±SD passes per night</th>
<th>Range of passes/night</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unknowns</td>
<td>15,556</td>
<td>100</td>
<td>100</td>
<td>11.3±32</td>
<td>0-396</td>
</tr>
<tr>
<td><em>Vespadelus darlingtoni</em></td>
<td>5,988</td>
<td>100</td>
<td>83</td>
<td>4.3±16.8</td>
<td>0-249</td>
</tr>
<tr>
<td><em>Chalinolobus gouldii</em></td>
<td>4,369</td>
<td>100</td>
<td>88</td>
<td>3.2±17.9</td>
<td>0-384</td>
</tr>
<tr>
<td><em>Falsistrellus tasmaniensis</em></td>
<td>3,100</td>
<td>100</td>
<td>77</td>
<td>2.3±9.4</td>
<td>0-165</td>
</tr>
<tr>
<td><em>C. morio-V. vulturnus</em></td>
<td>2,645</td>
<td>100</td>
<td>85</td>
<td>1.9±7.4</td>
<td>0-107</td>
</tr>
<tr>
<td><em>Nyctophilus spp.</em></td>
<td>978</td>
<td>100</td>
<td>77</td>
<td>0.7±2.4</td>
<td>0-29</td>
</tr>
<tr>
<td><em>V. darlingtoni-V. regulus</em></td>
<td>372</td>
<td>92</td>
<td>71</td>
<td>0.3±1.3</td>
<td>0-23</td>
</tr>
<tr>
<td><em>V. vulturnus-V. regulus</em></td>
<td>331</td>
<td>100</td>
<td>58</td>
<td>0.2±1.6</td>
<td>0-34</td>
</tr>
<tr>
<td><em>Chalinolobus morio</em></td>
<td>242</td>
<td>100</td>
<td>67</td>
<td>0.2±1.0</td>
<td>0-23</td>
</tr>
<tr>
<td><em>Vespadelus vulturnus</em></td>
<td>14</td>
<td>50</td>
<td>15</td>
<td>0.01±0.1</td>
<td>0-2</td>
</tr>
<tr>
<td><em>Vespadelus regulus</em></td>
<td>11</td>
<td>25</td>
<td>6</td>
<td>0.0±0.2</td>
<td>0-9</td>
</tr>
</tbody>
</table>
Variation in bat activity and species richness between landscapes

Models revealed that bat activity and species richness varied temporally and could be categorised into two periods – a ‘peak period’ between January and April and a ‘low period’ between May and December (see more below). During the peak period, bat activity varied markedly between habitat elements, with large patches, strips and narrow strips supporting double the amount of bat activity on average compared to small patches, individual trees and areas where no habitat was retained ($H = 81.598, df=6, P=<0.001$). During the low period, when bat activity declined by at least 50% in each habitat element, large strips were used significantly less compared to large patches and narrow strips ($H = 51.540, df=5, P = <0.001$) (Figure 25).

Species richness also varied between habitat elements during the peak and low period but was less pronounced than variations in bat activity. Large patches around the harvested edge and narrow strips had two to three more species than other habitat elements ($H = 28.580, df=5, P = <0.001$), but similar species richness was recorded across all other habitat elements (Figure 26). Species and species complexes also differed in activity patterns across habitat elements (see more below, discussed in next section) (Figure 27).
Chapter 6: Bat activity and species composition

Figure 25. Variation in average bat activity (passes per night) ± standard error at different habitat elements within timber production landscapes between January and April, and May to December. All landscapes combined.

Figure 26. Variation in mean species richness ± standard error at different habitat elements within timber production landscapes between January and April, and May to December. All landscapes combined.
Figure 27. Variation in activity of *C. gouldii*, *F. tasmaniensis*, *Nyctophilus* spp., *V. darlingtoni*, *C. morio*, *V. vulturnus* and unknowns at different types of forest retention measures (habitat elements) in timber production forests between January and April. All landscapes combined. Note Y-axis scales vary between species.
**Chapter 6: Bat activity and species composition**

*Relationship between bat activity and species richness and temporal, spatial and climatic factors*

Regression tree models revealed there were several spatial, temporal and climatic factors that were good predictors of bat activity and species richness at habitat elements. Month was the strongest variable in all of the models. Bat activity and species richness varied significantly over the survey period, being relatively higher from January to April compared to May to December (Figure 25 & Figure 26). Other spatial and climatic factors were: the amount of heterogeneity and edge in the surrounding 5 km landscape; the amount of mature forest in the surrounding 1 km landscape; distance to road and water; monthly and daily rainfall. All models except those for large patches performed reasonably well at explaining bat responses ($R^2 > 0.50$). However the amount of variance explained by variables did, however, vary between models and not all models included the same variables, as detailed below for each habitat element (forest retention measure) (Table 14).

At sites in large patches (reserves), bat activity was negatively influenced by the amount of daily rainfall and was positively influenced by distance to water sources. In contrast, species richness was positively associated with the amount of edge in the landscape (5km). Both model accuracies were poor ($R^2 < 0.50$) suggesting that other variables not measured in this study are likely to be better predictors of bat activity and species richness in large patches (reserves) (Table 14). Patterns of bat activity were highest in this habitat element for *C. morio-V. vulturnus* (Figure 27).

At large patches around the harvested stand edge, bat activity and species richness were both positively influenced by the amount of edge in the landscape (5km). Patterns of bat activity were highest in this habitat element for *C. gouldii* and *V. darlingtoni* (Figure 27).
At large strips, bat activity and species richness were both negatively influenced by the proportion of mature habitat availability in the landscape (1km). In landscapes where mature habitat availability was below 43% within 1 km, bat activity and species richness were highest (Figure 28). In landscapes with more than 43% mature habitat within 1km, both bat activity and species richness were higher at sites within 482m of a road. Overall, bat activity was greatest at large strips in landscapes with 16% to 43% mature habitat retained within 1km of the site.

At narrow strips, bat activity was greatest between October and February during the maternity season. No spatial or climatic variables were good predictors of bat activity at narrow strips. In contrast, species richness was positively influenced by the amount of edge in the landscape (5km) between June and September. Patterns of bat activity were highest in this habitat element for *F. tasmaniensis* (Figure 27).

At small patches, bat activity was highest between January and March when some females lactating and young are dispersing. During April, the onset of the mating season, the use of small patches was negatively associated with the amount of mature habitat in the landscape (1km). Bat activity was highest in small patches in landscapes where less than 16% mature forest was retained within 1km of the site (Figure 29). Species richness was high between January and April. No spatial or climatic variables were good predictors of species richness.

At individual trees, bat activity and species richness was greatest between February and April and positively influenced by amount of heterogeneity in the landscape (5km).

Where no habitat was retained, bat activity and species richness was greatest between November and February, particularly in areas less than 423m from roads. During other times of year, the use of areas where no habitat was retained increased with the amount of edge in the
surrounding landscape (5km).
Chapter 6: Bat activity and species composition

Figure 28. The relationship between bat activity and mature habitat availability in the surrounding 1km landscape at large strips between January and April.

Figure 29. The relationship between average bat activity and mature habitat availability in the surrounding 1km landscape at small patches between January and April.
Chapter 6: Bat activity and species composition

Table 14. The residual mean deviance and proportion of variance explained (R^2) by each model of bat activity and species richness at each habitat element.

<table>
<thead>
<tr>
<th>Habitat element</th>
<th>Bat activity</th>
<th>Species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Residual mean</td>
<td>R^2</td>
</tr>
<tr>
<td>Large patch (Reserve)</td>
<td>2.79</td>
<td>0.27</td>
</tr>
<tr>
<td>Large patch (Harvested edge)</td>
<td>1.94</td>
<td>0.58</td>
</tr>
<tr>
<td>Large strip</td>
<td>1.07</td>
<td>0.63</td>
</tr>
<tr>
<td>Narrow strip</td>
<td>1.45</td>
<td>0.50</td>
</tr>
<tr>
<td>Small patch</td>
<td>0.73</td>
<td>0.68</td>
</tr>
<tr>
<td>Individual tree</td>
<td>0.89</td>
<td>0.58</td>
</tr>
<tr>
<td>No retained habitat</td>
<td>0.19</td>
<td>0.57</td>
</tr>
</tbody>
</table>

DISCUSSION

Sustainable forest management requires an understanding of the effectiveness of management strategies to facilitate continual improvement (Lindenmayer & Franklin 2002). This is particularly so in regions where forest management strategies were developed based on little existing information about the habitat requirements of forest-dependent species (e.g. Tasmania - Taylor 1991). This study found that the most effective forest retention measures for bats implemented in Tasmania’s partially harvested dry eucalypt forests were large patches and strips, and narrow strips because these measures supported the highest bat activity and species richness. Although individual trees and small patches (wildlife habitat clumps) retained within the harvested stand supported less bat activity, species richness at such sites was similar to that recorded at the large patches and strips. Furthermore, bat activity at small patches was influenced by the composition of the matrix, in particular, mature habitat availability. This suggests that small ‘within-harvest area’ patches may still play a role in the maintenance of bat species in the production forest landscape and aid in recolonisation of harvested areas, particularly where mature habitat is scarce in the surrounding landscape. Together these findings suggest that the multi-spatial scale approach to forest retention provides habitat for
bats, facilitating recolonisation of harvested areas in the short to medium term (<20 years) and maintenance of bat species richness in timber production landscapes.

The influence of the landscape on the response of fauna to forest management strategies has been demonstrated by several studies (Kroll et al. 2012a; Vergara in press; Wardlaw et al. 2012). The premise of these studies is that understanding the effectiveness of forest retention measures cannot be fully understood without considering the influence of the matrix (Mazerolle & Villard 1999). For example, Kroll et al. (2012a) found that in landscapes where there was a relatively large amount of mature forest surrounding the harvested stand, the creation of hollows in the harvested stand was not an effective approach. Wardlaw et al. (2012) also found that the ability of many plant, bird and beetle species to recolonise harvested areas was reduced if there was relatively little mature forest in the surrounding landscape. For species dependent on mature forest elements, such as hollow-bearing trees, the amount of mature forest in the landscape could be an important factor in determining whether forest retention measures in a harvested stand are utilised.

Several temporal, spatial and climatic variables were also good predictors of bat activity and species richness at different patches and can further explain differences in the use of retained areas. Not surprisingly, time of year had the strongest influence. Temporal variation in bat activity is well recognised (Hayes 1997; Kuenzi & Morrison 2003; Milne et al. 2005; O'Donnell 2000), but there are few studies that have sampled bat activity and species richness throughout the year when undertaking effectiveness monitoring. Most studies sample during late spring and early summer. The rationale behind this approach is that this is the most important period to sample because it has: the highest bat activity as recorded by ultrasonic detectors; the maternity period when resource requirements, especially for females, are likely to be highest; and that bat activity is likely to be inflated in late summary when young become volant (i.e. Threlfall et al. 2012a; Webala et al. 2011). For effectiveness monitoring, however, this approach has a major limitation in that it only provides a ‘snap-shot’ of how bats and other
fauna use retained patches, which may vary throughout the annual cycle of bats as the spatial habitat requirements change (Kroll et al. 2012b).

The findings of this study demonstrate that the effectiveness of forest management strategies vary temporally. Between January and April (the maternity / mating season), large patches on the harvested area edge and narrow strips supported 50% more bat activity than large patches in reserves. However between May and December, both large patches in reserves and on the harvested edge, as well as narrow strips, supported similar bat activity. This pattern was similar but less pronounced for species richness, which varied by one to two species. High bat activity during the spring and summer months is generally associated with moderate temperatures, day lengths and insect availability, as well as the energetic requirements of lactation and juvenile dispersal. Low bat activity is generally associated with low temperatures and day lengths which reduce insect availability and increases in the energetic demands of thermoregulation (Lumsden & Bennett 2005; Sanderson & Kirkley 1998). These findings suggest that there are features of large patches and narrow strips on the harvested edge that make these patches more suitable to bats from a resource (i.e. insect or roost availability) or thermoregulatory perspective than large patches in reserves.

Both large patches on the edge of harvested forest and narrow strips share one feature in common: they have a relatively large area of linear edges. Linear edges created during timber harvesting operations function in the same way as natural forest gaps do in undisturbed forest – they create additional bat habitat by opening up areas of high vegetation density for commuting and foraging that would otherwise be inaccessible to those bat species that cannot maneuver through such habitat (Morris et al. 2010). This is consistent with data collected throughout Australia, where bat activity has been found to be higher on tracks and streams throughout regrowth and old growth forest (Cawthen et al. 2012; Law & Chidel 2002; Webala et al. 2011). Indeed, in this study the amount of edge in the landscape influenced bat activity and species richness at large patches around the harvested edge. Our results combined with
previous studies demonstrate the importance of linear edges for bats, such as tracks (Law & Chidel 2002; Webala et al. 2011), hedgerows (Boughey et al. 2012), riparian zones (Cawthen et al. 2012; Downs & Racey 2006; Law & Chidel 2002), intact woodland and harvested area edges (Downs & Racey 2006; Morris et al. 2010).

Individual trees and small patches are unlikely to provide all the resources that bats require and do not provide a greater thermoregulatory or resource advantage compared to larger patches which were readily accessible to bats. These patches are generally exposed and provide little edge for bats to commute and forage. They are also small in size and so the likelihood of containing a suitable available roost is greatly decreased. These findings differ to those from North America, where the use of small patches of trees has been found to be similar to that of the harvest edge (Hogberg et al. 2002). Such forest retention measures are likely to be more effective in landscapes where forest is highly fragmented or modified, such as agricultural landscapes (Fischer et al. 2010; Lumsden & Bennett 2005). Bats can travel relatively large distances (Lumsden & Bennett 2005), so in highly modified and fragmented landscapes, multiple individual trees and small patches are likely to provide key resources to bats and encourage recolonisation of harvested areas and facilitate connectivity (Russo et al. 2010). The findings of this study support this, as small patches were used more in timber production landscapes where there was less than 16% mature forest remaining within 1km of the harvested area. Therefore, the retention of individual trees and small patches may be effective in landscapes where there is little mature forest available close by.

No single forest retention measure is likely to benefit all bat species in an area. One of the main benefits of the multi-spatial scale approach to forest retention is that it is likely to cater for the diverse habitat requirements of forest-dependent species through ‘risk-spreading’ (Whitford & Stone 2004). Different bat species are known to respond differently to forest loss and modification (e.g. Webala et al. 2011) and this is related to differences in ecomorphology (Hanspach et al. 2012; Threlfall et al. 2012b). The findings of this study, that bat species varied
in their patterns of activity at different forest retention measures, demonstrate the value of the multi-spatial scale approach. For example, the high-flying less manoeuvrable *F. tasmaniensis* used open areas where no habitat had been retained twice as much as large patches in reserves, but used narrow strips twice as much as any other forest retention measure. Narrow riparian strips may be an important habitat element in Tasmania’s forests (Cawthen et al. 2012), but this could not be assessed in this study because few sites contained riparian reserves. In contrast there was little variation in the use of forest retention measures by the low-flying highly manoeuvrable *Nyctophilus* spp. most likely because these bat species can access open and closed forest patches. Results from other studies suggest that the response of bat species to forest management strategies will vary depending on forest structure in a given area (Law & Chidel 2002; Law & Chidel 2001; Webala et al. 2011). This may in part explain why *Nyctophilus* spp. readily used regrowth in dry eucalypt forests in this study, but avoided regrowth forest in wet eucalypt forests in other Tasmanian studies (Law & Law 2011; Rhodes 1996).

The findings of this study overcame many of the limitations recognised in previous research by including ‘unknown’ bat call identifications in the analysis. This precluded inferences of forest retention measure use being biased towards only bat species whose calls could be identified accurately, and replicating sampling both temporally and spatially (Sherwin et al. 2000). Using bat call surveys as a survey method is however not without its limitations, and these should be taken into account when interpreting the results for individual species. Firstly, not all species could be identified to species level, so inferences of habitat use patterns are based on bat taxa (e.g. *Nyctophilus* spp. for *N. sherrini* & *N. geoffroyi*). For *Nyctophilus* spp. in particular, although both species are known to occur in the study (Driessen et al. 2011). It is possible that the habitat use patterns inferred from bat call data reflect the habitat use patterns of only one species, as *N. geoffroyi* and *N. sherrini* are known to select habitat differently (Chapter 5). Secondly, this study did not sample insect biomass or diversity which is a probable to be a factor influencing bat activity and may be a strong driver of the temporal variation observed (Threlfall et al. 2011; Threlfall et al. 2012b). Excluding insect abundance or diversity from our
analysis likely resulted in poorer models, but forest managers are unlikely to survey insects when selecting habitat for bats, so other factors such as those measured in this study are more practical for the purposes of this study. Thirdly, the survey design did not take into account the vertical stratification in bat habitat use which may have resulted in overestimates and underestimates in bat activity of some species (Adams et al. 2009) but as dry eucalyptus forests were quite low in height, this is unlikely to be an issue compared to the tall wet eucalyptus forests. Lastly, bat call surveys do not take into account intra-specific variation in habitat use patterns or the value of forest retention measures for roosting which can only be obtained from radio-telemetry data (Chapter 4). Despite these limitations, this data set was robust and indicates seasonal and species-specific differences in the use of retained areas by bats which can help inform management practices.

**Management Considerations**

World-wide, the multi-spatial scale approach to mature forest retention is considered to be one of the most effective strategies for maintaining bat diversity in timber production landscapes (Adams et al. 2009; Dodd et al. 2012; Grindal & Brigham 1998; Jung et al. 2012; Morris et al. 2010; Patriquin & Barclay 2003). Because bats used forest retention measures differently and the extent of use varied temporally and spatially this approach is likely to be more appropriate than the ‘one-size-fits-all’ approach to forest management in catering for the habitat requirements of bats and maintaining bat species in the landscape. That said, the effectiveness of this approach will depend on the ability of land managers to implement strategies across multiple land tenures (e.g. public and private forest) and land managers (e.g. local council and state government). This is challenging but crucial as the findings of this study demonstrate the importance of mature forest availability for bats. For improvement of current forest management strategies, forest managers should consider the retention of forest patches that optimise the amount of edge in the stand; and the retention of small patches and large strips in landscapes where current and anticipated future amounts of mature forest habitat in the
landscape are rare or low. In landscapes where mature forest habitat is low in relation to past extents, regeneration of mature forest should also be a priority. Future research into the effectiveness of forest management strategies for bats should focus on how the type, amount and spatial arrangement of mature forest are influencing populations in terms of genetic diversity, abundance and reproductive success. The long-term success of the multi-spatial scale forest management approach will require such studies in addition to ongoing monitoring of whether retained habitat survives and continues to be used by bats as the forest regenerates. Without such research forest managers cannot understand how effective forest retention measures are and how to improve them, which is a necessary objective of ecologically sustainable forest management.
A timber production landscape adjacent a formal reserve (the Southwest National Park) – does the network of multi-spatial scale forest retention measures benefit biodiversity in such a landscape?
Chapter 7: General discussion

INTRODUCTION

Ecologically sustainable forest management has been described as the perpetuation of ecosystem processes and maintenance of ecosystem integrity whilst utilising forests for their timber production and non-timber values (Lindenmayer et al. 2000). The maintenance of biodiversity is an important part of ecologically sustainable forest management, not only because of the intrinsic value of the biota forests support, but also because of the important role many species play in maintaining the health of forest ecosystems and aiding in regeneration after disturbance (Burton et al. 1992). Understanding the effectiveness of different approaches to forest management for biodiversity conservation, and how effectively these are applied in practice, is crucial for the continual improvement of forest management strategies for biodiversity conservation (Lindenmayer & Franklin 2002). The overall aim of this thesis was to gather information that can be collectively used to assess the effectiveness of this multi-scale approach to forest management as applied in practice in Tasmania, at conserving hollow-using bats.

Though bats represent a large component of Tasmania’s terrestrial mammalian diversity, there is limited understanding of their distribution, abundance, echolocation calls (for bat call identification), reproduction, activity patterns and ecological requirements (Driessen et al. 2011). Such information is vital for developing and interpreting the results of studies such as effectiveness monitoring of forest management strategies (Chapters 5 and 6). Though some of this information, such as the timing of reproduction, is known from mainland conspecifics, such information cannot be readily transferred from one region to another. This is because of variation in the morphology, physiology and ecology of bat species across their range influences, their echolocation call attributes, timing of reproduction and activity patterns, and ecological requirements (Racey & Entwistle 2003). Recognising this, a large proportion of this thesis (Chapters 2 – 4) is dedicated to filling gaps in the understanding of Tasmanian bats with the findings informing the development and interpretation of the studies in Chapters 5 and 6.
Chapter 7: General discussion

This chapter synthesises the main findings of this thesis and discusses how they have contributed to expanding our knowledge of Tasmanian bats and evaluating the effectiveness of the multi-scale approach to forest management for bats. This chapter concludes by providing recommendations on the improvement of current forest management strategies for bats and other forest-dependent fauna.

**SYNTHESIS OF KEY FINDINGS**

*Tasmanian bats*

There are just over a 1000 bat species, almost a quarter of which are threatened (Mickleburgh et al. 2002). Australia’s most recent mammalian extinction was a bat, the Christmas island pipistrelle (Lunney et al. 2011). Like Tasmanian bats, this species was a hollow-using insectivorous micro-bat (Koch et al. 2008b). Reminiscent of so many species that have become extinct, little was understood of the Christmas Island pipistrelle’s distribution, abundance, reproduction and ecology to inform conservation initiatives when it was first found to be in decline. Though Tasmanian bats are currently not considered threatened (Driessen et al. 2011), like the Christmas island pipistrelle, no baseline data exists to adequately assess their conservation status. The studies undertaken as part of this thesis have provided a significant contribution to filling the gaps in the knowledge of Tasmanian bats to enable such assessment and to inform the development of management strategies for Tasmanian bats and their habitat.

One of the main approaches used in this thesis to collect data on Tasmanian bats was though bat call surveys. Bat call surveys are promoted as one of the most appropriate methods for surveying bats because in many regions species cannot be effectively detected through capture methods alone (e.g. species adapted to flying in open spaces - Duffy et al. 2000; Mills et al. 1996) and because capture methods are not always practical (e.g. wind farm monitoring at height- Johnson et al. 2004) or suitable for long-term monitoring (e.g. species declines - Brooks 2011). Bat call surveys are also less invasive, and do not require animals to be captured once a bat call identification key has been developed. Though in many regions not all bat species can be readily identified by their calls (Barclay 1999; Fenton 2003), bat call surveys can be a
valuable tool for collecting baseline data on bats if the limitations of this approach, such as the ability to identify bat calls, are fully understood (Walters et al. 2012).

One of the greatest challenges for anyone undertaking bat call surveys is the identification of bat call sequences. Specifically, deciding on the most accurate and efficient approach to bat call identification given the likelihood that not all calls can be identified accurately to species level. Various approaches to bat call identification are outlined in the literature, but few are compared (e.g. Adams et al. 2010; Herr et al. 1997; Parsons & Szewczac 2009). Chapter 2 provides one of the most comprehensive quantitative comparisons of different approaches to bat call identification, and provides details on developing a bat call identification key. By collating and comparing bat calls from throughout Tasmania, this study demonstrates the ability of the computer software package AnaScheme to accurately and efficiently identify bat call sequences, in particular, bat call sequences that overlap extensively in call attributes. This chapter also discusses alternative computer software packages that have the potential, like AnaScheme, to assist with bat call identification. Importantly for future bat research and monitoring in Tasmania, this chapter provides an approach to bat call identification that can be used to collect data to inform management of Tasmanian bats and their habitat without the biases associated with subjective bat call identification or statistical techniques. This approached to bat call identification is not Tasmanian bat specific and has the potential to be successful at identifying bat call sequences in other regions throughout the world.

The value of bat call surveys and the bat call identification key developed for Chapter 2 is exemplified by the discovery of the white-striped freetail bat in Tasmania during data collection for this thesis (chapter 3). This discovery demonstrates the power of bat call surveys as a bat survey approach, particularly for species not readily captured. The successfulness of this approach was also demonstrated by using bat call surveys to clarify the relationship between the activity and reproductive cycles of Tasmanian bats (Chapter 4) and evaluate the importance of different forest retention measures for bats (Chapter 6). It is important to note, however,
that bat call surveys do have their limitations. In Tasmania, the main limitation of this technique, as demonstrated in Chapter 2 and 6 is that not all species can be identified by their calls and so this approach cannot provide a complete inventory of Tasmanian bat species.

By using a combination of bat call surveys and bat capture Chapters 2 and 4 were able to clarify that Tasmanian bat species exhibit marked variation in their echolocation calls (Chapter 2), as well as in their reproductive and activity cycles (Chapter 4) compared to their mainland conspecifics. These differences likely reflect the size, location and glacial history of Tasmania and the influence these factors have had on bat morphology, physiology and ecology since Tasmania separated from mainland Australia (Driessen et al. 2011). The identification of such variation between bat populations is crucial because it confirms that information on the echolocation, reproduction and ecology of bats in one region cannot be readily transferred to another. If this were attempted, this could result in conducting bat surveys at inappropriate times of year (e.g. sampling outside of the maternity season in Chapter 5) or the misinterpretation of data (e.g. seasonal variation in bat activity in Chapter 6).

The effectiveness of forest management strategies for bats

Off-reserve forest management is promoted as an important strategy for biodiversity conservation (Lindenmayer & Franklin 2002), though little is known of the effectiveness of different management approaches. The data collected in Chapters 5 and 6 reveal that the multi-spatial scale approach to forest management is effective at maintaining bats in off-reserve areas such as timber production landscapes. By retaining mature forest elements at a range of spatial scales, such as in the form of individual hollow-bearing trees, as well as small and large mature forest patches and strips, bats can not only be maintained in timber production landscapes, but are also provided with suitable habitat that facilitates their recolonisation of regenerating forest stands.
Chapter 7: General discussion

The retention of a variety of different types, amounts and spatial arrangements of mature forest habitat is one of the main reasons why the multi-spatial scale approach to forest management is promoted to be effective for biodiversity conservation (Lindenmayer & Franklin 2002). Bats vary in their ecological requirements spatially and temporally to meet changes in their physiological, ecological and social needs (Lumsden & Bennett 2006). By retaining habitat at multiple spatial scales there is a greater likelihood that suitable habitat will be retained to cater for the range of roosting, foraging and commuting habitat preferences demonstrated by bats.

Tasmanian bats exhibit a range of roosting, foraging and commuting habitat preferences. The findings of Chapters 5 and 6 revealed that not all bat species shared the same roosting, foraging and commuting habitat preferences nor did each species use the same habitat for roosting as they did for foraging and commuting. This was particularly evident for maternal colonies of different species. Lactating females of all species foraged in small patches and large strips of regenerating forest but varied in their roost site selection at multiple spatial scales. For example, *Nyctophilus geoffroyi* readily used small patches and large strips to breed in whereas other species such as *Nyctophilus sherrini* and *Chalinolobus morio* avoided such patches. These findings imply that no single forest management strategy (e.g. ‘the one-size fits all approach’) is likely to meet all the habitat requirements all bat species as well as facilitate the recolonisation of regenerating forest and thus maintain bat species in timber production landscapes. This reinforces the conclusion that the multi-spatial scale approach to forest management, as applied in Tasmania’s dry eucalypt forests, is a viable and effective approach for bat conservation.

One of the most significant findings of this thesis was that the value of forest retention strategies for bats varies with landscape composition. This is not surprising as studies have found that the landscape has an important influence on the habitat use patterns and community structure of a variety of fauna including birds (Antongiovanni & Metzger 2005;
Chapter 7: General discussion

Jokimäki & Huhta 1996; Pardini et al. 2009; Tubelis et al. 2007; Vergara et al. 2013; Wardlaw et al. 2012), mammals (Caryl et al. 2012; Caryl et al. in press; Cawthen & Munks 2011; Flynn et al. 2011a; Flynn et al. 2011b; Pardini et al. 2009; Umetsu & Pardini 2007), reptiles (Pardini et al. 2009; Steen et al. 2012), amphibians (Pardini et al. 2009; Parris 2004) and invertebrates (Pardini et al. 2009; Wardlaw et al. 2012). What is significant about this finding for bats is that it could explain differences in habitat use patterns and species assemblages that have been observed across different landscapes and landscape contexts (e.g. urban areas) that vary in landscape composition.

There were several components of the landscape that were particularly important to bats. These were the amount of mature forest in the landscape (within 1km), the amount of landscape heterogeneity and edge in the broader landscape (within 5km) and distance to roads. Specifically, the findings of both Chapters 5 and 6 revealed that the type, amount and spatial arrangement of mature forest influenced both bat roosting and activity patterns in timber production landscapes. For example, bats used small patches and large strips of mature forest retained in young regenerating forest to a greater extent in landscapes where mature forest availability was relatively low compared to a landscape where mature forest was readily available. The relationship between the composition of the surrounding landscape and the use of small forest patches has also been noted in hollow-using birds (Kroll et al. 2012a) and arboreal marsupials (Banks et al. 2013). Together these findings suggest that the less mature forest available in the landscape, the greater the likelihood that retained habitat at smaller spatial scales (e.g. individual tree, small patch and strips) will be utilised by fauna, and thus the greater importance of retaining such habitat. By using bat ecomorphology, land managers may be able to predict how species will use retained forest habitat (Table 15) (Hanspach et al. 2012).
ARE TASMANIA’S FOREST MANAGEMENT STRATEGIES EFFECTIVE FOR CONSERVING FAUNA?

The findings of this thesis have important implications for understanding the effectiveness of Tasmania’s forest management strategies for conserving fauna. Unfortunately there is limited information on how fauna are responding to Tasmanian forest management strategies and how this varies in response to landscape composition. Though a range of studies have been undertaken on a variety of fauna including ground-dwelling small mammals (Stephens et al. 2012a), arboreal marsupials (Cawthen & Munks 2011; Flynn et al. 2011b), birds (Koch et al. 2009a; Koch et al. 2009b; Lefort & Grove 2009; MacDonald et al. 2005; MacDonald et al. 2002), invertebrates (Baker et al. 2009; Grove) and even bats (Cawthen et al. 2012; Law & Law 2011), for the most part, there has been a lack of consideration of the composition of the surrounding landscape when interpreting results. What these studies do provide us with is a consensus that, overall, Tasmania’s forest management strategies as a collective (i.e. the multi-spatial scale approach) is effective for conserving a wide range of fauna, but that each forest retention measure (e.g. large reserves or small patches) is not necessarily effective on its own at meeting the habitat requirements of all species. This is because not only do fauna vary in their habitat requirements, but each species varies spatially and temporally in the habitat they require as demonstrated by the findings of this thesis (Table 15). It is also important to note that though small patches, strips and individual trees may not cater for all the habitat requirements of a species, these retention measures do provide important habitat for facilitating the recolonisation of harvested areas and conserving species in the landscape (e.g. Cawthen & Munks 2011). This is particularly so in landscapes where large areas of mature forest have been cleared or are naturally rare.
Table 15. The diverse ecological requirements of Tasmanian bat species in timber production landscapes and their relationship with ecomorphology. Note that these preferences may be site specific depending on the landscape context.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ecomorphology</th>
<th>Roosting habitat</th>
<th>Foraging and commuting habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chalinolobus gouldii</em></td>
<td>Low freq calls; fast-flying, low manoeuvrability</td>
<td>Not assessed</td>
<td>The edges of large patches and to a lesser extent than large patches</td>
</tr>
<tr>
<td><em>Chalinolobus morio</em></td>
<td>Med to high freq calls; fast-flying, low manoeuvrability</td>
<td>Large patches of mature forest (&gt;350ha), especially for breeding, but will use strips, individual trees and small patches</td>
<td>Large patches and the edge of large patches</td>
</tr>
<tr>
<td><em>Falsistrellus tasmaniensis</em></td>
<td>Low freq calls; fast-flying, low manoeuvrability</td>
<td>Large patches of mature forest (&gt;350ha)</td>
<td>The edge of narrow strips and to a lesser extent large patch edges and partially harvested regrowth forest.</td>
</tr>
<tr>
<td><em>Nyctophilus geoffroyi</em></td>
<td>High freq calls; slow-flying, high manoeuvrability</td>
<td>Individual trees, small and large patches and strips</td>
<td></td>
</tr>
<tr>
<td><em>Nyctophilus sherrini</em></td>
<td>High freq calls; slow-flying, high manoeuvrability</td>
<td>Large patches of mature forest (&gt;350ha), especially for breeding, but will use strips, individual trees and small patches</td>
<td>Uses all patch types</td>
</tr>
<tr>
<td><em>Vespadelus darlingtoni</em></td>
<td>Med freq calls; fast-flying, low manoeuvrability</td>
<td>Not assessed</td>
<td>Large patch edges and strips and to a lesser extent large patches and narrow strips.</td>
</tr>
<tr>
<td><em>Vespadelus regulus</em></td>
<td>Med freq calls; fast-flying, high manoeuvrability</td>
<td>Not assessed</td>
<td>Large patch edges and strips and to a lesser extent large patches and narrow strips.</td>
</tr>
<tr>
<td><em>Vespadelus vulturnus</em></td>
<td>Med to high freq calls; fast-flying, high manoeuvrability</td>
<td>Not assessed</td>
<td>Large patches and large patch edges</td>
</tr>
</tbody>
</table>
CONSIDERATIONS FOR IMPROVEMENT OF FOREST MANAGEMENT STRATEGIES

There is a large amount of evidence to demonstrate that retaining forest in areas where forest is to be lost or modified (off-reserve forest management) is beneficial for biodiversity around the world (Baker & Read 2011; Banks et al. 2013; Kroll et al. 2012b; Lindenmayer et al. 2012). Although current forest management strategies are mitigating the impacts of forest loss and fragmentation on a variety of fauna species (Baker et al. 2009; Cawthen & Munks 2011; Cawthen et al. 2012; Flynn et al. 2011a; Flynn et al. 2011b; Grove & Yaxley 2005; Lefort & Grove 2009; Stephens et al. 2012a; Wardlaw et al. 2012), including bats, the long-term effectiveness of these management strategies can be improved by retaining a variety of different types of forest habitat at a variety of spatial scales ranging from the hollow to the stand scale, and by considering the composition of the landscape when deciding on the type, amount and spatial arrangement of mature forest to retained in an area to be retained.

Considering the composition of the landscape (the matrix) when managing habitat for biodiversity is a huge challenge. Unlike retaining habitat at smaller spatial scales (e.g. an individual tree), managing habitat at the landscape scale can involve forest stands or catchments that are managed by multiple land managers whose management objectives and strategies vary (Kroll et al. 2012a). Inconsistencies in forest management strategies have the potential to create landscapes devoid of large tracts of mature forest, which as shown in this thesis, are important habitat for many species. These deficiencies will be long-term, as it takes at least 100 years for mature forest elements to develop (e.g. hollow-bearing trees) (Koch et al. 2008a). Furthermore, though the retention of small patches and large strips are beneficial in maintaining biodiversity in landscapes where large tracts of mature forest are lost or naturally rare, it is unclear how the long-term persistence of species in such landscapes will be affected by reduced habitat availability (e.g. genetic structure: Stephens et al. 2012b). Recognising the importance of landscape scale forest management and consistency in forest management strategies across land tenures and land use regulatory systems is essential to ensuring that forest biodiversity is conserved in the long-term.
**Final Remarks**

Ultimately, species respond in different ways to forest management strategies depending on the taxon in question, the spatial and temporal scale at which forest is lost, modified and fragmented and the composition of the surrounding landscape. It is an almost impossible task to understand the effectiveness of forest management actions for all species given their range of responses, but through studying groups of species whose ecological characteristics are shared by other species, we can test ecological theory applicable to the conservation of multiple species (Koch et al. 2012). This is the approach that has been followed in this thesis. It is however crucial that basic research on both individual species and communities is undertaken to underpin management actions for biodiversity conservation, particularly given the potential for bat species to be shifting their ranges throughout the world. Such management actions must however be underpinned by sound scientific research which is integrated with community education, sound policy and action by government based on research and monitoring of outcomes (Lunney et al. 2011).
APPENDICES

An eastern falsistrelle (*Falsistrellus tasmaniensis*)
Appendices

APPENDIX 1. EXAMPLES OF TASMANIAN BAT REFERENCE CALL SONOGRAMS RECORDED USING ANABATS

Gould’s wattled bat (*Chalinolobus gouldii*)

Chocolate wattled bat (*Chalinolobus morio*)
Appendices

Eastern falsistrelle (*Falsistrellus tasmaniensis*)

Tasmanian long-eared bat (*Nyctophilus sherrini*)
Lesser long-eared bat (*Nyctophilus geoffroyi*)

Large forest bat (*Vespadelus darlingtoni*)
Large forest bat (*Vespadelus darlingtoni*)– low frequency call

Southern forest bat (*Vespadelus regulus*)
Little forest bat (*Vespadelus vulturnus*)
APPENDIX 2. ANASCHME BAT CALL IDENTIFICATION KEY

```python
def PulseKey(pulse):
    tail=end_frequency-model_frequency
    tail2=end_frequency-minimum_frequency
    curvxmodelstarslo=model_curvature*model_start_slope
    startxendslop1=model_start_slope-model_end_slope
    startxendslop2=model_start_slope*model_end_slope
    bandwidth=maximum_frequency-minimum_frequency

    if model_frequency < 9.9:
        if model_quality > 0.9:
            if (end_frequency - start_frequency > 2):
                return 'noise'
            if model_quality < 0.9:
                return 'noise'
        if within(model_frequency, 10, 16):
            if model_quality > 0.9:
                if freq_gap_stdev >372:
                    if duration <9.4 or average_time_between_pulses <15:
                        return 'noise'
                    if duration >9.4 and average_time_between_pulses >15:
                        return 'Tadarida australis'
                if freq_gap_stdev <372:
                    if average_time_between_pulses <15 or duration <5.1:
                        return 'noise'
                    if average_time_between_pulses >15 and duration >5.1:
                        return 'Tadarida australis'
        if model_quality < 0.9:
            return 'noise'

    if within(model_frequency, 16, 21.5):
        if model_quality > 0.9:
            if freq_gap_stdev >372:
                if duration <5.4:
                    return 'noise'
            if freq_gap_stdev <372:
                if average_time_between_pulses <15 or duration <5.1:
                    return 'noise'
                if average_time_between_pulses >15 and duration >5.1:
                    return 'Tadarida australis'
        if model_quality < 0.9:
            return 'noise'

    if within(model_frequency, 24, 39.67):
        if model_end_slope < -1.5193:
            if model_curvature > 1.06535:
                if model_curvature >=1.9365:
                    if mean_model_curvature < 2.0365:
                        return 'cgouldi'
                if model_curvature < 1.9365:
                    return 'Nycto sp.'
            if model_curvature >=1.9365:
                if mean_model_curvature < 2.0365:
                    return 'Vespadelus darlingtoni'
        if model_end_slope < -1.5193:
            if model_frequency > 33.07:
                return 'Chalinolobus Gouldii'
            if model_frequency >=33.0704:
                return 'Falsistrellus tasmaniensis'
        if model_end_slope < -1.5193:
            return 'Nyctophilus sp.'

    if within(model_frequency, 39.68, 41.51):
        if model_end_slope < -0.9237:
            return 'Nyctophilus sp.'
        if model_end_slope > -0.9237:
            return 'Vespadelus darlingtoni'

    if within(model_frequency, 41.52, 44.00):
        if model_end_slope < -2.4299:
            return 'Nyctophilus sp.'
        if model_end_slope > -2.4299:
            if model_start_slope >=-4.1064:
Appendices

return 'Vespadelus darlingtoni'
if model_start_slope < -4.1064:
    return 'Vespadelus darlingtoni or regulus'

if within(model_frequency, 44.01, 51.31):
    if tail < -1.42:
        return 'C.morio'
    if tail > -1.42:
        if end_frequency < 45.262:
            if start_endslo1 >= 2.67585:
                if model_slope >= 3.2506:
                    return 'Nyctophilus sp.'
                if model_slope < 3.2506:
                    return 'Chalinolobus morio or Vespadelus vulturnus'
            if start_endslo1 < -2.67585:
                if model_slope >= 3.7139:
                    return 'Nyctophilus geoffroyi'
                if model_slope < 3.7139:
                    return 'Vespadelus regulus-darlingtoni'
        if end_frequency >= 45.262:
            if model_curvature < 2.25:
                if model_slope >= 7.2206:
                    return 'Nyctophilus sp.'
                if model_slope < 7.2206:
                    if model_curvature >= 2.25:
                        if tail2 >= 1.015:
                            return 'Chalinolobus morio'
                        if tail2 < 1.015:
                            if model_curvature < 2.75:
                                return 'Chalinolobus morio or Vespadelus vulturnus'
                            if model_curvature >= 2.75:
                                return 'Vespadelus vulturnus'
            if within(model_frequency, 51.32, 56):
                if model_end_slope >= -15.5:
                    return 'Chalinolobus morio'
                if model_end_slope < -15.5:
                    if model_frequency < 46:
                        return 'Nycto sp'
                    if model_frequency >= 46:
                        return 'Chalinolobus morio'

if num_points < 8 or bandwidth < 2.1:
    return 'Unknown - C.morio/V.regulus/v.darlingtoni'

return 'Unknown'
APPENDIX 3. ANTI-PREDATION STRATEGIES IN TASMANIA’S HOLLOW-USING BATS

INTRODUCTION

Predation risk has a major influence on bat behaviour and is considered to be one of the main selection pressures on roost selection by hollow-using bats (Kunz & Lumsden 2003). However little is understood about how predators influence bat roost site selection and behaviour. Observations of predation on bats at roosts are relatively rare (Baker 1962; Borkin & Ludlow 2009; Dwyer 1964; Esberard & Vrcibradic 2007; Hammer & Arlettaz 1998; Twente 1954) and virtually nothing is known about anti-predation strategies in bats (Lima & O'Keefe 2013; Petrezekova & Zukal 2003). If predators influence bat behaviour, than an increase in predation risk should generally lead to a change in behaviour favouring a safer behavioural option (anti-predation strategy) most likely at some cost to the bat (i.e. foraging efficiency, thermoregulation) (Lima & O'Keefe 2013).

One might expect that roost selection by individual bats is in part in response to the day-to-day variation in predation risk (Lima & O'Keefe 2013). A range of bat roosting behaviour such as nocturnality, avoidance, coloniality, roost switching, adjusting the times and durations of emergence, changing the hollow of emergence, clustering during emergence and roost abandonment have been interpreted as an anti-predation strategy (Fenton et al. 1994; Petrezekova & Zukal 2003; Speakman 1991). However there is little information to support or refute whether bats use these behaviours in response to predation risk and if so, when and in what situations they are used (Lima & O'Keefe 2013).

Generally most predation on bats is opportunistic with only a few predators specialising on bats (e.g. The bat hawk, Macheiramphus alcinus) (Jones et al. 2012). Opportunistic bat predators include several centipede, frog, snake, bird and mammal species (including humans) (Baxter et
In most regions, owls are thought to be main predators of bats (Baxter et al. 2006). This is based on bat remains in regurgitated pellets (Garcia et al. 2005; Green et al. 1986; Hall & Blewett 1964; Khalafalla & Iudica 2012; Lesinski et al. 2012; Rosina & Shokhrin 2011; Wiley 2010; Yuan Li et al. 2010) and several owl predation events that have been reported (Baker 1962; Borkin & Ludlow 2009; Olsen 2011; Twente 1954). Bats can be captured in roosts during the day, presumably while torpid (e.g. by cats) (Scrimgeour et al. 2012) or on the wing as they emerge from roosts at night (e.g. by owls) (Lima & O'Keefe 2013).

In Australia, bats have a range of nocturnal predators including several owl species such as the southern boobook (Olsen et al. 2008), masked owl (Todd 2012) and barking owl (Stanton 2011); yawny frogmouths (Nick Mooney and Monika Rhodes pers comm.) and nightjars (Michael Pennay pers comm.). Other animals observed pursuing or having consumed bats include (but are unlikely not limited to): wedge tailed eagles, brown falcons, grey goshawks, Australian hobbys (Nick Mooney pers comm.), Tasmanian devils (Jillian Smith), spotted-tail quolls (Glen & Dickman 2008), cats (Phillips et al. 2001), foxes (Dwyer 1964) and water rats (Woollard et al. 1978). Information on how bats respond to predation risk by different predators (e.g. Birds versus mammals), in different situations (e.g. at roosts versus foraging) could provide valuable insights into habitat and roost choice (Lima & O'Keefe 2013).

This short note describes the situation and response of bats to a predation event by a southern boobook (*Ninox novaeseelandiae*) on a maternal colony of chocolate wattled bats (*Chalinolobus morio*). I use this observation and anecdotal and published observations to provide insights into anti-predation strategies used by bats and how predation risk may influence roost use and behaviour.
MATERIALS AND METHODS

In January 2011, lactating female Chocolate wattled bats with non-volant young were radio-tracked to their day-time roosts in Woodsdale, south-east Tasmania, Australia (552488E 5293966N). Roost emergence was monitored by two to three people. Each observation of roost emergence started approximately 30 minutes before the expected onset of emergence. The number of bats emerging, inter-species interactions and emergence behavior (e.g. emerging in clusters) were recorded by observers. Anabat detectors (SD2, Titley electronics, Ballina, Australia) were used as a secondary method of monitoring bats during emergence by listening to calls. Moon illumination and sunset times were calculated using the on-line tool time and date (http://www.timeandate.com). This study was undertaken under the guidelines of the University of Tasmania Animal Ethics Committee permit #A0010640 and the Department of Primary Industries Water and the Environment scientific permit #FA09132.

RESULTS

On 13th January 2011 a maternal colony of Chocolate wattled bats were located in a hollow with a large entrance size (>10cm) in a Eucalypt tree. Bats began emerging at 21:02. Bats emerged individually, but more often in clusters of up to 40 individuals. At 21:12, a Southern Boobook was observed on a nearby branch, approximately 20 meters from the roost tree. After several minutes, the Boobook flew to the roost entrance, hovering in mid-air in a reared ‘sitting position’, wings out, talons open directed into the roost. Bats continued to emerge and echolocate in clusters despite the presence of the Boobook. After a minute, the Boobook took flight from the roost and then returned, pursuing emerging bats as they circled the roost tree. After two failed attempts to capture a bat, an individual bat that had circled the roost tree was captured by its wing in the Boobook’s talons. The Boobook then pecked the bats body, the bat became immobile and the Boobook flew into nearby forest out of sight.
A total of 299 bats emerged from the roost that night, with several bats returning within an hour of the first bat emerging. On the following day, no radio-tracked bats used the tree where the predation event occurred. The individuals radio-tracked were instead found in a small colony of 17 individuals in a nearby tree. Two days later however, a smaller colony of five individuals, including a least one individual that experienced the predation event, was found roosting in the tree where the predation event occurred. Other radio-tracked individuals were roosting nearby in a roost of 155 individuals (Table 1).

Table 16. Changes in timing of emergence and colony size of Chocolate wattled bats before and after a predation event. Bold values indicate observations the night of the predation event.

<table>
<thead>
<tr>
<th>Date</th>
<th>Sunset time</th>
<th>Roost ID</th>
<th>Emergence time</th>
<th>Colony Size</th>
<th>Moon illumination</th>
</tr>
</thead>
<tbody>
<tr>
<td>4/01/2011</td>
<td>19:50</td>
<td>SW26.1</td>
<td>21:11</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>5/01/2011</td>
<td>19:50</td>
<td>SW26.2</td>
<td>21:24</td>
<td>86</td>
<td>0.6</td>
</tr>
<tr>
<td>6/01/2011</td>
<td>19:50</td>
<td>SW26.3</td>
<td>21:18</td>
<td>1</td>
<td>3.2</td>
</tr>
<tr>
<td>7/01/2011</td>
<td>19:50</td>
<td>SW26.4</td>
<td>21:10</td>
<td>130</td>
<td>7.8</td>
</tr>
<tr>
<td>10/01/2011</td>
<td>19:49</td>
<td>SW26.5</td>
<td>21:09</td>
<td>145</td>
<td>29.8</td>
</tr>
<tr>
<td><strong>13/01/2011</strong></td>
<td><strong>19:48</strong></td>
<td><strong>SW24.2</strong></td>
<td><strong>21:02</strong></td>
<td><strong>299</strong></td>
<td><strong>58.5</strong></td>
</tr>
<tr>
<td>14/01/2011</td>
<td>19:48</td>
<td>SW24.3</td>
<td>21:15</td>
<td>17</td>
<td>68.3</td>
</tr>
<tr>
<td>15/01/2011</td>
<td>19:47</td>
<td>SW24.2</td>
<td>21:15</td>
<td>5</td>
<td>77.6</td>
</tr>
<tr>
<td>15/01/2011</td>
<td>19:47</td>
<td>SW6.6</td>
<td>21:07</td>
<td>155</td>
<td>77.6</td>
</tr>
<tr>
<td>16/01/2011</td>
<td>19:47</td>
<td>SW6.6</td>
<td>21:05</td>
<td>341</td>
<td>85.9</td>
</tr>
<tr>
<td>18/01/2011</td>
<td>19:46</td>
<td>SW6.7</td>
<td>21:05</td>
<td>220</td>
<td>N/A</td>
</tr>
<tr>
<td>19/01/2011</td>
<td>19:45</td>
<td>SW6.7</td>
<td>21:08</td>
<td>1</td>
<td>97.6</td>
</tr>
</tbody>
</table>

**DISCUSSION**

Bat colonies emerging from a tree-hollow provide a concentrated (albeit fast-moving and small) food resource for nocturnal predators (Petzkelova & Zukal 2003). As a consequence, it is not
surprising that bats feature in the diet of nocturnal predators throughout the world. This is especially so for Owls (Khalafalla and Iudica, Hall and Blewett 1964, Green et al. 1986, Garcia et al. 2005, Wiley 2010, Yuan Li et al. 2010, Rosina and Shokhrin 2011, Lesinski et al. 2012), which are able to access and pursue bats in flight (Olsen 2011). It is therefore not surprising that bats have developed anti-predation strategies. The observations reported in this study demonstrate some of these strategies in use including clustering, delayed emergence and roost switching.

Clustering during emergence is proposed by Speakman (1992) to be increasingly used in the presence of a predator to decrease the probability of predation on the individual (safety in numbers). This strategy appears to be used by several bat species around the world (Fenton et al. 1994; Petrazelkova & Zukal 2003; Speakman 1995), especially in large colonies where it is most likely to be effective (Fenton 1994). This strategy seems to be effective, as Owls have been observed to be unsuccessful at predating upon bats when bats emerge in clusters from roosts in this study and by others (Temby pers comm; Baker 1962; Twente 1954). Indeed, Owls seem more successful predating on individual bats in mid-air (Olsen 2011) rather than directly at a tree hollow roost entrance.

Avoidance is another strategy employed by bats to minimise predation risk. Avoidance may be in the form of roost-switching (avoiding the location of the predation event) or fleeing the predator (Kunz & Lumsden 2003). In this study, bats were observed to switch roosts directly after the predation event. It is difficult to say however, whether this was in response the predation event, as roost-switching was a frequently observed during the radio-tracking study (Cawthen et al. unpublished data). Bats may switch roosts to avoid predators which may return to the roost tree the following night.

An alternative strategy most likely used when roost-switching or clustering is not effective is delaying the timing of emergence to avoid or reduce the likelihood of predation (Fenton et al. 1994). In my observation, C. morio did not delay emergence in the presence of a predator but
on the following night in an alternative roost with a smaller colony emergence was delayed. This may indicate that C. morio could not perceive the increased predation risk when the Boobook was present or that there was ‘safety in numbers.’ Delayed emergence is not an uncommon strategy in bats in response to predation risk. Tadarida australis has also been observed to delay emergence in response to the presence of predators, including humans. This species also stops echolocating and producing social calls in the presence of predators (Monika Rhodes pers comm.), a strategy not used by the C. morio in this study. However, because insectivorous bats are constrained by the emergence times of insects, they may not be capable of varying their emergence times greatly without effecting foraging efficiency (Baxter et al. 2006; Jones & Rydell 1994).

Bats may not alter their roosting behaviour at all, instead, using evasive manoeuvres in-flight to avoid predators (Lima & O'Keefe 2013). Although this was not observed in this study, several instances of evasive manoeuvres have been observed overseas (Lima & O'Keefe 2013) and in Australia. In Australia, a Saccolaimus flaviventris has been observed being pursued by a Barking Owl and using an aerobatic strategy to avoid predation. As the Owl approached, the bat pulled in its wings, dropped out of the Owls flight path and then re-extended its wing and altered direction (Luke Hogan pers comm.). Bats may also confront their predators in an attempt to avoid predation. For example, Chalinolobus gouldii has been observed being pursued by a nightjar and then change its flight to pursue and harass the nightjar (Michael Pennay pers comm.).

There are a range of anti-predation strategies used by bats which may influence bat habitat and roost choice, and other bat behaviours. Some of which, such as delayed emergence, are likely to reduce the amount of time spent foraging, and may result in changes to habitat selection, potentially reducing bat foraging efficiency. Therefore understanding anti-predation strategies used by bats is an important component of understanding bat behaviour. Future and previous
Appendices

studies should report movements and habitat selection of bats when exposed to predation events to inform our understanding of anti-predation strategies used by bats.
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