

**The Ecology and Conservation of the
White-striped freetail bat (*Tadarida australis*)
in Urban Environments**

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Synopsis

Of all anthropogenic pressures, urbanisation is one of the most damaging, and is expanding in its influence throughout the world. In Australia, 90% of the human population live in urban centres along the eastern seaboard. Before European settlement in the early 1800s, much of the Australia's East coast was dominated by forests. Many of the forest dependent fauna have had to adapt to forest fragmentation and habitat loss resulting from clearing for urbanisation. However, relatively few studies have investigated the impact of urbanisation on biodiversity. This is especially true for the remaining fauna in large metropolitan areas, such as Melbourne, Sydney and Brisbane.

The physical and conceptual context of this thesis is the increasing impact of urbanisation and the potentially threatening factors to forest dependent fauna. Bats were selected because they comprise a third of Australia's mammal species, and therefore form a major component of Australia's biodiversity. Very little is known about the ecology and conservation biology of hollow-dependent bats in general, but particularly in urban environments. The study was conducted in Brisbane, south-east Queensland, one of Australia's most biodiverse regions. More than a third of Australia's bat species occur in this region. A large insectivorous bat, the white-striped freetail bat (*Tadarida australis*), was selected to study two key resources in this urban area – hollow availability and foraging habitat. This thesis also examined if artificial roost habitat could provide temporary roosts for white-striped freetail bats and other insectivorous bats and assessed whether these bat boxes can be used as a conservation tool in urban environments where natural hollow-availability is limited.

The white-striped freetail bat is an obligate hollow-dweller and roosted largely in hollows of old or dead eucalypts throughout Brisbane's urban matrix. These roost trees harboured significantly more additional hollow-dependent species compared to control trees of similar age, height, and tree diameter. Roost cavities inside trees often exceeded 30 cm in diameter. Furthermore, maternity colonies used cavities of hollow trunks, which often extended into major branches, to roost in big numbers. Therefore artificial alternatives, such as small bat boxes, may provide temporary shelter for small roosting groups, but are unlikely to be suitable substitutes for habitat loss. Although five bat species used bat boxes during this study, the white-striped freetail bat was not attracted into bat boxes.

Roost-switching behaviour was then used to quantify associations between individual white-striped freetail bats of a roosting group. Despite differences in gender and reproductive seasons, the bats exhibited the same behaviour throughout three radio-telemetry periods and over 500 bat-days of radio-tracking: each roosted in separate roosts, switched roosts very infrequently, and associated with other tagged bats only at a communal roost. Furthermore, the communal roost exhibited a hub of socialising between members of the roosting group especially at night, with vocalisation and swarming behaviour not found at any of the other roosts.

Despite being spread over a large geographic area ($> 200 \text{ km}^2$), each roost was connected to others by less than three links. One roost (the communal roost) defined the architecture of the network because it had the most links. That the network showed scale-free properties has profound implications for the management of the habitat trees of this roosting group. Scale-free networks provide high tolerance against stochastic events such as random roost removals, but are susceptible to the selective removal of hub nodes, such as the communal roost.

The white-striped freetail bat flew at high speed and covered large distances in search for food. It foraged over all land-cover types found in Brisbane. However, its

observed foraging behaviour was non-random with respect to both spatial location and the nature of the ground-level habitat. The main feeding areas were within three kilometers of the communal roost, predominantly over the Brisbane River flood plains.

As the only mammal capable of flight, bats can forage above fragmented habitats. However, as this study showed, hollow-dependent insectivorous bats, including free-tailed bats, are specialised in their roosting requirements. The ongoing protection of hollow-bearing trees, and the ongoing recruitment of future hollow-bearing trees, is essential for the long-term conservation of these animals in highly fragmented landscapes. Furthermore, loss of foraging habitat is still poorly understood, and should be considered in the ongoing conservation of bats in urban environments.

Statement of Originality

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Monika Rhodes

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Preface

During this project I designed the study in collaboration with my supervisors Darryl Jones, Grant Wardell-Johnson and Carla Catterall; I collected all data, sometimes with the assistance of volunteers (see Acknowledgements); I undertook statistical analyses with guidance of my supervisors; drafted and revised all chapters and publications; and took all the photographs included in this thesis, with the exception of a few, which have been acknowledged.

Structure of this thesis

Each chapter in this thesis is written as manuscripts for publication as the aim was to publish as I write. Two of the chapters have been published and two have been submitted:

Chapter 3: Rhodes, M., and G. Wardell-Johnson. 2006. Roost tree characteristics determine use by the white-striped freetail bat (*Tadarida australis*, Molossidae, Microchiroptera) in suburban subtropical Brisbane, Australia. *Austral Ecology* 31:228-239.

Chapter 4: Rhodes, M., G. Wardell-Johnson, M. P. Rhodes, and B. Raymond. 2006. Applying network analysis to the conservation of habitat trees in urban environments: a case study from Brisbane, Australia. *Conservation Biology* 20: 861-870.

Chapter 5: Rhodes, M. Roost fidelity and fission-fusion dynamics of white-striped freetail bats (*Tadarida australis*). Submitted to *Journal of Mammalogy*, September 2005. Subject to revisions.

Chapter 6: Rhodes, M. and C. Catterall. Foraging behaviour and use of an urban landscape by white-striped freetail bats (*Tadarida australis*). Submitted *Journal of Zoology*, London.

I also intend to publish Chapter 7 (bat box study) after submitting this thesis for examination. However, at this stage, the last chapter is too long for publication and will need shortening.

Most chapters have been written with the support of at least one of my supervisors who were therefore included as co-authors. Chapter 4 had more than one co-author as the topic of *network theory* is a very complex mathematical field and needed the feedback of people specialised in this area. The involvement of co-authors is listed below.

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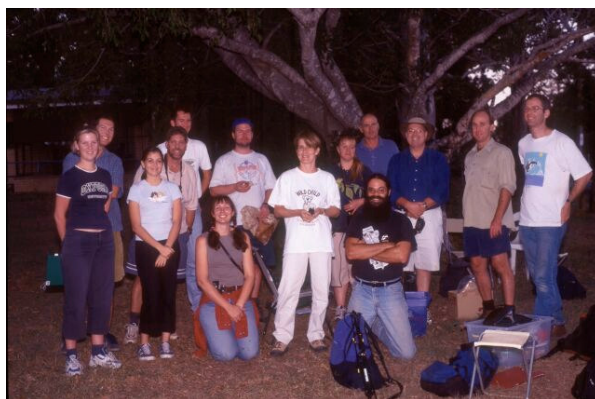


Plate 0.1. Radio-tracking team (Capture night, March 2002).

Although I undertook most sections of my PhD by myself, the long and difficult field work, mostly at night in public parks, would not have been possible without the help of many unpaid volunteers. I also received a lot of encouragement, moral support and critical feedback from friends and supervisors. I am also pleased to be part of a big network of bat researchers around the globe, stretching from Australia to New Zealand, Germany, Portugal, Canada and the USA (no doubt a *scale-free network* in itself, see Chapter 4 for definitions).

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Chapter 1

General introduction

1.1 Urbanisation and its impact on habitat loss and biodiversity

In his book “*Deforesting the Earth: from Prehistory to Crisis*” Williams (2003) concluded that deforestation is as old as the presence of humans on earth. It is, however, he explained, modern technology which has enabled humans to exploit natural resources (e.g., timber) more fully. Agriculture, logging practices and urbanisation have all resulted in fragmentation and clearing of native habitat and a global decline in biodiversity (Williams 2003). Hansen and Rotella (1999) argued that many large protected areas are established on relatively unproductive land, while areas targeted for forest exploitation, agriculture and development coincide with productive lands and hence high biodiversity. Areas with a high level of species diversity and endemism (hereafter *biodiversity hotspots*) often have above-average human population densities and growth rates with around 150 major cities presently located in or close to a hotspot (reviewed by Miller and Hobbs 2002).

In Australia, many major cities are located near areas of high conservation significance for forest fauna (Williams *et al.* 2001, National Forest Inventory 2003, Lunney 2004a), but only 13% of Australia’s forests are in protected areas (National Forest Inventory 2003). Forest fauna, however, are not limited to protected areas, but are found across a wide variety of habitats (Martin and Martin 2004). Lindenmayer and Franklin (2002) argued that conservation approaches must encompass the entire landscape, regardless of tenure, if biological diversity is to be retained. This is a view

echoed by Lunney (2004b: p. 2): *“If we let forest-dwelling species, or suite of species, define a landscape, we can arrive at a different way of conserving our forest fauna. Among the cultural obstacles we face are tenure boundaries between private and publicly owned land [...]”* This is especially true for urban environments where the majority of the human population share the same location as many species of Australia’s native fauna (Goldingay and Sharpe 2004).

Of all anthropogenic pressures, urbanisation is currently regarded as one the most damaging, and is expanding in its influence world-wide (Hooper and Vitousek 1997, McKinney 2002, Miller and Hobbs 2002, Jha and Bawa 2006). Hobbs and Mooney (1997) concluded that urban and suburban environments coincide with profound habitat fragmentation across the globe. In Australia 90% of the human population lives along the eastern seaboard, predominately in the three major cities of Sydney, Melbourne and Brisbane (Commonwealth of Australia 2003). Urbanisation has transformed the coastal forests of these regions, which formerly included a high level of species diversity and endemism (Williams *et al.* 2001, National Forest Inventory 2003, Lunney 2004b, Norman *et al.* 2004). This process has led to a mosaic of fragmented patches of native forests, separated by buildings, roads and industries within a human-modified environment (Catterall and Kingston 1993, Collins *et al.* 2000).

Despite these changes, some urban areas still retain a rich diversity of flora and fauna (Jonsson 1995, Queensland Museum 1995) and some species seem able to adapt well to human-dominated environments. Kühn *et al.* (2004) discussed that the high diversity of the flora in German cities persists in spite of urbanisation. However, in urban Oxford, U.K., Dickman (1987) found a rapid decline of vertebrate species richness with increased levels of urbanisation. Studies of urban avifauna have also found dramatic changes. While some urban areas retain native bird communities, these communities are often dominated by a small number of dominant

native species (Recher and Serventy 1991, Sewell and Catterall 1998, Jones 2003, Catterall 2004).

Collins *et al.* (2000) argued that urban ecosystems are dynamic and changing. Like natural ecosystems, urban ecosystems can recover from human-induced disturbances (e.g., altered landscapes, diverted waterways, increased nutrient levels, *etc.*) with forms of ecological successions within thirty years. This view is shared by Low (2002), who presented examples of endangered plants and animals which can be found in city centres but extinct in surrounding nature reserves. Whether a species becomes a '*winner*' or '*loser*' (Low 2002) will depend on its ecological requirements and how well these can be met in highly disturbed environments.

1.2 Hollows: a declining resource in urban environments?

When forest is replaced by urbanisation the forest fauna remaining in urban remnant bushlands or parklands must adapt to environmental changes. While Collins *et al.* (2000) and Low (2002) argued that some species can adapt to new urban environments, many hollow-dependent species can be disadvantaged by removal of hollow-bearing trees (Goldingay and Sharpe 2004, Rowston and Catterall 2004). In Australia, Gibbons and Lindenmayer (2002) highlighted the importance of hollows to more than 300 native species. Eucalypts, the predominant tree species of Australian forests and woodlands (Boland *et al.* 1992), generally support a greater number of hollows than rainforest species (reviewed in Gibbons and Lindenmayer 2002). With the continued drying of the Australian continent, eucalypt forests started to dominate rainforests by the late Miocene (White 1990). Keast (1985) and Archer *et al.* (1991) have argued that the increasing abundance of hollows during the Miocene is one

reason for the radiation of hollow-dependent birds such as parrots, cockatoos and also mammals such as possums, gliders and vespertilionid bats in Australia.

In the Northern Hemisphere, many tree hollows are formed by primary or secondary cavity excavators such as woodpeckers (Frank 1997). These cavities are used by a succession of hollow-dependent species such as bees, squirrels and insectivorous bats. In Australia, however, hollow development in eucalypts does not begin by excavation, but by damage to the heartwood and a succession of organisms, beginning with decay-causing fungi that gain entry through injuries in the tree (Wilkes 1982). Termites may then access the heartwood that contains fungal rot (McCaw 1983, Perry *et al.* 1985), excavating pipes slowly in a tree which can eventually extend into the main branches (Wilkes 1982, Perry *et al.* 1985, Gibbons and Lindenmayer 2002). Hollows in eucalypts ultimately form when the decayed heartwood is exposed where branches or the trunk break-off due to natural shedding or wind damage and the decayed wood is removed by animals, water or fire (Jacobs 1955, Saunders 1979, Mackowski 1987, Gibbons and Lindenmayer 2002).

Hollow-formation in eucalypts can take several hundred years, depending on tree species, tree location and history and the size of hollows (Mackowski 1987, Wormington 1996, Gibbons *et al.* 2000). For example, Mackowski (1984) estimated that it takes 40 years to form small hollows, and 220 years to form large hollows in blackbutt (*Eucalyptus pilularis*) in temperate Australia. Wormington (1996), on the other hand, calculated 150 years for small hollows and more than 166 years for large hollows to form in blackbutt in subtropical south-east Queensland. While hollow formation may commence from a young age, most authors agree that hollows suitable for larger fauna form rarely under the age of 120 years (Mackowski 1984, Inions *et al.* 1989, Mawson and Long 1994, Wormington 1996, Gibbons *et al.* 2000).

The long duration required for hollow formation and the anthropogenic pressure on hollow-bearing trees due to selective logging of old trees, removal of

trees for agriculture, or urban development may limit the availability of hollows for wildlife. For example, Gibbons and Lindenmayer (2002) demonstrated that the formation and loss of hollows are cyclic events. In unmanaged dry eucalypt forests, hollow numbers fluctuate within a narrow band of variation. This reflects a wide variety of disturbances, from loss of individual trees to intense fires. As unmanaged forests have a high diversity of different aged trees, they contain enough trees to eventually replace lost hollows. Forests managed for timber production have stands dominated by even-aged young trees, as well as few regeneration events to counter loss of mature and hollow-bearing trees (Ross 1999). Similarly, in rural areas, old hollow-bearing trees occur along riparian areas or as single, scattered individuals in paddocks, where regeneration is unlikely (Bennett *et al.* 1994, Gibbons and Boak 2002, Lumsden and Bennett 2005, Maron 2005).

While the impact of logging and agriculture on hollow-bearing trees has been studied in forested and rural environments, little research has been carried out in urban environments. The few studies in urban environments have been conducted in remnant forests (Harper *et al.* 2005a). However, a study of hollow availability for hollow-dependent fauna in the urban matrix has yet to be conducted.

1.3 Hollow-usage

Hollow-usage can be obligate or opportunistic, depending not only on the species but also on seasons and hollow availability (Gibbons and Lindenmayer 2002). For example, Lumsden *et al.* (1994, 2002) reported that lesser long-eared bats (*Nyctophilus geoffroyi*) can be flexible in their roost choice (e.g., under bark, in fissures or in buildings) but require tree hollows as maternity colonies. Similarly, Webb and Shine (1997, 1998) showed that an arboreal tree snake (*Hoplocephalus*

bungaroides) uses tree hollows only during the warmer months when rocks become too hot.

In Australia as elsewhere, hollows may provide several advantages and disadvantages to a roosting animal (Gibbons and Lindenmayer 2002, Kunz and Lumsden 2003). They provide roosting space (e.g., Saunders 1982), give protection against predators (e.g., Tidemann and Flavel 1987), and reduce energetic costs by providing stable microclimates (e.g., Sedgely 2001) or help to facilitate thermoregulation through passive re-warming (e.g., Turbill 2006). However, roosting in confined spaces makes it hard to avoid predators, especially when roosting in hollows with large entrances. Lace monitors (*Varanus varius*) and spotted-tailed quolls (*Dasyurus maculatus*) may gain access to otherwise concealed spaces (Mansergh and Huxley 1985, Belcher 1995). A shortage in hollow availability can also cause accumulation of parasites and competition between and within hollow-dependent species (Lindenmayer *et al.* 1997).

An ecological understanding of hollow-usage by particular species is important to derive appropriate management actions, especially in species that frequently switch between hollows. For example, a study of den-swapping behaviour of the mountain brushtail possum (*Trichosurus caninus*) by Lindenmayer *et al.* (1996) revealed that 16 radio-tracked individuals used more than 100 hollow-bearing trees within a 18-month period. Some species show even more pronounced roost lability. O'Donnell and Sedgely (1999) showed that the long tail bat (*Chalinolobus tuberculatus*) in New Zealand changes roosts on average every 1.2 days, and that roosts are seldom re-used.

1.4 Hollow-dependent fauna in urban Australia

At present, 15% of Australia's terrestrial vertebrates depend on hollows at some stage of their lives. These include 114 bird, 79 reptile, 27 amphibian, and 83 mammal species (Gibbons and Lindenmayer 2002). Much of the research on hollow-dependent species in urban environments in Australia has concentrated on birds and the more conspicuous mammals, such as gliders and possums, in the fragmented matrix of urban bushland remnants (Jones 2003, Goldingay and Sharpe 2004, Lunney 2004a, Lunney and Burgin 2004, Garden *et al.* 2006). However, the largest group of hollow-dependent mammals in Australia, the bats with 43 species, has been largely neglected (Gibbons and Lindenmayer 2002, Garden *et al.* 2006).

Although bats comprise approximately 20% of the world's mammal species, less than 7% of studies of mammalian life histories have focused on bats (Barclay and Harder 2003). Furthermore, bats are rarely considered in studies of habitat fragmentation and vertebrate species richness, despite the knowledge that habitat fragmentation and associated loss of roost sites are important factors in the decline of bat populations (Dickman 1987, Hall 1990, Sheffield *et al.* 1992, Barclay and Brigham 1996, Racey and Entwistle 2003, Parnaby and Hamilton-Smith 2004). Moreover, bats are extremely vulnerable to population declines due to low reproductive rates and long generation times, they stabilise only slowly after high rates of mortality (Sheffield *et al.* 1992, Barclay and Harder 2003, Racey and Entwistle 2003).

Information on the impact of habitat loss on bats mainly derived from studies conducted in forested or agricultural areas (Barclay and Brigham 1996, Law 1996, Lumsden 2004). Consequently our understanding of the effects of urbanisation and associated habitat loss on bats is fragmentary and limited. Studies on roosting habitat of urban bats have been mainly restricted to species that roost in caves or

human-made structures, such as buildings (Taylor *et al.* 1999, Hoyer and Spence 2004). Other studies have focused on identifying associations between species' foraging activities and habitat type of urban bats. Gaisler *et al.* (1998), for instance, recorded bat activity and relative species abundance in a central European city and found that activity was highest at the river and in long established suburbs with low-density housing, while it was lowest in the city centre and new housing estates. Similarly, Kirsten and Klomp (1998) recorded the highest bat activity and species abundance in, or close to, urban remnant vegetation in temperate Australia. Hourigan *et al.* (2006) found that only one species, the molossid *Mormopterus* species 5, was able to exploit all urban habitats in a tropical Australian city while the remaining 14 bats foraged close to natural vegetation with low numbers of street lights. These authors concluded that species which are able to forage on insects attracted by white street lamps, were the most successful urban bat species as these were able to forage away from remnant vegetation.

To date no study has examined the spatial foraging patterns and habitat preferences of any hollow-dependent bat species in urban Australia. Similarly, no study has investigated whether species that forage in open areas are affected by urbanisation. Such information is essential for the formulation of appropriate management recommendations for urban bat populations. The persistence of native wildlife, including bats, in cities will depend on the extent to which their resource requirements can be met within the urban landscape. These requirements include roosting and foraging demands (Kunz and Lumsden 2003, Racey and Entwistle 2003).

1.5 Nest boxes as alternative roost sites in urban environments?

Nest boxes are used world-wide as a substitute for natural tree hollows to provide nest sites for a range of hollow-dependent fauna. In this situation, nest boxes have been shown to maintain or increase populations of birds, mammals and marsupials (Thomas *et al.* 1979, Schemnitz 1980, Menkhorst 1984, Stebbings and Walsh 1985, Wardell-Johnson 1986, Tidemann and Flavel 1987, Tuttle and Hensley 2000, Smith and Agnew 2002, Harper *et al.* 2005b). At the same time, nest boxes have also been used as a tool for the study of hollow-using species, allowing researchers access to nests or roosts which are otherwise difficult to reach (Menkhorst 1984, Gerell and Lundberg 1985, Nagel and Nagel 1988, Boyd and Stebbings 1989, Lundberg and Gerell 1996, O'Shea 1998, Park *et al.* 1998, Kerth *et al.* 2001).

Most of the above-specified studies were carried out in forested environments, often in young timber plantations, to determine whether nest boxes may be a substitute for the loss of hollows. Although nest boxes are very popular for many households in urban backyards in some regions (Tuttle 1989, Tuttle and Hensley 2000), very little scientific research has been conducted on nest box usage in urban environments. In a 12-month study of nest box use in metropolitan Melbourne, southern Australia, Harper *et al.* (2005b) found that nest boxes were readily occupied by the common brushtail possum (*Trichosurus vulpecula*) and the common ringtail possum (*Pseudocheirus peregrinus*). The introduced common myna (*Acridotheres tristis*), an aggressive bird species, however, utilised these boxes especially in spring and summer, hereby reducing the availability of this resource for native species. In North America, bat boxes which have been installed next to residential houses in an attempt to attract displaced maternity roosts, have had mixed results. While Brittingham and Williams (2000) found that bat boxes were successful in attracting big brown bats (*Eptesicus fuscus*), Neilson and Fenton (1994)

found that nest boxes failed to attract little brown myotis (*Myotis lucifugus*). These results suggest that if nest boxes are to be used as a management tool for hollow-dependent species in cities or elsewhere, there is a greater need for understanding of the ecological requirements of the species at which these artificial roosts have been targeted.

1.6 Aim of this thesis

In a review of studies published in the journal *Conservation Biology* between 1995 and 1999, Miller and Hobbs (2002) found that less than six percent had been conducted in urban, suburban and ex-urban areas despite that many human settlements are located within biodiversity hotspots. However, despite the clear threat to these critical areas posed by urban development, little attention has been given by conservation biologists to addressing the effects of this form of land-use. Miller and Hobbs (2002: p. 333) concluded that “*development will continue with or without input from researchers*” and they urged conservation biologists to “*go beyond general guidelines derived from the theory of island biogeography or extrapolated from research conducted in the context of other land uses [...] and instead to begin to address specific questions directly related to settlement*”.

The physical and conceptual context of this thesis, therefore, is the increasing impact of urbanisation in one of the fastest growing urban areas in the world (Poole 1995, Queensland Government 2004), the greater Brisbane region in south-east Queensland (SEQ), Australia and the potentially threatening factors to Australia's second most abundant, but little known mammal group, the bats. In particular, I aim to examine two relevant key resources in this urban area - hollow (roost) availability and foraging habitat - for one particular group of bats, the molossids.

As Parnaby and Hamilton-Smith (2004) described, bats were wrongly portrayed in the 1980's as adaptable generalists due to their ability to fly across fragmented habitats. This has been proposed especially in relation to the open-space specialist bats, the molossids, which are able to exploit many habitat types in the pursuit of high-flying insects (Fenton and Rautenbach 1986, Arlettaz 1990, Carmel and Safriel 1998, Lee and McCracken 2002, Marques *et al.* 2004, Avila-Flores and Fenton 2005, Hourigan *et al.* 2006). At first sight, molossids may seem to be less affected by vegetation clearing and should be able to persist in urban environments. In spite of their apparent resilience to urbanisation, only a few studies have investigated the spatial foraging ecology of molossids in metropolitan cities or rural towns (Carmel and Safriel 1998, Lee and McCracken 2002, Avila-Flores and Fenton 2005, Hourigan *et al.* 2006). Furthermore, none of these studies have radio-tagged molossids to investigate their foraging and roosting requirements in highly urban areas.

This study specifically aims to investigate the roosting and foraging ecology of the white-striped freetail bat (*Tadarida australis*, Chiroptera: Molossidae) in the greater Brisbane region. The white-striped freetail bat is the largest molossid in Australia and despite being widespread and abundant, little is known about its roosting and foraging requirements, especially for urban populations (Churchill 1998). Its abundance makes it an ideal study animal for obtaining sufficient data for useful ecological knowledge to be developed which can improve conservation and management efforts.

1.7 Content of this thesis

This thesis consists of eight chapters. **Chapter 2** introduces the study species, the study area and the climate. **Chapters 3-7** include the results of field work conducted in metropolitan Brisbane and the surrounding area (greater Brisbane region).

Chapter 8 concludes with an overall discussion of the key findings arising from this study, and their implications.

Chapter 3 describes the roost tree characteristics, which determine roost selection by the white-striped freetail bat by answering the two main questions: (1) What are the tree and landscape characteristics of roost trees used by the white-striped freetail bat, and (2) What distinguishes these trees from control trees which may or may not contain colonies of the white-striped freetail bat? This information is essential to understand if hollow availability is a limited resource for the white-striped freetail bat in Brisbane and also to help formulate management recommendations for the general retention of habitat trees in metropolitan areas.

The most important roosting locations for one colony or roosting group, however, are not always obvious, especially in species such as hollow-dependent bats, which use multiple habitat trees as roosts. **Chapter 4** identifies several aspects to the network of day-roosts used by individual members of one roosting group of white-striped freetail bats: (1) It explores the application of network analysis to the bats' pattern of roost tree usage, and (2) considers the implications for habitat tree conservation.

The same network of day-roosts of the white-striped freetail bat is further investigated in **Chapter 5** as the ecological understanding of hollow-usage by this species is most important to derive appropriate management actions. Specifically, this chapter investigates the following questions: (1) How many bats use the communal roost or any other roost and do numbers fluctuate over the study period? (2) Does trapping at the roost influence roost usage? (3) To what extent do white-striped freetail bats show roost fidelity? (4) Do members of the colonial roosting group switch roosts and exhibit fission-fusion sociality? (5) Do they select roost-mates at random or do they share day-roosts with individuals captured and radio-

tracked at the same time? Furthermore, this chapter explores the nocturnal movements of individuals in relation to their day-roost locations.

Chapter 6 investigates the other key resource for the white-striped freetail bat – its foraging requirements in urban Brisbane. It uses information from radio-telemetry of foraging individuals to answer the following questions: (1) What is the emergence behaviour of the white-striped freetail bat?; (2) What are the spatial foraging patterns of this species in Brisbane?; (3) Do the bats show specific preferences for foraging habitat?; and (4) finally it identifies the importance of foraging habitat for the conservation of white-striped freetail bats.

In **Chapter 7**, bat boxes are explored as a conservation tool. Based on a study of 70 bat boxes, this chapter asks three questions: (1) Are bat boxes accepted by white-striped freetail bats or other insectivorous bats in Brisbane; (2) Which species adapt to artificial roosts most readily?; and (3) Does bat box usage and success depend on landscape characteristics, box design or box microclimate?

The last chapter (**Chapter 8**) summarises the main results of this thesis and puts them into context; especially with respect to the long-term survival of the white-striped freetail bat in urban environments.

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Chapter 2

Study species, study area and climate



Plate 2.1. The white-striped freetail bat (*Tadarida australis*).

Photo: Luke Hogan / Monika Rhodes

2.1 Introduction

The overall aim of my thesis was to investigate the effects of urbanisation on the ecology and conservation of a hollow-dependent species in an urban environment. For the study to be useful, I needed (i) an abundant hollow-dwelling species to obtain sufficient data for effective hypothesis testing; and (ii) an area which was formerly forested but had undergone recent and rapid changes due to urbanisation. This chapter comprises a review of the study species, the study area and its climatic conditions.

2.2 Study species

The white-striped freetail-bat (*Tadarida australis* (Gray, 1838)) belongs to the order Chiroptera, suborder Microchiroptera and the family of freetail-bats (Molossidae; Strahan 1998). Freetail-bats, also known as mastiff-bats due to their appearance, are found on all continents and include 12 genera and over 80 species (Strahan 1998).

The fur of the white-striped freetail bat is chocolate to dark brown dorsally and slightly lighter ventrally, although individuals with slightly reddish fur were recorded during this study (Appendix I). The ventral fur has distinct white stripes between body and wings. Individually distinctive horizontal white stripes and patches are common. The species has large, fleshy, forward-pointing ears. The ears are not joined and have characteristic protuberances along their edge (Plate 2.2). The upper lip is deeply wrinkled (hence 'mastiff-bats') and throat-pouches are present in both sexes, although these are non-secreting in females (Richards 1995, Churchill 1998b; Plate 2.3).



Plate 2.2. Dorsal view of ears of the white-striped freetail bat with the characteristic protuberances.



Plate 2.3. A male white-striped freetail bat with secreting throat gland.

The white-striped freetail-bat is the largest of all the Australian freetail-bats (Richards 1995, Churchill 1998a). Males weigh 26-35 (mean 33) g while females are usually heavier, especially during pregnancy (32-48 - mean 37 g). Their head and body length measures 85-100 (mean 92) mm, the tail length reaches 40-55 (mean 43) mm and their forearm length is between 57 and 65 (mean 61) mm (Rhodes and Richards in press; Appendix I).

The white-striped freetail bat is endemic to Australia and common to uncommon on the mainland, but absent from Tasmania. Until recently, white-striped freetail bats were believed to be absent from the tropical north of Australia (Richards 1995, Churchill 1998b). However, museum specimen collections (Western Australian Museum) and recent bat surveys (Milne and Nash 2003) have documented them from as far north as the tropical savannas in the Northern Territory. This indicates that the white-striped freetail-bat may occur throughout Australia (Rhodes and Richards in press).

The species produces audible echolocation calls. The characteristically long (up to 10 ms long) and flat (quasi-constant modulated) search calls range from 11 to 17 (14) kHz. Depending on the situation, this species also produces much shorter

and steep (frequency modulated) calls, including inaudible calls (> 20 kHz; Herr and Klomp 1997).

The white-striped freetail bat is capable of fast speeds (Norberg and Rayner 1987). As a molossid, it is adapted to aerial hawking of insects well above the vegetation due to long-narrow wings, high wing loading, aspect ratio and echolocation (Vaughan 1966, Norberg 1981, Norberg and Rayner 1987, Rhodes 1998, Schnitzler and Kalko 1998, 2001, McKenzie *et al.* 2002). This species is found in a range of habitats including forests, open woodlands, farmlands, semi-arid habitats, tropical savannas and urban environments. It typically roosts in small numbers (up to ten) in tree hollows but maternity colonies can include several hundred individuals (Richards 1995). Roosting almost always occurs in the hollows of trees; only very seldom does the white-striped freetail bat roost in rock caverns or buildings (Richards 1995, Hoyer 2002). White-striped freetail bats feed predominantly on moths (*Lepidoptera*), followed by beetles (*Scarabaeidae*) and bugs (*Hemiptera*; Vestjens and Hall 1977).

Female white-striped freetail-bats are monoestrous (Kitchener and Hudson 1982). Copulation, ovulation and fertilisation occur in late winter and females give birth between mid-December and the end of January (Kitchener and Hudson 1982). Juveniles are weaned by mid February (Appendix I). The white-striped freetail-bat is believed to be a non-hibernating species (Kitchener and Hudson 1982), but there is little known about its ecology and whereabouts during winter in the temperate regions of Australia. In Western Australia its range expands northward during the colder months (Bullen and McKenzie 2005). In the subtropics and tropics its audible search calls can be heard during mild winter nights, while they are usually absent in the temperate regions of Australia (Lumsden 1999).

There has been confusion concerning the nomenclature of *Tadarida australis* following Mahoney and Walton's (1988) suggestion of a change of the genus

synonym from *Tadarida* to *Nyctinomus*. However, the International Commission on Zoological Nomenclature (ICZN) recognises *Nyctinomus* as Geoffroy 1818, and therefore *Tadarida* (Rafinesque 1814) is more properly the genus synonym (Reardon 1999).

2.3 Study area

The study area, metropolitan Brisbane (27° 30' S, 153° 0' E), is located in subtropical coastal Australia, in the centre of the greater Brisbane region. This area covers approximately 3000 km² (Poole 1995). During this study, Brisbane City had a population of 1.6 million people with an average annual population growth of 2.4% (Queensland Government 2004). Brisbane was the fastest growing capital city in Australia in the year to June 2003 – at least twice the rate of any other Australian capital city. The population increase in 2003 was up 24% compared to the average growth over the previous four years. It is estimated that Brisbane's population will increase to 2.3 million by 2026 (Queensland Government 2004).

The greater Brisbane region lies within south-east Queensland (SEQ; *sensu* Young and Dillewaard 1999). This area has a high level of species richness and endemism (Norman *et al.* 2004). For example, more than half of the 300 Australian hollow-dependent vertebrates occur in SEQ (Smith and Lees 1998). Of the 26 insectivorous bat species found in this region, 22 permanently or partially use trees as roosts (Churchill 1998a, Strahan 1998; Table 2.1). The region's plant diversity is also remarkable. Two hundred and seventy-three species from 63 families are regionally endemic, with 556 species being on the northern and 355 species on the southern limits of their ranges (Norman *et al.* 2004). The vegetation of SEQ has been classified into 145 regional ecosystems, with all but 20 of these being dominated by forests (Queensland Government 1999, Young and Dillewaard 1999).

The topography of SEQ is characterised by coastal plains, sub-coastal ranges, occasional mountain peaks above 1000 m, and drainage systems and valleys (Catterall and Kingston 1993). European settlement commenced in the early 1820s. Since then, the originally continuous vegetation cover of woody trees and shrubs (approximately 23,000 km²) has been converted into a mosaic of cleared agricultural and other human-modified landscapes within which large and small forest remnants are scattered (Catterall *et al.* 1997). While vegetation has been retained on the peaks and ridges, the lowlands have been extensively cleared. Overall, 65% of native vegetation had been cleared in SEQ up to 1994, including 92% of the land below 20 m in altitude (Catterall and Kingston 1993, Catterall *et al.* 1997).

The bushland of the greater Brisbane region comprises many vegetation types, including subtropical rainforests, open eucalypt forests, melaleuca forests, woodlands, heathlands and mangroves (Catterall and Kingston 1993). The lowlands of greater Brisbane today represent a mixture of suburbs, substantial grassy areas with scattered trees (eucalypts or introduced) on parklands, golf courses and pastures, construction-dominated industrial and commercial precincts, and numerous smaller bushland remnants (Catterall 2004). Many of these forests show evidence of past logging, with few trees larger than 40 cm in diameter (Catterall *et al.* 1998). Outer metropolitan Brisbane is primarily composed of a patchwork of low density residential developments, pastures with scattered trees, as well as remnant bushlands, rainforest, *Melaleuca* forests and mangroves (Catterall 2004). The eastern edge of the greater Brisbane region borders Moreton Bay, a large bay separated from the Pacific Ocean by a chain of three large sand islands.

2.4 Climate and weather conditions

The climate in Brisbane is subtropical with annual summer rainfall of 1146 mm per year, predominantly dry winters, and an average maximum temperature of 25.5° C. The two main seasons are dominated by warm wet (summer season: October–April) and cool dry weather (winter season: May–September). During summer average minimum temperatures do not fall below 15° C while maximum temperatures reach up to 30° C, although seldom more than 35° C. Winter is characterised by average minimum temperatures below 15° C (9.5 – 13.8° C) and maximum temperatures of 20 to 25° C. Relative humidity remains stable throughout the year (61-71%), but mean monthly rainfall during summer reaches 122 mm compared to 58 mm in winter (Australian Government, Bureau of Meteorology).

During the three-year study (2001-2003) Australia experienced very dry conditions and above average maximum temperatures. In 2001 much of the eastern Australia suffered drought conditions with average temperatures higher than normal. Similarly during 2002, Queensland recorded warmer than average temperatures and rainfall was below median rainfall, especially following the onset of El Niño conditions in Autumn. During December of that year, 97% of the continent received below median rainfall, the dry conditions exacerbated by high temperatures. 2002 was Australia's fourth driest year on record. In 2003 the El Niño-related drought continued for much of Queensland, especially in Brisbane, with warmer than normal conditions. State rainfalls totals remained below normal, although they were above the corresponding totals for 2002 (Australian Government, Bureau of Meteorology).

Table 2.1. Microchiropteran species present in south-east Queensland (SEQ), their roost types, threatened species status and conservation status in south-east Queensland and Brisbane.

<i>Scientific name</i>	<i>Species</i>	<i>Roost type^b</i>	<i>Status^c</i>	<i>Conservation status in SEQ and Brisbane^d</i>
Emballonuridae				
<i>Saccolaimus flaviventris</i>	Yellow-bellied sheath-tail bat	T	Com	Significant (Brisbane)
Molossidae				
<i>Mormopterus beccarii</i>	Beccari's freetail bat	T, B	Com	
<i>Mormopterus norfolkensis</i>	East-coast freetail bat	T, (B)	Com	
<i>Mormopterus species 2^a</i>	Eastern freetail bat	T	Com	
<i>Tadarida australis</i>	White-striped freetail bat	T	Com	
Rhinolophidae				
<i>Rhinolophus megaphyllus</i>	Eastern horseshoe bat	C	Com	
Vespertilionidae				
<i>Chalinobus dwyeri</i>	Large-eared pied bat	C	Rare	
<i>Chalinobus gouldii</i>	Gould's wattled bat	T, B	Com	
<i>Chalinobus morio</i>	Chocolate wattled bat	T, B	Com	
<i>Chalinobus nigrogriseus</i>	Hoary wattled bat	T, (B)	Com	
<i>Falsistrellus tasmaniensis</i>	Eastern falsistrelle	T	Com	Considered declining with restricted distribution in SEQ; Significant (Brisbane)
<i>Miniopterus australis</i>	Little bentwing bat	C	Com	
<i>Miniopterus schreibersii</i>	Large bentwing bat	C, B	Com	
<i>Myotis macropus</i>	Large-footed myotis	C, B	Com	Considered declining, near threatened in SEQ
<i>Nyctophilus bifax</i>	Northern long-eared bat	T	Com	Significant (Brisbane)

Table 2.1. cont.

Scientific name	Species	Roost type^b	Status^c	Conservation status in SEQ and Brisbane^d
<i>Nyctophilus geoffroyi</i>	Lesser long-eared bat	T, B	Com	
<i>Nyctophilus gouldi</i>	Gould's long-eared bat	T	Com	
<i>Phoniscus papuensis</i>	Golden-tipped bat	N	Rare	
<i>Scoteanax rueppellii</i>	Greater broad-nosed bat	T, B	Com	Considered declining, near threatened in SEQ; Significant (Brisbane)
<i>Scotorepens orion</i>	Eastern broad-nosed bat	T, (B)	Com	Restricted distribution in SEQ
<i>Scotorepens species</i>	Little broad-nosed bat	T, B	Com	
<i>Vespadelus darlingtoni</i>	Large forest bat	T, B	Com	Restricted distribution in SEQ
<i>Vespadelus pumilus</i>	Eastern forest bat	T	Com	Significant (Brisbane)
<i>Vespadelus regulus</i>	Southern forest bat	T	Com	Restricted distribution in SEQ
<i>Vespadelus troughtoni</i>	Eastern cave bat	C	Com	Significant (Brisbane)
<i>Vespadelus vulturnus</i>	Little forest bat	T	Com	Restricted distribution in SEQ

^aCurrently undergoing taxonomic revision. This species is regarded as species 2 in Adams *et al.* (1988).

^bRoost type: C – caves and mines; T – tree cavities, under bark; N – abandoned bird nests; B – buildings, culverts, tunnels; brackets indicate the least common roost type.

^cStatus: Threatened status of bats according to Nature Conservation (Wildlife) Regulation 1994, Queensland Government (2005).
Com – common.

^dStatus in SEQ and Brisbane: Status according to the EPA Biodiversity Planning Assessment for South-east Queensland (2002) and Brisbane City Council Natural Assets Planning Scheme Policy, City Plan (2000).
Significant (Brisbane) – 'Animals that are rare in Brisbane, or animals that are uncommon in Brisbane and becoming rare' (BCC 2000).

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Chapter 3

Roost tree characteristics determine use by the white-striped
freetail bat (*Tadarida australis*, Chiroptera: Molossidae) in
suburban subtropical Brisbane, Australia

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Plate 3.1. One of the suburban roost trees used by white-striped freetail bats
(Brisbane Boys College, Brisbane).

Abstract

I examined factors affecting roost tree selection by the white-striped freetail bat *Tadarida australis* (Chiroptera: Molossidae), a large insectivorous bat in suburban Brisbane, Australia. I compared biophysical characteristics associated with 34 roost trees and 170 control trees of similar diameter, height, and tree senescence characters. Roost trees used by the white-striped freetail bat had significantly higher numbers of hollows in the trunk and branches ($P < 0.003$) and were more likely to contain a large trunk cavity with an internal diameter of > 30 cm ($P < 0.001$) than control trees. These trees also accommodated more species of hollow-using fauna ($P = 0.005$). When comparing roost trees with control trees of similar diameters and heights, roost trees were on average at a later stage of tree senescence ($P < 0.001$). None of the roost trees were found in the large forest reserves fringing the Brisbane metropolitan area despite these areas being used for foraging by the white-striped freetail bat. Although all tree locations in this study were in modified landscapes, roost trees tended to be surrounded by groups of trees and undergrowth. Roost trees provide important habitat requirements for hollow-using fauna in suburban, rural and forested environments.

3.1 Introduction

Hollow formation in eucalypts is a long and complex process and may take place over several hundred years, although rates of hollow formation are contentious (reviewed in Gibbons & Lindenmayer 2002). Estimates of time for eucalypts to develop hollows suitable for larger hollow-dependent fauna varies between studies, but is seldom less than 200 years (Mackowski 1984, Wormington 1996, Gibbons *et al.* 2000b). Hollow formation is associated with large tree diameter, advanced tree age, tree health and tree species. Location can also influence hollow formation, as

trees are more likely to develop hollows if under stress (Gibbons and Lindenmayer 2002). Basal injuries of the heartwood often allows fungi and insects, especially termites, to colonise the tree (McCaw 1983, Perry *et al.* 1985, Wilkes 1985a,b). Termites slowly excavate a pipe within the tree, eventually extending this into the main branches (Wilkes 1982, Perry *et al.* 1985, Gibbons and Lindenmayer 2002). Hollows then form where branches or the trunk break, or where branches are shed naturally (Jacobs 1955, Saunders 1979, Mackowski 1984). The decayed material inside the tree may then be excavated by hollow nesting birds, arboreal marsupials and invertebrates or removed by fire or drained by water (Gibbons and Lindenmayer 2002).

More than 300 native Australian vertebrate species use tree hollows for shelter, 83 of which are mammals (Gibbons and Lindenmayer 2002). Of these more than half are insectivorous bats (Gibbons and Lindenmayer 2002), which use hollows for day and/or night roosting. Roosts play important roles in the life of these mammals as they are used as maternity, bachelor, migrating, mating or hibernation sites (von Helversen 1989a, Siemers and Nill 2000, Kunz and Fenton 2003). They also facilitate energy conservation, and provide protection from weather and predators (Kunz and Lumsden 2003). Large tree diameters, tree age, proportion of dead branches in the crown (crown senescence), and tree species are significant factors predicting hollow availability and usage by vertebrates (Mackowski 1984, Bennett *et al.* 1994, Gibbons *et al.* 2000a, Lindenmayer *et al.* 2000, Gibbons and Lindenmayer 2002, Gibbons *et al.* 2002, Whitford 2002, Whitford and Williams 2002).

Bat roosting ecology in Australia has been studied mainly in forested areas or in remnant vegetation in rural areas (Tidemann and Flavel 1987, Lunney *et al.* 1988, Taylor and Sava 1988, Lunney *et al.* 1995, Herr and Klomp 1999, Law and Anderson 2000, Lumsden *et al.* 2002a, b). At present, little information is known on bat diversity and roosting requirements in urban areas in Australia or elsewhere (Frank 1994,

Holmes 1996, Everette *et al.* 2001, Guest *et al.* 2002). However, Australia is becoming increasingly urbanised. For example, the population in south-east Queensland (SEQ) doubled between 1976 and 2003 with the biggest increase in the greater Brisbane region. Sixty-five percent of native vegetation has been cleared in SEQ (Catterall and Kingston 1993). In metropolitan Brisbane itself only 1% of the pre-European vegetation remains unmanaged (Catterall and Kingston 1993). Most of Brisbane's forest reserves now consist of young regrowth, with few trees larger than 40 cm in diameter (Catterall *et al.* 1998).

The white-striped freetail bat (*Tadarida australis*, Chiroptera: Molossidae) is one of the largest Microchiroptera in Australia (weight: 25-40 g). It is a poorly studied species and little is known about its natural history (Richards 1995, Churchill 1998). This species is thought to be abundant in temperate and subtropical mainland Australia, including the urban environment. It is a fast-flying species and tends to forage in open areas, well above canopy height (Churchill 1998). The white-striped freetail bat is a tree-dweller. During the warmer months (September – May) it roosts in tree cavities in mature to overmature eucalypts either singly, in small groups of around 20 or in maternity colonies of up to 300 individuals (Richards 1995, Churchill 1998, M. Rhodes unpublished data). It enters large internal trunk cavities (> 30 cm internal diameter) through a range of unobstructed hollows on branches and/or the trunk itself (M. Rhodes, unpublished data).

Tree characteristics and usage of large hollows in Australia have been investigated for conspicuous vertebrates, such as possums, gliders, parrots and cockatoos (Saunders 1979, Saunders *et al.* 1982, Kavanagh 1984, Mackowski 1984, Menkhorst 1984, Smith and Hume 1984, Mackowski 1987, Smith and Lindenmayer 1988, Mawson and Long 1994, Garnett *et al.* 1999, Box 2001, Gibbons *et al.* 2002) but not for large hollow-using bats. This study investigated the characteristics of trees used as summer roosts by a large microchiropteran, the white-striped freetail bat, in

a fast growing metropolitan area and addressed the following questions: (i) What were the tree and landscape characteristics of roost trees used by the white-striped freetail bat?; and (ii) What distinguished these trees from control trees of similar diameter, height, senescence and land tenure, which may or may not contain colonies of the white-striped freetail bat?

3.2 Methods

Study area

The greater Brisbane region is located in subtropical coastal Australia (27° 30' S, 153° 0' E). The topography of the region is characterised by coastal plains, sub-coastal ranges, occasional mountain peaks above 1000 m, and drainage systems and valleys. The region comprises many vegetation types, including subtropical rainforests, open eucalypt forests, melaleuca forests, woodlands and heathlands (Catterall and Kingston 1993).

All field sites were located in the coastal lowlands below 120 m altitude in the Brisbane and Bremer River catchment area (Fig. 3.1). The landscape is undulating to hilly. It consists of a mosaic of mostly cleared urban settings with grassed lawns, parklands with scattered mature eucalypts (maturity classes *sensu* Jacobs 1955), dominated by forest red gum (*Eucalyptus tereticornis*), and bushland reserves ranging from less than one to 20 km² (*sensu* Catterall & Kingston 1993; Catterall *et al.* 1998). An exception is the Brisbane Forest Park, a large remnant forest reserve (28,500 ha; Fig. 3.1) on the margins of the urban environment. Outer metropolitan Brisbane is primarily composed of cleared pastures with scattered mature trees and larger bushland reserves (> 20 km²; Catterall & Kingston 1993; Catterall *et al.* 1998).

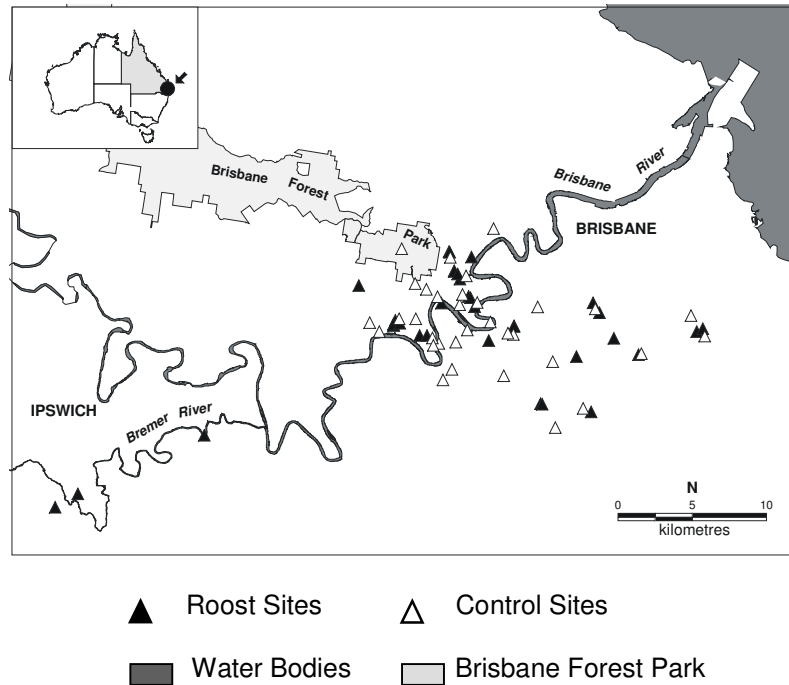


Fig. 3.1. Location of roost and control sites in the greater Brisbane region, south-east Queensland.

Sampling regime

Roost sites of the white-striped freetail bat were found either by opportunistic searches (checking for roosts at dusk by listening to their intense audible social calls or their echolocation behaviour while exiting) or by following radio-tagged individuals to their day-roosts. Two males and seventeen females were tracked during three different radio-tracking seasons and followed to new roost sites.

Tree and site characteristics were surveyed between May and October 2002 and 2003. This ensured that observations were carried out during the same season to avoid biases introduced by recording in different breeding seasons.

Tree level

Tree characteristics were measured of each roost tree and two control trees within a 100 m radius (Table 3.1). Control trees were sought which had similar tree attributes of diameter, height and senescence and were, if possible, the same species.

Additionally, one control site of similar land tenure was selected for each roost site using topographic image maps (scale 1: 25,000; Department of Lands, Brisbane) and then visited to determine suitability. For example, if a roost tree was found in a paddock with a stem diameter of 70 cm, 24 m height with some dead branches and visible hollows, three control trees in a paddock with similar tree and site attributes were then selected. I tried to match tree species and tree and site attributes as closely as possible. If more than three trees within a 100 m radius fitted the criteria then control trees were selected randomly.

Visible hollows were counted from the ground using binoculars. To overcome biases associated with the use of different observers (Gibbons and Lindenmayer 2002), I counted all hollows during the two years of sampling. Hollow sizes were estimated and assigned to four size classes (< 5, 5-10, 11-20, > 20 cm) in trunk and branches separately. Hollow locations were classified into four categories:

(i) unobstructed trunk; (ii) obstructed trunk; (iii) unobstructed branches and (iv) obstructed branches. Hollows were classified as obstructed if leaves, branches or other plant material (e.g., vines) covered them. This separation into obstructed/unobstructed hollows was necessary as all roost entrances used by the white-striped freetail bat had previously been found to be unobstructed (M. Rhodes, unpublished data). It was not possible to assess accurately the number or depths of hollows from below (Whitford 2002, Harper *et al.* 2004). However, the number of visible hollows counted from the ground can be taken as an index (Lindenmayer *et al.* 2000, Gibbons and Lindenmayer 2002, Harper *et al.* 2004).

Table 3.1. Habitat tree variables measured at tree and site level. Each variable was compared between roost and control trees (Mann-Whitney *U*-tests).

<i>Variable</i>	<i>Description</i>	<i>P-value</i>
Tree level		
Tree diameter (DBH)	Tree diameter at 1.3 m over bark to the nearest centimetre	0.37
Tree height	Measured either with an ultrasonic <i>Vertex</i> or a manual tree height measurer to the nearest metre	0.86
Tree alive/dead	1 = alive, 0 = dead	0.09
Tree condition	10 ordinal categories on a pictorial scale, modified from Gibbons <i>et al.</i> (2000b) and Whitford (2002)	< 0.001
Crown position	5 ordinal categories on a pictorial scale modified from Grimes (1978)	0.14
Crown density	6 ordinal categories on a pictorial scale modified from Grimes (1978)	0.05
Total number of visible hollows	a) in trunk b) in branches (see text for details, Fig. 3.4c)	a: < 0.003 b: < 0.001
Trunk cavity (> 30 cm)	Presence (1) or absence (0) of a big cavity inside the tree trunk	< 0.001
Tree species	Identified (BRI 2001) and categorised into eight groups (see text for details, Fig. 3.4b)	all > 0.07
Fire impact	Assigned from 6 categorical variables: 1 = intact, 2 = dry side < half tree, 3 = dry side > half tree, 4 = hollow-butt < half tree, 5 = hollow-butt > half tree	0.75
Termite infestation	Presence (1) absence (0) of a) termite mounts and b) termite trails	a: 0.14 b: 0.25
Other fauna present	Species and number of species/nests other than the white-striped freetail bat (see text and Fig. 3.4d for details)	0.005
Site level		
Basal area	Angle count sampling using a wedge prism (BAF 2) to assess the stand productivity in m ² ha ⁻¹ (Eyre <i>et al.</i> 2000)	0.30
Vegetation cover	7% cover categories for eight different height classes for grass & herbs, woody plants, bare soil, asphalt, buildings (see text for details)	all > 0.07
Topographic position	6 categorical variables: 1 = top, 2 = upper slope, 3 = mid slope, 4 = lower slope, 5 = flat, 6 = gully	all > 0.10
Slope	The general slope of the plot was measured with a clinometer in degrees. For flat areas = 0°	0.58
Aspect	Aspect of the downward slope recorded on a compass direction (in degrees): Flat areas = 0°. The aspect was then converted into a) 1+cos and b) 1+sin for multivariate analysis purposes	a: 0.59 b: 0.23
Altitude	Altitude of the plot in metres	0.08
Proximity to open water body	Measured to the nearest metre	0.46
Type of water body	1 = Brisbane River, 2 = creek, 3 = dam, 4 = pond, 5 = tanks/pools, 6 = other	0.09

Evidence of a major hollow cavity inside a trunk was determined by tree climbing where possible. In these cases, an infra-red custom-made endoscope (hollowscope) was inserted into hollows to verify and measure trunk cavities. If tree climbing was not possible I noted signs indicating trunk cavities such as draining cavities at the base of trunks, tree condition and broken main stems. Trunk cavities occur either inside the trunk or in a short section that connects the cavity to the main trunk (Gibbons and Lindenmayer 2002). I defined large trunk cavities as being large enough to accommodate vertebrates such as the common brushtail possum (*Trichosurus vulpecula*), sulphur-crested cockatoos (*Cacatua galerita*), or large colonies (> 25 individuals) of the white-striped freetail bat. These would require internal diameters of at least 30 cm (Inions *et al.* 1989). Only obvious and clearly identifiable trunk cavities were recorded in roost and control trees.

During measurements, each tree was observed for hollow-occupancy by fauna for at least half an hour. For each occupied hollow, the species, number of individuals and/or nests were recorded. Fauna observed during nightly observations of the roost trees were not included in these analyses.

Bio-physical tree attributes were measured or estimated using techniques adapted from several existing approaches (Table 3.1). These attributes included tree diameter at breast-height (DBH), height, tree condition (Gibbons *et al.* 2000a, Whitford 2002), senescence (crown position and crown density; Grimes 1978), fire impact and termite infestation.

Site level

Cover of grass and herbs, woody plants, bare soil, litter, asphalt and buildings were recorded in a 40 x 40 m plot centred at each roost and control tree. Seven percentage cover categories (1, 1-5, 5-10, 10-25, 25-50, 50-75, > 75%) for eight height classes (< 0.25, 0.25-1, 1-2.5, 2.5-5, 5-10, 10-20, 20-50 and > 50 m) were

used. In addition, basal area (Eyre *et al.* 2000), topography, proximity to, and type of the nearest permanent open water body were also assessed.

Statistical analysis

Dissimilarity among trees with respect to ten variables commonly associated with tree and site characteristics (Fig. 3.2a) was examined using the Bray Curtis Metric (Bray and Curtis 1957). Results were visually represented through 2-D semi-strong hybrid multidimensional scaling ordination (SSH MDS) with dissimilarity cut level at 0.9 in the package WinPATN (Belbin 1990, Belbin and Queensland 2003), referred to hereafter as the *habitat tree ordination* (Fig. 3.2a).

SSH MDS is widely used in the study of relationships between species assemblages (Digby and Kempton 1991, Kent and Peddy 1992, Belbin 1995) and seeks to provide, in few dimensions, an accurate representation of the similarity between samples (trees) on the basis of their attribute profiles (tree/site characteristics). Data were clustered using unweighted pair group arithmetic averaging (UPGMA) with β set at -0.1 (Belbin 1990). Under such conditions the clustering strategy is space-dilating and resists the formation of a single large group (Booth 1978). Range standardisation was used to reduce the effects of numerical dominance by particular variables.

The relationship of component variables with the ordination was explored using principal axis correlation (PCC procedure within WinPATN) and randomisation tests (with 1000 permutations) of the significance of correlation for each intrinsic variable (Monte Carlo Permutation Test (MCAO) procedure of WinPATN; Belbin 1995; Belbin *et al.* 2003). This procedure was also used to assess the relationship of extrinsic variables with the ordination axis. Because many data-sets were not normally distributed (Wilk-Shapiro statistics, W), Mann-Whitney U -tests with pairwise

comparison of ranks (Zar 1999) were used to determine whether roost and control trees differed with respect to particular individual variables. The differences between assemblages defined through cluster analysis and *a priori* (roost and control trees) were tested with analysis of similarity (ANOSIM in WinPATN, Belbin *et al.* 2003) with 1000 permutations.

3.3 Results

Roost locations

Thirty-seven roost trees were located over a three-year period between 2000 and 2003 (Fig. 3.1). Four roost trees were lost during that period (two removed by city council and property owner and two lost to wind). Three of these trees were destroyed before they could be measured, leaving 34 trees that could be assessed. The roost trees consisted of a mixture of maternity and non-breeding sites with solitary roosts ($n = 5$), small colonies (up to 25 individuals; $n = 24$) and five large colonies, at least two containing maternity roosts (25 - 291 individuals). White-striped freetail bats used roost trees scattered throughout the Brisbane and Bremer River catchment area (Fig. 3.1). The majority of roost trees ($n = 22$) were located on public land (Brisbane City Council, Ipswich City Council property and Crown land), while the rest ($n = 12$) were found on private property (Table 3.2).

Table 3.2. Numbers of roost trees used by the white-striped freetail bat in different locations in relation to tenure and plant cover. The numbers in brackets indicate the numbers of dead trees found in each location.

Tenure	<i>Open parkland^a</i>	<i>Forests/ Bushlands^b</i>	<i>Paddocks</i>
Public land	15	4 (3)	
Crown land	2	1 (1)	
Private land	8	2 (1)	2 (1)

^aOpen parkland included suburban parks, school grounds, golf courses and private property.

^b*Sensu* Catterall & Kingston 1993; Catterall *et al.* 1998.

Tree and site attributes

Four groups could be discerned on the basis of multivariate analyses of habitat tree variables (UPGMA, Bray Curtis Metric, $\beta = -0.1$; Fig. 3.2a). Group one and two consisted solely of dead trees (group one trees occurred in sites with large basal areas). Group three included mainly roost trees supporting relatively large bat colonies (> 25 bats) and a smaller group of control trees; both had large internal trunk cavities and an abundance of hollows in trunk and branches. Group four contained control trees and few roost trees supporting small bat colonies (< 25 bats) in dead-end branches. These trees were usually healthier and contained few hollows in the trunk and branches. The assemblages of the four groups derived by cluster analysis, and the two *a priori*-groups (roost/control trees) were significantly different from one another ($P < 0.001$; pair-wise ANOSIM).

All ten intrinsic variables used to derive the *habitat tree ordination* were significantly correlated with the ordination axis ($P < 0.001$; Fig. 3.2b). Extrinsic variables usually associated with habitat trees, such as vegetation cover, hollow-dependent fauna and hollows in trunk and branches, were significantly correlated with the ordination axis ($P < 0.05$; Fig. 3.3a-d).

I found no differences between roost and control trees in tree diameter, height, basal area, crown position, fire impact as well as vegetation cover, topographic position, slope, aspect, altitude, proximity to open water bodies and type of water bodies (Table 3.1, Fig. 3.4a). However, on a scale from 1 (dead tree) to 10 (healthy tree), roost trees were more decayed (7.9 ± 1.7 , $n = 34$) than control trees (8.9 ± 1.6 , $n = 170$; $U = 1710$, $P < 0.001$). Roost trees also had a slightly sparser crown density (2.56 ± 1.44 , $n = 34$) than control trees (2.99 ± 1.23 , $n = 170$; $U = 2301$, $P = 0.05$).

Despite all roost locations being found in highly modified landscapes, roost trees were usually surrounded by clumps of tall trees, determined by the basal area factor (BAF > 2). There was no difference in the basal area (BA) between roost (7.12 ± 3.85 , $n = 34$) and control trees (6.53 ± 3.90 , $n = 170$; $U = 2572$, $P = 0.30$; Fig. 3.4a).

PCC (Fig. 3.3) and Mann-Whitney U -tests (Fig. 3.4) showed similar results for the analysis of tree and site variables, with one exception. While Mann-Whitney U -tests showed no significant differences in the vegetation cover, the PCC showed that roost trees were associated with undergrowth cover (woody plants < 0.25, 0.25-1, 1-2.5, 2.5-5, 5-10, 10-20 m) and grass and herbs cover (0.25-1, 1-2.5 m), while control trees were positively associated with asphalt (Fig. 3.3a).

Tree species

All roost trees used by the white-striped freetail bat were eucalypts (28 trees living and six dead). The majority of live roost trees were forest red gums (*Eucalyptus tereticornis*, $n = 11$), followed by scribbly gum (*E. racemosa*, $n = 5$), tallowwood (*E. microcorys*, $n = 3$), grey box (*E. moluccana*, $n = 3$), spotted gum (*Corymbia citriodora* subsp. *variegata*, $n = 3$), grey gum (*E. propinqua* var. *propinqua* and var. *major*, $n = 2$), and narrow leafed ironbark (*E. crebra*, $n = 1$). Forest red gum was also the most common tree species in the control group (Fig. 3.4b). There were no significant differences in the abundance of different tree species between roost and control trees ($P > 0.11$ for any tree species, except for $P = 0.09$ for dead trees and $P = 0.07$ for others; $n = 34$, 170).

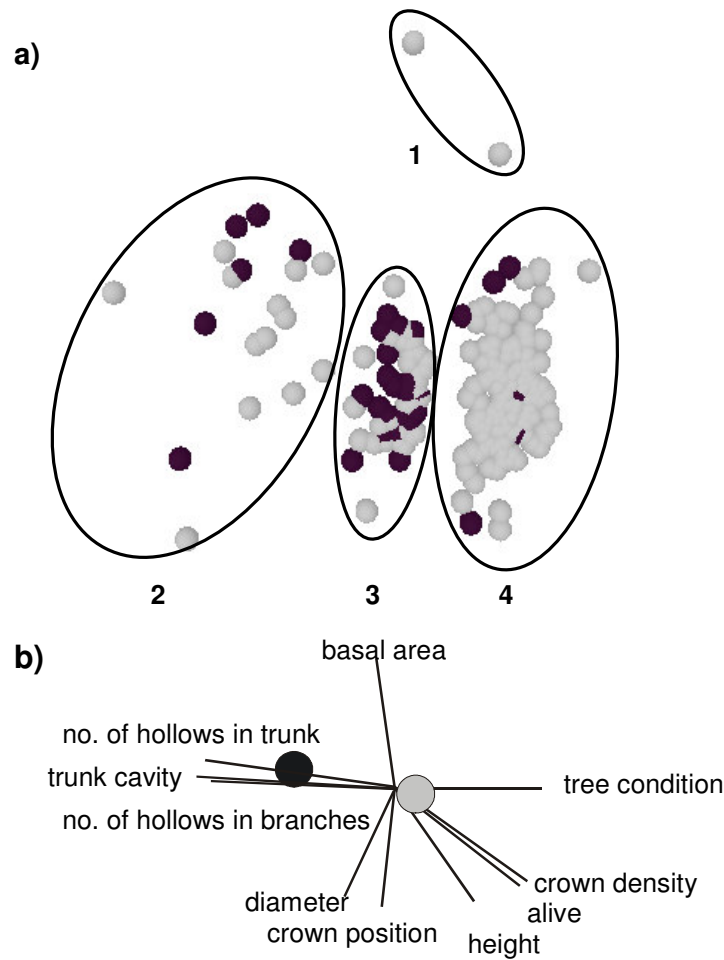


Fig. 3.2. a) Two-dimensional ordination (SSH MDS, stress = 0.16) of roost (black, $n = 34$) and control trees (grey, $n = 170$) based on ten intrinsic attributes (habitat tree ordination): Tree diameter, tree height, tree condition (alive/dead), basal area, tree condition, crown position, crown density, number of hollows in the trunk, number of hollows in branches, and trunk cavity. The solid lines enclose trees grouped by UPGMA (Bray Curtis Metric, $\beta = -0.1$).

b) Principal axis correlation (PCC) showing vectors of intrinsic attributes significantly associated (MCAO; $P < 0.001$) with the 2-D ordination, and *a priori* groups represented by their centroids (roosts = black, controls = grey). For example, roost trees are associated with higher number of hollows in trunk and in branches and the presence of a large trunk cavity (> 30 cm internal diameter) while control trees are positively associated with healthier tree condition, higher crown density and live trees. Basal area, diameter and crown position are significantly correlated to the ordination axis but are not associated with either roost or control trees.

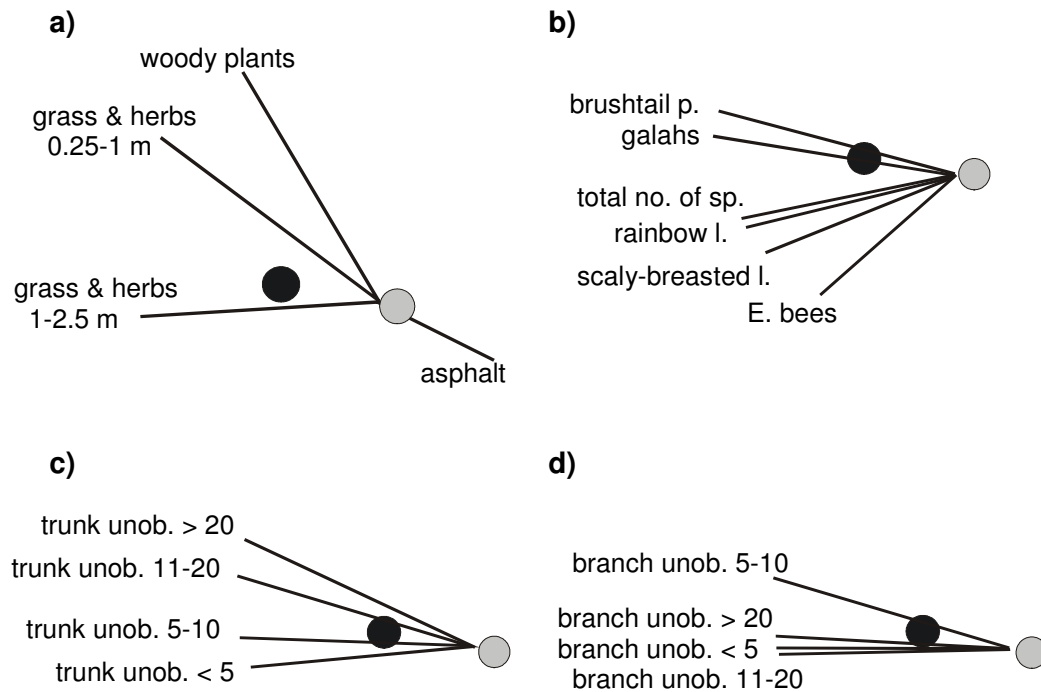


Fig. 3.3. Principal axis correlation (PCC), showing vectors of tree and site attributes significantly associated (MCAO; $P < 0.05$) with the 2-D ordination, and centroids of a priori plot groups shown in Fig. 3.2a (roosts = black, controls = grey). Vectors (attributes) pointing to the left of the ordination are associated with roost trees, to the right with control trees.

a) Vegetation and asphalt cover. The six vectors of the vegetation cover variables, woody plants (< 0.25, 0.25-1, 1-2.5, 2.5-5, 5-10, 10-20 m), are all significantly associated ($P < 0.001$) with roost trees and are almost identical. They are represented by one central vector (woody plants);

b) hollow-dependent fauna;

c) hollows of four different size classes (< 5, 5-10, 11-20, > 20 cm) found in unobstructed locations on the tree trunk; and

d) hollows of four different size classes (< 5, 5-10, 11-20, > 20 cm) found in unobstructed locations in branches.

Brushtail p. - common brushtail possum (*Trichosurus vulpecula*); galahs - (*Cacatua roseicapilla*); total no. of sp. - total number of hollow-using species other than the white-striped freetail bat; rainbow l. - rainbow lorikeets (*Trichoglossus haematodus*); scaly-breasted l. - scaly-breasted lorikeets (*Trichoglossus chlorolepidotus*); E. bees - European bee colonies (*Apis mellifera*).

Hollows

The total number of hollows in trunk ($U = 1968$, $P < 0.003$; $n = 34, 170$) and branches ($U = 821$, $P < 0.001$; $n = 34, 170$) were greater in roost trees than in control trees (Fig. 3.4c). When the hollows were separated into size and location categories, there was a clear difference between unobstructed and obstructed locations. Roost trees had more unobstructed large hollows (> 11 cm) in the trunk and branches than control trees ($P < 0.001$; $n = 34, 170$). These hollows were commonly used by the white-striped freetail bat to access internal roost cavities.

Eighty-two percent of roost trees contained large internal trunk cavities of at least 30 cm diameter. In most cases these cavities extended throughout the trunk and major branches. In comparison only 25% of control trees had large internal trunk cavities ($U = 1241$, $P < 0.001$; $n = 34, 170$).

Hollow-dependent fauna

Six of eight hollow-dependent species regularly observed in tree hollows were found significantly more frequently in roost trees than in control trees ($P < 0.01$; $n = 34, 170$; Fig. 3.4d). No significant differences between roost and control trees were found for the common myna (*Acridotheres tristis*) and native bee colonies (*Trigona* sp.). The total number of hollow-dwelling species was higher in roost than control trees ($U = 2042$, $P = 0.005$; $n = 34, 170$).

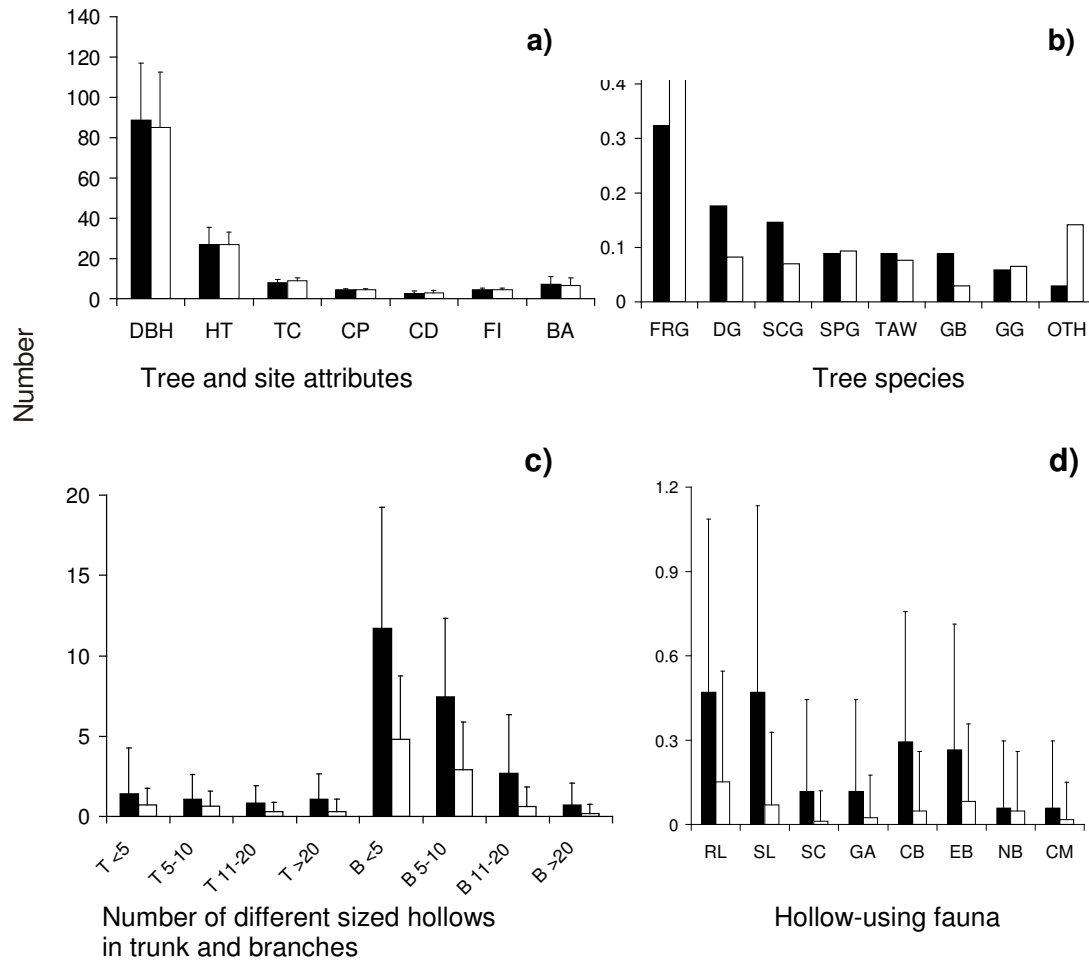


Fig. 3.4. Comparison between mean (\pm SD) of variables in roost (black) and control trees (white) for a) tree and site attributes; b) proportion of tree species; c) number of different sized hollows in trunk and branches; and d) number of hollow-using fauna.

a) DBH - diameter in breast-height (cm); HT - tree height (m); TC - tree condition; CP - crown position; CD - crown density; FI - fire impact; BA - basal area.

b) FRG - Forest red gum (*Eucalyptus tereticornis*); DG - Dead gum tree; SCG - Scribbly gum (*E. racemosa*); SPG - Spotted gum (*Corymbia citriodora* subsp. *variegata*); TAW - Tallowwood (*E. microcorys*); GB - Grey box (*E. moluccana*); GG - Grey gum (*E. propinqua* var. *propinqua* and var. *major*); OTH - Other eucalypt species.

c) T - hollow size categories (trunk - cm); B - hollow size categories (branch - cm).

d) RL - rainbow lorikeets; SL - scaly-breasted lorikeets; SC - sulphur crested cockatoos; GA - galahs; CB - common brushtail possums; EB - European bee colonies; NB - native bee colonies; CM - common mynas.

3.4 Discussion

Roost locations

This study showed that the white-striped freetail bat roosted in urbanised areas provided that suitable roost trees were available. Roost trees of the white-striped freetail bat were found in highly modified, often urbanised habitats (parklands, school grounds, golf courses and paddocks) or in remaining bushland or regrowth forest reserves (< 100 ha) surrounded by suburban housing. This result contrasted with previous studies on roost site selection by other microchiropterans in Australia. Other insectivorous bats choose roost trees primarily inside mature forests, even when they forage in open areas, such as rural environments, regrowth and clearfelled forests (Taylor and Sava 1988, Herr and Klomp 1999, Law and Anderson 2000, Lumsden *et al.* 2002a,b).

I assume that the generally open habitat of metropolitan Brisbane suited this fast, high-flying bat species because of its low manoeuvrability (Rhodes 1998). The white-striped freetail bat is able to fly at high altitudes (Richards 1995, Churchill 1998). It has a high wing loading and aspect ratio which enables it to achieve high agility at high speeds (Rhodes 1998). This agility may be important for foraging in open spaces as it is likely to contribute to the capture success of aerial prey (Aldridge 1987).

While the greater Brisbane region has large forest reserves available as roosting habitat for the white-striped freetail bat, none of the roost sites identified were found within these reserves. For example, the boundary of Brisbane Forest Park is located only four kilometres from the city centre and is one of the largest remaining conservation reserves in the greater Brisbane region (28,500 ha). It is connected to the extensive subcoastal mountain ranges of the D'Arguilar Range and consists of rugged land with ridges and deep gullies with a mixture of eucalypt

dominated forests and rainforests (Catterall and Kingston 1993). Although it has been previously logged (P. Howard pers. comm., 2004), I found scattered remnant habitat trees throughout the park. The present study revealed that no radio-tracked white-striped freetail bat roosted within Brisbane Forest Park (Fig. 3.1), despite recordings of them foraging in this park (Chapter 6). Tagged individuals frequently commuted more than 50 km per night from the roost to different foraging locations (M. Rhodes, unpublished data). Although the white-striped freetail bat is capable of travelling considerable distances, none of the roost trees used were found inside Brisbane Forest Park or any other larger forest reserves (> 100 ha).

It remains unclear as to why individual white-striped freetail bats in this study used roost sites in urban settings and small regrowth remnants rather than potential roost trees within neighbouring large forest reserves. The tree density of Brisbane Forest Park is no higher than that of the smaller regrowth forest reserves where roosts have been found. The wing morphology (Rhodes 1998) and echolocation behaviour (Herr and Klomp 1997) of this species suggests that it may be more suited to roost and forage in open (e.g., woodlands) than in forested habitats. However, a comparison of the roost ecology of this species in forested and woodland areas is needed.

Tree attributes

Studies on tree and habitat variables (e.g., tree species, tree health, tree diameter, tree height, canopy clutter and roost stand) of roost sites by hollow-dependent bats are largely reported for temperate species (Kunz & Lumsden 2003). In these situations most bat species selected trees that have large diameters, are taller than the surrounding trees and have less canopy clutter than the surrounding vegetation (Vonhof 1996, Sedgeley and O'Donnell 1999, Kunz and Lumsden 2003). This is because hollow formation and the number of hollows are significantly related to tree

diameter, tree health, tree species, tree age, tree location, tree position and fire events (reviewed in Gibbons & Lindenmayer 2002).

The white-striped freetail bat selected a wide variety of eucalypts as roost habitats but preferred overmature to dead eucalypts with large tree diameters (> 89 cm). The main difference between these roost trees and control trees of similar diameters and height were that roost trees were more decayed and had a higher number of hollows in the trunk and branches. Therefore tree health (level of senescence) was found to be an important tree characteristic in predicting hollow-availability and hollow types of similar sized trees in the greater Brisbane region. Physiological health (e.g., proportion of dead branches in the crown and large trunk cavities) was reported as a significant factor associated with vertebrate occupancy (Bennett *et al.* 1994, Lindenmayer *et al.* 2000, Gibbons and Lindenmayer 2002, Gibbons *et al.* 2002, Whitford 2002).

The vast majority (82%) of the roost trees had developed large trunk cavities, often extending throughout the trunk and major branches. These trunk cavities were accessed by the white-striped freetail bat through multiple unobstructed branch and/or trunk hollows (M. Rhodes, unpublished data). A clear flight path may result in energetic savings for bats (Vonhof 1996) and reduce the exposure to predators (Fenton *et al.* 1994), while the extent of the internal tree cavity size may limit the size of bat colonies (Vonhof 1996). The white-striped freetail bat is a highly colonial tree-dweller and large internal cavities will be an important feature in selecting suitable maternity sites as population numbers increase during parturition.

Hence I suggest that the quality and size of roost space is more important than the selection of specific tree species in roost choice by the white-striped freetail bat (Vonhof 1996, Sedgeley and O'Donnell 1999). Although I have not measured and compared microclimates in hollows of roost and control trees it is also likely to be an important factor in roost choice (Rieger 1996, Sedgeley 2001).

Hollow-dependent fauna

Mature trees with large numbers of different sized hollows provide important roosting opportunities for hollow-dependent fauna (Inions *et al.* 1989, Lindenmayer *et al.* 2000, Gibbons *et al.* 2002). In this study, rainbow and scaly-breasted lorikeets frequently bred during winter inside the same hollows also used by the white-striped freetail bat. These birds usually left these sites, following the fledging of their young, and before the bats returned to their summer roosts. No other bat species was found to use the roost trees used by the white-striped freetail bat in this study, despite these trees being observed at least once a month over a period of one to three years (M. Rhodes, unpublished data).

Introduced species pose a significant danger to native Australian wildlife through competition for the same roost spaces. In particular, I found honey bees frequently occupying large and deep hollows, a situation observed throughout Australia (Suckling and Goldstraw 1989, Mawson and Long 1994, Oldroyd *et al.* 1994, Lawler *et al.* 1995, Wood and Wallis 1998, Garnet *et al.* 1999). Similarly, the common myna is regarded as a major competitor for hollows (Pell and Tidemann 1997).

Urbanisation and habitat loss

All roost sites located in this study were in forest red gum associations of the Brisbane and Bremer River catchments, and the majority of eucalypts measured in both roost and control trees were forest red gums. This species occurs in open-forest or as scattered trees on alluvial flats (Boland *et al.* 1992). In Brisbane, this species dominates alluvial flats of the catchment areas surveyed; sites which are subject to occasional flooding (Catterall and Kingston 1993). The forest red gum association, together with the semi-evergreen vine thicket, has become the most highly reduced and fragmented vegetation complex following European settlement in the region in

the 1820s (Catterall & Kingston 1993). This study showed that stands of remnant mature eucalypt trees occur particularly along the river and creek lines, and can act as recruitment trees (trees that in time will develop hollows suitable as roost sites).

However, continuous land clearing and development in the greater Brisbane region is likely to lead to the loss of many of the remaining mature eucalypts. It is estimated that Brisbane's current population (2004) of 1.6 million will increase to 2.3 million by 2026 (Department of Local Government, Planning, Sport and Recreation 2004). Regardless, conservation issues concerning urban Brisbane are relevant to Australia's urban expansion in general, as most Australian cities are centred on areas of considerable conservation significance for hollow-dependent fauna (Lunney and Matthews 2004).

Habitat loss is often considered to be a main factor contributing to the decline of fauna, including bats, in an area despite continued provision of food and water (Kunz and Lumsden 2003, Racey and Entwistle 2003, Parnaby and Hamilton-Smith 2004). Almost two-thirds of the roost trees used by the white-striped freetail bat were found on public or Crown land, emphasising the importance of retaining mature habitat trees on public areas. With increasing fears of public liability most mature trees in public areas are intensively managed by city councils. Dead or potentially dangerous branches are trimmed, resulting in the loss of hollows in terminal branches while dead trees and trees that show signs of late stages of senescence are usually removed (Holmes 1996). Inventories of hollow-bearing trees that have become part of forest practices in Australia (Ross 1999, Law 2004) and elsewhere (Barclay and Brigham 1996, Spencer and Czaplewski 1997) should also be applied to urban environments as these are amongst the most highly managed landscapes.

Conclusion

Protecting individual habitat trees is not a long-term solution for the survival of hollow-dependent species in urban settings. Planning for the retention and protection of habitat trees must incorporate landscape features, landscape context, and management issues such as ongoing urbanisation and health and safety concerns. These factors then have to be combined with the roosting and foraging ecology of hollow-dependent species to maximise the chances of survival of these species in urban environments. Inventories of hollow-bearing trees are only useful if factors determining roost choice such as interspecific and intraspecific differences, seasonality, roost quality and roost competition are equally considered.

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Chapter 4

Applying network analysis to the conservation of habitat trees in urban environments: a case study from Brisbane, Australia

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Plate 4.1. The indiscriminate loss of trees, including habitat trees, due to a new suburban development in the study area (June 2002).

Abstract

In Australia over 300 vertebrates, including 43 insectivorous bat species, depend on hollows in habitat trees for shelter, with many species using a network of multiple trees as roosts. I used roost-switching data from white-striped freetail bats (*Tadarida australis*; Microchiroptera: Molossidae) to construct a network representation of day-roosts in suburban Brisbane, Australia. Bats were caught from a communal roost tree with a roosting group of several hundred individuals and released with transmitters. Each roost used by the bats represented a node in the network, and the movements of bats between roosts formed the links between nodes. Despite differences in gender and reproductive seasons, the bats exhibited the same behaviour throughout three radio-telemetry periods and over 500 bat days of radio-tracking: each roosted in separate roosts, switched roosts very infrequently, and associated with other bats only at the communal roost. This network resembled a scale-free network in which the distribution of the number of links from each roost followed a power-law. Despite being spread over a large geographic area ($> 200 \text{ km}^2$), each roost was connected to others by less than three links. One roost (the hub or communal roost) defined the architecture of the network because it had the most links. That the network showed scale-free properties has profound implications for the management of the habitat trees of this roosting group. Scale-free networks provide high tolerance against stochastic events such as random roost removals, but are susceptible to the selective removal of hub nodes. Network analysis is a useful tool for understanding the structural organisation of habitat tree usage and allows the informed judgment of the relative importance of individual trees and hence the derivation of appropriate management decisions. Conservation planners and managers should emphasise the differential importance of habitat trees and think of them as being analogous to vital service centers in human societies.

4.1 Introduction

Habitat loss is a major factor contributing to the decline of forest-dependent fauna (Lunney 2004). Land clearing for urban expansion, vegetation clearance on farms, and continued logging of older trees in forests are the primary causes of habitat loss for many native vertebrates (Holmes 1996, Lunney and Matthews 2004, Rhodes and Wardell-Johnson 2006). In Australia, mature eucalypts with large numbers of hollows of varying sizes provide important shelter for hollow-dependent fauna (Inions *et al.* 1989, Lindenmayer *et al.* 2000, Gibbons and Lindenmayer 2002, Gibbons *et al.* 2002). In many areas, forest practices have resulted in forests with insufficient numbers of tree hollows (Ross 1999). Similarly, in urban environments, dead trees, and trees that show signs of late stages of senescence are usually removed due to ongoing urbanisation and concerns of public liability (Holmes 1996, Rhodes and Wardell-Johnson 2006; Chapter 3). A recognition that the numbers of hollows are insufficient has led to the retention of mature eucalypts of over 40 cm diameter at 1.3 m height in some areas (Queensland Government 1999). However, knowledge of species' requirements for hollow-bearing trees remains cursory in the eucalypt-dominated vegetation of Australia. Furthermore, temporal and spatial changes in the use of hollows by particular species or by a range of taxa (intra- and interspecific use of hollows) have yet to be examined.

To find habitat trees, radio-tagged individuals are tracked back to their roosts (White and Garrot 1990a). This method is an excellent way to identify habitat trees that would otherwise not be found. The most important roosting locations, however, are not always obvious, especially in species such as hollow-dependent bats, which use multiple habitat trees as roosts (Lewis 1995). This poses a challenge for conservation planners because decisions regarding the protection or removal of

individual habitat trees are frequently made (e.g., during logging operations) without understanding of the relative importance of individual trees.

In nature, complex systems tend to be networked (Aloy and Russell 2004). Many of these natural systems can be represented by a network of nodes connected by links, in which the nodes represent entities in the system and the links between them represent relationships or interactions between the entities. Examples of network structures in biological systems include food webs (e.g., Solé & Montoya 2001) and social (e.g., Lusseau 2003), metabolic (e.g., Jeong *et al.* 2000), protein (e.g., Jeong *et al.* 2001), and yeast coexpression networks (e.g., Wuchty *et al.* 2003). Many real-world networks, including human networks such as the World Wide Web, display a scale-free degree distribution, whereby the number of links per node follows a power-law (Barabási and Albert 1999). A scale-free network has a large majority of nodes that have only a few links to other nodes and increasingly fewer nodes that have higher numbers of links. The nodes with the majority of links are often referred to as *hubs* (e.g., search-engines in the World Wide Web; Barabási 2002).

The structure of a network can offer insights into the functioning of the system that it represents (Strogatz 2001). Scale-free networks, for example, are remarkably tolerant to random node loss, which is most likely to be a node with few connections due to their greater number, and thus will have little effect on the connectivity of the network (Barabási and Albert 1999). An understanding of the network structure can therefore provide insights into which nodes and links are the most important for maintaining the cohesiveness of the network (e.g., Borgatti & Everett 1999; Flack *et al.* 2005).

Studies of bat ecology have revealed that species can be threatened by loss of roosting habitat despite the continued availability of food and water (Barclay and Brigham 1996, Holmes 1996, Kunz and Lumsden 2003, Racey and Entwistle 2003, Parnaby and Hamilton-Smith 2004). Identifying the most important roosting locations

would allow the prioritisation of management actions designed to conserve species. Network analysis is thus an important tool in biology and has the potential to lead to more effective conservation planning (Lusseau 2003, Croft *et al.* 2004).

Hollow-dependent bats provide good opportunities to investigate the social organisation between roosts because they switch roosts at regular intervals (Kunz and Lumsden 2003). I used a network approach to analyse the roost-switching behaviour of the white-striped freetail bat (*Tadarida australis*; Microchiroptera: Molossidae) in suburban Brisbane, Australia. The white-striped freetail bat is a widespread and abundant insectivorous bat species capable of commuting long distances (Churchill 1998). In summer, white-striped freetail bats roost in large cavities in mature eucalypt trees scattered over several hundred square kilometers (Rhodes and Wardell-Johnson 2006). This relatively large microchiropteran (around 40 g) gives birth to a single young between mid December and the end of January and forms large communal roosts (Richards 1995, Churchill 1998). Many of these trees are found in public parklands and are in danger of being removed by land management agencies due to the potential danger to people from falling limbs (Rhodes and Wardell-Johnson 2006, Chapter 3).

I used this study to investigate retention of habitat trees in a fast-growing city by using network analysis to answer the following questions: (i) What is the network topology of day-roosts used by individual members of a suburban roosting group of white-striped freetail bats?; and (ii) Can network analysis be applied to help devise management recommendations in quantifying the conservation status of individual habitat trees used by these bats?

4.2 Methods

Study area

Brisbane is a fast-growing metropolitan city in the center of south-east Queensland (27° 30' S, 153° 0' E) that covers an area of 3000 km² (Poole 1995). It is estimated to increase in population from 1.6 million in 2004 to 2.3 million by 2026 (Queensland Government 2004). The climate is subtropical with monsoonal summer rainfall (800 mm per year), predominantly dry winters, and an average maximum temperature of 25.5° C (Australian Government, Bureau of Meteorology, July 2005). The region is characterised by coastal plains, subcoastal ranges with the drainage systems and valleys containing many vegetation types, including subtropical rainforests, open eucalypt forests, *Melaleuca* forests, woodlands and heathlands (Catterall and Kingston 1993).



Fig. 4.1. Roost sites of white-striped freetail bats in metropolitan Brisbane, south-east Queensland, Australia. The arrow indicates the position of the communal roost.

Captures

I captured white-striped freetail bats with mist nets from a roost tree in a public park, four kilometres south of Brisbane's central business district. A large roosting group of up to 300 bats roosted in the internal cavity of the tree and entered the roosting space through several trunk and branch hollows (Rhodes and Wardell-Johnson 2006). This tallowwood (*Eucalyptus microcorys* F. Muell.) had a diameter of 100 cm diameter at 1.3 m height, was 24 m in height, and was characterised by a hollow trunk and many dead-end branches. It was surrounded by clumps of similar-sized tallowwoods and could not be distinguished *a priori* based on external tree attributes (Rhodes and Wardell-Johnson 2006, Chapter 3). This roost site, also used as a maternity roost during summer, is referred to hereafter as the *communal roost*.

Bats were captured while exiting their roost at dusk. I recorded species, gender, mass, forearm length, and reproductive status for all captured bats. Females without visible nipples and/or with hair growing over their nipples were classified as non-reproductive females. Pregnancy was detected by gently palpating the abdomen. During the lactation and post-lactation periods all females were checked for engorged mammary glands. If the breasts were swollen and milk was found the females were classified as lactating. Males were checked for their reproductive status by determining whether their epididymides were distended or regressed. Juveniles (young of the year) were identified by metacarpal-phalangeal joints that had not yet fused (Racey 1974). Individuals not used for the radio-telemetry study were released at the roost site immediately after handling.

Radio-telemetry

I carried out radio-tracking during three reproductive stages: pregnancy (November 2001), lactation (February 2003), and post-lactation (March 2002). In the first season (November 2001) I fitted five individuals (three pregnant females and two non-

reproductive males) with transmitters (model BD-2G, Holohil Systems, Carp, Ontario; Table 4.1). Each transmitter had a weight of 1.6 g and a battery life of nine weeks. I used Vetbond (3M, St. Paul, MN) to attach the transmitters between the scapulae. This adhesive is widely used to bond tissues together for veterinary procedures and is safe for attaching transmitters (Hamilton and Barclay 1994).

Limited data was obtained from the transmitters used in the first season, so I used collar transmitters in the second season (March 2002). Three post-lactating females were fitted with MD-2C collar transmitters (Holohil Systems, Carp, Ontario; 1.6 g weight, ten weeks battery life; Table 4.1) attached by a very thin cotton thread inserted through a small, flexible plastic tube and knotted together at the back of the neck. I also fitted LT2 two stage collar transmitters (Titley Electronics, Ballina, NSW; weight 1.6 g, up to six weeks battery life; Table 4.1) to the necks of three post-lactating females with customised surgical rubber bands. I glued the collar transmitters of both types and their aerials to the back of each individual. All collars were designed to break apart because reliable retrapping was impossible.

The MD-2C collar transmitters from the second season proved successful. Therefore in the third season (February 2003), I fitted eight non-reproductive females with slightly heavier collar transmitters (model MD-2C Holohil Systems, Carp, Ontario; 1.9 g, 16 weeks battery life; Table 4.1) to increase signal strength and detectability. I also used a thicker cotton thread to keep the transmitter attached for up to 16 weeks. The four different types of transmitter I used during the three tracking seasons represented 3.2–5.1% of the bat's body mass, which is within the limits suggested by Aldridge and Brigham (1988; Appendix I).

I radio-tracked individuals from air (light aircraft) and on land (cars) with omnidirectional antennas (model RA-5A, Telonics, Mesa, AZ) and Regal 2000 telemetry receivers (Titley Electronics, Ballina, NSW). Once I detected signals on the ground, I used a three-element, hand-held, uni-directional antenna (model AY/C Yagi Antenna,

Titely Electronics, Ballina, NSW) to locate the bats in their roost trees. Location coordinates; tree species, diameter, and height; roost entrance, size of roosting group of each roost, and distances between the communal roost and the new roost locations were noted. I checked the location of day-roosts for each bat daily. Additionally, nocturnal radio-telemetry was conducted from elevated positions to triangulate the positions of each bat every 15 minutes for up to six hours per night (White and Garrot 1990b). The vicinity of the communal roost was well suited for stationary radio-tracking at night because of its relatively high elevation. This allowed me to follow the movements of the tagged bats and to simultaneously observe the communal roost.

Roost counts

I conducted roost counts (communal and new roosts) by counting the emerging bats against the ambient light. The counts were conducted at least once a week for each roost site. I used Anabat detectors (Titely Electronics, Ballina, NSW) to confirm species identification (Herr and Klomp 1997). I stopped counting 30 minutes after the last bat had exited or until bats could not longer be heard inside the roost, whichever was later. At the communal roost bats often began to visit before all had left; hence, I were only able to obtain a minimum estimate for the group size. To avoid double counting of individuals, I stopped counting once bats re-entered the roost.

Table 4.1. Radio-telemetry data from 19 white-striped freetail bats gathered during three seasons (2001-2003) in Brisbane, Australia.

Season and bat no.	Gender^a	Repro._b	Tracking days (n)	Transmitter type^c	Days in CR^d	Group size of CR (n)	New roosts (n)^e	Group size of new roosts (n)
2001			<i>22 (total)</i>			<i>59</i>		
01	M	NR	22	BD-2G	C, 20		1	21
02	F	preg	1	BD-2G	C		1	15
03	F	preg	1	BD-2G	C		1	15
04	F	preg	1	BD-2G	C		-	-
05	M	NR	1	BD-2G	C		-	-
2002			<i>22 (total)</i>			<i>291</i>		
06	F	PL	18	MD-2C	C, 3, 5, 7, 13, 14		1	18
07	F	PL	22	MD-2C	C, 3, 5, 7		1	1
08	F	PL	18	MD-2C	C		1	1
09	F	PL	10	LT2	C		-	-
10	F	PL	10	LT2	C, 4, 10		-	-
11	F	PL	2	LT2	C, 2		-	-
2003			<i>88 (total)</i>			<i>120</i>		
12	F	NR	11	MD-2C	C		1	3
13	F	NR	88	MD-2C	C, 2, 4, 5, 6, 7, 9, 11, 19,		2	7; 20
14	F	NR	60	MD-2C	C, 4		2	4; 1
15	F	NR	41	MD-2C	C, 3, 4, 5, 6, 7		2	5; 3
16	F	NR	88	MD-2C	C, 2		1	7
17	F	NR	44	MD-2C	C, 5, 6, 7		2	5
18	F	NR	60	MD-2C	C		1	1
19	F	NR	11	MD-2C	C, 9, 11		1	1

^aGender: F - female; M - male.

^bRepro.: Reproductive status of each bat; NR - non-reproductive; preg - pregnant; PL - post-lactating.

^cSee text for explanations of transmitter types.

^dDays in CR (communal roost): Radiotracking days in which bats were found roosting in the communal roost (e.g., bat 01 was found on Capture night (C) and on day 20).

^eNew roosts (n): Number of roosts other than the communal roost used by each bat.

Analysing the roost network topology

I used data from bats with reliable roost-switching information to construct a network representation of the day-roosts, in which each day-roost formed a node. I placed links between any two nodes that were visited by the same bat.

I anticipated a network of roosts in which each node would have approximately the same number of links to other nodes. This is known as a random network and is a well-studied network topology (Erdős and Rényi 1960). The distribution of node degree (k , the number of links from a node) in such a network follows a Poisson distribution. This gives a clear peak at $k \equiv \langle k \rangle$ (i.e., the most common value of the node degree is the average node degree of the network). The numbers of nodes with higher or lower node degree decays exponentially ($P(k) \approx e^{-k}$ for $k \ll \langle k \rangle$ and $k \gg \langle k \rangle$; Erdős and Rényi 1960).

An alternative class of network, which has been found in many natural systems, is the degree distribution in a scale-free network that follows a power-law $P(k) \approx k^{-\gamma}$ (Barabási and Albert 1999). Scale-free networks are highly heterogeneous, with a few highly linked nodes (hubs) and many nodes with few links (Barabási 2002).

4.3 Results

Roost sites and roost switching behaviour

A total of 100 bats were captured: 19 in November 2001, 23 in March 2002, and 58 in February 2003. Nineteen bats were fitted with transmitters during these three radio-telemetry seasons (Table 4.1). The bats were tracked on average 26.9 days (range = 1-88 days; $n = 19$), resulting in 509 days of radio-tracking (Table 4.1). During the three-year study, I found 17 new roost sites (Fig. 4.1). The traditional method of attaching transmitters between the scapulae failed for the white-striped freetail bat.

Two bats (02, 03) lost their transmitters the next day in their new day-roosts, and two bats (04, 05) were tracked only for a few hours after release. This left me with one male (01) to track for more than one day in the first radio-tracking season (Table 4.1). In the following two radio-telemetry periods I used collar transmitters and were able to track individuals up to 16 weeks until they lost their transmitters (usually in their day-roosts) or moved out of the area (Table 4.1). In March 2002 the collar transmitters of three bats (09, 10, and 11) had insufficient range (< 1 km), and no additional roosts were located. However, their visits to the communal roosts were recorded (Table 4.1).

The roosts covered a geographic area of more than 200 km². Each individual trapped at the communal roost subsequently moved into separate roost trees with much smaller roosting groups (< 21 individuals; Table 4.1). None of the bats roosted together in the same day-roost, with the exception of the communal roost. The bats switched roosts on average every 10.6 days (range = 5-23 days). Twelve of the 19 bats returned at irregular intervals to the communal roost (average: 7 days, range = 2-20 days), and three did not roost in the communal roost again during their tracking period (Table 4.1). Tagged bats also visited the communal roost at night, even though they did not roost there during the day (Chapter 5). This included bats 08 and 18 that did not use the communal roost again after trapping (Table 4.1).

Roost searches revealed three other communal roosts with roosting groups of over 120 individuals and ten roosts with smaller groups (< 30 bats) within the geographic envelope covered by the roost network (M. P. Rhodes 1998; Rhodes and Wardell-Johnson 2006; M. Rhodes, unpublished data). The tagged bats did not visit any of these roosts during the three radio-tracking seasons.

Roost-network topology

I obtained roost-switching information from 14 bats (Table 4.1) with which I constructed a network representation of the day-roosts. I expected a homogeneous network among the 18 day-roosts inhabited by the tagged bats. Thus, I anticipated that the roost tree network would conform to a random network, where each node would have approximately the same number of links (Fig. 4.2a) and the probability of linkages would follow a Poisson distribution (Fig. 4.2b). Instead, the network diagram revealed that one tree, the communal roost, held the majority of links (15), a small subset of roosts ($n = 4$) had two links, and a large number of roosts ($n = 13$) had only one link (Fig. 4.3a). The network resembled a scale-free network because the number of roosts that had links to exactly k other roosts fitted a power-law, with $P(k) \approx k^{-0.88}$ ($R^2 = 0.95$; Fig. 4.3b). The network had one major hub –the communal roost– that had many more links than any other node. The average path length (the number of links that lie on the shortest path from any node to any other node) of this roost network was relatively short (2.2 ± 0.5 links). Thus, each bat in this population could potentially interact with other individuals through a path of less than three links, despite being spread over a large area.

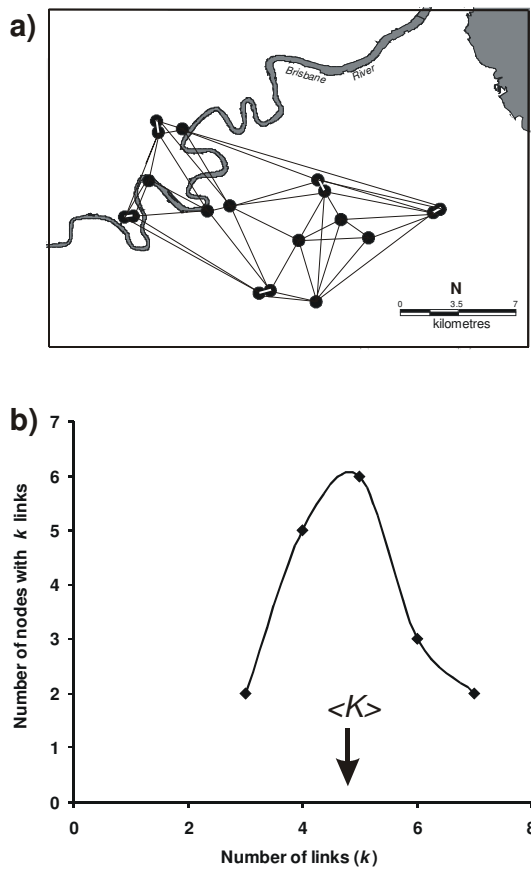


Fig. 4.2. Expected connectivity between roost sites of white-striped freetail bats in the greater Brisbane region (lines indicate the possible links [movements] between different roost sites [nodes]):
a) random network of roost trees in which each node has approximately the same number of links (k); and
b) probability of linkage $P(k)$ follows a Poisson distribution with a peak at $k \approx \langle k \rangle$, around which the numbers of nodes decay exponentially ($P(k) \approx e^{-k}$ for $k \ll \langle k \rangle$ and $k \gg \langle k \rangle$).

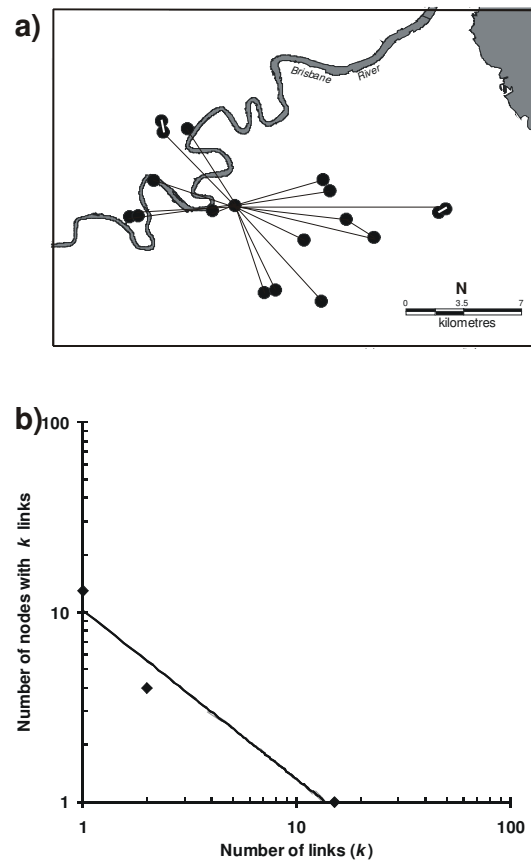


Fig. 4.3. Observed connectivity between roost sites of white-striped freetail bats in the greater Brisbane region:
a) roost network resembling a scale-free network in which most nodes have only a few links but one node (the hub) holds the majority of links; and
b) distribution of the number of links from each node is consistent with a scale-free network in which the probability of linkage $P(k)$ follows a power-law, with $P(k) \approx k^{-0.88}$ ($R^2 = 0.95$).

4.4 Discussion

Roost network topology

I used network analysis to identify the network structure of day-roosts used by individual members of a roosting group of white-striped freetail bats. This roost network was characterised by one dominant hub with many links (in this case the communal roost). My data are limited: the distribution of the number of links per node contains only three points and spans only a single order of magnitude. Nonetheless, this roost network does not represent a random topology (Erdős & Rényi 1960) and can be best described by a scale-free network model (Barabási & Albert 1999; Barabási 2002). Furthermore, the roost network remained the same during a period of over 500 bat days of radio-telemetry, regardless of the gender and reproductive season.

Despite the large geographic range of the roost network, each tree was connected to the hub through a path with a maximum length of two links (Fig. 4.3a). Results of empirical studies of food webs show that indirect effects across short paths (path length of two or three links) can be as important as direct effects (Williams *et al.* 2002). The highly connected hub node in this study is the key to the short path length of the roost network because members of the same roosting group can be distributed over a large area, thus reducing the competition for food and shelter but maintaining a cohesive roost network (Lewis 1995).

I postulate that this network is only one part of a much larger roost network of white-striped freetail bats in the greater Brisbane region. Other roosts in the region may form other roost networks with similar distribution models to the one I studied. Only a few white-striped freetail bats would need to visit roosts belonging to other roost networks to form links between roost networks, ultimately leading to the formation of one large network, a network similar to the World Wide Web (Albert *et*

al. 1999). Similarly, the long-tailed bat (*Chalinolobus tuberculatus*) has overlapping foraging ranges of groups, but roosting occurs in three geographically distinct adjacent areas. Nonetheless, some individuals move infrequently between groups, thereby linking local groups (O'Donnell 2000).

White-striped freetail bats switched roosts on average every eleven days and showed strong roost fidelity to their individual roost sites, visiting no more than three roost trees. In contrast, many other hollow-dependent bat species switch roosts on an almost a daily basis, resulting in many occupied roost trees (Kerth and König 1999, O'Donnell and Sedgeley 1999, Kunz and Lumsden 2003, Willis and Bringham 2004). Despite the low number of roost trees used by the white-striped freetail bat, none of the bats roosted together in any of the same day-roosts other than in the communal roost. However, at the same time these individuals were observed to visit the communal roost at night without roosting there during the day (Chapters 5, 6). This further strengthens the evidence that the communal roost tree plays a pivotal role in the roost network of the white-striped freetail bat.

Robustness and fragility of the bat roost network

Scale-free networks are robust against stochastic events such as random node removals (e.g., Albert *et al.* 2000; Cohen *et al.* 2000, Flack *et al.* 2005) because the majority of nodes in the network have only a few connections to other nodes. A random attack is more likely to remove one of these nodes than a well-connected one, so network connectivity remains largely unaffected (Fig. 4.4a).

In contrast, the removal of a well-connected hub has a more marked effect on the connectivity of the network (Albert *et al.* 2000). Consequently, the loss of the communal roost, the hub, of the white-striped freetail bat is likely to have a serious effect on the roosting group by disaggregating the roost network into small and isolated clusters of roosts (Figs. 4.4b). This may reduce the functionality of the roost

network by complicating interactions between individuals in different roosts.

Analogies may include the damage to scale-free networks constructed to serve human social needs (e.g., power blackouts caused by power plant failure; Barabási 2002). In such a situation, the loss of the central hub affects many individuals and can result in a serious disruption in function.

Other types of networks respond quite differently to node loss. Random networks, for example (e.g., road networks), are less susceptible to systematic attack. Node loss in random networks has little impact regardless of whether nodes are selected indiscriminately or in decreasing order of connectivity (Albert *et al.* 2000).

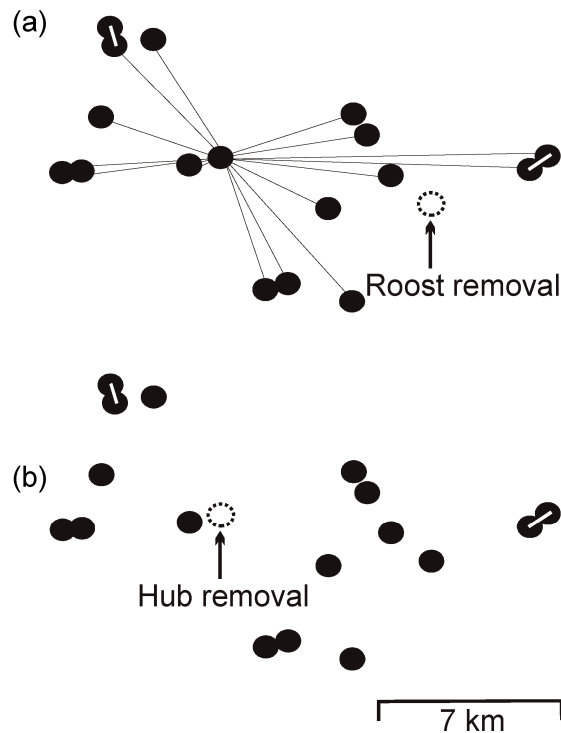


Fig. 4.4. Loss of a roost in a day-roost network of a roosting group of white-striped freetail bats:
a) loss of a smaller node; and
b) loss of the hub node (communal roost) in a scale-free network.

Although the conservation significance of these findings is profound, the hub in this network could not have been predicted *a priori*. A hub is a node with a large number of links to other roosts, not necessarily a large number of inhabitants. Apart from its central location with respect to other sites and its larger roosting group size, no attribute or pattern of attributes differentiated the hub or any of the other communal roosts from other day-roost sites (Rhodes and Wardell-Johnson 2006, Chapter 3). In this study the communal roost had the majority of connections to other roosts and the highest number of bats – making it a network hub as well as a hub of social activity. This suggests a need to understand network structures before conservation measures of individual habitat trees can be implemented effectively.

During this study the communal roost, together with many other trees, was identified by the local management agency (Brisbane City Council) as being dangerous to the public, thus triggering possible management actions such as removal or pruning of dangerous limbs. Communication of the importance of this roost tree allowed appropriate protection measures to be implemented (Rhodes 2003). The relatively high priority of this particular tree has led to measures for ongoing protection, thus ensuring the stability of this roost network for the immediate future.

Using network theory to model conservation approaches

The long-term effect of node removal on a real-world biological network is difficult to predict with certainty (Flack *et al.* 2005). Solé and Montoya's (2001) results show that food webs with power-law scaling have a high resistance to secondary extinction when species are randomly removed but are extremely susceptible to selective attacks. Conversely, Lusseau (2003) reports that a dolphin social network with scale-free properties does not fragment under simulated targeted attack. The issue is

further complicated by the dynamic nature of many biological networks, whereby some aspects of the network can adapt and respond to external perturbations.

In the roost network I examined, the links were not fixed physical entities (such as a cable in a power network); rather, they represented the movements of individual bats. It is likely that the bats will respond to the removal of a roost tree by seeking a new roost. Thus it is difficult to predict the precise consequences of the removal of a particular roost. It is clear, however, that of all possible choices, the removal of the hub node is likely to have the most profound effect. Presumably, in a forested landscape that featured many hollows, a networked system such as the one I examined could cope with the occasional loss of a hub (e.g., through wind or fire). However, in fragmented landscapes or those dominated by young stands of trees, it is likely that such a system would be less able to sustain the simultaneous removal of many hollow-bearing trees. In such situations, these essential habitat components have become rare and limiting (Barclay & Bringham 1996; Gibbons & Lindenmayer 2002; Lunney 2004).

General conservation applications

The network structure of animal residences has not been used previously to address problems in conservation biology. Through my examination of the network topology, I was able to make conservation and management recommendations for the roosting habitat of the white-striped freetail bat (Rhodes 2003). This illustrates the importance of my approach in areas such as forest conservation and urban planning, where decisions are often made concerning the protection or removal of habitat trees (Barclay and Bringham 1996, Lindenmayer and Franklin 2002). In complex networks lacking a readily predictable hub, cost-effective conservation planning suggests that the allocation of resources should be toward understanding network patterns.

My approach can be applied to other fauna groups but works especially for endangered or vulnerable species that depend on habitat trees (e.g., koalas and gliders; Claridge and van der Ree 2004, Rowston and Catterall 2004, Smith 2004). The adoption of network-based approaches will allow a more predictive understanding of complex ecological networks and could lead to a better understanding of habitat tree networks. Ecologists can model the effects of node removal (e.g., Figs. 4.4a, b), identify the relative prioritisation for protection of particular habitat trees, and determine the appropriate protection measure for each system, regardless of its topology. This would allow more efficient use of management resources and improved outcomes for biodiversity conservation.

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Chapter 5

Roost fidelity and fission-fusion dynamics of white-striped freetail bats (*Tadarida australis*)

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Plate 5.1. A white-striped freetail bat with a MD-2C-collar-transmitter attached.

Abstract

The white-striped freetail bat (*Tadarida australis*) is a common, insectivorous bat species in the temperate and subtropical regions of Australia. Despite its abundance, very little is known about its roost ecology. I used roost-switching data collected during three radio-tracking seasons to examine roost fidelity and roosting associations of a colonial summer roosting group. Bats were trapped from a large communal roost in subtropical urban Brisbane, Australia. A total of 132 radio-tracking days and nights provided 509 bat-days of data; with each bat being tracked on average 26.9 ± 28.6 SD. Seventeen new roost trees were found, scattered throughout an area of over 200 km². Roost cavities were located inside eucalypt trees > 83 cm diameter at 1.3 m height. White-striped freetail bats switched roosts every 10.6 ± 7.9 days. Tagged bats spent the majority of their time away from a communal roost in day-roosts with smaller roosting groups despite being caught in the communal roost with up to 300 individuals. I quantified associations between pairs of tagged bats using a pair-wise sharing index (PSI). The consistent negative PSI-values obtained during this study indicated that members of the roosting group shared roosts less often than predicted by chance. However, bats associated at night at the communal roost, even when they did not occupy it during the day. For every day-visit recorded per bat at the communal roost, each bat visited the same roost twice at night during the period of night-time observations. This suggests that nocturnal movements of individuals should be included in assessments of associations between individuals. I postulate a fission-fusion pattern based on individual movements to and from one communal site. This roost represents a center for the group, both in geographical and behavioural terms. I also argue that the roost network of one communal roost and many satellite roosts may be seen as a single inter-connected unit.

5.1 Introduction

In some mammal societies, stable social groups frequently divide into sub-groups for varying periods of time before rejoining (e.g., Robinson and Janson 1987; Packer *et al.* 1990; Henzi *et al.* 1997; Bräger 1999). This phenomenon is known as *fission-fusion* (Kummer 1971). The mechanisms driving this behaviour are not fully understood but have been discussed in the context of resource availability, the maintenance of long-term relationships, and predation pressure (Robinson and Janson 1987; Henzi *et al.* 1997). The dynamics of separation and re-grouping are usually described by examining group membership of individuals and determining the proportion of time these individuals spent together using association indices (e.g., Henzi *et al.* 1997; Kerth and König 1999; Willis and Brigham 2004; Cross *et al.* 2005).

Insectivorous bats are a suitable taxon in which to study fission-fusion dynamics as many species are known to shift roosts regularly (Kunz and Lumsden 2003). Bats roost in natural (e.g., caves, rock crevices, tree hollows, tree foliage) or human-made structures (buildings, mines, bat boxes). Roost changes may be influenced by season, reproductive stage, food availability, thermoregulation, predation pressure, parasite accumulation and/or site disturbances (Lewis 1995; Kunz and Lumsden 2003). Some species shift roosts almost daily (roost lability; e.g., O'Donnell and Sedgely 1999), while others remain at the same site over several years (roost fidelity; e.g., McCracken and Bradbury 1981). In recent years the definition of the term 'bat colony' (Bradbury 1977) has altered. A colony is now seen as a social unit of individuals based on the interactions of members (reviewed in Burland and Worthington Wilmer 2001). However, this social unit of roosting bats may still split into several subunits during the day (Kerth and König 1999, O'Donnell 2000, Kerth *et al.* 2001). In some bat species, individuals appear to associate with

certain roost mates more than others and roost in non-random aggregations spread over several roost sites, despite daily changes of roost sites, fluctuating group sizes and overlap of foraging ranges (O'Donnell 2000; Vonhof *et al.* 2004; Willis and Brigham 2004).

The white-striped freetail bat, *Tadarida australis* (Microchiroptera: Molossidae (Gray, 1838)), is an endemic insectivorous species of mainland Australia (Churchill 1998; Rhodes and Richards in press). The species is a fast flyer which typically feeds at high altitudes (Churchill 1998). In urban areas of south-east Queensland it roosts in hollows of large eucalypts (Rhodes and Wardell-Johnson 2006). Ovulation, copulation and fertilisation occur in the late Austral winter (Kitchener and Hudson 1982). Females give birth between mid-December and mid-January and congregate in tree roosts of several hundred individuals (Rhodes and Richards in press). Although thought to be abundant, little is known about its roost ecology (Churchill 1998; Rhodes and Richards in press).

The overall objective of this study was to investigate the roost-switching behaviour of a known colonial summer roosting group of white-striped freetail bats at one communal roost. Specifically I examined the following questions: (i) How many bats use the communal roost and other roosts associated with the communal roost?; (ii) Does trapping at the communal roost influence its roost usage?; (iii) To what extent do white-striped freetail bats show roost fidelity?; (iv) Do members of the colonial roosting group switch roosts and exhibit fission-fusion sociality?; (v) Do white-striped freetail bats select roost-mates at random or do they share day-roosts with individuals captured and radio-tracked at the same time?; And (vi) do tagged bats associate at night at any of the known roost sites?

5.2 Methods

Study area

The field sites were located in the Brisbane River catchment area, which includes metropolitan Brisbane and its outer suburbs in subtropical eastern Australia (27° 30' S, 153° 31' E, Fig. 5.1). The landscape is undulating and dominated by a mosaic of mostly urban developments with planted gardens, as well as parklands with scattered mature eucalypts, dominated by forest red gum (*Eucalyptus tereticornis*). The metropolitan region includes bushland reserves, ranging in area from one to 20 km². The fringes of metropolitan Brisbane are dominated by cleared pastures with scattered mature trees and larger bushland remnants (Catterall and Kingston 1993).

Capture and examination

White-striped freetail bats were captured in mist nets while exiting at dusk from one roost tree used by several hundred individuals (hereafter *communal roost*). This tree was located in a suburban park, four kilometres south of Brisbane's central business district. Four sets of mist-nets (0.1-10 m high and 18 m wide) were erected in a V-shape around the tree roost exit to capture exiting bats at dusk. Mist nets were removed after one hour even if bats still remained in the roost.

Pregnancy was detected by gently palpating the abdomen. Lactating females had swollen mammary glands from which milk could be expressed. Females without obvious nipples and/or with hair growing over their nipples were classified as non-reproductive females. Reproductive males were identified by distended epididymides. Adults were distinguished from juveniles (young of the year) by fusion of the metacarpal-phalangeal joints (Racey 1974). Individuals not used for radio-tracking were released at the roost site immediately after processing.

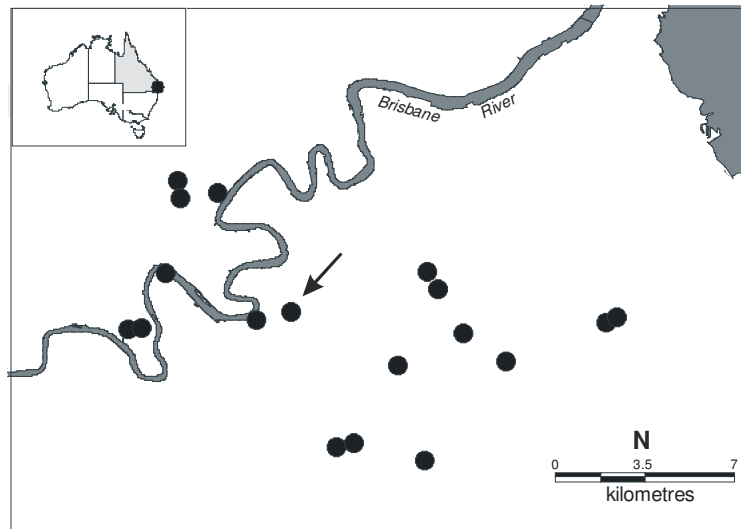


Fig. 5.1. Location of roost sites of a roosting group of white-striped freetail bats in Brisbane, south-east Queensland, Australia. The arrow indicates the location of the communal roost.

Telemetry

I radio-tracked white-striped freetail bats during three different radio-tracking seasons: 22 radio-tracking days during November 2001 (pregnancy season), 88 days from February to May 2003 (lactation to post-lactation period), and 22 days and in March and April 2002 (post-lactation). In the first tracking period (November 2001), individuals were fitted with 1.6g transmitters (model BD-2G, Holohil Systems, Carp, ON, Canada; Table 5.1) using Vetbond (3M, St. Paul, MN, USA) to attach the transmitters between the scapulae (Hamilton and Barclay 1994).

In the second season (March-April 2002) six collar-transmitters from two different suppliers were used to test their effectiveness for this high and fast flying bat species (Fenton and Rautenbach 1986). Three transmitters were 1.6 g models (MD-2C, Holohil Systems, Carp, ON, Canada; Table 5.1) attached by a thin cotton thread which was inserted through a small, flexible plastic tube and knotted together at the

back of the neck. The other three were 1.6 g LT2 two stage models (Titley Electronics, Ballina, NSW, Australia; Table 5.1) with customised surgical-rubber bands placed around the necks. The collar-transmitters of both types and their aeriels were also glued to the back of each individual in order to keep the transmitter and aerial fixed dorsally, avoiding unnecessary friction and reducing disturbance for each bat. All collars were designed to break open, as reliable re-trapping was impossible.

In the third season (February-May 2003) eight adult females were fitted with 1.9g collar-transmitters (model MD-2C Holohil Systems, Carp, ON, Canada; Table 5.1) to increase signal strength and detectability, and a thicker cotton thread was used to keep the transmitter attached for up to 16 weeks. Transmitters of all three types represented 3.2 – 5.1% of mean body mass (Aldridge and Brigham 1988; Appendix I).

To locate new roost sites a car with an omni-directional antenna mounted on the roof (model RA-5A, Telonics, Mesa, AZ, U.S.A.) and Regal 2000 telemetry receivers (Titley Electronics, Ballina, NSW, Australia) were used to locate the signals as airspace restrictions and signal interference precluded use of aircraft for aerial tracking. Once signals were detected, a three-element, hand-held unidirectional antenna (model AY/C Yagi Antenna, Titley Electronics, Ballina, NSW, Australia) in combination with a Regal receiver was used to locate the bat in its day-roost. The location of day-roosts were tracked daily as long as the transmitters were attached to the bats.

Roost counts

Counts of the roosting group at the communal roost started 17 months prior to tracking in order to observe patterns of roost usage before trapping commenced. This continued until the end of the study period (July 2000 - June 2003). Tagged bats

were followed back to new roost sites (hereafter *satellite roosts*) and roosting group sizes were estimated by counting bat exits. Roosts were observed from the ground, ca. five metres away from the tree where the roost entrance was visible against the ambient light but where bats could not see the observer (emergence was otherwise delayed). Ultrasonic detectors (Anabat; Titley Electronics, Ballina, NSW, Australia) were used to confirm species identification (Herr and Klomp 1997). Observation started 30 min before sunset and counting stopped 30 min after the last bat exited and bats could no longer be heard inside the roost. Counts were made once a week for each roost site during summer, and once a month during winter. At the communal roost, bats approached the roost and entered it before all others had left; hence, I was only able to obtain a minimum estimate for the group size. To avoid double counting of individuals, I stopped counting once bats re-entered the roost. Satellite roosts found in the summer season of 2001/2002 were also observed in the following summer season (2002/2003). Observations of satellite roosts stopped in June 2003.

Roost-switching behaviour

Once roost trees were located via telemetry, I recorded location co-ordinates with GPS and measured biophysical tree and site characteristics (e.g., tree species, diameter, height, roost entrance characteristics; see Chapter 3). To assess the roost-switching pattern of individuals I mapped the movements of bats between their diurnal roost sites and measured the distances between consecutive roost sites per bat using GPS coordinates on a digital aerial photograph with a resolution of 0.6 m (Mapview; Queensland Department of Natural Resources 2002). The percentage of roost-use per roost tree per bat was calculated by dividing the number of days spent by each bat in a particular roost location by the total number of tracking days.

Roost-sharing behaviour

I used a *pair-wise sharing index* (Willis and Brigham 2004, 2005) to assess whether tagged white-striped freetail bats selected roost mates at random or whether bats shared roosts with individuals captured and radio-tracked at the same time. This index compares the observed rate of roost co-occupancy of pairs of bats to an expected value. The expected value is calculated based on the individual roost-switching behaviour of each bat in the pair, combined with the number of simultaneous days that both bats were tracked (Willis and Brigham 2004, 2005). Positive values indicate that the bats were sharing roosts more often than expected by chance, while negative figures indicate the bats shared roosts less often than expected by chance, with zero indicating random roost selection (Willis and Brigham 2004). I only included bat pairs for which I knew the exact roost location of both individuals on at least five simultaneous days (Willis and Brigham 2004).

Nocturnal use of the communal roost and surrounding area

One radio telemetry station was located at the communal roost. The high elevation of this site made it well suited to following the movements of tagged bats via radio-tracking, and also permitted simultaneous observation of the communal roost and surrounding area. Tracking was conducted each night, usually spanned three to six hours after sunset, although the communal roost was also tracked between midnight and sunrise on two occasions. Time, location and length of stay of each tagged bat at the communal roost were recorded.

Nocturnal use of other roosts

In addition to the observation of the communal roost, satellite roosts were observed once a week from sunset for up to three hours. On one occasion the satellite roost used by bat 06 was observed from sunset to sunrise. Exiting and entering behaviour were recorded for tagged or untagged bats. In addition, I checked for signals from tagged bats every 15 min and if tagged bats visited the satellite roost or its surrounding area.

Statistical analysis

Tracking data were pooled due to the small sample size of different sexes and the lack of different reproductive stages. Data are presented in the text as means \pm SD. Mann-Whitney *U*-tests were used to compare samples because many data sets were not normally distributed (Wilk-Shapiro statistics, *W*). Correlations between variables were tested using Spearman *R* (Zar 1999). Significance was assessed at an alpha of 0.05.

5.3 Results

Captures

I captured 100 bats at the communal roost on three trapping nights. In November 2001, two non-reproductive males and 17 pregnant females were captured. In March 2002, the majority of individuals captured were volant, almost fully grown juveniles (12 males and three females), indicating that the reproductive season had ended (Churchill 1998). The remaining eight bats were adult, post-lactating females. In February 2003, trapping was conducted during the expected lactation period when I predicted that the offspring were old enough to be left behind in the roost. All 58 bats captured were females and none showed any signs of reproduction (neither pregnant

nor lactating), possible due to severe local drought in that year (Australian Government, Bureau of Meteorology).

Telemetry

I tracked 19 individuals over 132 nights (509 bat-days; Table 5.1). Each bat was tracked on average 26.9 days \pm 28.6 SD ($N = 19$). Three pregnant females and two non-reproductive males were tagged in the first radio-tracking period (November 2001). Two females groomed off their transmitters in day-roosts the next day and the transmitter signals from another two bats (one female, one male) were not heard again after tagging and release, leaving one male to follow for 22 days (Table 5.1). In March and April, 2002, six post-lactating females were tracked between two and 22 days. In the last season (February-May 2003) I tracked eight non-reproductive females between ten and 88 days before the transmitters were groomed off or bats had moved out of the area (Table 5.1).

Table 5.1. Radio telemetry data for 19 white-striped freetail bats gathered during November 2001, March-April 2002 and February-May 2003 in urban Brisbane, Australia.

<i>Season and bat no.</i>	<i>Gender^a</i>	<i>Repro.^b</i>	<i>Tracking days (n)^c</i>	<i>Trans-mitter type^d</i>	<i>Days in CR^e</i>	<i>Group size of CR (n)^f</i>	<i>SR (n)^g</i>	<i>Distance SR to CR (m)^h</i>	<i>Group size of SR (n)ⁱ</i>	<i>Nocturnal visits (n) to RA, CR, Passing^k</i>
2001			<i>22 (total)</i>			59				
01	M	NR	22	BD-2G	C, 20		1	5100	21	0, 0, 0
02	F	Preg	1	BD-2G	C		1	6750	15	0, 0, 0
03	F	Preg	1	BD-2G	C		1	1350	15	0, 0, 0
04	F	Preg	1	BD-2G	C		-	-	-	0, 0, 0
05	M	NR	1	BD-2G	C		-	-	-	0, 0, 0
2002			<i>22 (total)</i>			291				
06	F	PL	18	MD-2C	C, 3, 5, 7, 13, 14		1	5100	18	3, 3, 1
07	F	PL	22	MD-2C	C, 3, 5, 7		1	5600	1	1, 2, 0
08	F	PL	18	MD-2C	C		1	5700	1	1, 1, 1
09	F	PL	10	LT2	C		-	-	-	1, 0, 1
10	F	PL	10	LT2	C, 4, 10		-	-	-	0, 0, 0
11	F	PL	2	LT2	C, 2		-	-	-	0, 1, 0

Table 5.1. cont.

Season and bat no.	Gender^a	Repro.^b	Tracking days (n)^c	Transmitter type^d	Days in CR^e	Group size of CR (n)^f	SR (n)^g	Distance SR to CR (m)^h	Group size of SR (n)ⁱ	Nocturnal visits (n) to RA, CR, Passing^k
2003			<i>88 (total)</i>			120				
12	F	NR	11	MD-2C	C		1 ⁺	5500	3	1, 0, 0
13	F	NR	88	MD-2C	C, 2, 4, 5, 6, 7, 9, 11, 19,		2 ⁺	8500 7000	7 20	10, 6, 1
14	F	NR	60	MD-2C	C, 4		2 ⁺	13100 13500	4 1	6, 2, 1
15	F	NR	41	MD-2C	C, 3, 4, 5, 6, 7		2 ⁺	6600 6600	5 3	2, 2, 0
16	F	NR	88	MD-2C	C, 2		1	7800	7	15, 5, 0
17	F	NR	44	MD-2C	C, 5, 6, 7		1 ⁺	6250	5	1, 0, 0
18	F	NR	60	MD-2C	C		1	5900	1	8, 3, 2
19	F	NR	11	MD-2C	C, 9, 11		1	5750	1	1, 0, 0

^aGender: F - female, M - male.

^bRepro.: Reproductive status of each bat; NR - non-reproductive, Preg - pregnant, PL - post-lactating.

^cTracking days (n): Number of radio-tracking days where bat was accounted for.

^dTransmitter type: See text for explanations of transmitter types.

^eDays in communal roost (CR): Radio-tracking days where bats were found roosting in the communal roost (e.g., bat 01 was found on capture night [C] and on day 20).

^fGroup size of CR (n): Maximum number of bat exits at the communal roost counted during peak summer months (December-early March).

^gSatellite roosts (SR) (n): Number of roosts other than the communal roost; - = no data; + - not all day-roost were found

^hDistance to CR (m): Distance from satellite roosts to the communal roosts (m).

ⁱGroup size of SR (n): Maximum number of bat exits counted at each satellite roost.

^kNocturnal visits (n): Number of times each bat has been recorded to visit the roost area (RA), communal roost (CR) or passing through the roost area for a short period of time (< 2 min) during night-time tracking

Roost trees

The communal tree, a tallowwood (*Eucalyptus microcorys*), had a height of 24 m, a diameter of 100 cm (at 1.3 m height) and the roost entrance was located on the trunk, six metres above ground. In addition to the communal roost, I found 17 other roost trees used by tagged bats (Fig. 5.1). The average diameter of satellite roost trees was 82.8 ± 29.6 cm with heights ranging from eleven to 43 m (25.0 ± 9.2 m; $n = 17$). The average height of roost entrances at the satellite roost was 15.8 ± 6.3 m. Roost entrances were in branches or trunks, often leading to a larger trunk cavity with internal diameters of > 30 cm (Rhodes and Wardell-Johnson 2006; Chapter 3).

All roost trees were eucalypts: *Corymbia citriodora* subsp. *variegata* ($n = 2$), *Eucalyptus propinqua* ($n = 1$), *E. microcorys* ($n = 2$, including the communal roost), *E. moluccana* ($n = 1$), *E. racemosa* ($n = 5$), *E. tereticornis* ($n = 2$) and dead eucalypts that were not be identified to species ($n = 5$).

Roost counts

White-striped freetail bats did not use the communal roost during the Austral winter months of June and July. Bats returned between late August and early September (mating season; Kitchener and Hudson 1982; Fig. 5.2a). The communal roosting group size increased continuously and peaked during summer (December to March). In summer 2002/2003, however, numbers remained relatively low until rain relieved the drought conditions in early February. Bat numbers decreased from late March and bats started to vacate the communal roost from mid April to mid May (Fig. 5.2a). Trapping and tracking did not influence the bats' roost usage as the pattern at the communal roost remained the same between July 2000 and June 2003 (Fig. 5.2a).

Roost occupancy at the satellite roosts showed similar trends, although with much smaller roosting group sizes (Fig. 5.2b,c; Table 5.1). Except for one satellite

roost (used by bat 02 in November 2001), none of the satellite roosts were re-used (tagged or untagged) during observations (Fig. 5.2b,c).

Day-roost-switching

Most individuals returned to the communal roost at regular intervals, although not all returned on the day following capture (Table 5.1). Of the 19 bats tracked, I obtained roost-switching data for 14 bats (Table 5.1, Fig. 5.3). These 14 bats spent most of the radio-tracking days in primary satellite roosts ($64.6 \pm 34.4\%$), followed by time in unknown roosts ($23.1 \pm 34.2\%$), the communal roost ($9.7 \pm 29.4\%$) and secondary satellite roosts ($2.6 \pm 5.7\%$; 5.4a, b). They switched roosts on average every 10.6 ± 7.9 days and despite being captured in the communal roost they spent most their days roosting away from the communal roost (Mann-Whitney *U*-test; $n = 14, 14$; $U = 0.00$, $P < 0.001$; Fig. 5.4a, b). None of these individuals roosted together other than in the communal roost.

Four bats did not use the communal roost again (Table 5.1, Fig. 5.4a, b). The remaining ten bats returned to the communal roost 2.1 ± 2.3 times for up to five consecutive days ($n = 32$). The interval between revisits varied from one to 20 days (7.0 ± 4.5 ; Table 5.1). There was no significant correlation between the number of days each bat was tracked and the number of revisits to the communal roost ($n = 14$; $R = 0.35$, $P = 0.21$).

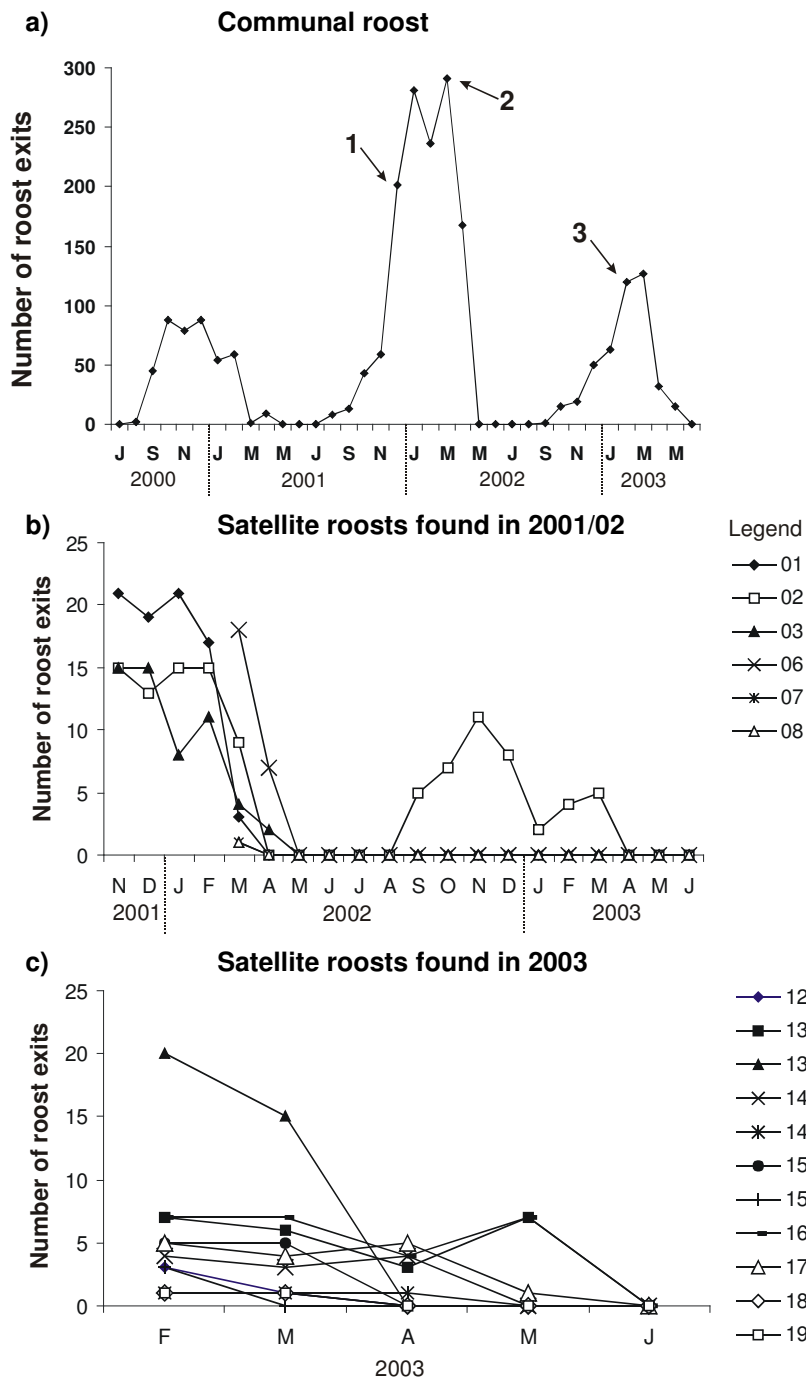


Fig. 5.2. Counts of bats exiting at dusk at the communal roost (a) and at satellite roosts (b, c). If multiple roost counts were made in a month, the highest number is shown.

a) Counts at the communal roosts (July 2000 - June 2003). Numbers 1-3 indicate timing of the three capture events at the roost.

b) Counts for bats 01 to 03 and 06 to 08. Bats 01-03 were caught in November 2001 and their satellite roosts were observed from November 2001 until July 2003. Bats 06-08 were caught in March 2002 and satellite roosts were observed from March 2002 until July 2003.

c) Counts for bats 12-19. Bats were caught in February 2003. Bats 13-15 used two satellite roosts during the period of observations. Satellite roosts of these bats were observed from February to June 2003.

Bat 12 left the communal roost area immediately after release, returned the next night for a short visit of five minutes, but was subsequently not found during night or day for 22 consecutive radio-tracking days; suggesting that it roosted and foraged in a different area. This bat then returned for eleven radio-tracking days to one satellite roost before the signal was no longer detected. The satellite roosts of the three bats fitted with LT2 collar-transmitters were not found, although day roosting and/or night visits at the communal roost were observed (Table 5.1).

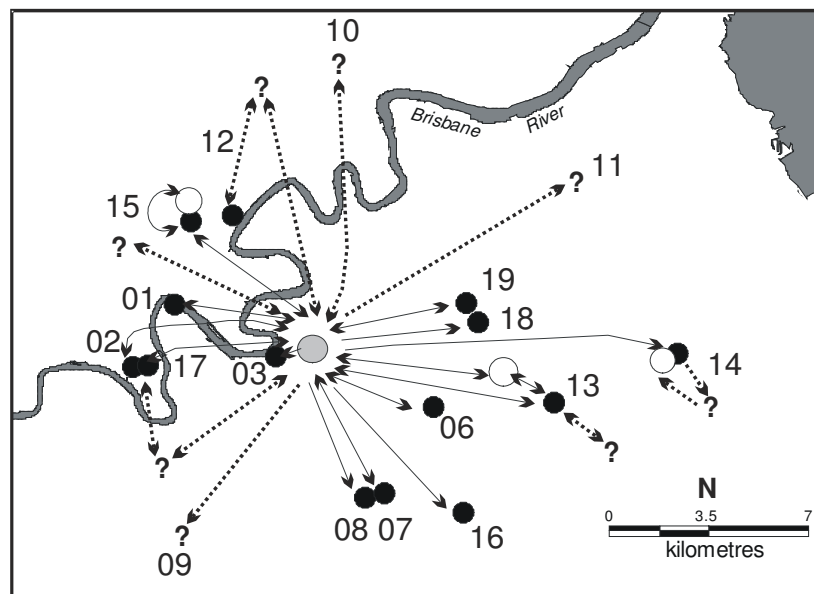


Fig. 5.3. Roost-switching pattern of individual white-striped freetail bats in urban Brisbane, Australia. Arrows indicate movements and directions between roost sites of each bat. Unknown roost location/s are indicated through dotted lines, based on known directions of radio-fixes.

Grey – communal roost; black – primary satellite roosts;
white – secondary satellite roosts; ? – unknown roost location/s.

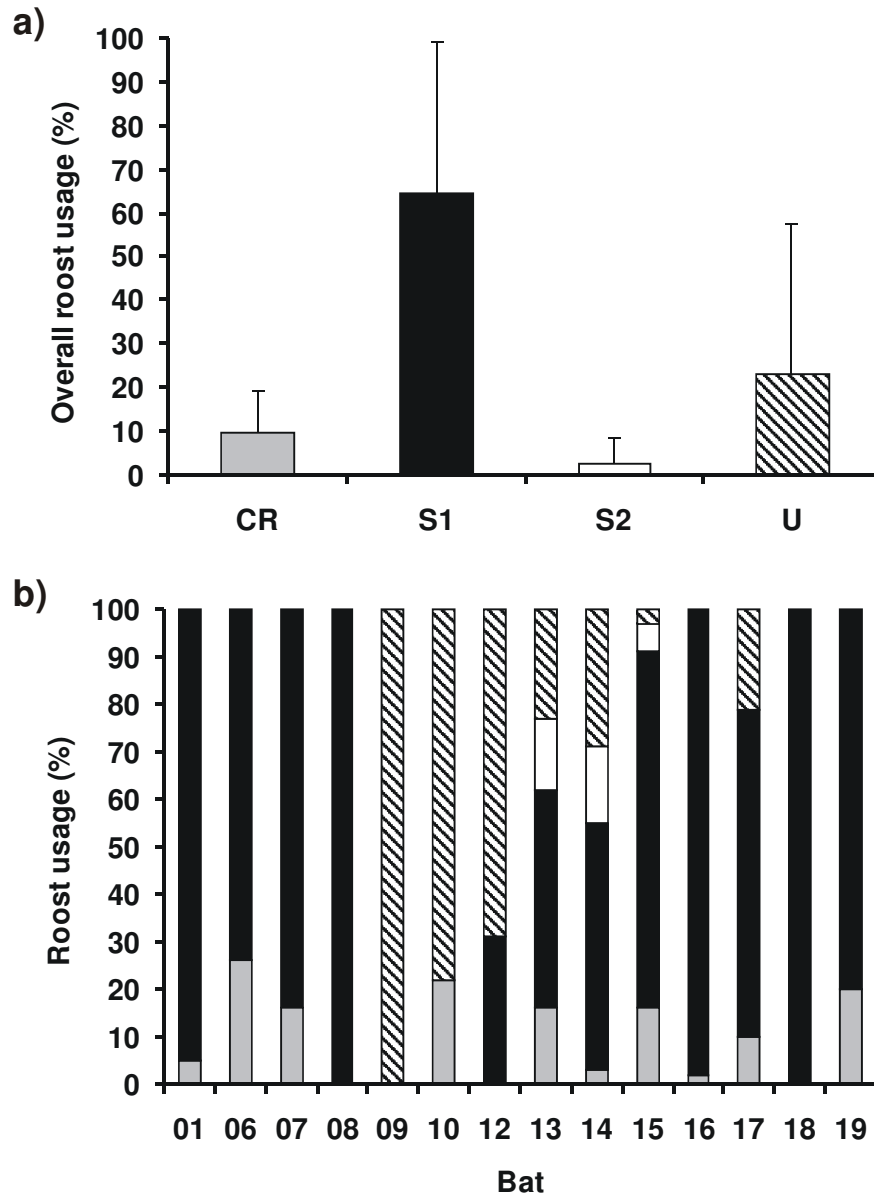


Fig. 5.4. Roost usage of 14 white-striped freetail bats in urban Brisbane, Australia.

a) Overall roost usage of different roost sites for the 14 bats examined, expressed as percentage (means \pm SD) of total days tracked; communal roost (CR), primary satellite (S1), secondary satellite (S2) and unknown roost location/s (U);

b) Percentage of roost usage per individual bat. The number of tracking days per bat is indicated above each bar. The shading of CR, S1, S2 and U correspond to Fig. 5.4a.

Roost-sharing behaviour

I calculated the pair-wise sharing index for ten individuals of 30 different pair-wise combinations (three in 2002 and 27 in 2003; in 2001 I had no bat pairs to compare). Values of the pair-wise sharing index of all pairs were negative (-0.55 ± 0.19 ; $n = 30$, $N = 10$), indicating that roost switching did not lead to the same roosts. There was no difference in PSI values between tracking periods in 2002 and 2003 (Mann-Whitney U -test, $n = 3$, 27 ; $U = 25.0$, $P = 0.28$), indicating that this lack of association persisted between seasons.

Nocturnal use of the communal roost and surrounding area

During nocturnal radio-tracking, bats visited the communal roost, the roost area or passed-through the roost area on their way from the satellite roosts to their foraging areas, even when they did not occupy it during the day ($n = 82$, $N = 13$; Table 5.1). Overall, bats visited the communal roost area more frequently ($n = 50$, $N = 12$) than the communal roost itself ($n = 25$, $N = 9$; Table 5.1). Visits to the communal roost lasted up to 180 min, with an average of 38.6 ± 39.6 min per bat ($n = 25$, $N = 9$). In comparison, mean visit duration to the communal roost area was 18.1 ± 14.2 min ($n = 50$, $N = 12$) for up to 59 min. Nevertheless, the overall time bats ($n = 25$, $N = 9$) spent inside the communal roost at night compared to the time bats ($n = 50$, $N = 12$) circling the roost area was similar (964 versus 906 minutes, respectively). Occasionally, two or more tagged bats visited the communal roost simultaneously ($n = 4$ occasions on 4 different nights) or circled together over the communal roost area ($n = 20$ occasions on 12 different nights).

I also observed tagged and untagged bats flying in groups of up to 20 bats around the communal roost tree. These group sizes changed continuously as different individuals joined and left the swarm. This behaviour was observed

throughout the night, from end of December to mid/end of February (2000-2002) and until mid March in 2003. Throughout the night, loud and audible social calls could be heard from inside the communal roost and from individuals flying over the roost site. This social behaviour started as soon as the first bats visited the roost (10-20 min after the first emerged) and ended just before dawn. Heavy thunderstorms and rain did not change this behaviour.

Nocturnal use of satellite roosts

Contrary to observations at the communal roost, bats inside satellite roosts rarely vocalised before emergence. No bats returned to the roosts during the first three hours after sunset and I did not observe any swarming behaviour. Swarming did also not take place during all-night observations at the satellite roost of bat 06. No other tagged bat, other than bat 06, visited this roost location.

5.4 Discussion

Roost fidelity and roost-sharing behaviour

Hollow-dependent bats show a wide spectrum of roost-switching behaviour, from daily roost changes (roost lability) to high levels of roost fidelity. Kunz and Lumsden (2003) categorised three such groups: species that shift almost daily; bats that shift every three to ten days; and those that are faithful to one site for a long period of time. The roost-switching behaviour of white-striped freetail bats was characterised by infrequent roost changes and loyalty of each bat to a very small number of roost sites. This behaviour groups them into the medium spectrum of roost fidelity (Kunz and Lumsden 2003).

During this study, most satellite roosts were not reused in subsequent tracking seasons. In contrast, the communal roost was used each year, but it is not

known whether the same individuals revisited this roost year after year. Similarly, the noctule bat (*Nyctalus noctula*) does not reuse roost trees between years and 60% of known roost sites remain vacant on average (Kronwitter 1988). North American big brown bats (*Eptesicus fuscus*) on the other hand, reuse roosts from previous years (Willis and Brigham 2004) while New Zealand's long-tailed bats (*Chalinolobus tuberculatus*) rarely reuse roosts (O'Donnell and Sedgely 1999).

The capture of solely non-reproductive females in early February 2003 was unexpected as the exit counts at the communal roost were within the range of the previous years where the communal roost was also used as a maternity roost. Roost counts at this roost over a three-year period demonstrated that bat numbers remained high during summer and that capture events did not influence usage of this roost. On the other hand, this study showed that tagged bats spent 90 % of their days in satellite roosting groups away from the communal roost, although individuals returned at irregular intervals. As only a small percentage of bats caught at the communal roost tree were tagged, the movements of the majority of bats remained unknown. These untagged bats may have formed part of the small groups observed at multiple satellite roosts. Individuals of the same colonial roosting group were dispersed over a number of roosts on any given day, as found in other forest-dwelling bats (O'Donnell and Sedgely 1999; Willis and Brigham 2004). I therefore I postulate that a network of separate roosts used by members of one communal roosting group should be considered as one single inter-connected unit (Chapter 4). This network of tree roosts may function in a similar manner as larger roosts, such as caves, as proposed by Willis and Brigham (2004).

Research into the fission-fusion sociality among other cavity-roosting bats has demonstrated strong associations between individuals where bats tend to associate with certain preferred roost mates (Heise and Schmidt 1988; Kerth and König 1999; O'Donnell and Sedgely 1999; Vonhof *et al.* 2004; Willis and Brigham 2004). The

application of the same methodology as Willis and Brigham (2004, 2005) allowed comparison of roost-sharing behaviour of a roosting group of white-striped freetail bats with that of a roosting group of American big brown bats, which demonstrated fission-fusion roosting patterns. The majority of big brown bats' pair-wise combinations showed positive values of the pair-wise sharing index indicating that this individuals associated with roost-mates more often than predicted by chance (Willis and Brigham 2004). In contrast, the negative values I obtained indicate that tagged white-striped freetail bats shared roosts less often than predicted by chance. Despite the small sample-size in the present study, the data showed consistently negative values with small variance, suggesting that tagged bats may have actively avoided each other. This behaviour remained the same over three radio-tracking seasons and regardless of reproductive stages. However, none of the tagged bats had dependent offspring in the communal roost. It is feasible, therefore, that lactating females may show different roost-switching dynamics to that observed here. I hypothesise that lactating females shift roosts less often due to the large energetic costs involved with shifting non-volant young between roosts (reviewed in Kunz and Lumsden 2003).

Pregnant, non-reproductive and post-lactating bats, on the other hand, might recognise a predatory cost of such a large aggregation and chose to stay away. The audible and loud vocalisation (echolocation and social calls) recorded at the communal roost (M. Rhodes, unpublished data) may alert predators, such as tawny frogmouths (*Podargus strigoides*), to a large congregation of bats (Fenton *et al.* 1994). At the communal roost I regularly observed a female tawny frogmouth move from its nearby roost to a perch opposite the bats' roost entrance, once bats began producing echolocation calls. This predator then chased bats after they emerged. For a fast flying bat species, such as the white-striped freetail bat, the most vulnerable time for predation may be during emergence (Black *et al.* 1979; Czechura 1983)

although they may also be affected by diurnal terrestrial predators which may enter the roost through the large hollows connecting to the roost cavity (Mansergh and Huxley 1985). Carpet pythons (*Morelia spilota variegata*) and lace monitors (*Varanus varius*) are common in urban Brisbane (Queensland Museum 1995).

It remains unclear why roost-switching was only observed between satellite roosts and the communal roost, but not between satellite roosts. Apart from the central location of the communal roost and its larger colony size, no measurable physical characteristics or tree attribute measured differentiated the communal roost from other day-roost sites (Rhodes and Wardell-Johnson 2006, Chapter 3). Thus, measured tree and site attributes may not have had an influence on the individuals' roost-switching behaviour. Further work is therefore required to investigate the roost-switching behaviour of white-striped freetail bats at other roost sites, including satellite roosts and other communal roosts found in the same study area.

Nocturnal fission-fusion dynamics

Since Kummer (1971) applied the concept of fission-fusion to primates, this pattern of social behaviour has been studied in a variety of mammalian taxa, including cetaceans, microchiroptera, primates and ungulates (e.g., Robinson and Janson 1987; Packer *et al.* 1990; Henzi *et al.* 1997; Bräger 1999; Kerth and König 1999; Chilvers and Corkeron 2002; Vonhof *et al.* 2004; Willis and Brigham 2004; Cross *et al.* 2005). Fission-fusion societies, however, vary greatly as the degree of association among individuals differs between species and within species. Cross *et al.* (2005) argued that traditional association and fission-fusion indices are more likely to represent a fission and fusion history of groups rather than individual preferences because individual choices may be limited by environmental constraints (e.g., predation).

In microchiropterans, descriptions of fission-fusion societies have been based on diurnal roost sharing behaviour of dyads (Kerth and König 1999; O'Donnell and Sedgeley 1999; Vonhof *et al.* 2004; Willis and Brigham 2004) presumably because associations between individual bats during the night are difficult to obtain. This study demonstrated that fission-fusion sociality can occur despite negative day-roost-sharing associations. Individual white-striped freetail bats met at night at a central location even if they did not always associate during the day. Hence, a colony of white-striped freetail bats may be better described by their social interactions, as has been proposed by Burland and Worthington Wilmer (2001). My data are consistent with a fission-fusion social structure. However, in contrast to other such societies among bats, the fission and fusion events I observed reflect movements by individuals to and from one communal roost as well as nocturnal activity in, at or near at the same roost site. In other systems, fission-fusion appears to result from switching between trees within a large population of diurnal roosts. This suggests that previous studies might have underestimated strengths of associations within bat colonies because they might not have looked at nocturnal behaviour. I therefore propose that nocturnal movements of individual bats should be included in assessments of associations. Furthermore, it may be possible that the social organisation of fission-fusion societies in bats is not always dependent on attractions between certain individuals but between individuals and the roosting group as a whole (c.f., Kerth and König 1999) or as a result of passive aggregation (Wilkinson 1985).

Given that the communal roost was also used as a maternity roost, the individuals of this fission-fusion society may be related to one another, as has been found in other bat species (Kerth and König 1999). Searches for additional roosts in metropolitan Brisbane revealed another 13 roosts: three communal roosts with roosting groups of over 120 individuals and ten roosts with less than 30 bats (Rhodes

and Wardell-Johnson 2006, Chapter 3). However, none of the tagged bats visited these roosts while being tracked, despite these sometimes being geographically closer to the satellite roosts than the communal roost used by the bats in this study. It is possible that these other roosts were part of different roost networks of white-striped freetail bats with members of other networks rarely interconnecting, as has been found for long-tailed bats in New Zealand (O'Donnell 2000).

At this stage, an adequate explanation of the observed pattern of splitting up during the day and meeting at night at a central roost is limited by the lack of comparable studies of the white-striped freetail bat. I hypothesise however, that a large inter-connected network of individual roost trees may enable the colonial roosting group to have alternative roost sites should the primary roost be damaged or destroyed (Lewis 1995). Visits to the communal roost may ensure that members of the same roosting group locate each other and share information on potential other roost sites (Kerth *et al.* 2006). On the other hand, regular visits at a central roost may serve as a mechanism for information exchange on foraging sites (Wilkinson and Boughman 1998). Information about feeding sites may be important for hollow-dependent bats, such as the white-striped freetail bat, where multiple roosts are distributed over a large area. Further work is required to address these questions.

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Chapter 6

Foraging behaviour and use of an urban landscape by
white-striped freetail bats (*Tadarida australis*)



Plate 6.1. The white-striped freetail bat in free-flight.

Photo: N. Speechly

Abstract

The persistence of native wildlife in cities will depend on the extent to which their resource requirements can be met within the urban landscape. Knowledge of these requirements will enable urban designs that support more native fauna. Insectivorous bats require different resources for diurnal roosting and nocturnal feeding. However, feeding ecology and spatial use of habitat are poorly known for most species. The white-striped freetail bat (*Tadarida australis*) is a fast-flying insectivorous bat, which feeds at high altitudes on airborne insects. I assessed the species' use of the urban landscape in the city of Brisbane, Australia. Position fixes from radio-telemetry of 14 non-reproductive individual bats, each tracked across multiple nights, were used to quantify spatial foraging movements and habitat preference during two summers. The bats commuted to feeding areas at a median flight speed of 42.9 km/h, within the first 30 minutes after they left their day-roosts; the flight speed dropped significantly (to a median of 6.7 km/h) once they commenced foraging. The bats foraged over all habitat types, but preferred river flood plains. Day-roosts were widely scattered across the urban landscape, however most night-time foraging activities were concentrated over a localised area, which was closer to a communal roost visited periodically by all bats, than to their day-roosts (median distances from the bats' feeding locations to the communal roost and day-roosts were 2.5 km and 6.2 km respectively). The white-striped freetail bat appears tolerant of deforestation and capable of persisting in an urban landscape, provided that suitable foraging habitat is retained and roost trees are protected.

6.1 Introduction

Insectivorous bats are an important, but frequently overlooked, component of terrestrial biodiversity (Barclay and Harder 2003). In order to persist in human-dominated landscapes, these nocturnal bats require suitable feeding habitat which provides a supply of airborne insects, as well as suitable roost sites to provide day-time shelter (Racey and Entwistle 2003). It is well documented that the loss of roosting habitat has had a negative effect on bat populations world-wide (Hall 1990, Sheffield *et al.* 1992, Kunz and Lumsden 2003, Racey and Entwistle 2003). However, the species-specific responses of bats to anthropogenic changes in foraging habitat appear more varied. For example, logging of native forests can negatively affect some species, while others seem to gain feeding habitat when logging opens up the forest canopy (Barclay and Brigham 1996, Rhodes 1996, Kunz and Lumsden 2003, Racey and Entwistle 2003).

Urbanisation involves a variety of changes to potential foraging habitat. Often these include clearing of native forest, accompanied by the creation of a new land-cover mosaic whose elements include built-up areas, open grassy parkland, suburban gardens and remnant forest patches. Many bat populations have declined in urban areas (Guest *et al.* 2002), although the specific reasons for such declines are poorly understood (Racey and Entwistle 2003). In order to predict future trends in the distribution and abundance of bat species, a better knowledge is needed of their preferences and requirements for particular habitat elements within the urban mosaic.

Bat species which have been advantaged by the opening of foraging habitat that occurs with forest clearing are typically adapted to aerial hawking of insects well above the vegetation (Norberg and Rayner 1987, Schnitzler and Kalko 1998). Bats in the family Molossidae (free-tailed bats) are specialised in such aerial hawking of

high-flying insects (Vaughan 1966). Their long, narrow wings are suited for long-distance, fast flights and high-altitude feeding, and this gives them improved access to scarce but predictable food resources (Norberg and Rayner 1987, Rhodes 1998, Bullen and McKenzie 2001, McKenzie *et al.* 2002). Molossids have been found in all urban habitat types, from forest remnants to build-up areas (Avila-Flores and Fenton 2005, Hourigan *et al.* 2006). However, the presence of such species within urban areas does not indicate that they will inevitably persist in the face of increasing urbanisation. The foraging habitat requirements of molossid bats are poorly known, because their fast flight has made them difficult to study (Marques *et al.* 2004). Hence, it has been difficult to predict their longer-term responses to urbanisation.

The endemic white-striped freetail bat (*Tadarida australis*) is the largest of all Australian molossids (35-40 g). The white-striped freetail bat flies a fast, relatively straight path in search of high-flying insects, and feeds predominantly on moths, beetles and bugs (Vestjens and Hall 1977, Rhodes 1998, Bullen and McKenzie 2001, Rhodes and Richards in press). Studies of their roosting habitat have shown that they depend on large, hollow-bearing trees (Rhodes and Wardell-Johnson 2006; Chapter 3). However, it is unknown whether their distribution in urbanising areas may also be affected by their foraging habitat requirements. Previous work on this species' feeding ecology has been limited to selective visual observations close to the ground (Rhodes 1998, Bullen and McKenzie 2001, McKenzie *et al.* 2002). Here I quantitatively assess the species' foraging patterns within the urban landscape of Brisbane, Australia.

In Australia, the majority of people live along the eastern seaboard, in areas which were forested before European settlement commenced in the late 18th century (Lunney 2004). While urban areas are among the most fragmented landscapes in Australia, research on the impact of urbanisation on wildlife is just emerging (Lunney and Burgin 2004). The present study uses information from radio-telemetry of

foraging individuals to answer the following questions: (i) What is the emergence behaviour of the white-striped freetail bat?; (ii) What are the spatial foraging patterns of this species in Brisbane?; (iii) do the bats show specific preferences for foraging habitat? Finally I consider whether feeding or roosting habitat are more important to the conservation of the white-striped freetail bat in urban areas.

6.2 Methods

Study area

The study was conducted in metropolitan Brisbane, subtropical coastal Australia. Brisbane is the centre of a region undergoing rapid urbanisation. Around the time of writing, Brisbane's human population was 1.6 million, with an average annual population growth of 2.4% (Queensland Government 2004). The region's topography is heterogeneous, and includes coastal plains, sub-coastal ranges, occasional mountain peaks above 1000 m, and drainage systems and valleys. Native vegetation associations include rainforests, eucalypt forests and woodlands, melaleuca forests, heathlands and mangroves (Catterall *et al.* 1997).

Over the past two centuries the region changed from an almost continuous cover of woodlands and forests to a mosaic of agricultural and human settlement. Larger tracts of native forests (> 800 ha) still persist in the greater Brisbane region, although they are less frequent in lowland areas (< 160 m altitude; Catterall *et al.*, 1997). Land cover in the lowlands today comprises a mixture of suburbs, substantial grassy areas with scattered trees in parklands, golf courses and pastures, construction-dominated industrial and commercial precincts, and numerous smaller bushland remnants (Catterall *et al.* 1998, Catterall 2004).

Study species

I studied the foraging patterns of the white-striped freetail bat in Brisbane by radio-tracking individuals belonging to one summer roosting group. Earlier studies of this roosting group had revealed a network of roost trees that were distributed over an area of around 200 km² (Fig. 6.1; Rhodes *et al.* 2006; Chapter 4). This consisted of several day-roosts with average roosting group sizes of around eight bats (hereafter *satellite roosts*), and one central roost (hereafter *communal roost*) which had an average roosting group size of 156 bats over three summer seasons. Although bats spent the majority of their days in the satellite roosts, they returned on average every 11 days to the communal roost (Chapters 4, 5). The communal roost was also used as a maternity roost. All roost trees were eucalypts (which here refers to species of *Eucalyptus* and *Corymbia*). These trees are found throughout Brisbane in parklands, golf courses, paddocks and regrowth forests (Rhodes and Wardell-Johnson 2006, Chapter 3). Females are monoestrous. Copulation, ovulation and fertilisation occur in late winter and females give birth between mid-December and the end of January (Kitchener and Hudson 1982). Juveniles are weaned by mid February (M. Rhodes, unpublished data). *Tadarida australis* is a non-hibernating species, but there is little knowledge about its ecology and whereabouts during winter (Kitchener and Hudson 1982, Rhodes and Richards in press).

Emergence behaviour

I recorded bat emergence behaviour at the communal roost with custom-made infrared cameras (Bionomic Ecological Consulting, Winmalee, NSW) and ultrasonic detectors (Anabat; Titley Electronics, Ballina, NSW). Recording started 30 minutes before the first bats left the roost. Additional visual observations were made from the radio-tracking position at the communal roost.

Captures and radio-tracking

I captured 81 bats from their communal roost tree, which was located in a suburban park (27° 30' S, 153° 31' E). Four mist-nets were positioned in a V-shape (0.1-10 m high and 18 m wide) surrounding the tree roost exit (6 m above the ground). The park contained scattered large remnant eucalypts; otherwise the area was covered by mown grass. Bats were captured at dusk while exiting. Radio-tracking was carried out during two summers in 2002 and 2003. Fourteen bats were radio-tagged; all were non-reproductive females, and transmitters used in both seasons represented $\leq 5.1\%$ of the bat's body mass (Aldridge and Brigham 1988).

In the first radiotelemetry season (March 11 – April 1, 2002) I used collar-transmitters from two different companies to test their effectiveness for this high and fast flying bat species (Fenton and Rautenbach 1986): three bats were outfitted with MD-2C models (Holohil Systems, Carp, ON; 1.6 g weight, 10 weeks battery life) and three bats were fitted with LT2 two stage collar-transmitters (Titley Electronics, Ballina, NSW, Australia; weight 1.6 g, six weeks battery life). The aerials of the collar-transmitters were additionally glued to the back of each individual to avoid friction. Collars were designed to break open as recapture was unlikely. In the second radio-tracking period (February 8 – May 5, 2003) eight slightly heavier collar-transmitters (model MD-2C Holohil Systems, Carp, ON; 1.9 gram, 16 weeks battery life) were used to increase signal range.

Bats were tracked from three fixed telemetry stations on elevated positions (Fig. 6.1). Each station consisted of a three-element, hand-held uni-directional antenna (model AY/C Yagi Antenna, Titley Electronics, Ballina, NSW) and a Regal 2000 telemetry receiver (Titley Electronics, Ballina, NSW). Bearings and signal strength were recorded every 10 to 20 minutes with synchronised watches. Tracking was conducted for three to six hours per night, usually between sunset and midnight.

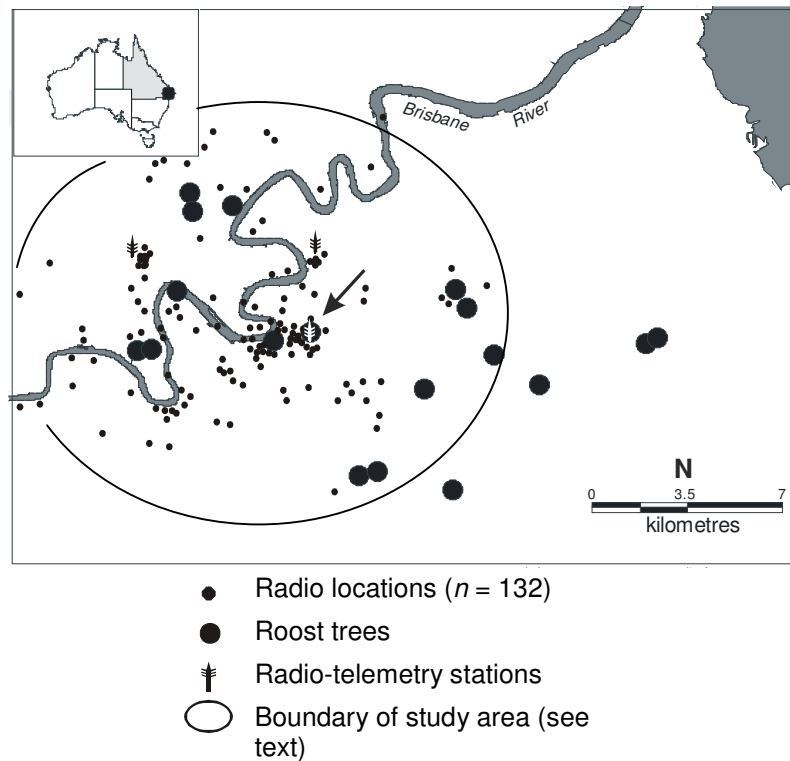


Fig. 6.1. Study area and radio-fixes of bats from the roosting group of the white-striped freetail bat in Brisbane, south-east Queensland, Australia. Map also shows locations of roost trees. The arrow points to the communal roost.

Accuracy of radio-fixes

Before radio-tracking commenced, I placed each of the 14 transmitters in different habitats and altitudes and then detected them from the three fixed telemetry stations (Fig. 6.1). Transmitters located on ground or in lower tree hollows were not always detected in some cases, or the recovered signals had bounced due to the hilly landscape, resulting in unacceptable error polygons of greater than 2 km^2 (Tidemann *et al.* 1985, Harris *et al.* 1990, White and Garrot 1990). However, when radio-transmitters were placed on elevated and exposed positions, readings from the three radio-tracking stations were accurate with errors of generally less than 500 m^2 . In these situations, signals could be detected from up to 12 km away.

The white-striped freetail bat is a high-flying species, so signals were typically transmitted from high above the ground. Therefore, bouncing signals were not a problem. However, due to the bats' fast flight, simultaneous readings from the radiotelemetry stations more than 60 seconds apart were discarded to minimise errors in the analysis. A mobile radio-tracking station (car) was regularly used to confirm the radio-tracking locations of free-flying bats. This showed that the signal range of free-flying bats was more than 12 km. However, to minimise errors, I excluded radiotelemetry fixes (hereafter "*radio-fixes*") outside this range from my analysis. Radio signals received from bats known to be stationary (e.g., within their roost tree-hollows) did not vary in their strength, compared with intermittent signal strengths received from flying bats.

Analysis of flight speeds and distances

I excluded data from the first trapping night to reduce effects of capture and handling on my results. Analyses of exact spatial positions of foraging bats were restricted to those recorded from all three fixed radio-telemetry stations. Only bats with MD-2C models (Holohil Systems, Carp, ON) were analysed because the LT-2 transmitters gave weaker, less reliable signals. For these spatially-explicit data, 110 radio-tracking nights were available, and resulted in a total of 461 bat-nights of radio-tracking for 11 bats. The average number of tracking nights per bat was 41 nights \pm 8.7 SE (range: 11-88 nights).

Commuting and foraging flights

I divided flights into two categories: commuting and foraging flights. Preliminary analyses of radio-tagged bats in 2001 revealed that the bats typically reached foraging sites within 30 minutes. Therefore data recorded within the first 30 minutes of emergence from the day-roosts were considered commuting flights.

The day-roost locations of each bat were known before foraging measurements were taken. Signals were detected from the radio-tracking stations once bats were in free-flight. I measured commuting speed using distances (in metres) between the day-roost and one commuting fix after emergence of the bat, and the time taken to travel between them (in minutes; $n = 50$ bat-nights, $N = 9$ bats). Foraging flight speed (> 30 min after emergence) was calculated based on distances between two foraging fixes and the time taken to travel between them ($n = 18$, $N = 8$). Each measurement consisted of two radio-fixes recorded 10 to 20 min apart. For both, commuting and foraging flight speeds, only one reliable measurement was randomly chosen per bat per night.

Travel distances during foraging

To determine where bats foraged in relation to their day-roosts I measured two distances: the distance between a foraging fix of a bat on a given night and its day-roost ($n = 21$ bat-nights, $N = 8$ bats) and the distance between the same foraging fix and the communal roost ($n = 21$, $N = 8$).

To provide information on the extent to which the bats remained within particular foraging areas within nights versus between nights, I measured the distance between one foraging fix of one night and one foraging fix from another night, for the same bat (distance between nights foraging; $n = 13$ bat-nights, $N = 8$ bats). This was compared with the distances between fixes of bats obtained at different times within particular nights (distance within nights foraging; $n = 18$, $N = 7$).

Flight directions in relation to the communal roost

Data on the directional locations of a much larger number of bat-records than used for flight speeds and distances were collected at the permanent telemetry station located next to the communal roost. Observers at this telemetry station could also

simultaneously record activities at the communal roost. For analyses, I included all directional radio-fixes recorded from each individual ($N = 14$) per night throughout both seasons of study. Up to 25 radio-fixes per bat per night were recorded. The overall tracking period per bat ranged between two and 88 nights. In 2002, a total of 277 radio-fixes were recorded for six bats and in 2003 a total of 1537 radio-fixes for eight bats. The total data set of 1814 radio-fixes for 14 bats consisted of 613 commuting flights and 1201 foraging flights.

Of the 1814 radio-fixes I calculated the percentage of times each bat ($N = 14$) visited the communal roost, during commuting and foraging flights separately. I refer to any visit to the roost tree or roost area as "*visits to the communal roost*". The data set consisted of 108 total visits during commuting (15 visits in 2002 and 93 visits in 2003) and 74 total visits during foraging (23 visits in 2002 and 51 visits in 2003).

A season-long picture of the foraging direction used by each bat was constructed by counting each radio-fix during commuting and foraging flights within 10° intervals from the communal roost (0-10, 11-20, [...], 351-360°). Radio-fixes recorded at the communal roosts (visits) were excluded.

Landscape characteristics of feeding habitat

I analysed environmental attributes of foraging areas to test whether the white-striped freetail bat preferentially foraged over any forms of land cover. There were 132 precise triangulated radio-tracking locations from 11 bats with MD-2C transmitters. Each of these locations was assessed with respect to land cover types (16 variables, see below), its physical context (four variables, see below) and its subcatchments and flood-proneness (14 variables, see below).

Land cover types

I measured the percentage of different land cover types in circles of radius 500 m or 1000 m, centred around each bat radio-fix. Measurements were made using a grid of 100 evenly-spaced points within each circle, which was overlaid on an aerial photograph which also showed topographic contours (1: 25,000 topographic image map; Department of Lands, Queensland Government 1995). This map provided information on elevation, waterways, vegetation, roads, train lines, and residential as well as industrial areas. The map resolution enabled identification of single objects, such as trees and houses. Each buffer (500 and 1000 m radius) was counted twice for every location to minimise counting errors.

The 16 land cover types were: grass; scattered trees (single standing tree surrounded by grass); riparian vegetation (any type of vegetation growing along drainage lines; such as mangroves, trees or grass); open water (river, creek, lake, dam); total native forest cover; native forest cover within different sized remnant patches (< 5 ha, 5-20 ha, 20-100 ha, > 100 ha); and open woodland (areas of trees with no understorey, due to thinning or grazing); residential developments (low to high density housing); new urban developments (areas which were developed during or after radio-tracking); industrial areas; roads; train lines; and bare ground (ground not covered by vegetation, such as in quarries).

Physical landscape variables

I measured four physical landscape variables for each bat radio-fix on the same topographic image map: altitude (to the nearest 5 m), distance to nearest drainage line (river or creek), distance to major drainage line (Brisbane River), and distance to the communal roost.

Flood and catchment areas

The location of flood plains was assessed using the "Flood Map of Brisbane and Suburbs" (Cityplan 2000, Brisbane City Council). This map delineated the extent of major floods since 1841 and showed areas subject to inundation for flood heights up to 10 m. A radio-fix anywhere within this zone was recorded as over a "*flood-inundated area*". Each bat radio-fix was also assigned to one of 13 water catchment area, using catchment maps (Strategy Plan for the Management of Brisbane Waterways, Volume 2 – Drawings: Catchment and Planning Units; Brisbane City Council, April 1990).

Random locations

To determine if the bats' foraging areas were randomly associated with land cover types and landscape characteristics the habitat attribute values of radio-fixes were compared with those of a set of random spatial locations. Random spatial locations ($n = 132$ points) were obtained using a random number generator (Microsoft Excel 97-SR1, Microsoft Corporation, Santa Rosa, CA) to produce easting and northing coordinates, which were constrained to lie within the same geographical study area as the radio-fixes (Fig. 6.1).

Statistical analysis

Because many data sets were not normally distributed (Wilk-Shapiro statistics, W), I used Mann-Whitney U -tests (Zar 1999) to compare flight speed and distances, and to determine whether bat radio-fixes and random locations differed with respect to particular landscape variables. Results are presented as mean and/or median \pm standard error (SE) and range. Significance was assessed at an alpha of 0.05.

Analyses were performed using STATISTICA 4.5 for Windows 97 (StatSoft, Tulsa, Oklahoma). The multivariate difference in habitat characteristics between the two a

priori groups, bat radio-fixes and random locations, was also compared with analysis of similarity (ANOSIM and SIMPER in PRIMER software; Clarke and Warwick 2001).

6.3 Results

Emergence behaviour at the communal roost

Bats emerged on average 29.9 ± 1.54 minutes after sunset ($n = 60$). Bats inside the roost vocalised loudly and audibly in the late afternoon during summer; this chatter of more than 50 bats could be heard up to 100 m away. Before leaving the roost, bats protruded their heads outside the hollow, moving them to the left and right while producing inaudible echolocation calls. Around civil twilight, when the sky was still partially illuminated, the bats started to emerge. They launched themselves, giving a series of inaudible calls, and dived rapidly downwards for 3-5 m. The bats then flew in a straight line, often only one meter above ground, towards the open section of the park, while producing their characteristic echolocation search calls (Herr and Klomp 1997). Floodlights from a nearby sports ground made visual observations possible. Bats then increased in height by spiralling upwards high above the roost tree for up to two minutes before they left the roost area. The flight path could be clearly followed by listening to the loud audible echolocation calls.

Flight speeds and distances

During commuting the bats flew very fast in a relatively straight line. They commuted at a median speed of 42.9 ± 2.5 km/h and covered a median distance of 5.6 ± 0.4 km in 10-20 min (Table 6.1). Flight speeds of over 60 km/h were confirmed by following tagged bats with a car, a hand-held uni-directional antenna and a telemetry receiver. Once the bats reached their feeding sites, they flew in large zigzags and speed measured during 10-20 min observation periods decreased significantly to a median

foraging speed of 6.7 ± 1.1 km/h (Fig. 6.2, Table 6.1). The median distance travelled during this time was significantly smaller during foraging (1.6 ± 0.3 km; Table 6.1) than during commuting (5.6 ± 0.4 km).

Although bats roosted in day-roosts away from the communal roost, foraging sites were located significantly closer to the communal roost (2.5 ± 0.4 km; Table 6.1) than to their day-roosts (6.2 ± 0.6 km). Compared with the large distances travelled during commuting, the bats tended to concentrate their foraging in comparatively small areas. The median distances travelled by foraging bats between different radio-fixes did not differ significantly whether these fixes were made within a single night or between different nights. The median distance also remained relatively constant regardless of how many nights had elapsed between radio-fixes (Fig. 6.3; Table 6.1). However, bats occasionally travelled considerable distances between different foraging areas (up to 11 km; Fig. 6.3).

Table 6.1. Comparison of flight characteristics of the white-striped freetail bat during commuting and foraging. *U*, *P* show results of Mann-Whitney *U*-tests.

Variable 1 Name; n ^a	Variable 2 Name; n ^a	Unit	Variable 1 values				Variable 2 values				U	P
			Mean	Median	SE	Range	Mean	Median	SE	Range		
Commuting speed ^b ; 50	Foraging speed ^c ; 18	km/h	43.6	42.9	2.5	13-81	7.4	6.7	1.1	1-19	9	<0.001
Commuting distance; 50	Foraging distance; 18	km	6.6	5.6	0.4	1.7-16	1.9	1.6	0.3	0.4-4.7	28	<0.001
Distance DR ^d to feeding; 21	Distance CR ^e to feeding; 21	km	5.6	6.2	0.6	0.9-11	2.9	2.5	0.4	0.4-6.8	87.5	<0.001
Distance between nights foraging; 13	Distance within night foraging; 18	km	3.4	2.1	0.8	0.7-11.4	1.9	1.6	0.3	0.4-4.7	80.5	0.14
Commuting fixes at CR ^f ; 14	Foraging fixes at CR ^g ; 14	%	18.1	15.9	3.0	0-40	6.0	2.6	2.4	0-31	32.5	<0.01

^a*n* - The number of bat-measurements, except for the last row (fixes at CR), where *n* is the number of individual bats.

^bCommuting speed – Based on distance travelled during 10-20 min within the first 0-30 min after leaving the roost.

^cForaging speed – Based on distance travelled during 10-20 min, at various times (30-266 min) after leaving the roost (Fig. 6.3).

^dDistance day-roosts (DR) - Distance travelled by a bat from the day-roost to the feeding area (km).

^eDistance communal roost (CR) - Distance travelled by a bat from the communal roost to the feeding area (km).

^fCommuting fixes at CR – Percentage of commuting fixes recorded at the CR.

^gForaging fixes at CR - Percentage of foraging fixes recorded at the CR.

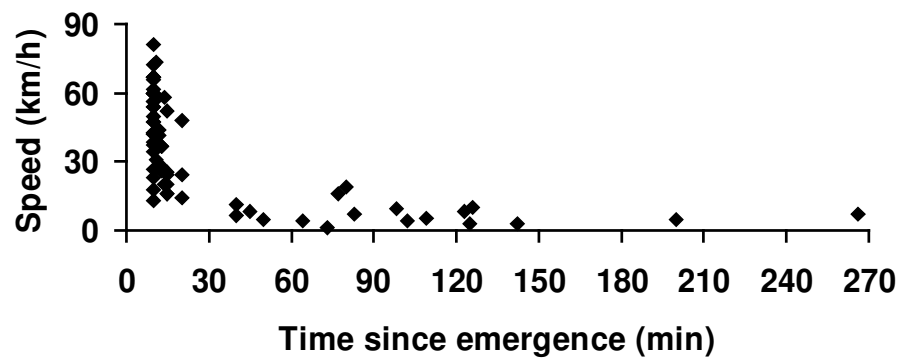


Fig. 6.2. Speed of white-striped freetail bats measured during commuting (0-30 min since emergence; $n = 50$) and foraging flights (30-266 min since emergence; $n = 18$).

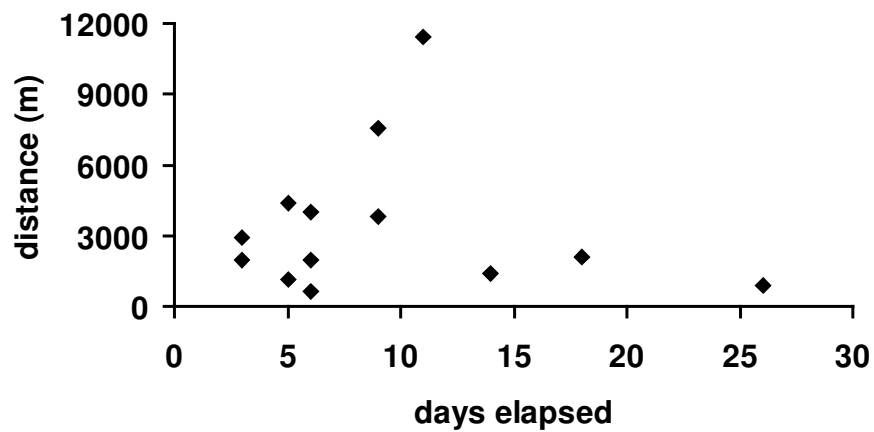


Fig. 6.3. Distances travelled by white-striped freetail bats between foraging locations on different nights ($n = 13$).

Direction of flights

Flight directions in relation to the communal roost

Overall, bats visited the communal roost significantly more often during commuting than during foraging (18% of bats were recorded over the roost while commuting, compared with 6% while foraging; Table 6.1). Of the 14 bats, seven were recorded more during commuting than during foraging, five visited the communal roost only during commuting, one was recorded there more times during foraging than during commuting, and one bat never visited the communal roost at night, although it was recorded there during the day.

I recorded radio-fixes of commuting bats at similar frequencies from all directions relative to the communal roost (Fig. 6.4). In contrast, during foraging flights more than 95% of radio-fixes were located at 220° to 300° (Fig. 6.4). This pattern was the same for both radio-tracking seasons (Fig. 6.4).

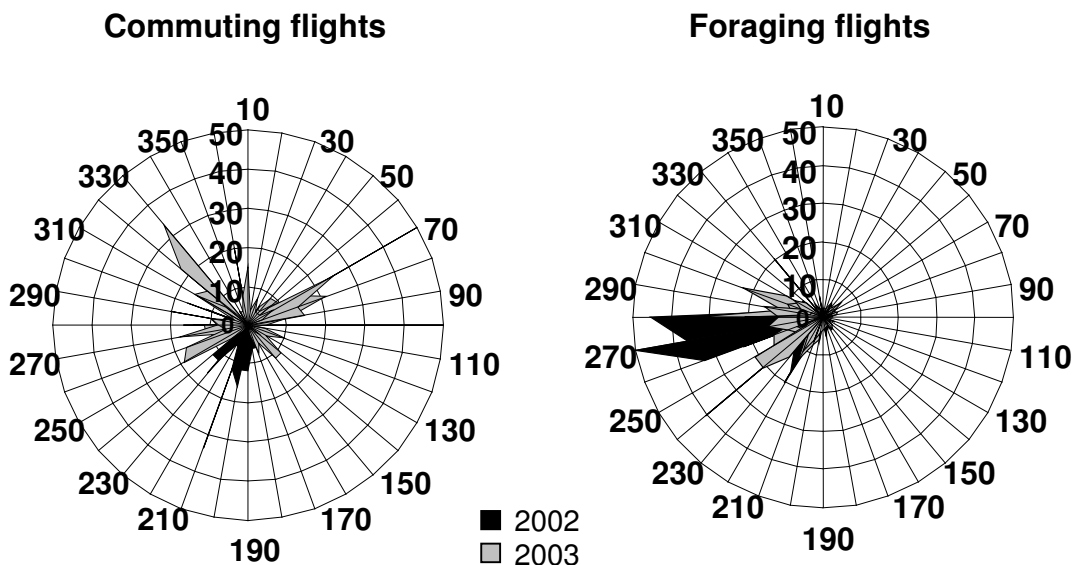


Fig. 6.4. Radar graphs showing direction (in 10° intervals) and proportion (%) of radio-fixes during commuting flights and foraging flights, relative to the location of the communal roost, for 239 recorded radio-fixes in 2002 and 1395 recorded radio-fixes in 2003.

Commuting and foraging flight directions, and flight paths based on precise radio-fixes within one selected night, are shown in Figs. 6.5 and 6.6 respectively, for the same four individual bats. During commuting the majority of recordings peaked towards the direction of the day-roosts. In comparison, most foraging radio-fixes were located in areas east to south-east of the communal roost (at directions of 200-300°; Fig. 6.5).

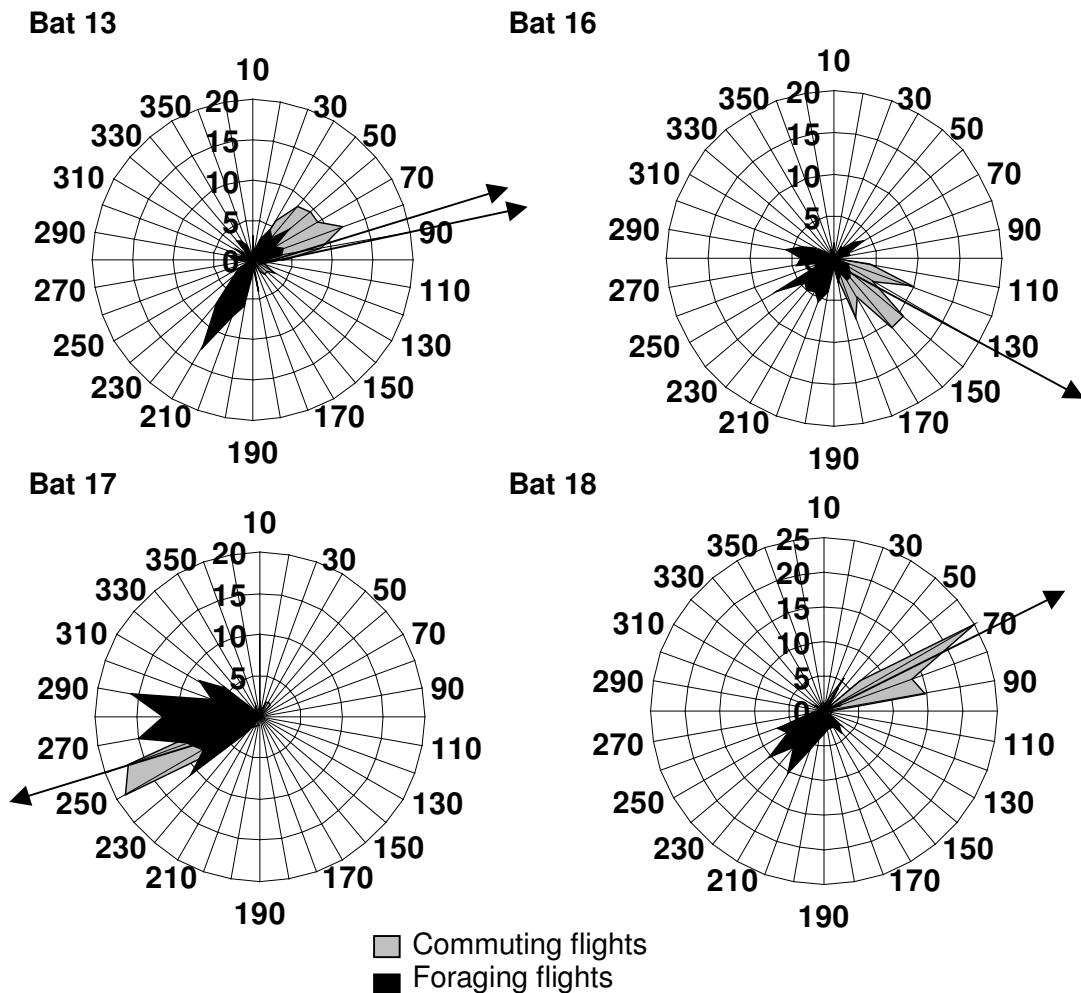


Fig. 6.5. Radar graphs showing direction (in 10° intervals) and proportion (%) of radio-fixes during commuting flights (grey) and foraging flights (black) for four white-striped freetail bats tracked in 2003. Arrows indicate directions of day-roosts.

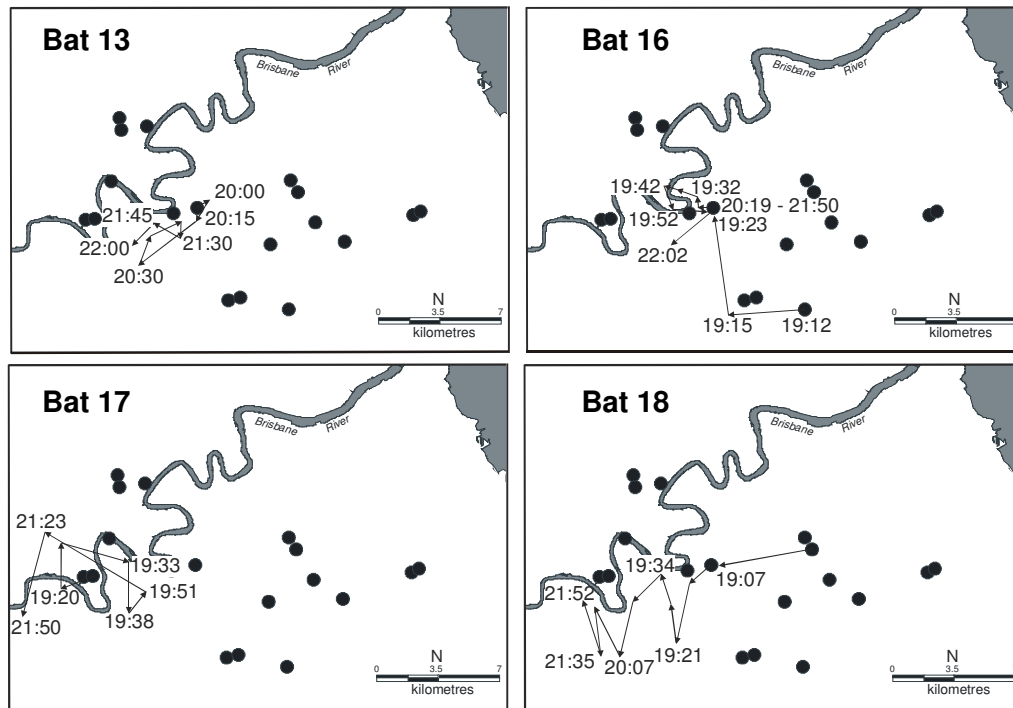


Fig. 6.6. Typical commuting and foraging radio-fixes observed for four white-striped freetail bats on February 12, 2003 between sunset and 22:00 h. Closed circles show the locations of all roost trees. Arrows indicate movements and directions between radio-fixes of each bat.

Bat 13 roosted in the communal roost during this day, while bats 16, 17 and 18 roosted in separate day-roosts. Bats emerged within an hour of each other. Bats 16 and 18 flew past the communal roost on their way to the foraging areas. Bat 16 returned to the communal roost area for a 91 min stay inside the roost (20:19–21:50 h). The locations of fixed tracking stations are as shown in Fig. 6.1.

Landscape characteristics of feeding habitat

The characteristics of the ground-level habitat beneath the radio-fixes of foraging bats differed significantly from the habitat characteristics at randomly generated locations ($n = 132, 132$; $R = 0.05$, $P = 0.001$). Results from SIMPER indicated that distance to the communal roost (42%), distance to the Brisbane River (36%) and distance to the nearest drainage line (12%) were the factors most strongly associated with the multivariate pattern of difference between bat fixes and random locations.

Overall, bats foraged over all land cover types in the study area. Most radio-fixes were, however, located in the grass-dominated flood plain of the Brisbane River, close to the communal roost (Table 6.2). These sites are seasonally-inundated wetlands, consisting mainly of open grassy areas with interspersed large eucalypts, and also having a relatively high cover of open water and riparian vegetation. These areas had remained largely undeveloped by urban housing due to the high flood risk. The predominance of grassland was maintained by human management (clearing, grazing and mowing). The riparian vegetation, especially along the Brisbane River, consisted of mangroves, single standing old eucalypts and undergrowth (shrubs, herbs and grasses). The flood-inundated wetlands of the creek catchment areas (which were all small tributaries of the Brisbane River) in the study area were less frequently visited (Table 6.2). Bat radio-fixes were occasionally located above areas with a high percentage of forest cover. However, only for very small forested patches (< 5 ha) were they found more frequently above forest compared with random locations (Table 6.2). While there were no significant differences between bat radio-fixes and random locations in the percent of land occupied by residential development, the bats seemed to avoid areas with a high percentage of roads (Table 6.2).

Table 6.2. Values of land cover attributes (measured in 500 m and 1000 m radii) and physical landscape variables, compared between radio-fixes ($n = 132$) of the white-striped freetail bat and random locations ($n = 132$). U , P show results of Mann-Whitney U -tests; values where $P > 0.05$ are listed in the footnote.

Variables n = 132, 132	Unit	Bat random locations				Random locations				U	P
		Mean	Median	SE	Range	Mean	Median	SE	Range		
Land cover (500 m buffer)											
Grass ^a	%	11.9	7.0	1.3	0-81	7.4	4.0	0.8	0-41	7118.5	0.01
Riparian vegetation	%	6.8	4.0	0.7	0-39	4.7	3.0	0.5	0-19	7637	0.07
Forest patch < 5 ha	%	2.1	0	0.5;	0-22	0.1	0	0.1	0-5	7233	< 0.001
Forest 5-20 ha	%	0.2	0	0.2	0-20	0.6	0	0.3	0-24	8186.5	0.01
Water	%	3.7	0	0.7	0-40	3.1	0	0.7	0-46	7838.5	0.05
Roads	%	5.7	5.5	0.4	0-21	8.3	8.0	0.6	0-31	6892	0.003
Land cover (1000 m buffer)											
Grass	%	10.9	8	0.9	0-55	7.7	6	0.6	0-30	7067.5	0.08
Riparian vegetation	%	8.1	8	0.6	0-29	5.6	5	0.4	0-19	6847.5	0.02
Roads	%	4.8	4	0.3	0-18	9.1	8.3	0.4	0-26	4018	< 0.001
Train lines	%	2.0	0	0.3	0-14	1.1	01	0.2	0-9	7196	0.005
Forest < 5 ha	%	2.0	0	0.5	0-21	0.4	0	0.1	0-10	7440	0.003
Physical											
Distance to river	km	1.3	0.9	0.1	0-5.4	2.6	1.9	0.2	0-9.8	5733	< 0.001
Distance to CR ^b	km	4.5	3.9	0.3	0.3-11.7	6.5	6.5	0.2	0.8-12.3	5392	< 0.001
Presence/absence flood area	1/0	0.5	0	0.04	0-1	0.2	0	0.04	0-1	6732	< 0.001
Presence/absence river ^c	1/0	0.4	0	0.04	0-1	0.3	0	0.3	0-1	7524	0.02
Presence/absence creek ^d	1/0	0.6	1	0.04	0-1	0.7	1	0.04	0-1	7524	0.02

^aGrass - Total grass cover.

^bDistance to communal roost (CR) in km.

^cPresence/absence river - Presence or absence in the Brisbane River catchment area.

^dPresence/absence creek: Presence or absence in any of the creek catchment areas.

Non-significant variables: Scattered trees (500/1000 m), total forest cover (500/1000 m), forest patch 5-20 ha (1000 m), forest patch 20-100 ha (500/1000 m), forest patch > 100 ha (500/1000 m), woodland (500/1000 m), residential developments (500/1000 m), new developments (500/1000 m), industrial areas (500/1000 m), bare ground (500/1000 m), altitude, distance to nearest drainage line (see text for more details).

6.4 Discussion

Spatial foraging behaviour and use of the urban landscape

The present study is the first to investigate the spatial foraging behaviour and habitat use at a landscape scale by radio-tagged molossids within an urban environment.

Previous studies of molossids' spatial foraging patterns in areas of human settlement have measured bat activity with sound recordings (Carmel and Safriel 1998, Lee and McCracken 2002, Avila-Flores and Fenton 2005, Hourigan *et al.* 2006); a method which does not enable the assessment of individual movements.

High flight speeds are common in molossids, and this enables them to regularly traverse long-distances (Norberg and Rayner 1987). In the present study the white-striped freetail bats travelled large distances (up to 20 km) to reach the feeding areas at median speeds of 43 km/h. Median speeds of 30 km/h have been reported from hand-released white-striped freetail bats in Western Australia (Bullen and McKenzie 2005). Based on its wing morphology, the predicted maximum flight speed for white-striped freetail bats (V_{mr} , where the cost of transport is least and the bat is able to cover the biggest air distance for available energy; Bullen and McKenzie 2001; Norberg and Rayner 1987; Rhodes 1998) would be 20.4 km/h, which is considerably smaller than the observed commuting speeds in the present study. Similarly, Marques *et al.* (2004) found that the observed median speed of flight to foraging areas of a European molossid bat (50 km/h) was 2.5 times its predicted maximum speed based on morphology. This suggests that flight speed predictions based on morphology underestimates speed capabilities of fast-flying species, especially during commuting.

Even when foraging, molossids are fast fliers. The white-striped freetail bat is notable for its fast, straight-line interception of prey (McKenzie *et al.* 2002, Bullen and McKenzie 2004). Such fast-flying foragers must use unobstructed air spaces well

above the tallest trees or other structures (Churchill 1998). Therefore, I could expect molossids not to show preferences for specific habitat features. However, the observed foraging behaviour of the white-striped freetail bat in urban Brisbane was non-random with respect to both spatial location and the nature of the ground-level habitat. The bats showed a significant preference for foraging over flood plain areas, within three kilometres of the communal roost. The bats also showed an apparent preference for foraging over very small forest patches, although this may simply reflect a greater probability that forested areas on flood plains occurred mainly as small (< 5 ha) patches, whereas more extensive forest patches were restricted to higher elevations (Catterall *et al.* 1997). Likewise, the bats' apparent preference for foraging over railway lines may have been due to a concentration of the rail transport network in the flood plain areas.

During commuting, the bats flew across several creek flood plain areas, but moved on and foraged mainly over the seasonally-inundated wetlands of the Brisbane River. In Townsville (northern tropical Australia), foraging white-striped freetail bats concentrated over grassland (areas with sparse trees, such as golf courses), and suburbs established 20-50 years ago (Hourigan *et al.* 2006). Similar habitats were used by foraging white-striped freetail bats in this study. The flood plains of the Brisbane River are surrounded by medium to high density housing developments interspersed with small forest remnants and golf courses, and the bats in the present study frequently foraged over these areas even though they showed a clear preference for the flood plains.

Other free-tailed bats with similar ecology to the white-striped freetail bat also over forage a range of habitats including modified human landscapes and rural environments. For example, the Brazilian free-tailed bat (*Tadarida brasiliensis*) forages over large parks and illuminated areas in metropolitan cities and rural towns (Lee and McCracken 2002, Avila-Flores and Fenton 2005) and the European free-

tailed bat (*Tadarida teniotis*) in rural Israel forages high above scrub vegetation, open water and rural settlements (Carmel and Safriel 1998). In rural Portugal the European free-tailed forages predominately over stone pine and cork oak woodlands, but also over alluvial plains and mountainous areas (Carmel and Safriel 1998, Marques *et al.* 2004).

The quality of the local habitat with respect to the supply of airborne insects may be a driving force behind the white-striped freetail bats' foraging habitat preference. The links between flood plain habitat, aerial insect availability, and foraging behaviour in the study region merit further investigation. Lee and McCracken (2002) found that the Brazilian free-tailed bat, which feeds on insects at heights of up to 1200 m (McCracken *et al.* 1997), has the same spectrum of insect families in its faecal pellets as found in insect traps on-ground, indicating that insect abundance on-ground could indicate prey availability in higher altitudes.

Minimising the flight distance between the foraging area and the communal roost also seems to have been important to the bats in the present study. This could have involved either the choice of a communal roost close to the foraging area, or choice of a foraging area as close as possible to the roost. The communal roost appears to have an important role in these bats' social organisation (Rhodes *et al.* 2006, Chapters 4 and 5). Other bat species, such as the northern bat (*Eptesicus nilsoni*), forage close to their central day-roost site when insect abundance is high (de Jong 1984). However proximity to day-roosts and energy savings can not explain why white-striped freetail bats commuted large distances to reach their feeding sites if they could have roosted in the communal roost in the first place. At this stage, the benefits of roosting apart (Chapter 5) but foraging in similar areas are unknown and no comparable literature on similar roosting and foraging behaviour of bats is available. I hypothesise that regular nocturnal visits to this roost may be used to share information on potential other roost sites as found in other fission-fusion bat

societies (Kerth *et al.* 2006). Bats may have also avoided roosting in a large communal group because of a high predation risk (Fenton *et al.* 1994). On the other hand, regular nocturnal meetings may indicate that information on feeding sites was exchanged (Wilkinson 1992, 1995, Wilkinson and Boughman 1998). Although white-striped freetail bats foraged mainly over the same area, my data showed that bats foraged over all other urban habitats, often in pairs despite roosting apart. Dyads may have followed each other to localised and highly variable food resources. More studies are needed to link the species' nocturnal fusion dynamics with information exchange on roosting or feeding sites.

Impact of urbanisation on the white-striped freetail bat

Insectivorous bats may be better equipped than other forest-dependent fauna to persist in fragmented habitats, due to their ability to cross open spaces. This is especially true for the open-space specialists, the molossids, which are able to exploit many different habitat types, including urban environments, in the pursuit of high-flying insects (Fenton and Rautenbach 1986, Arlettaz 1990, Carmel and Safriel 1998, Lee and McCracken 2002, Marques *et al.* 2004, Avila-Flores and Fenton 2005, Hourigan *et al.* 2006). This suggests that molossids may be resilient to effects of deforestation, especially since white-striped freetail bats foraged extensively over unforested areas in Brisbane. The white-striped freetail bat may have always been an open-space specialist, but no information is available on its foraging preferences before European settlement commenced.

However, the survival of a bat species depends also on availability of roosts (Kunz and Lumsden 2003, Racey and Entwistle 2003). The white-striped freetail bat in Brisbane roosts mainly in hollows of large old or dead eucalypt trees (Rhodes and Wardell-Johnson 2006). These roost sites are progressively being removed by ongoing clearing for new urban developments, and through tree-lopping in existing

urban areas due to concerns for public safety. Furthermore, despite its flexible foraging behaviour, the white-striped freetail bat concentrated its foraging in a relatively small area, which are currently being increasingly developed. An estimated quarter of the bats' foraging area during the present study comprised new clearing or construction for urban development, and many of these areas were located near the Brisbane River ($> 4 \text{ km}^2$; see Methods for measurement information based on aerial photography). The insect supply provided in these new urban developments (in which a large part of the ground is covered by impervious surfaces) is likely to differ greatly from that provided by flood-prone grasslands. Both the security of feeding habitat and the protection of roost sites need attention in order to conserve the white-striped freetail bat in urban environments.

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Chapter 7

Acceptance of artificial roost habitat by insectivorous bats in the greater Brisbane region



Plate 7.1. Bat box check in Toowong Cemetery, Brisbane.

Photo: B. Thomson

7.1 Introduction

Logging, farming and urbanisation are recognised world-wide as a threat to habitat, including hollow-bearing trees (Barclay and Bringham 1996, Gibbons and Lindenmayer 2002, Lindenmayer and Franklin 2002, Smith and Agnew 2002, Lunney 2004, Lunney and Burgin 2004). In south-east Queensland, Australia, the number of hollow-bearing trees are below targets set by Queensland's Code of Practice for Native Forest Timber Production (Queensland Department of Natural Resources 1998). Furthermore, hollow-bearing trees in the greater Brisbane region, the largest urban area within south-east Queensland, are under-represented in parklands, forest reserves and on private property alike (Rhodes and Wardell-Johnson 2006). Ongoing loss of natural hollows is likely to have significant and long-term impacts on Australian fauna. Over 300 native Australian vertebrate species use tree hollows for shelter (Gibbons and Lindenmayer 2002) and 127 of these occur in south-east Queensland (Smith and Lees 1998). Of the 26 insectivorous bat species found in this region 22 are hollow-dependent (Churchill 1998, Strahan 1998).

Nest boxes have been used world-wide as wildlife management tools and have been shown to maintain or increase populations of birds and mammals (Thomas *et al.* 1979, Schemnitz 1980, Menkhorst 1984, Stebbings and Walsh 1985, Wardell-Johnson 1986, Tidemann and Flavel 1987, Tuttle and Hensley 2000, Smith and Agnew 2002, Harper *et al.* 2005b, Long *et al.* 2006). Nest boxes can also be used as a tool for studying the biology of hollow-using species, because they allow researchers access to nests otherwise difficult to reach (Menkhorst 1984, Gerell and Lundberg 1985, Nagel and Nagel 1988, Boyd and Stebbings 1989, Lundberg and Gerell 1996, O'Shea 1998, Park *et al.* 1998, Kerth *et al.* 2001).

In metropolitan areas where hollow-bearing trees are limited (Holmes 1996, Harper *et al.* 2005a, Rhodes and Wardell-Johnson 2006), nest boxes may be the

only source of hollows for wildlife populations and may, therefore, provide essential roosting habitat for insectivorous bats, enabling these species to persist in urban environments. In Europe and the U.S., bat boxes have been shown to provide suitable roosts for many bat species, especially where roost sites have become scarce (Stebbins and Walsh 1985, Schwarting 1994a,b, Dietrich 1998, Tuttle and Hensley 2000, Flaquer *et al.* 2006). Bats use nest boxes as solitary, dispersal, migration, mating, or maternity roosts (König and König 1995, Dietrich 1998) with the time each bat spends in boxes depending on its status as a transient, immigrant or resident bat (Boyd and Stebbings 1989). However, in many situations immigration into boxes by adults appears to be a minor source of recruitment; the majority of bats using boxes tend to be females born in the boxes and returning to reuse the boxes as maternity roosts (Boyd and Stebbings 1989, Brittingham and Williams 2000, Bender and Irvine 2001, Flaquer *et al.* 2006).

In Australia, there have been few systematic studies of the use of bat boxes (Golding 1979b, Bender and Irvine 1995, O'Shea 1998, Bender and Irvine 2001, Smith and Agnew 2002, Bender 2005). While some useful information is available on design, construction and placement of nest boxes in Australia, little attention has been paid to outcomes (Gibbons and Lindenmayer 2002); most studies are descriptive and there has been little discussion of landscape factors which might contribute to occupancy rates (Smith and Agnew 2002). Also lacking in Australia are comparisons of different bat box designs and species usage. In general, most Australian bat box designs have been adapted from those used in the northern hemisphere (Stebbins and Walsh 1985, Tuttle and Hensley 2000). However, roosting requirements of northern hemisphere bats may differ to that of Australian species due to their long evolutionary history of roosting in trees with different cavity characteristics. For example in the northern hemisphere, cavities are found in conifer and deciduous trees and snags compared to cavities in large eucalypts in Australia

(Kunz and Lumsden 2003; Chapters 1 and 3). In nature, competition for available roost space has resulted in species exhibiting preferences for roost sites with markedly different physical dimensions and other parameters (Menkhorst 1984) yet these issues have not been considered when comparing the suitability of boxes to different species.

Bats belong to the Order Chiroptera, the second largest order of mammals, with approximately one thousand species world-wide (Kunz and Fenton 2003). Despite this, remarkably little is known of the life history and conservation status of the majority of species (Barclay and Harder 2003). This lack of information is seriously constraining attempts to understand how bats are being impacted by global threats such as habitat loss and urbanisation. Food and roosting habitat are essential for the survival of hollow-dwelling bats (Schwartz 1994b, Barclay and Brigham 1996, Racey and Entwistle 2003). As the only mammals capable of flight, bats have been falsely portrayed as able to compensate for changes in availability of habitat and food sources by moving to new areas in search of these resources (Parnaby and Hamilton-Smith 2004). However, the loss of old-growth forests and mature trees due to logging and urbanisation has progressively reduced the availability of roosting habitat, forcing bats to move even when food resources are plentiful (Boyd and Stebbings 1989, Sheffield *et al.* 1992, Parnaby and Hamilton-Smith 2004).

The white-striped freetail bat (*Tadarida australis* (Gray, 1838)) is a large molossid endemic to mainland Australia. In metropolitan Brisbane, subtropical coastal Australia, it prefers to roost in cavities of old and dead eucalypts. However, hollow availability for this species is limited in metropolitan Brisbane (Rhodes and Wardell-Johnson 2006; Chapter 3). This chapter presents the results of a study of 70 bat boxes monitored over a three-year period in the greater Brisbane region, south-east Queensland, Australia. Specifically, I aimed to investigate (i) Whether bat boxes are accepted by white-striped freetail bats or other insectivorous bats in a subtropical

metropolitan city; (ii) Which species adapt to artificial roosts most readily; and (iii) If the use of bat boxes depend on microclimate, landscape characteristics, or number of boxes in an area. I also discuss whether bat boxes can be used as a potential tool for the conservation of insectivorous bats in metropolitan Brisbane.

7.2 Methods

Study area and bat species

Field sites were located in the coastal lowlands of the greater Brisbane region (< 120 m altitude), south-east Queensland, Australia (27° 30' S, 153° 0' E; Fig. 7.1). The greater Brisbane region comprises some 3000 km² (Poole 1995), and it is estimated that the population in this region will increase from 1.6 million in 2004 to 2.3 million by 2026 (Queensland Government 2004). The climate is subtropical with annual summer rainfall of 1146 mm per year, predominantly dry winters, and an average maximum temperature of 25.5° C (Australian Government, Bureau of Meteorology).

The topography of the greater Brisbane region is characterised by coastal plains, sub-coastal ranges, occasional mountain peaks above 1000 m with drainage systems and valleys. Vegetation types vary from rainforest, to open eucalypt forests and woodlands, melaleuca forests and woodlands as well as heathlands and mangroves (Catterall and Kingston 1993).

Metropolitan Brisbane is dominated by a mosaic of mostly cleared urban settings with grassed lawns, low-growing ornamental plants, leafy cover of low native and introduced subtropical or tropical trees and sparse tall eucalypts, parklands with scattered mature eucalypts, and predominantly small bushland remnants (Catterall and Kingston 1993, Catterall *et al.* 1998). These small reserves consist of young regrowth, with few trees larger than 40 cm diameter (Catterall *et al.* 1998).

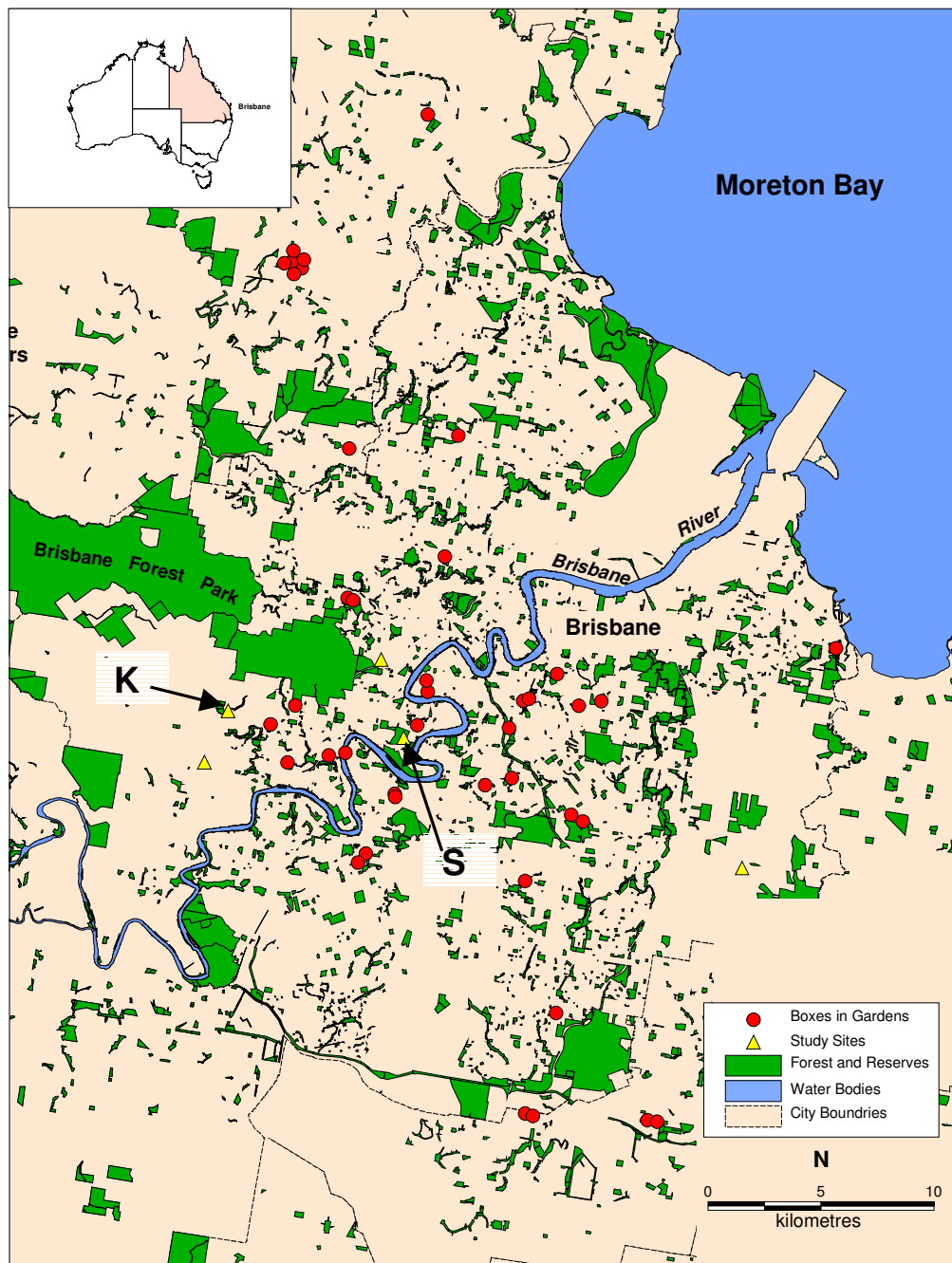


Fig. 7.1. Location of bat boxes in backyards ($n = 40$; red circles) and on experimental sites ($n = 5$; yellow triangles) in relation to land cover types in the greater Brisbane region, south-east Queensland, Australia. Forests and reserves include Commonwealth, State, and Brisbane City Council forests, but not private tenures.

K – Kenmore Hill Experimental Site; S – St. Lucia Experimental Site.

Despite dense urbanisation there are several large bushland remnants in the greater Brisbane region, especially the Brisbane Forest Park which covers 28,000 ha, with its western boundary only 4 km from Brisbane's central business district (Fig. 7.1). The fringes of the metropolitan area is primarily composed of cleared pastures with scattered mature trees and larger bushland remnants (Catterall and Kingston 1993).

Construction and design of boxes

Bat boxes were built from 15 mm laminated plywood (Australian Nestbox Company, Gordon Park, Queensland, Australia). Privately owned boxes were coated with a dark green, non-toxic exterior paint to increase longevity under subtropical weather conditions (Tuttle and Hensley 2000). Bat boxes on experimental sites remained unstained. Aluminium plates covered removeable lids of each box to minimise moisture entry and to reduce bird damage (Fig. 7.2). Lids were secured with two screws onto the box as cockatoos are known to gain entry by chewing on the lids and forcing the lids open (F. Box, pers. comm. 2000). Grooves were inserted onto all inner walls (including landing pad and inner lid) to allow better hanging conditions for the bats (Tuttle and Hensley 2000, Wendorf 2004). The boxes were mounted directly onto the trees with two long screws. A metal spacer was placed on each screw between box and tree to allow tree-growth (Fig. 7.2).

I tested three basic box types (Fig. 7.2, Table 7.1) which varied in dimensions, internal volumes and size of entrance slits. Box types 1a,b were adapted from the Stebbings and Walsh design (1985), which was found to successfully attract bats in the U.K. (Boyd and Stebbings 1989) and in Victoria, temperate southern Australia (Bender and Irvine 1995, 2000). The back wall extended below the box to allow the bats to land and climb up into the box through the slit on the underside (Fig. 7.2). Box type 1a had an entrance slit of 15 x 117 mm to allow most bat species to enter while it excluded larger hollow-using vertebrates, such as the common

brushtail possum (*Trichosurus vulpecula*) or sugar gliders (*Petaurus breviceps*; Bender and Irvine 2000). Box type 1b had a smaller entrance slit (12 x 117 mm) to exclude larger bat species.

Box types 2 and 3 had larger internal volumes. Type 2a had a 18 x 202 mm front entrance slit, while box type 2b had a bottom entrance slit of 18 x 202 mm entrance slits with the back wall extended below (Fig. 7.2, Table 7.1). The slightly larger entrances of 18 mm were chosen to test whether these might attract larger bat species.

Types 3a,b were adapted from Richards and Tidemann (1988) and had front facing entrance slits, located at the lower end of the front boards. They also consisted of two internal chambers, separated by a wooden board with a round access hole (3 cm diameter) placed in the middle. The entrance slit of type 3a measured 15 x 202mm and type 3b measured 12 x 202 mm (Fig. 7.2, Table 7.1).

Experimental Procedure

I sought people interested in being involved in a long-term bat conservation study through a broad media appeal (radio stations, State and local newspapers; newspapers of Griffith University and The University of Queensland; and newsletters of naturalist organisations). As a result 34 participants purchased 52 bat boxes, supplemented with 18 boxes that I added subsequently.

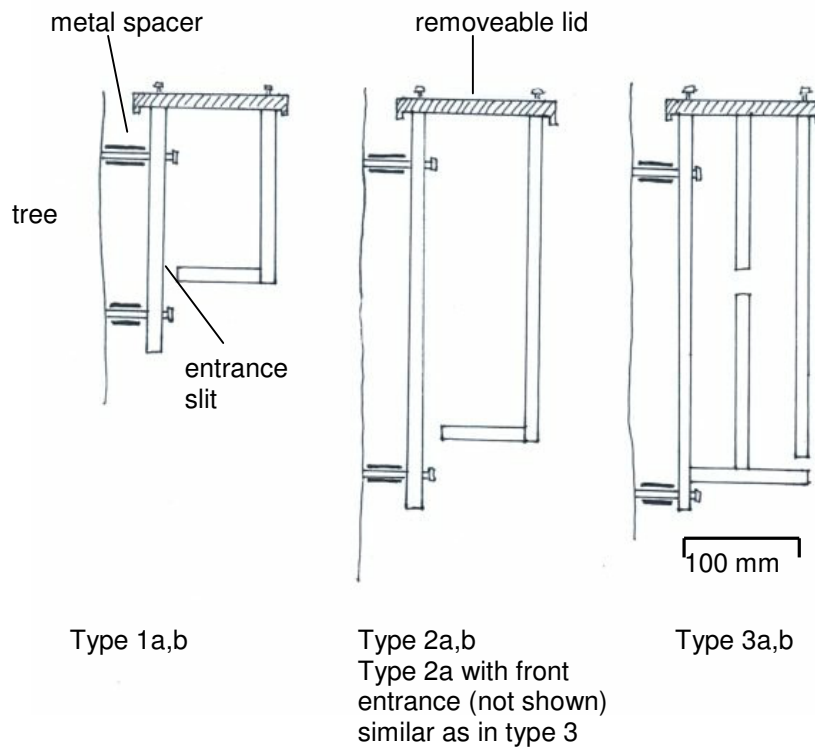


Fig. 7.2. Side views of the bat box designs used in the present study.

Table 7.1. Number of boxes, height, width and length, internal volume, the entrance size and general specifications of box types 1a,b, 2a,b and 3a,b used in the present study in Brisbane.

Box type	No of boxes (n)^a	Height (mm)	Width (mm)	Length (mm)	Internal volume (cm³)	Entrance size (mm)	Specifications
1a	40 (B)	170	120	98	2000	15 x 117	Bottom entrance
1b	5 (E)	170	120	98	2000	12 x 117	Bottom entrance
2a	5 (E)	430	205	98	8600	18 x 202	Front entrance
2b	5 (E)	430	205	98	8600	18 x 202	Bottom entrance
3a	5 (E)	430	205	100	8800	15 x 202	Front entrance, double compart. ^b
3b	5 (E)	430	205	100	8800	12 x 202	Front entrance, double compart.

^aNumber of boxes installed in backyards (B) and on experimental sites (E).

^bCompart. - compartment

A total of 70 boxes were installed between October and November 2000. Boxes were mounted on average 4.98 ± 0.03 SE ($n = 70$, range 4.1-5.5 m) above ground, on a tree trunk free of branches (Stebbins and Walsh 1985, Tuttle and Hensley 2000). Boxes faced eastwards to ensure exposure to the morning sun and to avoid the hot afternoon sun.

Boxes in backyards

For the first part of the study I installed 35 type 1a boxes on trees in 27 private properties (Figs. 7.1, 7.2). Where private properties did not have suitable trees, type 1a boxes ($n = 5$) were erected in three nearby public parklands. All of these boxes (*boxes in backyards* hereafter) were located randomly throughout metropolitan Brisbane (Fig. 7.1).

Boxes on experimental sites

A range of different bat box designs (types 1a,b, 2a,b and 3a,b; Fig. 7.2) were tested at five sites ($n = 30$; Fig. 7.1). The sites (*experimental sites* hereafter) were located on private properties ($n = 3$; in the suburbs of Kenmore Hills, Pullenvale and Burbank) and on public land ($n = 2$; St. Lucia Golf Links and Toowong Cemetery). All experimental sites consisted of open woodland with tall eucalypt stands, with few or no hollows. I used only sites from which the understorey had been thinned or removed and replaced by lawn. On each experimental site, six boxes were installed on separate tall trees (native *Eucalyptus* species) 25-50 m apart. On one experimental site (Toowong Cemetery), only four boxes could be installed in close proximity because of a lack of suitable tall trees. The remaining two boxes were located at a distance of 100 and 150 m from these boxes.

Bat box inspections and handling of bats

Due to the subtropical climate and the lack of distinctive seasons in Brisbane, I divided the year into two main seasons based on climate data (Australian Government, Bureau of Meteorology): Warm wet months (October–April, *summer* hereafter) and cold dry months (May–September, *winter* hereafter). During summer the average minimum temperatures do not fall below 15° C while the maximum temperatures often exceeds 30° C, although seldom more than 35° C. Winter is characterised by average minimum temperatures below 15° C (9.5 – 13.8° C) and maximum temperatures of 20 to 25° C. Relative humidity remains stable throughout the year (61-71%), but mean annual rainfall during the summer reaches 122 mm compared to 58 mm in winter (Australian Government, Bureau of Meteorology).

Boxes were monitored over a period of 30 months (January 2001 – June 2003; $n = 544$). Each box was checked at least once during each season and up to eight times per box (2-4 times/year). In 2001 boxes were inspected four times a year (twice per season), but due to logistical reasons boxes were only checked once per season in 2002 and 2003.

Boxes were individually inspected by opening the lid and removing the bats for identification. Species, gender, mass, forearm length, and reproductive status were recorded. Individuals were placed immediately back into the box after handling. In the absence of bats, the box was assessed for any signs of bat occupancy (guano, urine stains). Number and location of fresh bat droppings as well as the size and location of fresh urine stains were recorded. This allowed the tracking of box use between inspections and seasons (Nagel and Nagel 1988, Arnett and Hayes 2000). The rate of box usage (%) was calculated as the number of times boxes were used divided by the number of boxes checked (some boxes were not accessible on all occasions). Fauna other than bats occupying the boxes was also recorded.

Temperature and relative humidity

In 2002 and 2003 I monitored temperature (degree Celsius) and relative humidity (%). Before inspecting boxes, I measured ambient temperatures and relative humidity (" T_a , RH_a " hereafter), as well as temperatures and relative humidity inside boxes (" T_{box} , RH_{box} " hereafter) with a commercially available temperature data logger (HOBO-Temp, Onset Computer Corporation, Pocasset, MA) and a custom-made relative humidity data-logger (Griffith University, Nathan, Queensland). Internal measurements were taken by inserting temperature and relative humidity sensors simultaneously 15 cm into each box (measured from the entrance slit). In boxes with two compartments, only the first was accessible with sensors. Ambient measurements were taken 15 cm below each entrance slit. All measurements were obtained within one minute period and the data obtained at the 30 second mark were used for analysis.

The exact time (hr/min/sec), length of recordings (in seconds), as well as general weather and cloud conditions were recorded during each measurement. Relative humidity was recorded immediately, while temperature data was downloaded after each field day onto a laptop, using BoxCar Pro, version 4, software for Windows (Onset Computer Corporation, Pocasset, MA) and later cross-checked with the timing of measurements.

I measured box temperature and relative humidity twice per box per season, however temperature data logger failure, and the occupancy of ants in boxes prevented some data collection. Overall, 71 temperature readings (40 during the summer and 31 during the winter) and 144 relative humidity readings (48 during the summer and 96 during the winter) were conducted between January 2002 and June 2003.

The effects of seasonality on bat box temperature and relative humidity, the effects of box design (small = box types 1a,b; large = types 2a,b and 3a,b) and stain

(painted/unpainted) on box temperature and relative humidity were analysed. I examined actual temperature and relative humidity data and additionally the difference in temperature and relative humidity between internal and ambient measurements ($T_{\text{box}} - T_{\text{a}}$ and $RH_{\text{box}} - RH_{\text{a}}$). This was to analyse the direct comparison of microclimates between different boxes. As bat box inspections were conducted over different days and different seasons, ambient temperature and weather changed accordingly.

At experimental sites I analysed the effects of microclimate on box choice by bats. Temperature and relative humidity of boxes containing bats during measurements were compared with readings for boxes which did not contain bats. I distinguished between boxes housing bats versus boxes with evidence of use (e.g., bat guano or stains) because all boxes on experimental sites were used during this study. I was interested if at the time of readings there was a difference in temperature and relative humidity between used and unused boxes. These comparisons were possible on experimental sites as boxes on each site were located near each other and were checked in close succession. Therefore, microclimate data could be used to test the hypothesis that temperature and relative humidity were influenced box choice by bats.

Landscape characteristics

Environmental attributes of each bat box site were analysed to investigate whether landscape variables, such as land cover types and physical attributes, influenced the box occupancy. I measured each attribute in five different circular buffers (100, 500, 1000, 2000, 5000 m) centred around each bat box location.

Percentages of four land cover types were measured by overlaying five different radii (see above), each with a grid system of 100 identical elements each over a topographic image map (scale 1: 25,000; State of Queensland Department of

Land 1995). These included the percentage of grass, build-up area, permanent open water (such as river, creek, dams, sea) and total forest cover (dry sclerophyll forest).

In addition, I measured 12 physical landscape variables for each bat box on a topographic aerial image map (scale 1: 25,000; 5 m contour interval; The State of Queensland Department of Lands, 1995): altitude (to the nearest 5 m), distance to nearest open water body (river, creek or dam), distance to the forests differing in sizes (1-20, 20-100, and > 100 ha). The number of bat boxes within different buffers (100, 500, 1000, 2000, 3000, 4000, 5000 m) were also measured as bat literature suggested that a high number of boxes in one area attracts more bats (Schwartz 1990, 1994a).

Statistical Analysis

Data are presented as mean and/or median \pm standard error (SE) and range. Data sets were checked for normality (Wilk-Shapiro statistics, *W*) and non parametric statistics were applied because many data-sets were not normally distributed.

Temperature and relative humidity data were analysed with Mann-Whitney *U*-tests with pairwise comparison of ranks (Zar 1999). Spearman's rank order correlations (Zar 1999) were used to compare variables of box usage by bats (number of times boxes were used by bats in winter, summer and overall; presence/absence of dwelling bats in boxes and the number of species in boxes) against the four types of land cover types and the 12 physical landscape variables (see previous paragraph). Additionally, box usage by bats (number of times boxes were used by bats in summer, winter and over both seasons; presence/absence of dwelling bats in boxes; and the number of species in boxes) was correlated against number of times boxes were used by ants in summer, winter and over both seasons. Significance was assessed at an alpha of 0.05. Analyses of the data were performed using STATISTICA 4.5 for Windows 97 (StatSoft, Tulsa, Oklahoma).

7.3 Results

Bat box usage

All but three bat boxes were used at least once during the three-year study (37 boxes in backyards and all 30 boxes on experimental sites). Usage increased steadily with up to 87% of boxes being used (Figs. 7.3a, b). In most cases bat box usage was confirmed from the occurrence of fresh bat guano and stains inside boxes. On some occasions, bats were caught inside boxes (see below). Ants excluded bats by building nests inside boxes and blocking-off the entrance slits with bark material, even when the boxes had been used in the previous season by bats (Figs. 7.3a, b). In contrast to bat occupancy, ant presence remained relatively stable throughout the project regardless of the year and season (Figs. 7.3a, b). In backyards, ants occupied on average 21.1% of boxes (± 2.6 SE; range: 12.2 - 33.3%; $n = 8$), while the rate was about half on experimental sites (11.6 ± 1.9 SE; range: 3.3 - 20%; $n = 8$). Ants were therefore competing with bats for the available roosting space.

Bat species

Twenty-four bats of five species were captured in boxes on five occasions during winters of 2001-2003. Bats were found on two of the five experimental sites (St. Lucia Golf Links and Kenmore Hills; Fig. 7.1; Table 7.2). No bats were caught during summer or in backyard boxes. Some bats escaped while being retrieved from the boxes and therefore could not be measured (Table 7.2). All bats were non-reproductive. Most roosting groups consisted of one male and several females. Only twice did bats roost as individuals; an unidentified vespertilionid and a male Gould's long-eared bat (*Nyctophilus gouldi* (Tomes, 1858)).

I captured eight Gould's wattled bats (*Chalinolobus gouldii* (Gray, 1841)), five northern long-eared bats (*Nyctophilus bifax* Thomas, 1915), four Gould's long-eared bat (*N. gouldi*), six greater broad-nosed bats (*Scoteanax rueppellii* (Peters, 1866)), and one small vespertilionid (Table 7.2; Plate 7.2.). Identification of the vespertilionid bat was impossible, as I was unable to retrieve this bat from the narrow compartment of its box. Its appearance was consistent with a little broad-nosed bat (*Scotorepens* species (Gray, 1843)), a little bentwing bat (*Miniopterus australis* Tomes, 1858) or a chocolate wattled bat (*Chalinolobus morio* (Gray, 1841)). All three species occur in this region (Churchill 1998) and are likely to use bat boxes (Smith and Agnew 2002, Bender 2005). Two bat species, the northern long-eared bat and the greater broad-nosed bat, are listed as rare in Brisbane (Brisbane City Council 2000; Table 2.1, Chapter 2).



Plate 7.2. Four of the five bat species found in bat boxes during the present study: a) northern long-eared bat (*N. bifax*); b) Gould's long-eared bat (*N. gouldi*); c) Gould's wattled bat (*C. gouldii*); and d) greater broad-nosed bat (*S. rueppellii*).

Photos: a) T. Low; b-d) M. Rhodes.

Large bat droppings were found in large quantities (> 50) in box type 2a (Kenmore Hill experimental site). The guano was similar to those found in box type 3a where the greater broad-nosed bats were roosting and the guano size was much larger than the guano found in the remaining boxes. I therefore assume that greater broad-nosed bats might have roosted first in box type 2a prior moving into 3a. However, it also could have been guano from another large bat species, such as the white-striped freetail bat (*Tadarida australis*). However, white-striped freetail bats were never caught in boxes.

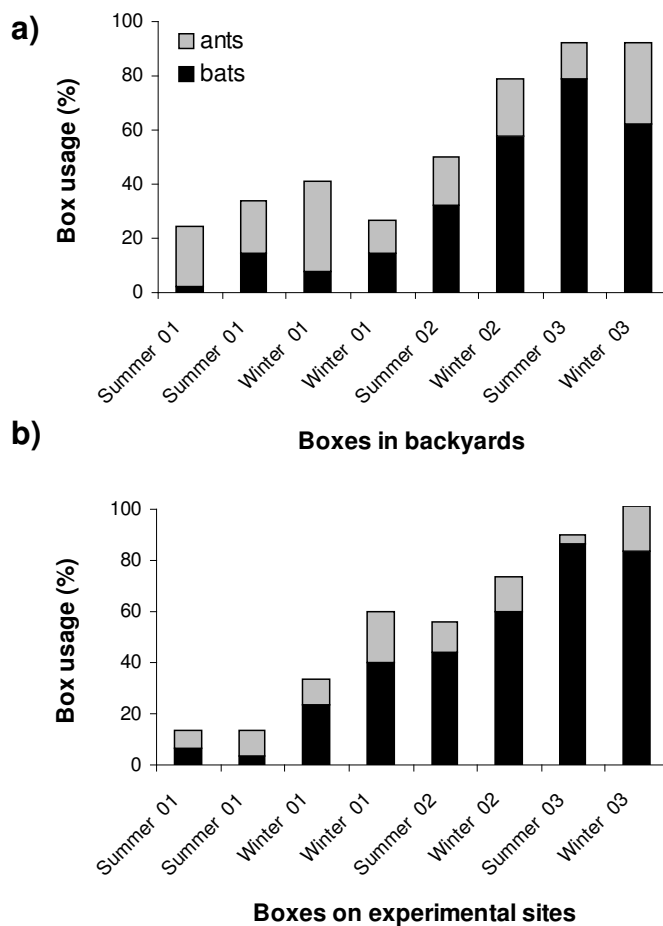


Fig. 7.3. Box usage (%) of bat boxes located in a) backyards ($n=40$) and b) experimental sites ($n=30$) for bats (black) and ants (grey). Proof of bat usage was determined by either locating bats inside boxes or by indirect signs, such as bat guano and urine stains. During 2001 boxes were checked every three months, resulting in two inspections per season. Summer (October-April); winter (May-September).

Fauna other than bats

Bat boxes were also used by fauna other than bats (Figs. 7.4a, b). Fauna were identified to genus or species and combined into broad taxonomic groups for analysis. As with bats, the rate of box usage (%) was calculated as the number of times boxes were used divided by the number of boxes checked.

After bats, spiders were the second largest fauna group present, occupying 30.1% of boxes during summer and 25.7% during winter (Figs. 7.4a, b). Most spiders consisted of different species of huntsman and were pooled into a taxonomic group of huntsman (Figs. 7.4a, b): Over the three-year project 29.9% were grey huntsman (*Holconia immanis*), 18.4% were giant green huntsman (*Typostola sp.*), 9.8% were brown huntsman (*Heteropoda jugulans*), 23% were unidentified huntsman, and 1.7% were unidentified huntsman hatchlings. Additionally, boxes hosted a range of other spiders: 6.3% red house spiders (*Nesticodes rufipes*), 0.6% daddy-long-legs (*Pholcus phalangiodes*) and 10.3% unidentified spiders.

Occasionally ants were seen foraging inside boxes but most represented established colonies, which filled the box completely and sealed the entrance with bark and other plant material. More than eight ant species used the boxes, the majority belonging to the genus *Polyrhachis*. During summer ant nests were found in 13.3% of all boxes, while during winter it increased slightly to 16% (Figs. 7.4a, b).

Cockroaches frequently occupied boxes, especially during summer (17.4%) while usage dropped in winter to 8.7% (Figs. 7.4a, b). The majority of cockroaches (all data combined) were German cockroaches (*Blattella germanica*; 54.3%), followed by Australian cockroaches (*Periplaneta australasiae*; 12.3%), bush cockroaches (*Methana marginalis*; 8.6%), American cockroaches (*Periplaneta americana*; 3.7%), and barred cockroaches (*Cosmozosteria subzonata*; 1.3%). 19.8% of recorded cockroaches were not identified to species.

Hedge grasshoppers (*Valanga irregularis*) were encountered on 3.8% of inspections during summer and 3.2% during winter. Grasshoppers and geckoes often shared the same box. Geckos were found in the same ratio in summer and winter (2%). Geckoes were most likely to be the native dubious dtella (*Gehrya dubia*) or the introduced Asian house gecko (*Hemidactylus frenatus*) but confirmation was impossible as geckos escaped the boxes before identification could take place.

Other animals ("other fauna") used the boxes infrequently during summer (2%) and winter (4.4%; Figs. 7.4a, b). These included unidentified skinks ($n = 8$), mud wasp nests ($n = 5$), caterpillars ($n = 2$), unidentified crickets ($n = 2$), one common tree snake (*Dendrelaphis punctulatus*) and one scorpion (*Liocheles waigiensis*). Furthermore I detected bite marks from galahs (*Cacatua roseicapilla*; $n = 3$) on the lid and scratch marks on the box ($n = 1$), especially around the entrance slit. These were most likely made by a lace monitor (*Varanus varius*), a known predator of bats and a common species in Brisbane (Mansergh and Huxley 1985, Queensland Museum 1995).

Table 7.2. Dates, bat species, number of bats found and measured, gender ratio, weight and forearm measurements, choice of box type and box site location in Brisbane.

<i>Species^a</i>	<i>Dates</i>	<i>Gender ratio^b</i>	<i>Wt (g)^c</i>		<i>FA (mm)^d</i>		<i>No of times (n) bat box type was used^e</i>						<i>Site^f</i>
			Mean	SE	Mean	SE	1a	1b	2a	2b	3a	3b	
<i>C. gouldii</i> (7/8)	30/06/2003	6F, 1M	14.8	0.5	43.6	0.5	1		1				S
<i>N. bifax</i> (4/5)	10/06/2001	3F, 1M	8.7	0.6	41.9	0.7					1		K
<i>N. gouldi</i> (4/4)	10/09/2001 3/06/2003	1F, 3M	9	0.5	40.7	0.4	1	2					K
<i>S. rueppellii</i> (6/6)	04/06/2002 23/06/2003	5F, 1M	28.5	1.2	54.3	0.6					2		K
Vespertilionid ^g (0/1)	04/06/2002	1?										1	K

^aSpecies: Bat species (Number of individuals measured/total number of bats found in box).

^bGender ratio: number of females (F) to males (M); ? - not identified.

^cWt (g): Mean \pm SE of body weight.

^dFA (mm): Mean \pm SE of forearm length.

^eNo of times (*n*) a bat box type was used: Number of times bat species occupied box type 1a-3b.

^fSite: Box site location; S – St Lucia experimental site; K – Kenmore Hills experimental site.

^gVespertilionid: Unidentified vespertilionid bat, see text for more detail.

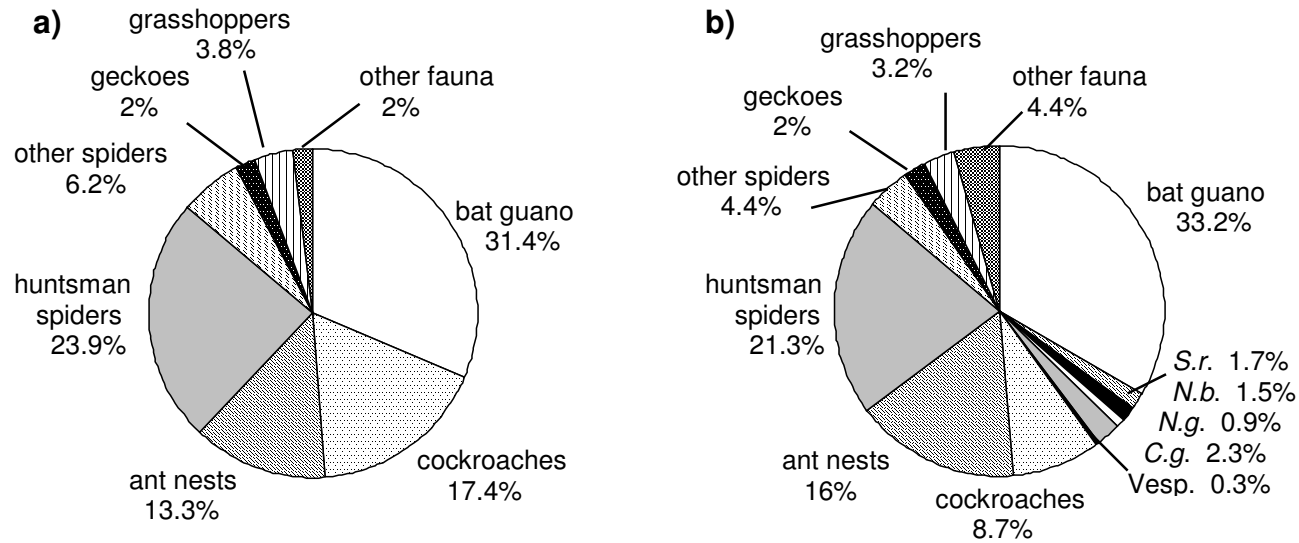


Fig. 7.4. Overall mean percentages of fauna found in bat boxes during a) summer and b) winter between January 2001 and June 2003 ($n = 544$ individual bat box inspections). Data included bat guano, which was used as indication that bat boxes had been used by bats prior inspections. Except for bat species, fauna presented in these graphs were lumped into broad taxonomic groups (see text for more detail).

S.r. - *Scoteanax rueppellii* (greater broad-nosed bat); N.b. - *Nyctophilus bifax* (northern long-eared bat); N.g. - *Nyctophilus gouldi* (Gould's long-eared bat); C.g. - *Chalinolobus gouldii* (Gould's wattled bat); Vesp. - unidentified Vespertilionidae (see text for details); other fauna - fauna, which occupied boxes infrequently, such as snakes, wasps, caterpillars, etc. (see text for detail).

Effects of season, design and paint on bat box temperature and relative humidity

Effects of seasonality on bat box temperature and relative humidity

T_{box} and T_a were significantly warmer during summer, while RH_{box} and RH_a were significantly higher during winter (P for all measurements ≤ 0.02 ; Table 7.3a). This was a direct response to seasonal climatic fluctuations. There were no differences in T_{box} , T_a , RH_{box} , or RH_a between seasons (Table 7.3b). T_{box} was always significantly higher than T_a during summer ($U = 371$, $P = 0.001$; $n = 41, 41$) and during winter ($U = 272$, $P = 0.02$; $n = 29, 29$; Table 7.3c). And while RH_{box} also trended higher especially during summer, results were not significant (Table 7.3c).

Effects of design on bat box temperature and relative humidity

Temperature and relative humidity measured in small boxes (types 1a,b) and large boxes (types 2a,b; 3a,b) were compared to assess the effects of bat box design on box temperature and relative humidity. To avoid biases in data collected at different times, only differences between internal and ambient temperature ($T_{\text{box}} - T_a$) and relative humidity ($RH_{\text{box}} - RH_a$) were compared (Table 7.4). In small boxes the differences were not significant, indicating that the differences of temperatures and relative humidity remained stable throughout the seasons (Table 7.4a). In comparison, large boxes had significant higher temperatures ($U = 12$, $P = 0.04$; $n = 8, 8$) and relative humidity ($U = 120$, $P = 0.02$; $n = 15, 29$) during summer (Table 7.4a).

However, when differences in temperature and relative humidity were compared between bat box types (small/large) within the same season, large boxes had significantly larger differences in temperature ($U = 40$, $P = 0.004$; $n = 31, 8$) and relative humidity ($U = 108.5$, $P = 0.002$; $n = 33, 15$) during summer (Table 7.4b). No significance between box types was found during winter (Table 7.4b).

Effects of paint on bat box temperature and relative humidity

Differences in temperature ($T_{\text{box}} - T_{\text{a}}$) and relative humidity ($RH_{\text{box}} - RH_{\text{a}}$) in small boxes (types 1a,b) were compared between painted and unpainted boxes within the same season (Table 7.5). During summer, unpainted boxes had significantly greater differences between ambient and internal temperatures ($U = 11$, $P = 0.03$; $n = 29$, 3) but no significant differences between ambient and internal relative humidity ($U = 43$, $P = 0.07$; $n = 27$, 6). There were no significant differences in temperature ($U = 36.5$, $P = 0.9$; $n = 19$, 4) and relative humidity ($U = 334.5$, $P = 0.8$; $n = 54$, 13) between painted and unpainted boxes during winter (Table 7.5).

Effects of microclimate on bat box choice

On experimental sites internal temperature, ambient temperature and relative humidity were compared between boxes housing bats during inspections and those which did not contain bats. None of the four measurements ($T_{\text{box}} - T_{\text{a}}$ and $RH_{\text{box}} - RH_{\text{a}}$) were significantly different between both groups (P for all measurements ≥ 0.3 ; Table 7.6). Therefore, I found no evidence to support the hypothesis that bat box' microclimates influence box choice by bats during this study.

Landscape characteristics, ant infestation and number of bat boxes in an area

Spearman's rank order correlations were used to associate box usage by bats with environmental factors, such as land cover types, physical landscape variables, ant infestation and number of boxes in an area (Table 7.7). The most significant results were negative correlations between box success ('*number of times boxes were used by bats*') and ant infestations, regardless of the season (for all measurements: $R_s \geq -0.29$, $P \leq 0.02$; Table 7.7). Of the four land cover types and the 12 physical landscape variables, only the distances to small forest remnants (1-20 ha; all

measurements $R_s \geq 0.3$, $P < 0.02$) and medium sized forest remnants (20-100 ha; all measurements $R_s \geq 0.29$, $P < 0.02$) had a significant influence on box success. The percentage of grass in a 5000 m radius was negatively associated with box success ($R_s = -0.31$, $P < 0.01$). The presence/absence of bats ('*bats in boxes*') was significantly correlated with the number of boxes, especially within a 2 km radius ($R_s = 0.42$, $P < 0.001$; Table 7.7), the percentage of grass within a 1 km ($R_s = 0.24$, $P = 0.05$), as well as the percentage of forest within a 5 km radius of a box ($R_s = 0.23$, $P = 0.05$). Similarly, the chance of attracting more than one species ('*number of bat species*') into boxes increased with the number of boxes, especially in a 2 km radius ($R_s = 0.42$, $P < 0.001$), the percentage of grass within 1 km radius ($R_s = 0.24$, $P < 0.05$), and percentage of forest cover within 5 km radius around a bat box ($R_s = 0.24$, $P = 0.05$; Table 7.7). The percentage of build-up areas was weakly negatively correlated with number of bat species ($R_s = -0.23$, $P = 0.06$; Table 7.7).

Table 7.3. Comparison of temperatures and relative humidity measured in 70 bat boxes in 2002 and 2003. Variables were compared with Mann-Whitney U -tests between a) internal and ambient measurements within the same season; b) $T_{\text{box}}-T_{\text{a}}$ and $RH_{\text{box}}-RH_{\text{a}}$ between seasons; and c) measurements of the same variable (e.g., T_{box}) between the two seasons (summer: October-April, winter: May-September).

Variable 1 Name; n	Variable 2 Name; n	Unit	Variable 1 Mean	Variable 1 Median	Variable 1 SE	Variable 1 Range	Variable 2 Mean	Variable 2 Median	Variable 2 SE	Variable 2 Range	U	P
a) Actual data measured between seasons												
T_{box} , summer; 41	T_{box} , winter; 29	°C	27.9	28	0.4	19.1-31.1	19.8	19.1	0.6	15.5-28.5	45.5	<0.001
T_{a} , summer; 41	T_{a} , winter; 29	°C	25.9	25.6	0.4	16.2-30.2	18.1	18.4	0.6	14-27.6	57	<0.001
RH_{box} , summer; 52	RH_{box} , winter; 98	%	51.3	48.5	1.7	33-83	56.8	57.5	1.3	32-83	1874	<0.01
RH_{a} , summer; 51	RH_{a} , winter; 97	%	48.8	47	1.6	31-78	54.7	54.5	1.5	28-80	1877.5	0.02
b) Differences of internal and ambient measurements between seasons												
$T_{\text{box}}-T_{\text{a}}$, summer; 40	$T_{\text{box}}-T_{\text{a}}$, winter; 30	°C	1.9	1.6	0.2	(-0.4)-5	1.7	1.5	0.2	(-2)-4.2	561	0.6
$RH_{\text{box}}-RH_{\text{a}}$, summer; 48	$RH_{\text{box}}-RH_{\text{a}}$, winter; 96	%	1.8	2	0.5	(-7)-9	2.2	1	0.4	(-5)-16	2272.5	0.9
c) Actual internal versus ambient measurements, same season												
T_{box} , summer; 41	T_{a} , summer; 41	°C	27.9	28	0.4	19.1-31.1	25.9	25.6	0.4	16.2-30.2	371	0.001
T_{box} , winter; 29	T_{a} , winter; 29	°C	19.8	19.1	0.6	15.5-28.5	18.1	18.4	0.6	14-27.6	272	0.02
RH_{box} , summer; 52	RH_{box} , summer; 51	%	51.3	48.5	1.7	33-83	48.8	47	1.6	31-78	1142	0.2
RH_{a} , winter; 98	RH_{a} , winter; 97	%	56.8	57.5	1.3	32-83	54.7	54.5	1.5	28-80	4371	0.3

Table 7.4. Comparison of differences in temperatures and relative humidity ($T_{\text{box}}-T_a$ and $RH_{\text{box}}-RH_a$). Temperature and relative humidity measured outside boxes were sometimes higher than inside boxes, resulting in negative values (listed in brackets). Data were compared a) between same box types and different seasons, and b) same season but different box types (Mann-Whitney U -tests).

Variable 1 Name; n	Variable 2 Name; n	Unit	Variable 1				Variable 2				U	P
			Mean	Median	SE	Range	Mean	Median	SE	Range		
a) Same box type, different seasons^a												
Small boxes: $T_{\text{box}}-T_a$, summer; 31	Small boxes: $T_{\text{box}}-T_a$, winter; 23	°C	1.6	1.3	0.2	(-0.4)-5	1.7	1.5	0.2	0.3-4	315.5	0.5
Small boxes: $RH_{\text{box}}-RH_a$, summer; 33	Small boxes: $RH_{\text{box}}-RH_a$, winter; 67	%	1.9	1.5	0.4	(-7)-16	2.4	2	0.5	(-5)-16	901	0.1
Large boxes: $T_{\text{box}}-T_a$, summer; 8	Large boxes: $T_{\text{box}}-T_a$, winter; 8	°C	3	2.7	0.4	2-4.8	1.6	1.6	0.6	(-2)-4.2	12	0.04
Large boxes: $RH_{\text{box}}-RH_a$, summer; 15	Large boxes: $RH_{\text{box}}-RH_a$, winter; 29	%	3.7	3	0.6	0-9	1.9	0.5	0.6	(-2.5)-10	120	0.02
b) Same season, different box types^b												
Small boxes: $T_{\text{box}}-T_a$, summer; 31	Large boxes: $T_{\text{box}}-T_a$, summer; 8	°C	1.6	1.3	0.2	(-0.4)-5	3	2.7	0.4	2-4.8	40	0.004
Small boxes: $RH_{\text{box}}-RH_a$, summer; 33	Large boxes: $RH_{\text{box}}-RH_a$, summer; 15	%	1.9	1.5	0.4	(-7)-16	3.7	3	0.6	0-9	108.5	0.002
Small boxes: $T_{\text{box}}-T_a$, winter; 23	Large boxes: $T_{\text{box}}-T_a$, winter; 8	°C	1.7	1.5	0.2	0.3-4	1.6	1.6	0.6	(-2)-4.2	90	0.9
Small boxes: $RH_{\text{box}}-RH_a$, winter; 67	Large boxes: $RH_{\text{box}}-RH_a$, winter; 29	%	2.4	2	0.5	(-5)-16	1.9	0.5	0.6	(-2.5)-10	858.5	0.4

^aBox types: small bat boxes - types 1a,b; large bat boxes - types 2a,b and 3a,b (see Fig. 7.2 and text for details).

^bSeasons: Summer (October-April), winter (May-September).

Table 7.5. Comparison of differences in temperatures and relative humidity ($T_{\text{box}}-T_a$ and $RH_{\text{box}}-RH_a$) between painted and unpainted boxes of the same box design (types 1a,b) during summer and winter (Mann-Whitney U -tests). Temperature and relative humidity measured outside boxes were sometimes higher than inside boxes, resulting in negative values (listed in brackets).

Variable 1 Name; n	Variable 2 Name; n	Unit	Variable 1				Variable 2				U	P
			Mean	Median	SE	Range	Mean	Median	SE	Range		
Painted: $T_{\text{box}}-T_a$, summer; 29	Unpainted: $T_{\text{box}}-T_a$, summer; 3	°C	1.5	1.3	0.2	(-0.4)- 4.4	3.1	2.4	0.9	2-5	11	0.03
Painted: $RH_{\text{box}}-RH_a$, summer; 27	Unpainted: $RH_{\text{box}}-RH_a$, summer; 6	%	1.3	1.5	0.6	(-7)-9	-0.7	-1	0.7	(-3)-2	43	0.07
Painted: $T_{\text{box}}-T_a$, winter; 19	Unpainted: $T_{\text{box}}-T_a$, winter; 4	°C	1.7	1.5	0.2	0.3-4	1.9	1.6	0.7	0.7-3.7	36.5	0.9
Painted: $RH_{\text{box}}-RH_a$, winter; 54	Unpainted: $RH_{\text{box}}-RH_a$, winter; 13	%	2.4	2	0.5	(-5)-16	2.2	1	1.1	(-5)-12	334.5	0.8

^aSeasons: Summer: October-April; Winter: May-September.

Table 7.6. Temperature and relative humidity compared between boxes housing bats during inspections and those which did not contain bats (Mann-Whitney *U*-tests). Boxes were located on experimental sites.

Variable 1 Name; n	Variable 2 Name; n	Unit	Variable 1				Variable 2				U	P
			Mean	Median	SE	Range	Mean	Median	SE	Range		
T _{box} : boxes with bats, 4	T _{box} : boxes without bats, 8	°C	21	21	0.5	19.8-22.2	20.9	21.4	1.0	16.8-25.2	53	0.9
T _a : boxes with bats, 4	T _a : boxes without bats, 8	°C	19.4	19.3	0.2	19.1-19.8	18.9	18.8	0.7	15.5-21.9	10	0.3
RH _{box} : boxes with bats, 11	RH _{box} : boxes without bats, 31	%	62	63	4.4	35-79	60.4	64	2.5	33-80	162.5	0.8
RH _a : boxes with bats, 11	RH _a : boxes without bats, 31	%	59.7	64	5.3	32-80	58.5	64	2.9	28-80	653.5	0.7

Table 7.7. Most significant results from the Spearman's rank order correlation matrix (see text for more detail). The 34 variables which were compared against each other are listed as footnotes^a.

<i>Variable 1</i>	<i>Variable 2</i>	<i>n</i>	<i>R_s</i>	<i>P</i>
No of times boxes were used by bats (winter)	No of times boxes were used by ants (winter)	68	-0.46	<0.0001
No of times boxes were used by bats (all seasons)	No of times boxes were used by ants (winter)	68	-0.41	<0.001
No of times boxes were used by bats (all seasons)	No of times boxes were used by ants (all seasons)	68	-0.38	<0.002
No of times boxes were used by bats (summer)	No of times boxes were used by ants (summer)	68	-0.29	<0.02
No of times boxes were used by bats (winter)	Distance to forest remnant (20-100 ha)	68	0.4	<0.001
No of times boxes were used by bats (all seasons)	Distance to forest remnant (20-100 ha)	68	0.29	<0.02
No of times boxes were used by bats (winter)	Distance to forest remnant (1-20 ha)	68	0.36	<0.01
No of times boxes were used by bats (all seasons)	Distance to forest remnant (1-20 ha)	68	0.3	<0.02
No of times boxes were used by bats(winter)	% of grass cover in 5000 m radius	68	-0.31	<0.01
Bats in boxes	No of boxes in 2000 m radius	68	0.42	<0.001
Bats in boxes	% of grass cover in 1000 m radius	68	0.24	0.05
Bats in boxes	% of forest cover in 5000 m radius	68	0.23	0.05
No of bat species	No of boxes in 2000 m radius	68	0.42	<0.001
No of bat species	No of boxes in 3000 m radius	68	0.3	<0.02
No of bat species	% of forest cover in 5000 m radius	68	0.24	0.05
[No of bat species	% of build-up in 500 m radius	68	-0.23	0.06]

^a1 - No. of times boxes were used by bats (all seasons).

2 - No. of times boxes were used by bats during summer.

3 - No. of times boxes were used by bats during winter.

4 - Bats in boxes: presence/absence of bats.

5 - No. of bat species.

6 - Colony present (more than one bat).

7 - Ant infestation: presence/absence.

8 - No. of ant infestations (all seasons).

9 - No. of ant infestations (summer).

10 - No. of ant infestations (winter).

11 - Distance to nearest water body.

12 - Distance to forest 1-20 ha.

13 - Distance to forest 20-100 ha.

14 - Distance to forest >100 ha.

15 - No of boxes in 100 m radius.

16 - No of boxes in 500 m radius.

17 - No of boxes in 1000m radius.

18 - No of boxes in 2000 m radius.

19 - No of boxes in 3000 m radius.

20 - No of boxes in 4000 m radius.

21 - No of boxes in 5000 m radius.

22 - Altitude.

23 - % of grass cover in 500 m radius.

24 - % of grass cover in 1000 m radius.

25 - % of grass cover in 5000 m radius.

26 - % of forest cover in 500 m radius.

27 - % of forest cover in 1000 m radius.

28 - % of forest cover in 5000 m radius.

29 - % of build-up area in 500 m radius.

30 - % of build-up area in 1000 m radius.

31 - % of build-up area in 5000 m radius.

32 - % of water in 500 m radius.

33 - % of water in 1000 m radius.

34 - % of water in 5000 m radius

7.4 Discussion

General bat box acceptance and bat box design

Over the three-year period of this study all but three boxes were used by bats and bat box acceptance increased steadily to over 80%. Evidence of use was, however, based mostly on the presence of fresh bat guano and urine stains inside (Haensel 1987, Nagel and Nagel 1988, Schwarting 1990, Shilton 1994, Arnett and Hayes 2000, Chambers *et al.* 2002). Infrequent box usage by bats has been reported in several bat box studies, where single individuals often used boxes for a day before moving on (Nagel and Nagel 1988, Shilton 1994, König and König 1995, O'Shea 1998). This roost switching behaviour likely reflects natural roost lability of some microchiroptans as many bat species shift daily between natural roost sites (e.g., Lewis 1995, O'Donnell and Sedgeley 1999, Willis and Brigham 2004).

To enhance usage rates, Schwarting (1990, 1994a) suggested an increase in the number of boxes in order to allow bats to remain in an area. In particular, the author recommended installing boxes in clusters of five in close proximity (not more than 50 m apart) and with many boxes distributed evenly throughout an area and all habitat types (Schwarting 1990, 1994a). The data of this study suggests that clusters of six boxes on one site (as found on experimental sites) were more likely to keep bats in an area than single distributed boxes over a large area (backyard sites). Only on experimental sites did I find dwelling bats and the amount of guano found was higher in boxes on experimental sites than in backyard boxes.

On the other hand, Boyd and Stebbings (1989) advised the setting of boxes on trees in two groups of four and in two different heights facing all directions. This has the additional advantage of bats being able to choose a suitable box depending on the season as some studies have found the aspect of boxes to be an important factor in box acceptance, especially during the breeding season (Schwarting 1990,

1994a, Flaquer *et al.* 2006). In contrast, Shilton (1994) and Smith and Agnew (2002) found no preference for box aspect.

In the present study there was an apparent preference by smaller and medium sized bat species for boxes with small and medium (12 or 15 mm) entrance slits and often also the smaller internal volumes while the largest bat species detected here, the greater broad-nosed bats, roosted in a large box with 18 mm entrance slits (Table 7.2). Due to the small sample sizes, however, I was unable to undertake detailed analyses. In the USA boxes had better acceptance rates if the internal volumes were larger (Tuttle and Hensley 2000) while the opposite was found in Europe (Gerell 1985).

Other box studies emphasise the importance of bat box design. The physical sizes of bat boxes are often not the limiting factor to the group size of bats as most can hold many more bats than is usually found in them (Park *et al.* 1998). Therefore, box design might be more important. Crevice roosting bats, for instance, prefer different box designs than bats which use large tree cavities. Schwarting (1994a) found that partitions inside the box especially attracted crevice-roosting bat species. Similarly, Flaquer *et al.* (2006) had twice as many bats in boxes with compartments than in boxes without compartments and that the abundance of bats varied seasonally according to box type. In the present study, northern long-eared bats, greater broad-nosed bats and an unidentified vespertilionid roosted only in boxes with compartments, while the Gould's wattled bats and Gould's long-eared bats occupied boxes without compartments.

Box acceptance is also improved by providing protection from wind and moisture, although ventilation is important (Heise 1980, Tuttle and Hensley 2000). In boxes with entrance slits on the bottom of the box, the chimney effect draws air up and traps warm air in the top part of the boxes. This is particularly important for boxes in temperate regions (Schwarting 1994a). In this study, dwelling bats were

only found during winter in boxes. However, while boxes with bottoms might improve thermal qualities of boxes on cold days, they also require regular cleaning as they harbour more parasites than boxes without bottom panels (Tuttle and Hensley 2000).

In Germany, box success was improved by providing sawdust-concrete or porous concrete boxes as they give better protection against woodpeckers and weather (Gerell 1985, Schwarting 1990, 1994a). Partitions and landing areas can be roughened, scratched or grooved horizontally, or covered with durable UV resistant plastic screening to attract bats (Tuttle and Hensley 2000). The location of boxes will also influence box success as boxes on poles and houses were used twice as quickly and in bigger numbers as the same boxes mounted on trees (Tuttle and Hensley 2000, Flaquer *et al.* 2006).

Species use of bat boxes

Five species of bats used bat boxes during this study. Two of these species are commonly found in Brisbane (Gould's wattled bats and Gould's long-eared bats), while two are of significance (northern long-eared bats and greater broad-nosed bats), being listed in Brisbane City Council's Natural Assets Planning Scheme as '*rare or are uncommon in Brisbane and becoming rare*' (Brisbane City Council 2000). None of bats using boxes were the white-striped freetail bat despite the provision of larger boxes. Instead, these large boxes were occupied by another large microbat, the greater broad-nosed bat.

Single male white-striped freetail bats have been found in bat boxes in the Organ Pipe National Park, southern Victoria (Bender 2005). These boxes were of similar size and shape as boxes used in this study (Stebbing and Walsh design; box type 1). However, these individuals visited the boxes over one season and not in the following year. Therefore new bat box designs were trialled based on the roost tree characteristics of Chapter 3 (Rhodes and Wardell-Johnson 2006), but has so far

failed to attract white-striped freetail bats. Instead, Gould's wattled bats have used these boxes (L. Evans, pers. comm. 2006).

In contrast, bat boxes erected in an urban reserve in Melbourne, Victoria, have successfully attracted white-striped freetail bats (Evans *et al.* 2006). These roosting groups of up to eight bats were selective in their bat box choice, using only long, rectangular upright facing boxes and ignoring other boxes types provided in the same area. This suggests that the white-striped freetail bat has very specific roosting requirements, which are not fully understood. The shape of bat boxes accepted by white-striped freetail bats in urban Melbourne were similar to the natural roosts used by the bats in Brisbane (Chapter 3). I found white-striped freetail bats roosting in hollow branches and trunks, with cavities often greater than 30 cm in diameter (Rhodes and Wardell-Johnson; Chapter 3). However, the present study commenced before the specific roost requirements were known for this species.

Box competition

The entrances of bat boxes used in this study were designed to exclude predators (Schwarting 1994a) and other arboreal mammals, such as common brushtail possums, common ringtail possums, feathertail gliders, sugar gliders, squirrel gliders and yellow-footed marsupial mice. These marsupials have been found to use nest boxes originally designed for bats in Australia (Bender and Irvine 2000, 2001, Smith and Agnew 2002). Similarly, in the northern hemisphere, wasps, hornets, birds, mice and squirrels use bat boxes regularly (Gerell 1985, Schwarting 1990, König and König 1995, Tuttle and Hensley 2000).

While the boxes used in this study successfully excluded arboreal mammals occurring in Brisbane (such as the possums and gliders), they did not prevent frequent ant infestations. Ants occupied up to 30% of boxes and in some areas were

present year round. Similarly, in temperate Australia, ants and wasps occupied many boxes which would be usually used by bats (Bender and Irvine 2000, 2001).

In the present study the application of talcum inside the boxes and water-proof marine grease around the metal spacers between tree and box proofed effective in repelling ants. The sticky grease prevented ants from crossing while talcum blocked the stigmas, the breathing holes in the cuticula of ants, and nests were quickly abandoned after application. Both methods reduced the ant but not bat occupancy. However, bat urine usually decreased the effectiveness of talcum and the grease on the spacers also dried out over time. Therefore, these measures only reduced ant infestation for up to three months.

In 2002, I trialled three bat boxes without bottom panels and three compartments on trees where boxes had been regularly infested with ants (Goodrich 2002, Rhodes 2002; Appendix II). I placed the boxes one metre below the ant infested boxes and found that the open bottom ones were never infested while the others remained filled with ant nests. On one experimental site (Kenmore Hills), bats used the new box within three weeks of mounting (D. Tobart, pers. comm. 2002). This suggests that box design can help reduce ant infestations in subtropical areas. Similarly, in the US, open bottom boxes are also less likely to be occupied by birds, mice and squirrels (Tuttle and Hensley 2000).

Smith and Agnew (2002) suggested that a box type similar to the designs in this study will exclude reptiles and birds. I frequently found geckos in backyard boxes and once a common tree snake in a double compartment box (type 3a). While the geckos most likely did not influence box usage by bats, the common tree snake may be regarded as a potential predator.

Microclimate in bat boxes

In Brisbane, box occupancy fell during summer, and bats were captured only during winter. Similarly, in a nest boxes study in subtropical south-east Queensland, 150 km north of Brisbane, occupancy rates of nest boxes fell during summer (Smith and Agnew 2002). Overall, bat boxes in Brisbane had higher temperatures and relative humidity than the ambient microclimate. Overheating is a known problem in boxes during hot summer days (König and König 1995, Lourenço and Palmeirim 2004). In a study of microclimates of nest boxes and natural cavities McComb and Noble (1981) showed that nest boxes were generally hotter and had a lower relative humidity compared to natural cavities. Solar radiation on the flat surface of nest boxes results in rapid and uniform heating of the box' surface. Natural cavities, in comparison, are usually round or oval in outline and are progressively heated throughout the day (McComb and Noble 1981).

Colour, for example, can be used to influence box temperatures with dark colours tending to increase temperature inside boxes while lighter colours have the opposite effect (Tuttle and Hensley 2000). In Mediterranean climates, black boxes are selected by the soprano pipistrelle (*Pipistrellus pygmaeus*) over white and grey boxes as the temperatures measured inside the black boxes resembled the temperature inside house roosts (Lourenço and Palmeirim 2004). However, black boxes were abandoned on very hot days when the temperature exceeded the thermal neutral zone of this species ($> 40^{\circ}\text{C}$; Lourenço and Palmeirim 2004).

In Brisbane, summer temperatures in bat boxes (T_{box}) did rarely exceed 30°C . Therefore, overheating was most likely not the reason for the drop of box occupancy and the lack of bats caught in boxes. A more likely explanation for the pattern I observed is that bats form large maternity colonies during summer and may therefore prefer natural roosts with larger volumes. Furthermore, maternity colonies and

pregnant females are often found in roosts, including bat boxes, with high temperatures to minimise energetic costs of thermoregulation (Kerth *et al.* 2001, Flaquer *et al.* 2006). High roost temperatures accelerate gestation, the growth of young and increase the survival during winter (Kerth *et al.* 2001, Sedgeley 2001, Speakman and Thomas 2003). Therefore, bat boxes provided for summer populations should be much larger than the boxes used in this study with a wider thermal range (Lourenço and Palmeirim 2004) .

In winter bats might have switched to cooler boxes to reduce metabolic rate and energy expenditure by lowering their body temperature (Kerth *et al.* 2001, Chruszcz and Barclay 2002, Speakman and Thomas 2003, Turbill 2006). The energy saving during torpor for bats of the sizes found in this study could be up to 90% of the resting metabolic rate (C. Willis, pers. comm. 2006; Speakman and Thomas 2003). More research needs to be conducted to link bat box design, box microclimate, bat box acceptance and thermoregulatory needs of subtropical bats in Australia.

Landscape characteristics and box occupancy

In Brisbane, boxes were more likely to be used if they were situated close to a small (1-20 ha) and medium (20-100 ha) sized forest reserves, while boxes mounted next to the Brisbane Forest Park, the largest reserve in Brisbane, were rarely used. It is likely that small and medium sized forest might be depleted of natural hollows as many forest reserves in Brisbane consist of young regrowth, with few trees larger than 40 cm in diameter (Catterall *et al.* 1998). Younger trees harbour usually fewer hollows as hollow formation and numbers of hollows are significantly related to tree diameter, tree health, tree age, tree location and fire events (reviewed in Gibbons and Lindenmayer 2002). Bats, therefore, may have used bat boxes in the near vicinity of young regrowth forest reserves. Large forest reserves, on the other hand, might still provide an abundant range of natural roost sites. Similarly, Smith and

Agnew (2002) argue that where hollows occur in high numbers, native mammals tend to use this in preference to nest boxes. In Germany however, box acceptance is independent of hollow density in forests, but instead depends on where boxes are placed (Schwaring 1994a,b). Boxes along forest paths or on forest edges were primarily used as dispersal and migration roosts, while boxes inside forest are predominantly used as maternity roosts (Schwaring 1994a). In another study, proximity to water was an important factor in bat box choice (Tuttle and Hensley 2000). In the present study, however, I did not find evidence that percentage of water or distance to water influenced box occupancy, probably because the study area had many permanent water bodies and boxes were located on average 380 m from any permanent water source.

In Brisbane, boxes were more likely to contain bats if they were installed in an area with high grass cover within one kilometre and high forest cover within five kilometres. Grass cover may affect insect abundance (Emery and Emery 2004) and therefore prey availability for bats. Bats may have chosen a bat box away from their natural hollows in forests to reduce commuting costs (Boyd and Stebbings 1989). At this stage, no systematic study has been conducted in the urban land use of microchiroptans in Brisbane, with the exception of the white-striped freetail bat (Rhodes and Wardell-Johnson 2006, Rhodes *et al.* 2006; Chapters 3-6) and little information is available on the roosting and foraging ecology of other urban bat populations in the greater Brisbane region. More studies are therefore needed to investigate roosting and foraging home-ranges of these bats in order to make appropriate management recommendations on the suitability of bat boxes in urban areas.

Cost and benefits of bat boxes

Bats are characterised by a life history similar to large mammals with high survival and low reproduction rates (Barclay and Harder 2003). Therefore, bat populations recover slowly from disturbances and loss of suitable roosts, especially maternity sites (Barclay and Harder 2003). In these cases, bat boxes can be an important tool in the conservation of a bat species (Lourenço and Palmeirim 2004, Flaquer *et al.* 2006). Other studies have shown that nest boxes can be successful in increasing the populations of insectivorous birds or bats in order to control outbreaks of insect pests (Thomas *et al.* 1979, Walton 2001). Furthermore, nest boxes have successfully maintained populations of several species of squirrels, waterfowl, kestrels, owls and martins in farmland or urban environment (Schemnitz 1980). Boyd and Stebbings (1989) argued that frequent recaptures of individual bats in boxes indicate that there are few alternative roost sites in areas such as forestry plantations. The increase of the population in boxes is explained, therefore, by the reduced commuting distance from previously used roosts.

However, occupancy of boxes also varies between sexes, species, seasons and where boxes are located (Shilton 1994, König and König 1995, Schmidt 1998). Bat boxes are often used only for a short period of time and occasionally as maternity colonies and the causes of failure are poorly understood (Wolz 1986, Neilson and Fenton 1994, Lourenço and Palmeirim 2004). Furthermore, different hollow-depending species use boxes of different designs and during different seasons for different reasons (Menkhorst 1984). For example, a 30-year study of bat boxes in Germany has revealed that the same bat species use different bat box designs as dispersal, mating, migrating, winter and maternity roosts (König and König 1995, Dietrich 1998). Bats usually need several years before they accept boxes (Dietrich 1998, Bender and Irvine 2001). Experience also showed that even after 19 years, new bat species were attracted into boxes because the box design was changed

(Dietrich 1998), highlighting the need to understand bat box designs for each species if boxes are to be used as a conservation tool.

This study aimed to investigate the attraction of different bat species to different box designs. It succeeded in attracting at least five bat species although some of these were common and opportunistic species such as the Gould's wattled bat and the Gould's long-eared bat. These bat species readily occupy bat boxes, regardless of the design and location (O'Shea 1998, Bender and Irvine 2001, Smith and Agnew 2002, Bender 2005). There is little information on the effects of artificially increasing population levels of common native, introduced or pest species on populations of other species in the same study area (Gibbons and Lindenmayer 2002). Catterall (2004) found in a study of bird diversity in Brisbane, that formerly forested areas that were cleared and urbanised showed avifaunal changes of time, where large-bodied birds exclude small foliage-feeding birds.

Overseas studies have shown that boxes are often occupied by dominant bat species (Gerell 1985, Nagel and Nagel 1988, Schwarting 1990, König and König 1995), and that these often evict other, usually smaller, bat species (e.g., *Myotis myotis* evicts *M. daubentoni*; *Pipistrellus nathusii* evicts *P. pipistrellus*; and *Nyctalus noctula* and *N. leisleri* evict *P. nathusii*; König and König 1995). On the other hand, some boxes may be used by several species simultaneously (Schmidt 1988). The reasons why some bats evict other bats and other species roost in mixed groups remain unclear (König and König 1995). Further research should be conducted to understand bat box requirements of different Australian bat species, and should be preferably focused on endangered species.

Nest boxes can also be an important tool for education and research into the biology of hollow-using species, as they allow access to nests that would otherwise be inaccessible (Menkhorst 1984). Boxes in my study attracted two bat species (greater broad-nosed bats and northern long-eared bats) declared as significant in

Brisbane with one species, the greater broad-nosed bat, returning over two successive winters. The ecology of these species is largely unstudied (Hoye and Richards 1995, Parnaby 1995, Churchill 1998, Brisbane City Council 2000). If these bats can be successfully attracted into bat boxes and during different seasons of the year, boxes may be used to study these species in more detail, similar to studies elsewhere (Golding 1979a, Boyd and Stebbings 1989, Lundberg and Gerell 1996, Park *et al.* 1998, Kerth and König 1999, Kerth *et al.* 2001).

Conclusion

Extensive logging, farming and urbanisation lead to the loss of natural habitat and consequently the decline of hollow-dependent fauna (Gibbons and Lindenmayer 2002, Lindenmayer and Franklin 2002, Lunney 2004). In areas affected by these processes, nest boxes have successfully been used to assist population recoveries (Schemnitz 1980, Menkhorst 1984, Lourenço and Palmeirim 2004, Flaquer *et al.* 2006). However, while nest boxes play an important role in conservation and management of hollow-dependent fauna, they usually only provide a temporary substitute for natural roosts (Gibbons and Lindenmayer 2002, Wendorf 2004). Consequently, the primary goal should be to preserve hollow-bearing trees or other roost sites (such as caves) with appropriate management plans and inventories (Gibbons and Lindenmayer 2002). The present bat box study was successful in attracting several bat species into boxes. However, box choice by these species is still poorly understood and future research should focus on the systematic study of box design, microclimate, landscape factors and different species usage throughout seasons and years. In areas with a remaining high biodiversity of native species, such as subtropical Brisbane, the ultimate goal should be to preserve overall biodiversity and to avoid upsetting community dynamics in favour of species that can adapt more easily to boxes.

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Chapter 8

Conclusion and Management Implications

8.1 Introduction

Urbanisation is now regarded as one of the most damaging and expanding influences world-wide, resulting in profound habitat fragmentation across the globe (Hobbs and Mooney 1997, Hooper and Vitousek 1997, McKinney 2002, Miller and Hobbs 2002, Jha and Bawa 2006). In Australia, the great majority of the human population is clustered in a series of concentrated urban centres along the eastern seaboard, transforming the coastal forests of these regions into a mosaic of forest fragments and human-modified environments (Catterall and Kingston 1993, Catterall *et al.* 1997, Collins *et al.* 2000, Williams *et al.* 2001, Commonwealth of Australia 2003, National Forest Inventory 2003, Lunney 2004b, Norman *et al.* 2004). Yet, despite the anthropogenic influence on these urban environments, little attention has been given by biologists to the effects of urbanisation in Australia or elsewhere (Miller and Hobbs 2002). This is especially important for forest dependent species, which must adapt to smaller forest remnants divided by many, often large, cleared and human-made land (Lunney 2004a). Many of these forest species are hollow-dependent, but information on the hollow-availability and foraging requirements in urban areas is limited in Australia (Gibbons and Lindenmayer 2002, Lunney and Burgin 2004).

Bats, especially molossids, may appear better equipped than other forest dependent fauna to persist in fragmented habitats due to their ability to fly and cross

open spaces (Avila-Flores and Fenton 2005). However, hollow-dependent molossid still require suitable roost sites to persist (Hall 1990, Sheffield *et al.* 1992, Barclay and Brigham 1996, Racey and Entwistle 2003, Parnaby and Hamilton-Smith 2004). Hollow-availability may be a limiting resource for molossid species in areas from which forests have been cleared. On the other hand, molossids may be more flexible during foraging; for example they may be able to use the air space above urban habitats when feeding on high-flying insects (Carmel and Safriel 1998, Lee and McCracken 2002, Marques *et al.* 2004, Avila-Flores and Fenton 2005, Hourigan *et al.* 2006).

This thesis explored the impact of urbanisation in one of the fastest growing urban areas in the world, the greater Brisbane region in south-east Queensland (SEQ), Australia (Poole 1995, Queensland Government 2004) on Australia's second most abundant, but little known mammal group, the bats. In particular, I examined two relevant key resources in this urban area - hollow (roost) availability and foraging habitat - for one abundant molossid species, the white-striped freetail bat (*Tadarida australis*), and how these findings might be incorporated into considerations of the conservation of insectivorous bats in highly urban environments.

8.2 Summary of key findings

The abundance of the white-striped freetail bat in a city such as Brisbane made it an excellent study animal, allowing me to address questions that would not have been possible with rare or endangered species (Marzluff and Sallabanks 1998). The species' ability to cover large areas during foraging made it an appropriate study animal to examine foraging ecology across the urban matrix, which may not have been possible for species restricted to very small foraging areas. This thesis also examined if artificial roost habitat can provide temporary roosts for the white-striped

freetail bat and other insectivorous bats and assessed whether bat boxes can be used as a conservation tool in urban environments where natural hollow-availability is limited.

This chapter synthesises the main results from the original questions asked in **Chapters 3-7**, followed by a discussion on the implications for the conservation of the white-striped freetail bat in urban environments.

1. Hollow availability is limited in metropolitan Brisbane.

In **Chapter 3** I investigated two main questions: (1) What were the tree and landscape characteristics of roost trees used by the white-striped freetail bat?; and (2) What distinguished these trees from control trees of similar diameter, height, senescence and land tenure, which may or may not contain colonies of the white-striped freetail bat?

Roost trees of white-striped freetail bats were found either by tracking bats returning to new roost sites or through opportunistic searches. Over a three-year period only 34 roost trees were identified. Other hollow-dependent bat species are known to use more roost trees over the same tracking period (e.g., O'Donnell and Sedgeley 1999, Kunz and Lumsden 2003). All roost sites were located in hollows in eucalypts, often containing large cavities inside the tree trunk. Roost trees of the white-striped freetail bat were frequently found in highly modified, often urbanised habitats (parklands, school grounds, golf courses and paddocks) or in remaining bushland or regrowth forest reserves (< 100 ha) surrounded by suburban housing. This result contrasted with previous studies on roost site selection by other microchiropterans in Australia where roost trees were primarily in mature forests, even when the the bats foraged in open areas, such as rural environments, regrowth

and clearfelled forests (Taylor and Sava 1988, Herr and Klomp 1999, Law and Anderson 2000, Lumsden *et al.* 2002a,b).

The white-striped freetail bat selected a wide variety of eucalypts as roost habitats, but preferred old and dead eucalypts with large tree diameters (> 89 cm). The main difference between these roost trees and control trees of similar diameters and height were that roost trees were more decayed and had a higher number of hollows in the trunk and branches. Therefore tree health (level of senescence) was an important characteristic in predicting hollow-availability and hollow types of similar-sized trees in the greater Brisbane region. Physiological health (e.g., proportion of dead branches in the crown and large trunk cavities) was reported as a significant factor associated with vertebrate occupancy (Bennett *et al.* 1994, Lindenmayer *et al.* 2000, Gibbons and Lindenmayer 2002, Gibbons *et al.* 2002, Whitford 2002).

The results of **Chapter 3** showed that hollow-availability is limited in metropolitan Brisbane. Stands of remnant mature eucalypts occur particularly along the river and creek lines, and can act as recruitment trees. However, continuous land clearing and development in the greater Brisbane region due to increasing human population growth (Queensland Government 2004) is likely to lead to the loss of many of the remaining mature eucalypts. Conservation issues concerning urban Brisbane are relevant to Australia's urban expansion in general, as most Australian cities are centred on areas of considerable conservation significance for hollow-dependent fauna (Lunney and Matthews 2004).

2. Some roost trees are more important than others: habitat tree conservation in urban environments.

Chapter 4 aimed to explore whether network analysis could be applied to help devise management recommendations by quantifying the relationships between individual habitat trees used by one roosting group of white-striped freetail bats. I used roost-switching data collected over three seasons to construct a network representation of day-roosts in suburban Brisbane. I anticipated a network of roosts, where each roost had, on average, the same number of links to any other roost in the network. The results, however, showed a different roost network, with one roost, the communal roost, defining the architecture of the network because it had the most links to other day-roosts. Despite the large geographic range of the roost network (around 200 km²), each tree was connected to the hub through a path with a maximum length of two links. The highly connected hub tree in this study allowed members of the same roosting group to be distributed over a large area, potentially reducing competition for food and shelter but maintaining a cohesive roost network at the same time (Lewis 1995).

Furthermore, I suggest that network theory will be a useful in predicting conservation significances of individual roost trees for some bat species. The scale-free network demonstrated in this study can provide high tolerance against random roost removals, but will be susceptible to the selective removal of the hub tree (in this case the communal roost; Barabási and Albert 1999, Albert *et al.* 2000). The hub in this network could not have been predicted *a priori*. Apart from its central location with respect to other sites and its larger roosting group size, no attribute or pattern of attributes that I measured differentiated the hub tree or any of the other communal roost trees from other day-roost trees (**Chapter 3**). Communication with the local city council helped to formulate appropriate protection measures for each identified roost

tree (Rhodes 2003). Roost trees are now protected by Brisbane City Council (BCC) and are not allowed to be trimmed or removed by BCC staff without consultation.

3. *White-striped freetail bats roost apart but meet at night.*

Chapter 5 aimed to investigate the roost-switching behaviour of the white-striped freetail bat. Specifically I tested the hypothesis that members of one roosting group captured at the communal roost, selected day-roost sites with other members of the communal roost.

White-striped freetail bats exhibited the same roost-switching behaviour throughout three radio-telemetry periods and over 500 bat-days of radio-tracking: each roosted in separate roosts, switched roosts every eleven days on average, and associated with other bats only at the communal roost. I quantified associations between pairs of tagged bats using a pair-wise sharing index (Willis and Bringham 2004, 2005). The consistent negative value I obtained during this study indicated that members of the same colonial roosting group avoided roosting together. Yet despite this result, tagged white-striped freetail bats frequently met at the communal roost at the night. This roost-switching behaviour contrasts with that of big brown bats (*Eptesicus fuscus*) which associated with roost-mates more often than predicted by chance (Willis and Bringham 2004).

In microchiropterans, descriptions of fission-fusion societies are based on diurnal roost sharing behaviour of dyads (Kerth and König 1999, O'Donnell and Sedgeley 1999, Vonhof *et al.* 2004, Willis and Bringham 2004). I argue, however, that the fission-fusion pattern found in the white-striped freetail bat was based on individual movements between different roosts at night rather than diurnal group-roosting dynamics. Furthermore I postulated that the network of separate roosts used by hollow-dependent bats should be considered as one single inter-connected unit

(**Chapter 4**), similar to spatially large roosts, such caves, mines or buildings, as proposed by Willis and Brigham (2004).

4. The white-striped freetail bat's foraging behaviour was non-random with respect to both spatial location and the nature of the ground-level habitat.

In **Chapter 6** I investigated the other key resource for the white-striped freetail bat – its foraging habitat requirements in urban Brisbane. Specifically I aimed to identify its spatial foraging patterns and habitat preferences. I hypothesised that, due to the white-striped freetail bat's wing morphology, it would use all habitat types equally, similar to what has been found in other free-tailed bats (Arlettaz 1990, Carmel and Safriel 1998, Marques *et al.* 2004, Avila-Flores and Fenton 2005).

I used position fixes from radio-telemetry to quantify spatial foraging movements and habitat use. As expected the white-striped freetail bat flew at high speed and foraged over all landcover types, including grass-dominated flood plains, forests, suburbs and industrial areas. However, its observed foraging behaviour was non-random with respect to both spatial location and the nature of the ground-level habitat. The main feeding areas were within three kilometers of the communal roost and it foraged predominantly over the Brisbane River flood plains. Much of these areas were undeveloped by urban housing due to high flood risk. Vegetation in preferred foraging areas was dominated by large proportion of grass, riparian vegetation and scattered trees and the area provided water year-round. Similarly, in northern Queensland, foraging areas of the white-striped freetail bat had a small spatial distribution and it was not recorded over all surveyed urban habitats (Hourigan *et al.* 2006). The quality of the local habitat for insects may be the driving force behind the foraging habitat preference. The impact of the loss of foraging habitat for this species is still little understood but should be considered together with

the protection of its roost sites in the long-term conservation of the white-striped freetail bat in urban environments.

5. Bat boxes may not be a substitute for roost habitat loss for the white-striped freetail bat.

Chapter 7 explored bat boxes as a conservation tool for white-striped freetail bats and other insectivorous bats in urban areas and investigated two main questions: (1) Are bat boxes accepted by white-striped freetail bats or other insectivorous bats in Brisbane? and, (2) Does bat box usage and success depend on landscape characteristics, box design or box microclimate? This information could be useful in determining whether boxes can substitute for hollow-bearing trees.

Over the three-year period of this study, bat box acceptance in Brisbane increased steadily to over 80%. This study was successful in attracting several bat species into boxes. Two of these are listed as rare in Brisbane, two were common species, and one was an unidentified vespertilionid bat. No white-striped freetail bats used boxes. Furthermore, most boxes were only used occasionally. Infrequent box usage by bats has been reported in several bat box studies, where single individuals often used boxes for a day before moving on (Nagel and Nagel 1988, Shilton 1994, König and König 1995, O'Shea 1998). In Brisbane, boxes were more likely to be used if they were situated in clusters of at least six boxes within 50 m of each other, in an area with high grass cover within one kilometre, high forest cover within five kilometres radius, especially small and medium sized forest remnants. Regardless of season, boxes of all types were always significantly warmer and had a higher humidity than simultaneously recorded ambient microclimates. Box size and colour influenced internal microclimates, with unpainted boxes, and large boxes exhibiting

greater temperature and humidity gradients during summer. However, bat box microclimates did not influence box choice by bats during this study.

At this stage, box acceptance and usage by bats is still poorly understood. Acceptance may be influenced by multiple factors, such as landscape variables, natural hollow abundance, box design, locale climate at locations, microclimate inside boxes and the species' ecology. Further research is needed to understand the factors influencing box usage for each species, especially for the white-striped freetail bat.

8.3 Management implications for the white-striped freetail bat in urban environments

The white-striped freetail bat was able to cover large areas in search for high-flying insects as do other molossids (Lee and McCracken 2002, Marques *et al.* 2004, Avila-Flores and Fenton 2005). This suggests that the white-striped freetail bat is well suited to the present structure of urban landscapes, provided that suitable foraging habitat is retained and, most importantly, that roost trees are protected. Destruction of roost sites already appears to be one of the most important factors in the decline of bat populations generally, despite continued provision of food and water (Sheffield *et al.* 1992, Barclay and Brigham 1996, Kunz and Lumsden 2003, Parnaby and Hamilton-Smith 2004).

My thesis (**Chapters 4-6**) highlights the pivotal role of the communal roost for roosting groups of white-striped freetail bats in Brisbane. While it is difficult to predict the precise consequences of the removal of specific roost trees, **Chapter 4** suggests that removal of the communal roost could have a devastating effect. In the fragmented landscape of urban environments with relatively young stands of trees (Queensland Department of Natural Resources 1998, Queensland Government

1999, Rhodes and Wardell-Johnson 2006), it is likely that such a roost network currently used by the white-striped freetail bat would be not able to sustain the simultaneous removal of many hollow-bearing trees.

Nest boxes have been used as a wildlife management tool to maintain or increase population levels (Thomas *et al.* 1979, Schemnitz 1980, Menkhorst 1984, Stebbings and Walsh 1985, Wardell-Johnson 1986, Tidemann and Flavel 1987, Tuttle and Hensley 2000, Smith and Agnew 2002, Harper *et al.* 2005). The bat box study in Brisbane (**Chapter 7**) demonstrated that some bat species can be readily attracted into bat boxes. However, no evidence of usage by the white-striped freetail bat was recorded, despite the provision of larger boxes with larger entrance slits.

Studies in southern Australia showed that bat boxes attracted single male white-striped freetail bats in the Organ Pipe National Park and small roosting groups of up to eight white-striped freetail bats in urban Melbourne (Bender 2005, Evans *et al.* 2006). Future approaches might be able to attract more suburban white-striped freetail bats into boxes. However, the results of my thesis suggest a highly complex roost network a fission-fusion social network centred around one communal roost (**Chapters 4-6**). This roosting pattern should be taken into account if artificial roosts are to be used as a successful conservation tool for white-striped freetail bats.

Even if white-striped freetail bats can be attracted to bat boxes and single habitat trees can be retained, these are only be short-term solutions for habitat loss. Future planning must incorporate landscape features, landscape context, and management issues such as ongoing urbanisation and health and safety concerns. These factors then have to be combined with the roosting and foraging ecology of hollow-dependent species, such as the white-striped freetail bat (**Chapters 3-7**), to maximise the chances of the persistence of these species in suburban environments.

8.4 Future directions

A number of questions remain to be answered about the roosting and foraging ecology of the white-striped freetail bat. For example, the role of the communal roost in the ecology of this species needs further investigation. Do other roosting groups in Brisbane or anywhere in Australia show similar behaviour as the one studied? What is the real function of a central roost? Answering these questions will help understanding evolution of sociality in general.

It is possible that the roosting group of white-striped freetail bats consisted of close family members, as found in other fission-fusion bat societies (e.g., Kerth and König 1999). However, genetic relatedness would not explain why these white-striped freetail bats roosted away from the communal roost 90% of their time, even though they visited the roost regularly at night. Therefore the importance of other factors such as predator avoidance and roost temperatures should be investigated. These factors were important components in the roost choice by other microchiropterans (reviewed in Kunz and Lumsden 2003). I hypothesise that the benefits of splitting (e.g., predator avoidance and roost microclimate) are combined with the benefits of maintaining social relationships and information exchange on feeding sites.

Information exchange about food resources is one form of co-operation found in bats (Wilkinson 1995). The frequent fission-fusion of the roosting group of white-striped freetail bats in urban Brisbane (**Chapter 5**) is a good opportunity to test whether information transfer occurs in this group. If information on feeding sites were exchanged at the communal roost between individuals which roosted apart during the day, I would expect to find them to have overlapping feeding areas and a change of feeding sites at the same time. However, if bats roost and forage apart than I should find individual foraging sites. In the latter case, insect abundance and

landscape factors, such as land cover type, might be more important in defining feeding sites than coloniality and information exchange (Kerth *et al.* 2001).

Anecdotal evidence obtained during the radio-tracking study suggested that bat pairs repeatedly foraged in the same area. These areas varied each night. Bat-pairs could be found foraging together in Brisbane's central business district during one night and over forests the next night; sometimes in close proximity to the radio-tracking station. However, despite this observed behaviour, all bats mostly foraged over the flood plains of the Brisbane River close to the communal roost (Fig. 6.4; **Chapter 6**). It remains unclear why bats chose their communal roost because of its proximity to their normal feeding area or *vice versa*. While Vestjens and Hall (1977) have described the diet of the white-striped freetail bat (moths, beetles and bugs), it remains unclear whether preferred insects depend on aquatic habitats. Further studies are clearly needed to link habitat preference and food resource of this species.

In Brisbane the white-striped freetail bat was an obligate hollow-user. It relied on old eucalypts with large internal hollows. Maternity colonies often used large cavity spaces of hollow trunks and branches of one tree to roost in large numbers. Therefore artificial alternatives, such as small bat boxes, are unlikely to be suitable substitutes for habitat loss. Furthermore, box choice by bats in Brisbane or anywhere in Australia is still poorly understood and future research should focus on the systematic study of box design, microclimate, landscape factors and different species usage throughout seasons and years.

Declines in bat species once abundant in certain areas, such as the Brazilian free-tailed bat (*Tadarida brasiliensis*), require conservation attention today (Hutson *et al.* 2001). Urbanisation may affect abundant bat species via habitat loss, degradation and fragmentation. These influences include the loss or reduction in the quality of foraging habitat and food resources as well as the loss of roosts (reviewed in Racey

and Entwistle 2003). Introduced species, such as European honey bees and the common myna pose a significant danger to hollow-dwelling bats through competition for the same roost spaces (**Chapter 3**). Additionally, pesticides and pollutants (especially DDT, DDE, lead, cadmium and arsenic) may also contribute to the decline of urban bat populations as they are responsible for heavy mortality especially in young bats (Schmidt 1990, Thies and Gregory 1994). Further threats to bats include persecution and disruption at roost sites (Ferris 2006), often because of well-established superstition.

At present, the white-striped freetail bat is considered an abundant bat species in Australia, including in urban areas (Duncan *et al.* 1999). This appears to be due to its audible echolocation calls which are easily detected. However, baseline surveys are necessary in order to verify its distribution and abundance (von Helversen 1989, Racey and Entwistle 2003). Furthermore, quantifying population levels via recorded echolocation calls can be deceptive, as simple detection of these calls does not impart information on population numbers. Although the calls of white-striped freetail bats are frequently recorded in Brisbane (M. Rhodes, unpublished data), this thesis revealed an unexpectedly low number of roost trees in urban Brisbane, which might indicate that this species is not as abundant as previously thought. However, without precise knowledge about the white-striped freetail bat's population levels researchers will be unable to compare present with future abundance data and will hence face difficulties determining whether urbanisation affects urban white-striped freetail bat populations.

8.5 References

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Appendix I

Additional Data

Description of bats and radio-transmitters used in the radio-tracking study.

<i>Bat ID</i>	<i>Gend.^a</i>	<i>Weight (g)^b</i>	<i>FA (mm)^c</i>	<i>Transm. Model^d</i>	<i>Radio freq.^e</i>	<i>Transm. weight (g)^f</i>	<i>%^g</i>
04/11/2001					150.		
01	M	34.5	61.5	BD-2G	008	1.6	4.6
02	F	38	60.6	BD-2G	037	1.6	4.2
03	F	38	59.1	BD-2G	057	1.6	4.2
04	F	39.5	60.8	BD-2G	079	1.6	4.0
05	M	32.2	59.1	BD-2G	098	1.6	4.9
10/03/2002					Collars 151.		
06	F	35	60.6	MD-2C	101	1.62	4.6
07	F	42.5	63.8	MD-2C	119	1.62	3.8
08	F	38	62	MD-2C	140	1.62	4.2
09	F	37	62.3	LT1	199	1.2	3.2
10	F	36.5	62.5	LT1	457	1.6	4.3
11	F	34	58.6	LT1	877	1.2	3.5
08/02/2003					Collars 150.		
12	F	37.2	61.4	MD-2C	120	1.9	5.1
13	F	36.7	61.6	MD-2C	139	1.9	5.1
14	F	38.5	62.2	MD-2C	158	1.9	4.9
15	F	38	61	MD-2C	180	1.9	5
16	F	37.7	61.1	MD-2C	199	1.9	5
17	F	37.5	61.7	MD-2C	220	1.9	5
18	F	39	61.4	MD-2C	240	1.9	4.8
19	F	40.5	62	MD-2C	258	1.9	4.6

^aGender: F – Female; M – Male.

^bWeight (g) – Body mass (g) of each bat.

^cFA - Forearm length (mm) of each bat.

^dTransm. Model – Transmitter model used per bat; Collars - collar-transmitters.

^eRadio freq. – Prefix of each radio frequency per season (e.g., 150 and 151) and individual radio frequency per bat.

^fTrans. weight (g) – Weight of each transmitter (g).

^g% - Percentage of transmitter weight per bat's body mass.

Roost locations, tree species, tree variables, maximum group size per roost, and distance to the communal roost (CR) used by radio-tagged white-striped freetail bats.

Bat No.	Roost	Roost location^a	Tree species^b	DBH (cm)^c	Tree height (m)	Height of roost entrance (m)	Group size (n)	Distance to CR^d (km)
All 19	CR	BCC, park	E. MIC	100	24	6	291	-
01	Roost 1	PP, river bank	E. TER	156	43	30	21	5.1
02	Roost 1	PP, regrowth	DEAD	36	12	12	15	6.75
03	Roost 1	PP, golf course	E. MOL	113	24	11	15	1.35
06	Roost 1	CL, regrowth	DEAD	82	11	13	18	5.1
07	Roost 1	BCC, regrowth	E. RAC	59	24	15	1	5.6
08	Roost 1	BCC, regrowth	E. RAC	93	30	15	1	5.7
12	Roost 1	BCC, park	C. CIT	103	28	20	3	5.5
13	Roost 1	BCC, park	E. MAJ	47	25	14	7	8.5
13	Roost 2	PP, regrowth	E. TER	95	43	25	20	7.0
14	Roost 1	PP, paddock	E. RAC	85	25	7	4	13.1
14	Roost 2	PP, regrowth	E. RAC	77	30	12	1	13.5
15	Roost 1	BCC, park	E. MIC	60	24	18	5	6.6
15	Roost 2	BCC, park	DEAD	35	15	13	3	6.6
16	Roost 1	BCC, park	E. RAC	104	30	20	7	7.8
17	Roost 1	BCC, park	C. CIT	90	33	22	5	6.25
18	Roost 1	BCC, park	DEAD	67	15	15	1	5.9
19	Roost 1	regrowth BCC, regrowth	DEAD	89	15	15	1	5.75

^aRoost location: BCC – Brisbane City Council; park – BCC parklands; regrowth – BCC regrowth forest remnants; PP – private property; paddock – private horse paddock.

^bTree species: E. MIC - *Eucalyptus microcorys*; E. TER - *Eucalyptus tereticornis*; DEAD – dead eucalypt; E. MOL - *E. moluccana*; E. RAC - *E. racemosa*; C. CIT - *Corymbia citriodora* subsp. *variegata*; E. MAJ - *E. propinqua* var. *major*.

^cDBH – Diameter at breast height (1.3 m).

^dCR – communal roost.

Data of white-striped freetail bats captured during the period of the present study.

<i>Capture No.</i>	<i>Gend.^a</i>	<i>FA (mm)^b</i>	<i>Weight (g)^c</i>	<i>Age/Reprod.^d</i>	<i>Other features^e</i>
04/11/2001; Yeronga Park (communal roost)					
01	F	61.4	39.5	Adult/ Preg.	Previous breeder
02	F	60.6	38	Adult/ Preg.	Transmitter 150.037; first breeder
03	F	60.8	39.5	Adult/ Preg.	Transmitter 150.079; first breeder
04	F	59.1	38	Adult/ Preg.	Transmitter 150.057; white spot on hind-head
05	F	60.8	39	Adult/ Preg.	Previous breeder
06	F	61.1	37	Adult/ Preg.	Previous breeder
07	F	60.2	41.5	Adult/ Preg.	White spot on shoulder; previous breeder
08	M	61.5	34.5	Yearling?	Transmitter 150.008; throat gland secreting (Plate 2.3)
09	F	61.1	36	Not preg.	Extended stripes across belly from both sides, but not touching (Plate 2.1); nulli parous
10	F	60.8	40	Adult/ Preg.	Previous breeder
11	F	61.9	38	Adult/ Not preg.	Previous breeder
12	F	61.5	37.4	Adult/ Preg.	Thick white stripes; previous breeder
13	F	59.5	41	Adult/ Preg.	One white stripe in the middle and across belly; first breeder;
14	F	62.2	43	Adult/ Preg.	First breeder
15	F	60.7	34.5	Adult/ Not preg.	Nulli parous
16	F	60.8	35	Adult/ Preg.	$\frac{3}{4}$ stripes; previous breeder
17	F	60.3	41	Adult/ Preg.	Thick white stripes; first breeder;
18	F	60.6	36	Adult/ Preg.	Some white spots; first breeder
19	M	59.1	32.2	Yearling?	Transmitter 150.098; throat gland not secreting

Capture data cont.

Capture No.	Gend.^a	FA (mm)^b	Weight (g)^c	Age/ Reprod.^d	Other features^e
10/03/2002; Yeronga Park (CR)					
20	F	63	28	Juvenile	
21	M	63.5	28	Juvenile	Short stripes from armpit to about ½ cm above leg; testis visible
22	F	58.6	34	Adult/ post lact.	Transmitter 151.877; one stripe across chest; reddish fur, skinny bat
23	F	62.25	37	Adult/ post lact.	Transmitter 151.199; half stripe across chest: I- -I
24	F	62.5	36.5	Adult/ post lact.	Transmitter 151.457
25	F	63.8	42.5	Adult/ post lact.	Transmitter 151.119; white spot on left chest
26	F	60.6	35	Adult/ post lact.	Transmitter 151.101
27	M	58	27	Juvenile	White stripes, big white spot in middle of chest, 2 side bars I- -I
28	M	61.9	30.5	Juvenile	White stripes across chest, brown patch both sides; mites
29	M	61.4	26	Juvenile	
30	M	61.3	27	Juvenile	
31	F	62	38	Adult/ post lac	Transmitter 151.140; previous breeder
32	M	58.3	26.9	Juvenile	
33	F	64	33	Juvenile	
34	F	57.6	24	Juvenile	Dark fur; white stripes
35	M	61.2	33.5	Juvenile?	
36	M	60.2	29.5	Juvenile	Mites
37	F	62.1	33.5	Adult post lac	Lots of mites
38	M	62.1	32	Juvenile	
39	M	62	32	Juvenile	Grey to brown fur
40	F	62.5	38.5	Adult post lac	
41	M	59	28.5	Juvenile	
42	M	60.1	26	Juvenile	Almost stripeless

Capture data cont.

Capture No.	Gend.^a	FA (mm)^b	Weight (g)^c	Age/Reprod.^d	Other features^e
23/12/2002; Wulkuraka Park					
43	F	59.5	37	Adult; not obviously pregnant	Engorged breasts, does not seem to lactate; nulli parous - first breeder?; two white stripes across chest height and white dots underneath
44	F	62.5	34.5	Adult/not pregnant	Previous breeder; very skinny
45	F	61.6	36.5	Adult/not pregnant	Previous breeder; very skinny
46	F	59	40.5	Adult/not pregnant	Previous breeder; chocolate-brown fur
47	F	60.35	44	Adult/Preg.	Very pregnant, belly swollen; previous breeder
48	F	61.35	47.5	Adult/Preg.	Very pregnant, belly swollen; first breeder
49	F	62.9	37	Adult/not pregnant	Previous breeder
05/01/2003; Kenmore					
50	F	61.4	37.5	Adult/not pregnant	Dark chocolate-brown fur, darker dorsal; previous breeder
51	F	58.4	33	Adult/not pregnant	Light brown colour, few spots ventral; previous breeder
52	F	60.9	35.7	Adult/not pregnant	Dark colouration as bat #50; few very small white spots on left chest; previous breeder
53	F	59.9	37	Adult/not pregnant	Dark, as #50; small vene in right wing punctured: injury; previous breeder
54	F	64.5	31.1	Adult/not pregnant	Light brown fur; nipples underdeveloped, but have little black tip; nulli parous
22/01/2003; Wulkuraka Park					
55	F	58.9	41	Adult/NR	Two big and thick white stripes across chest, white stripes just above uropetagus, chocolate-brown dorsal fur; nipples are swollen, but completely pink, no black pigmentation
56	F	60	41.5	Adult/NR	Normal stripes, dark fur; previous breeder
57	F	63.1	43	Adult/NR	Normal stripes, dark fur; previous breeder
58	F	59.05	38	Adult/NR	White stripe around top of right nipple, similar stripe on left, not as prominent; previous breeder

Capture data cont.

Capture No.	Gend.^a	FA (mm)^b	Weight (g)^c	Age/Reprod.^d	Other features^e
59	F	61	38.5	Adult/ NR	Right nipple smaller and less pigmented than left one; previous breeder
60	F	63.35	39	Adult/ NR	2 white spots on right breast side; white tip on both nipples; previous breeder
08/02/2003; Yeronga Park (CR)					
61	F	64.1	37.2	Adult/ NR	Transmitter: 150.120; previous breeder
62	F	61.6	36.7	Adult/ NR	Transmitter: 150.139 previous breeder
63	F	61.1	37.7	Adult/ NR	Transmitter: 150.199; choc-brown fur; white fur in groin
64	F	60.8	36	Adult/ NR	Previous breeder
65	F	60.5	38	Adult/ NR	Obvious scar on dorsal and ventral left side; left leg permanently extended; previous breeder
66	F	61.4	36	Adult/ NR	Previous breeder
67	F	61.7	37.5	Adult/ NR	Transmitter: 150.220; choc brown fur with sandy brown ventral side; previous breeder
68	F	57.2	39.5	Adult/ NR	
69	F	61.3	34.5	Adult/ NR	Choc-brown with white band half way down on ventral side; previous breeder
70	F	60.6	37.5	Adult/ NR	Choc-brown with white speckles on underside; previous breeder
71	F	61.9	37.5	Adult/ NR	Previous breeder
72	F	60.8	34	Adult/ NR	Previous breeder
73	F	61.5	34	Adult/ NR	Previous breeder
74	F	59.2	33	Adult/ NR	Previous breeder
75	F	60.2	36.5	Adult/ NR	Ears flecked with pink looks like mite bites/scars; previous breeder
76	F	60.7	37	Adult/ NR	Sandy fur ventral, choc-brown dorsal
77	F	60.2	36.5	Adult/ NR	White fur next to nipple; previous breeder
78	F	61.5	36.5	Adult/ NR	Canines quite worn ;choc brown; previous breeder

Capture data cont.

Capture No.	Gend.^a	FA (mm)^b	Weight (g)^c	Age/Reprod.^d	Other features^e
79	F	62.2	38.5	Adult/ NR	Transmitter: 150.158; previous breeder
80	F	60.9	36.5	Adult/ NR	White flecks/spotts on abdomen; previous breeder
81	F	61.4	39	Adult/ NR	Transmitter: 150.240; previous breeder
82	F	60.1	37	Adult/ NR	White spots on back ;darkly pigmented skin; previous breeder
83	F	60	37.5	Adult/ NR	Sandy fur on ventral; white spots near tail join; previous breeder
84	F	61.5	35	Adult/ NR	White spots on abdomen; previous breeder
85	F	60.9	37.5	Adult/ NR	Darker choc-brown; white L shape pattern under each arm; previous breeder
86	F	61.3	35	Adult/ NR	White spots on back; previous breeder
87	F	61	37.5	Adult/ NR	White tuff on belly button; previous breeder
88	F	61.3	37.5	Adult/ NR	Partial white barring across midline; previous breeder
89	F	62.1	34	Adult/ NR	High tick infestation on wings, previous breeder
90	F	61.3	38.5	Adult/ NR	Tail fused in a 'club' shape - infection?, photo taken; previous breeder
91	F	60.1	37.5	Adult/ NR	White patch on back of head; previous breeder
92	F	60.4	37	Adult/ NR	Previous breeder
93	F	62	36.5	Adult/ NR	Transverse white crescent on abdomen; dark chocolate brown
94	F	62.5	35	Adult/ NR	Choc brown dorsal and paler ventral
95	F	58.9	32.5	Adult/ NR	Previous breeder
96	F	60.9	37	Adult/ NR	Rich brown dorsal and grey-brown ventral with red tones on head; previous breeder
97	F	60.4	37	Adult/ NR	Dark choc-brown; previous breeder
98	F	59.7	34.5	Adult/ NR	Right forearm scarred like it has been burnt – blistered; previous breeder
99	F	59.9	35	Adult/ NR	Rich brown; previous breeder
100	F	61	38	Adult/ NR	Transmitter: 150.180: broad white transverse ventral band (1 cm across) with ca. 1 cm break in midline; photo taken: "Tatiana". Previous breeder

Capture data cont.

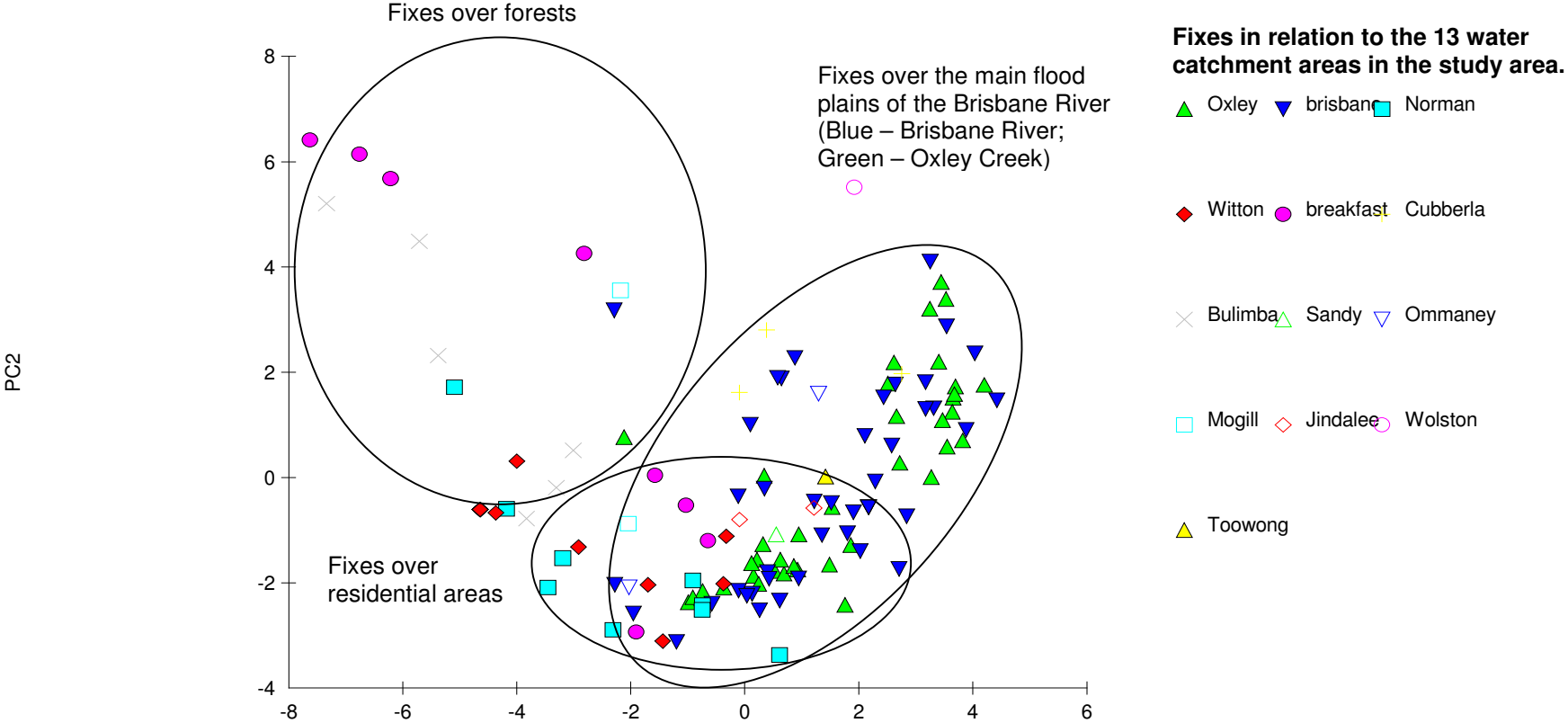
Capture No.	Gend.^a	FA (mm)^b	Weight (g)^c	Age/Reprod.^d	Other features^e
101	F	60.5	37	Adult/ NR	Rich brown; previous breeder
102	F	60.8	35	Adult/ NR	Rich brown dorsa; tiny white spots in small patch between shoulder blades on back; previous breeder
103	F	57.8	36.5	Adult/ NR	Medium choc-brown dorsal and paler brown ventral; previous breeder
104	F	61.1	35.5	Adult/ NR	Rich red brown dorsal and pale brown ventral; previous breeder
105	F	60.3	35.5	Adult/ NR	Very dark brown dorsal with white fleck/spot on left shoulder; previous breeder
106	F	60.1	36.5	Adult/ NR	Rich brown; previous breeder
107	F	60.5	34.5	Adult/ NR	Rich brown; previous breeder
108	F	58.8	31.5	Adult/ NR	Rich brown; previous breeder
109	F	62	40.5	Adult/ NR	Transmitter: 150.258; white spot on upper chest/lower throat: bow tie!; Amorphic donat-shaped white patch on rump; previous breeder
110	F	61	39	Adult/ NR	Blurred white shoulder patch on left; white transverse bar on left chest near nipple; previous breeder
111	F	59.8	34	Adult/ NR	Previous breeder
112	F	61.5	39	Adult/ NR	White transverse extension towards midline from white stripe on left side (near nipple); previous breeder
113	F	62.5	40	Adult/ NR	Previous breeder
114	F	60	32.5	Adult/ NR	Previous breeder
115	F	58.5	36.5	Adult/ NR	Teats regressed; previous breeder
116	F	61.4	41	Adult/ NR	Previous breeder
117	F	60.9	38	Adult/ NR	Teats regressed; previous breeder
118	F	59.9	36.5	Adult/ NR	Teats regressed; previous breeder

^a Gender: F – Female; M – Male.^b FA – Forearm length (mm) of bat.^c Weight – Body mass (g) of bat.^d Age/Reprod.: Age: Adult; Juvenile - young of the year; Yearling – Offspring from the last breeding season; Reproductive status of each bat: Preg – pregnant; post lac – post lactating; NR – non-reproductive.^e Other features – Individual markings, injuries, or other information gathered for each bat.

Calculated pair-wise sharing index (PSI) per bat-pair (Chapter 5).

<i>Bat-pair</i>	<i>PSI</i>
2002	
06x07	-0.31
06x08	-0.51
07x08	-0.47
2003	
12x13	-0.65
12x14	-0.76
12x15	-0.76
12x16	-0.99
12x17	-0.86
12x18	-0.86
13x14	-0.39
13x15	-0.29
13x16	-0.42
13x17	-0.34
13x18	-0.5
13x19	-0.42
14x15	-0.48
14x16	-0.5
14x17	-0.4
14x18	-0.42
14x19	-0.54
15x16	-0.57
15x17	-0.27
15x18	-0.44
15x19	-0.78
16x17	-0.55
16x18	-0.76
16x19	-0.84
17x18	-0.46
17x19	-0.55
18x19	-0.7

Principal Component Analysis of radio-tracking fixes of foraging white-striped freetail bats.



PC2 Variation:	12%
500m residential	-0.384
500m road:	-0.257
1000m road:	-0.259
1000m forest>100ha:	0.255
1000m total forest:	0.263

PC1 Variation:	21%
500m total forest:	-0.259
1000m riparian veg:	0.272
1000m forest > 100 ha:	-2.43
1000m total forest:	-0.275
Altitude:	0.315
Distance to water:	0.241

Appendix II has not been published. It is available in the original document held in the Griffith University Library.