

**Seasonal home range and foraging movements  
of the Wahlberg's epauletted fruit bat  
(*Epomophorus wahlbergi*) in an urban  
environment**

DOMINIC PAUL ROLLINSON

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## ABSTRACT

Urbanisation through the process of habitat loss and fragmentation has caused drastic changes in ecosystem dynamics around the world. Many species can no longer survive in these urban areas; however there are those species that have been able to survive and in fact thrive in the newly created habitats. With increasing urbanisation it is important that animals are able to adjust to a life in close association with humans. One such group of organisms which has adjusted well to urbanisation is the suborder Megachiroptera (Chiroptera). Some species from this suborder have benefited from increased food and roost resources in certain urban areas. Exotic fruiting plants (introduced purposely and accidentally) as well as increased cultivated gardens have provided additional food sources in some urban environments, while man-made structures, and increased suitable vegetation, have provided additional roosting opportunities. Although these urban dwelling species live in close association with humans, very little is known of their ecology in urban areas. Wahlberg's epauletted fruit bat *Epomophorus wahlbergi* is one such species of which little is known of its suburban ecology despite its increased presence in many urban areas.

This study on the ecology of *E. wahlbergi* was conducted from February to October 2011 in the urban environment of Pietermaritzburg, South Africa. The aim was to examine foraging movements and habitat use of *E. wahlbergi* in this urban environment. The objectives were to determine seasonal differences in foraging movements and home range sizes in this urban environment. In addition the roosting dynamics and roost characteristics of *E. wahlbergi* in this urban environment were determined,

In late summer, it was found that individual *E. wahlbergi* movements ranged considerably, with some bats making extensive flights to different parts of town while others stayed in particular areas throughout; no bats were recorded to have left the urban environment. Some of the larger distances covered in a single night's movements were two and five km. In late summer roosting fidelity varied between individual bats; all the individual bats changed their roosts at least once during late summer. Some individuals had as many as three known daytime roost sites. There was a difference in home range size between the sexes; with females occupying a larger home range size than males. This variation in movement patterns of individual bats suggests that their social interactions, roost site preferences, or dietary preferences vary between individuals in late summer.

A significant difference in home range size and habitat use by *E. wahlbergi* was found between winter and spring, with home range sizes being larger in winter. The increased home range sizes and habitat use in winter were a consequence of bats feeding on the fruits of the alien invasive *Syringa* (*Melia azedarach*) with few other trees in fruit. Consequently bats had to move greater distances for food in winter. In spring, fruit availability was greater and more varied including both indigenous and exotic fruits. Consequently in winter, the bats were more reliant on a few fruiting species to meet their dietary requirements than during spring. Bats changed their roosts regularly in summer, winter and spring. There was considerable variation in roost temperatures however roost temperatures were higher than ambient temperatures. Roosts in man-made structures were higher in temperature than those in natural vegetation. This study suggests the importance of temperature in the selection of daytime roosts, however other factors such as predator avoidance and proximity to food resources are also considered in selection of daytime roosts.

Within the order Chiroptera, species from the suborder Microchiroptera have generally not been well represented in urban areas, it is important that the reasons for this be better understood. Further research is still required to better understand the ecology of urban dwelling species as well as to understand the reasons why many species are not able to adjust to urban environments.

## PREFACE

The data described in this thesis were collected in the Republic of South Africa from September 2010 to December 2011. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs and co-supervision of Dr Joy Coleman.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

*D. Rollinson*

.....

Dominic Rollinson

February 2012

I certify that the above statement is correct...

*Downs*

.....

Professor Colleen T. Downs

Supervisor

February 2012

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### DECLARATION 1 - PLAGIARISM

I, Dominic Paul Rollinson, declare that

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### DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

#### Publication 1

**DP Rollinson, CT Downs and J Coleman. Movements and foraging dynamics of Wahlberg's epauletted fruit bat in an urban environment, during late summer.**

*Author contributions:*

DPR conceived paper with CTD and JC. DPR collected and analysed data, and wrote the paper. CTD and JC contributed valuable comments to the manuscript.

#### Publication 2

**DP Rollinson, CT Downs and J Coleman. Seasonal differences in foraging dynamics, habitat use and home range size of Wahlberg's epauletted fruit bat in an urban environment.**

*Author contributions:*

DPR conceived paper with CTD and JC. DPR collected and analysed data, and wrote the paper. CTD and JC contributed valuable comments to the manuscript.

#### Publication 3

**DP Rollinson, CT Downs and J Coleman. Roost temperature and roost fidelity of Wahlberg's epauletted fruit bat, in an urban environment.**

*Author contributions:*

DPR conceived paper with CTD and JC. DPR collected and analysed data, and wrote the paper. CTD and JC contributed valuable comments to the manuscript.

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## Chapter 1

### Introduction

The movement of organisms is considered a complex process that depends on the individual's ability to perform tasks as well as the nature of the landscape on which it moves (Getz & Saltz, 2008). Recently great interest has been shown in better understanding the movements of a variety of animal and plant taxa. This interest in movement ecology has even been called a new movement ecology paradigm (Nathan, 2008). Understanding movement ecology is important for a number of reasons; most importantly it is seen as a crucial component of climate change, habitat fragmentation, biological invasions and the spread of pests and diseases (Nathan, 2008). Foraging movements are important as they influence the spatial distribution as well as genetic structure of plant populations (Heithaus & Fleming, 1978).

It is important to better understand the movements of animals as this will shed more light on the ecology, life history, behaviour and conservation of most animals (Rubenstein & Hobson 2004). It is particularly important to study movement patterns of threatened and endangered species as this may aid conservation strategies. With the advancement of modern radio-telemetry equipment and techniques, animal movements may be monitored without having to rely on chance encounters of mark-recapture studies (Koehler, Reynolds & Anderson, 1987). Advancements in radio-telemetry technology have meant that transmitter weights have decreased dramatically; this now means that they can be attached to smaller animals such as mice, rats, squirrels (Koehler *et al.*, 1987) and bats (Bonaccorso *et al.*, 2002).

Research on the movements of bats (order Chiroptera) has increased recently, in particular research on the migratory movements of specific species (Spencer, Palmer & Parry-Jones, 1991; Rodrigues & Palmeirim, 2007; Richter & Cumming, 2008; Fraser, McKinnon & Diamond, 2010). It is important to understand the movements (foraging and reproductive) of bats as many species are considered threatened, and by better understanding their movements, the ecology of many species will be better understood. Furthermore, an understanding of the migratory movements may enhance conservation efforts of bats (Rodrigues & Palmeirim, 2007). In addition, many bat species are

important ecosystem components (Whittaker & Jones, 1994; Shilton *et al.*, 1999; Hodgkison & Balding, 2003). In order to conserve bats it is important to understand their roosting requirements, and protect all their known roosting areas that are used throughout the year (Rodrigues & Palmeirim, 2007). It is also important to know the foraging movements and habitat use of bats. Certain bat species will take specific routes to get to their feeding areas (Best & Hudson, 1996), and these routes need be conserved. For example, the endangered gray bat (*Myotis grisescens*) will follow rivers and waterways for up to 70 km in order to reach open water bodies over which it forages for insects (Best & Hudson, 1996). Some frugivorous bats are also known to travel large distances on foraging flights, sometimes up to 100 km (Taylor, 2005), which means they have important implications for the dispersal of seeds.

More recently the order Chiroptera has been split into two suborders; Pteropodiformes and Vespertilioniformes (Eick, Jacobs & Matthee, 2005). Previously Chiroptera were split into the two suborders Megachiroptera and Microchiroptera. The primary differences between the two former suborders include; Megachiroptera are generally larger than Microchiroptera, Megachiroptera (with a few exceptions) do not use echolocation while Microchiroptera are reliant on echolocation, and Microchiroptera lack a claw on the second toe of the forewing while Megachiroptera do not. Megachiroptera eat fruit, nectar and pollen while Microchiroptera are generally insectivorous. Pteropodiformes now include; Pteropodidae, Hipposideridae, Rhinolophidae and Megadermatidae, and so are not just confined to the Pteropodidae, while Vespertilioniformes incorporates all other bat families (Monadjem *et al.* 2011). In this thesis we have chosen to use the terms Megachiroptera and Microchiroptera.

Within the order Chiroptera, the two families Phyllostomidae and Pteropodidae include many frugivorous species, however the family Phyllostomidae also includes nectarivorous, insectivorous, carnivorous, and folivorous species (Kunz, 1982). Frugivorous Phyllostomidae are represented throughout the New World while Pteropodidae are represented in the Old World (Fleming, Breitwich & Whitesides, 1987). Although many of these species from the two families are frugivorous, there are differences in the foraging zones that they dominate. Phyllostomidae bats have radiated into basic feeding zones; canopy tree feeders and understory feeders while Pteropodidae

are canopy and forest-edge feeders (Fleming *et al.*, 1987). Community diversity of Phyllostomidae bats is usually higher than the diversity of Pteropodidae (Fleming *et al.*, 1987)

### **Bats as seed dispersers**

Animals that are seen as important seed dispersers of fruit and seeds include birds and mammals, and to a much smaller degree; reptiles, fish and amphibians (Corlett, 1998). Diurnal and nocturnal frugivores produce qualitatively and quantitatively different seed dispersal patterns, due to differences in abundance of species', food habits, movement patterns and seed passage rates (Fleming, 1988).

Martinez and Gonzalez-Taboada (2009) identified dispersal modeling as one of the main research goals in plant ecology, due to its importance in shaping plant communities. Dispersal distances are seen as critical to the dynamics of various ecological and biogeographical processes; some of these processes include recruitment patterns, range expansion, genetic structure and community diversity (Nathan & Muller-Landau, 2000). Long distance dispersal events are responsible for the ability of plants to achieve fast migration rates and so be able to respond to environmental changes (Clark, Macklin & Wood, 1998). However evaluating seed dispersal is considered complicated as it is difficult to determine which deposited seeds originate from which tree, due to the large amount of overlap of individual seed shadows (Turchin, 1998). Seed dispersal is not always considered in a positive light with regards to conservation and ecology, as seed dispersers can often aid in the establishment and spread of alien invasive plant species (Trakhtenbrot *et al.*, 2005).

Birds are seen as extremely important dispersers of seeds especially for long-distance dispersal and hence are thought to have a major importance in a biogeographical context (Debussche & Isenmann, 1994). Patterns of seed dispersal by birds can be monitored in a number of ways; 1) indirectly, by observing the actions of fruit-eating birds, 2) indirectly, by analysing the spatial patterns of fleshy-fruited plant seedlings, and 3) directly by collecting seeds that are visible on the ground (Debussche & Isenmann, 1994; Jordaan, Johnson & Downs, 2011). Frugivorous bird species often have substantial

foraging ranges, as they often need to move from fruiting trees in different areas (Levey, 1988).

Some bird species appear to be more effective as seed dispersers than mammals (including bats), as birds are more likely to swallow the entire fruit and thus transport the seed away from the parent tree, while mammals will often separate the seed from the fruit and deposit the seed beneath the parent tree (Howe & Smallwood, 1982). This demonstrates the importance of birds as seed dispersers in Africa, especially in areas where hunting for bushmeat has resulted in declines of large- to medium-sized seed dispersers. Birds and bats seem to be the least affected by hunting (Fa *et al.*, 2005), as more effort seems to be put into hunting larger animal species (Coad *et al.*, 2010). However, in other areas, such as certain Pacific Islands, fruit bats are hunted extensively, to such an extent that their numbers have become dangerously low (Craig *et al.*, 1994). This lowering of the numbers of fruit bats may have an adverse effect on the dispersal of certain species of fruiting plants.

In other regions such as the tropics, primates constitute around 25 % and 40 % of frugivore biomass and hence perform extremely important ecosystem functions (Chapman, 1989). Large proportions (60 %) of the seeds they eat and then defecate still remain viable and so these primates contribute to seed dispersal (Chapman, 1989), just as many Chiroptera species do.

Frugivorous bats are known to play important roles in seed dispersal in tropical communities and exhibit mutualistic co-evolutionary relationships with food plants (Dumont, 1999). A number of bat species are known to remove fruits from trees and then fly with them to nearby feeding roosts (Morrison, 1978), which helps with seed dispersal and hence forest regeneration. The regeneration of some forests, such as those in Africa, rely heavily on frugivorous bats, especially of the family Pteropodidae (Thomas, 1984). It is particularly important to conserve fruit bats in Africa as many other large- to medium-sized seed dispersers are in serious decline (Fa *et al.*, 2005). Thomas (1984) found that in successional areas in Cote d'Ivoire, 75 % of the fruits from eight different tree species were removed at night, and 95 % of seeds were dispersed by bats.

Frugivorous bats feed on fruit in an unusual fashion; juice is extracted by squeezing the pulp between the palate and tongue (Shilton *et al.*, 1999). In this way very

little of the fruit is actually consumed and the rest (including skin and seeds) is spat out. These areas beneath feeding roosts, where the rejected sections of the fruit are spat out, are known as bat spats. However not all the seeds are spat out and some of the smaller seeds are in fact digested (Shilton *et al.*, 1999). Research has shown that seeds from bat spats of certain plant species have a better probability of germination than seeds that have not been digested by bats (Shilton *et al.*, 1999; Jordaan *et al.*, 2011). Travaset (1998) found similar results when testing the seed germination of 200 plant species after passage through the gut of vertebrate frugivores. It was found that seed dispersers often have a positive effect on the ability and rate of germination of the seeds in approximately half of the seeds they consume (Travaset, 1998). The animals which were tested included birds, non-flying mammals, bats, reptiles and fish (Travaset, 1998). Overall it was found that enhancement of germination of the seeds occurred roughly twice as often as inhibition (Travaset, 1998). Bats are known to disperse seeds in two general categories 1) by plucking large-seeded fruits and the subsequent discarding of the seed (generally at a nearby site), and 2) unintentional ingestion and subsequent defecation or oral ejection of small seeds (Whittaker & Jones, 1994). Generally frugivorous bats in Africa do not ingest seeds or skin but discard them as part of their spats (Fenton *et al.*, 1985). These spats are usually a distance away from the parent tree and so contribute to seed dispersal (Fenton *et al.*, 1985).

Although birds and bats both eat and disperse fruits, they have different preferences as to which types of fruits they will eat (Baker, Baker & Hodges, 1998). Based on sugar content of Old World fruits, it was suggested that bats of the suborder Megachiroptera would seek fruits of higher sucrose content (Baker *et al.*, 1998). However recent research of fruit available and food preferences shows a range in sugar preference (Coleman & Downs, 2012; Downs, Mqokeli & Singh, 2012; Wilson & Downs, 2012). Species from the suborder Megachiroptera have also been known to chew leaves (folivory), which further illustrates their broad dietary range (Kunz & Diaz, 1995).

There also appears to be a difference in the colour of the fruits chosen by bats known as the 'bat dispersal syndrome' (Hodgkison & Balding, 2003). The distinct morphology of the fruits chosen by bats shows just how important bats are as fruit dispersers, as well as how little dietary overlap exists between bats and other frugivores

(Fleming, 1979). In the Neotropics fruits dispersed by bats are morphologically different from those fruits dispersed by birds, and can be differentiated by humans based on colour and odor (Fleming, 1988). Phyllostomid bats generally consume dull green fruits which give off a distinct odor when ripe, while birds tend to consume fruits which are red, purple and blue in colour and are generally odourless (Fleming, 1988; Korine, Kalko & Herre, 2000).

Species from the wild fig genus *Ficus* form an important dietary component of Pteropodid bats (Taylor, 2005). Wild figs may attract a high diversity of frugivores because of the absence of toxic compounds (Janzen, 1979b) and high calcium content found in the pulp (O'Brien, Kinnaird & Dierenfeld, 1998). However, figs are very high in fibre content, which will have negative effects on the digestive rate, with a low protein and fat content (Tello, 2003). Despite the fact that a large amount of seeds are consumed and hence dispersed by a number of different frugivores, it has been shown that up to 55 % of fig seed crop are destroyed by parasitic wasps (Janzen, 1979a). However the wasps do play a vital role as they pollinate the fig, and only once the wasps have pollinated the figs, do they become appealing to other frugivores, such as fruit bats (Janzen, 1979b), thus reducing conflict between pollinator and frugivore (Dumont *et al.*, 2004). Figs that the wasps successfully oviposit are known as gall figs (Dumont *et al.*, 2004). Although gall figs are not completely avoided by bats (Phua & Corlett, 1989), seed figs are preferred (Dumont *et al.*, 2004). Gall figs not taken by frugivores and instead deposited under the parent tree, are thought to be used by the parent tree for their nutrients, especially when there is a lack of resources (Harrison & Yamamura, 2003).

A further difference between bats and birds as seed dispersers is the gut retention time of ingested seeds. Pigeons and doves are considered by some to be the most important dispersers of seeds, as they eat large amounts of fleshy fruits and travel large distances to forage (Ridley, 1930; Bucher & Bocco, 2009). Pigeons and doves retain seeds in their gut for long periods of time (as long as 12 h) which means the seeds may be transported relatively large distances before defecation. Generally not all species of bird retain seed in the gut as long as pigeons and doves, however they do seem to retain seed longer than most bat species. Wolton *et al.* (1982) found that gut retention time for bats increases with animal size. For some of the larger species, gut retention time lasted up to

70 min (Wolton *et al.*, 1982) while some of the smaller bats average 12-30 min (Tedman & Hall, 1985). As mentioned, most southern African Pteropodid species discard seeds in spats rather than passing them through the gastrointestinal tract (Fenton *et al.*, 1985), however small seeds may be swallowed and remain in the gut overnight and hence may be dispersed further distances (Shilton *et al.*, 1999).

The „bat dispersal syndrome’ in the Paleotropics is morphologically variable and involves fruits of a number of different colours (reds, purples, greens and blues), often with distinct odors when ripe (Eby, 1998). Other characteristics of fruits that are regularly consumed by fruit bats of the Paleotropics include species with special modes of presentation. These fruits are produced directly from the bole of the tree’s main branches, or at the end of long pendulous stalks (Hodgkison & Balding, 2003). Further criteria that the larger Pteropodids of the Paleotropics may use to select fruit include; plant height, available crop density per tree and tree species (Utzurum, 1995), as well as those fruits with unfresh, rancid or musty odor when ripe (Whittaker & Jones, 1994).

### **The role of bats in reforestation**

The diversity of seed dispersers is believed to be reduced in forests which are considered disturbed and/or fragmented compared to undisturbed forests (Kirika *et al.*, 2007). Bats and birds are believed to be the most important dispersers of seeds in these fragmented and transformed habitats (Galindo-Gonzalez, Guevara & Sosa, 2000). In Neotropical rainforests 80 % of trees and shrubs are thought to rely on bats and birds for seed dispersal (Howe & Smallwood, 1982). Bats and birds are seen as important seed dispersers as they disperse seeds of pioneer and primary species, thus possibly connecting forest fragments and maintaining plant diversity (Galindo-Gonzalez *et al.*, 2000). Consequently they contribute to recovery of woody vegetation in disturbed areas (Whittaker & Jones, 1994; Galindo-Gonzalez *et al.*, 2000). In pastures in Mexico Galindo-Gonzalez *et al.* (2000) found that 32 % of seeds were dispersed by bats only, 47 % by birds only, while 21 % of the seeds were dispersed by both bats and birds. Birds are generally able to disperse larger seeds due to their larger gullet sizes than bats which can only ingest small seeds (Whittaker & Jones, 1994). Due to the differences in foraging behaviour between birds and bats it means they will produce different seed shadows



(Galindo-Gonzalez *et al.*, 2000). Birds deposit most of the seeds from a perched position under the canopy while bats tend to defecate in flight (Galindo-Gonzalez *et al.*, 2000). Although these dispersed seeds are unlikely to lead to the full recovery of the forest, the seed dispersers at some disturbed sites are still considered to be efficient and abundant (Galindo-Gonzalez *et al.*, 2000).

The reforestation of islands that have been completely deforested by natural disasters, such as volcanoes, can be largely attributed to bats and birds (Whittaker & Jones, 1994). This was the case with the recolonisation and eventual reforestation of the island of Krakatau, which was left sterile after massive volcanic activity in 1883 (Whittaker & Jones, 1994). The fruit bat species' (*Pteropus* species) found on Krakatau and its neighbouring islands are thought to forage up to 70 km in a night, and so it is conceivable that seeds may be spread large distances to different islands by the bats (Marshall, 1983). Although the exact numbers of plant species brought to the island by bats is not known, what is known is that bats and birds have played an important role in the recolonisation of the island (Whittaker & Jones, 1994).

Across many Pacific islands, bats are considered extremely important seed dispersers and along with birds, are some of the few frugivores found on the islands (McConkey & Drake, 2002). The loss of vertebrates such as flying foxes (large Pteropodidae species of south-east Asia and Australia) and doves, on Pacific islands, has had a negative effect on natural forest processes such as seed dispersal (McConkey & Drake, 2002). A loss of seed dispersers will have a greater affect on a Pacific island forest than a continental forest, as island trees rely on fewer seed dispersers than continental trees (McConkey & Drake, 2002), thus emphasising the importance of bats as seed dispersers and reinforcing the importance of their conservation.

### **Bats in urban environments**

Animals have been categorised in terms of their persistence to urbanization, either as urban avoiders, urban adapters or urban exploiters (McKinney, 2002). Megachiroptera (including *Epomophorus wahlbergi*) are categorized as urban adapters, as they benefit from but do not rely on additional resources in the suburban environment. Many species from the suborder Megachiroptera can often be seen roosting in cities and suburbia,

presumably as a response to loss of suitable forest habitat or alternatively due to availability of suitable roost and feeding opportunities in this transformed landscape (Birt *et al.*, 1998). In Australia a number of flying fox species have lost a considerable amount of potential habitat and resources due to development since European settlement (Markus & Hall, 2004). A number of native and exotic fruit-bearing plants have been identified as food substitutes to those plants that would traditionally make up large components of flying foxes' diets (Markus & Hall 2004). Some of these fruiting trees such as bananas (*Musa acuminata*), paw-paws (*Asimina triloba*), peaches (*Prunus persica*) and mangoes (*Mangifera indica*) are now more readily available to the flying-foxes as they are cultivated in orchards (Tidemann, 1997). Gardens have also been identified as a source of leguminous foliage which is occasionally used as a protein supplement (Richards, 1995). In urban environments there is likely to be an increase in the amount of potential roosting resources as well as foraging resources, as fruit and floral resources may increase in abundance, detectability and reliability due to the watering of these plants in gardens (Markus & Hall, 2004).

Foraging movements of various flying fox species in urban environments in Australia have been well documented (Markus & Hall, 2004; McDonald-Madden *et al.*, 2005; Parris & Hazell, 2005; Schmelitschek *et al.*, 2009). Markus and Hall (2004) followed the foraging movements of the black flying fox (*Pteropus alecto*) in the urban environment of Brisbane, Australia. They found that individuals would only visit two to three foraging sites per night and that they would return to these foraging sites two or three times a night. A number of the tracked bats were found to return to the same foraging sites for weeks and even months, suggesting a large degree of foraging fidelity, even during winter and summer months (Markus & Hall, 2004). Depending on which roost the bats used, they would average between 2.9 and 7.5 km to specific foraging sites (Markus & Hall, 2004). Fleming (1988) found that the Phyllostomid bats *Carollia perspicillata*, *Artibeus jamaicensis* and *Phyllostomus hastatus* spend relatively little time on the wing while foraging, and appear to forage in an energetically conservative fashion. The bats would take fruit from a number of different trees (native and exotic) during summer, while during winter the diversity of fruits taken was reduced (Markus & Hall, 2004).

Some insectivorous bat species also thrive in urban environments compared with natural environments and are generally less affected by urbanisation as they can cover large distances per night, move fast between habitat patches and are able to quickly react to resource fluctuations and roost availability (Jung & Kalko, 2010). Jung and Kalko (2010) observed a number of insectivorous bat species in South America across different environments; forest and town. They found that foraging activity was highest around streetlights in town, intermediate in the dark areas of town and lowest in the forested areas. Another reason for these bat species being able to live in urbanised habitat is because of the abundance of suitable roosting sites, such as in houses and under bridges (Keeley & Keeley, 2004). This again shows how some bat species have been able to adjust to certain urban environments and in many cases they have been able to thrive as if in a natural environment. This ability to be able to adjust to urban life may be because of plasticity in terms of physiology, behaviour and feeding ecology of the species.

### **Wahlberg's epauletted fruit bat**

Wahlberg's epauletted fruit bat (*E. wahlbergi*) is a relatively large frugivorous bat species that is common throughout Africa, south of the Sahara. *Epomophorus wahlbergi* belongs to the suborder Megachiroptera within the family Pteropodidae which consist of the Old World fruit bats (Taylor, 2005). The males average 169 mm in length and 145.7 g in weight while females are smaller and average 140 mm in length and 112.3 g in weight (Taylor, 2005). They are a pale buffy-brown to brown on the upperparts and are a pale buffy-brown on the underparts (Taylor, 2005). Males have glandular patches on the shoulder which are covered with long white hairs, while both sexes have white patches at the base of their brown ears (Taylor, 2005). It can only be distinguished from Gambian epauletted fruit bat (*Epomophorus gambianus*) by careful examination of the number of ridges on the palate. *Epomophorus wahlbergi* has only one ridge on the palate behind the molars, while *E. gambianus* has two ridges behind the molars (Taylor, 2005).

In southern Africa *E. wahlbergi* occurs from central Mozambique and eastern Zimbabwe in the north, down along the east coast to as far south as the Western Cape. It is common throughout the province of KwaZulu-Natal, where it is found in savanna, woodland and forest margins as long as there are fruit-bearing trees in the area. Although

they generally only occur in areas with a mean annual rainfall of more than 700 mm, they can be found in river valleys in drier areas with a minimum annual rainfall as low as 250 mm (Taylor, 2005).

Although *E. wahlbergi* favour soft fruits, such as those from wild figs (*Ficus* spp.) (Table 1), they will take a wide range of fruits from a number of different indigenous species as well as from orchards (Taylor, 2005). They will also feed extensively on cultivated fruits such as mango, guava (*Psidium guajava*), bananas, peaches and pawpaws (Sowler 1983). They are known to carry the fruit some distance before eating, after which the juice is swallowed and most of the rest of the fruit is spat out (Sowler, 1983; Monadjem *et al.*, 2011). According to Shilton *et al.* (1999), despite external fruit handling, frugivorous bats are reported to swallow as much as 80 % of small (> 0.5 mm<sup>2</sup>) seeds. Only small seeds are digested because the gastrointestinal tract is very narrow in most fruit bats (Shilton *et al.*, 1999). In South Africa *E. wahlbergi* is thought to cause damage to litchi (*Litchi chinensis*) orchards, however this damage is minimal and most of the damage by fruit bats can be attributed to Egyptian rousettes (*Rousettus aegyptiacus*) (Jacobsen & Du Plessis, 1976).

**Table 1** Indigenous tree species known to be eaten by *E. wahlbergi* in southern Africa (Coates Palgrave, 1981; Monadjem *et al.*, 2011).

Species	Size of Fruit (cm)	Colour of Fruit	Fruiting period
<i>Upaca kirkiana</i>	2.5-3	Rusty-yellow	October-December
<i>Upaca sansibarica</i>	1.5-2	Yellow	June-July
<i>Adansonia digitata</i>	12	Yellowish-grey	April-May
<i>Parinari curatellifolia</i>	3.5-5	Russet-yellow	October-January
<i>Pseudolachnostylis maprouneifolia</i>	2	Pale Yellow	May onwards
<i>Ficus sur</i>	3-4	Pink-red	September-March
<i>Ficus trichopoda</i>	2.5	Red	September-March
<i>Ficus natalensis</i>	1	Yellow-brown	March-January
<i>Ficus sycamorus</i>	3	Yellow-orange	July-December
<i>Voaconga thouarsii</i>	7-9	Dark green	December-September
<i>Tabernaemontana ventricosa</i>	2.5-4	Dark green	April-September
<i>Syzigium cordatum</i>	1.5	Purple	November-March
<i>Bridelia mucrantha</i>	0.8	Blackish	January-March

<i>Euclea natalensis</i>	0.7-1.0	Black	October-June
<i>Eugenia capensis</i>	1.6	Purplish-black	April-November
<i>Ekebergia capensis</i>	1.5	Pink-red	December-April
<i>Annona senegalensis</i>	4	Yellow-orange	December-March
<i>Podocarpus latifolius</i>	1-1.5	Fleshy	December-February
<i>Afrocarpus falcatus</i>	1.5	Yellow	September-May
<i>Sideroxylon inerme</i>	1.2	Purplish-black	July-January
<i>Rauvolfia caffra</i>	1.3	Black	October-March
<i>Halleria lucida</i>	1	Black	August-
<i>Sclerocarya caffra</i>	3.5	Yellow	February-June
<i>Trichelia emetica</i>	2.5-3	Creamy-brown	December-March
<i>Harpephyllum caffrum</i>	2.5	Red	August
<i>Mimusops caffra</i>	2	Orange-red	April-September

*Epomophorus wahlbergi* are known to forage solitarily, removing fruits from the plants and then consuming the fruit some distance away in small trees or vine tangles (Taylor, 2005). The areas where the fruit is consumed are known as feeding roosts (Voigt, Farwig & Johnson, 2011). In a night's foraging an individual bat can easily consume more than its body weight in fruit and can harvest 10-80 fruits. During the night's foraging the bats commute between the daytime roosts, feeding roosts and one or more resource patches (Fenton *et al.* 1985). Scouting flights are taken occasionally when the bats fly over their home ranges looking for any ripening fruit; these scouting flights are often done on darker moonless nights when predatory risks are reduced. After the night's feeding the bats return to their daytime roosting sites which may be in natural vegetation or man-made structures in colonies of up to a hundred individuals. *Epomophorus wahlbergi* often return to the same roosting site however they are known to change between a number of different roosting sites on an unpredictable cycle (Fenton *et al.*, 1985). These bats are often found in coastal cities and will regularly roost along busy streets such in Durban and various cities in Mozambique (Taylor, 2005).

### **Aim**

The aim of this project was to determine the seasonal differences in foraging dynamics and home range size as well as roosting dynamics of *E. wahlbergi*, in the urban environment of Pietermaritzburg, KwaZulu-Natal, South Africa.

## Objectives

The objectives were to determine seasonal differences in foraging dynamics and home range sizes in this urban environment by radio-tracking the bats and following their movements. Any differences and/or similarities in home range size and foraging movements between individual bats were also investigated. In addition, the roosting dynamics and roost characteristics of *E. wahlbergi* in this urban environment were determined. It was hypothesised that home range size and habitat use of *E. wahlbergi* differs between seasons in an urban environment. It was predicted that home range size would increase during winter compared with spring, as greater distances would need to be travelled during winter when food resources were scarcer. It was also predicted that bats would show very little roost fidelity and would regular change day roost locations possibly as a result of temperature changes at the roost.

This thesis is presented as chapters prepared as manuscripts for submission to international peer-reviewed Journals as follows:

Chapter 2: Movements and foraging dynamics of Wahlberg's epauletted fruit bat in an urban environment, during late summer.

Chapter 3: Seasonal differences in foraging dynamics, habitat use and home range size of Wahlberg's epauletted fruit bat in an urban environment.

Chapter 4: Roost temperature and fidelity of Wahlberg's epauletted fruit bat in an urban environment.

Chapter 5: Concluding chapter

As chapters have been prepared as stand-alone manuscripts, some overlap and repetition between chapters has been unavoidable.

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## Chapter 2

### **Movements and foraging dynamics of Wahlberg's epauletted fruit bat in an urban environment, during late summer.**

**D. P. Rollinson<sup>1</sup>, J.C. Coleman & C. T. Downs<sup>1,2</sup>**

<sup>1</sup> School of Life Sciences, University of KwaZulu-Natal,  
Private Bag X01, Pietermaritzburg, 3209, South Africa

<sup>2</sup> Tel: 033 260 5127

Fax: 033 260 5105

Email: [downs@ukzn.ac.za](mailto:downs@ukzn.ac.za)

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#### **Abstract**

Many bat species are commonly found in cities and towns throughout southern Africa. However, their movements within the urban environment are often poorly known or understood. This initial study focused on the movements of Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) within the urban environment of Pietermaritzburg, South Africa, during late summer. A number of *E. wahlbergi* (n = 8) were caught in the urban environment of Pietermaritzburg and fitted with radio-transmitters. Their movements were then followed for the next 12 days and nights. Their movements ranged considerably with some of the bats making large flights to different parts of town while others stayed in particular areas; no bats were recorded to have left the urban environment. Some of the larger distances covered in a single night's movements were 2 and 5 km. Roosting fidelity varied between individual bats, as some bats changed roosts regularly while others stayed at the same roost throughout. The different movements of individual bats suggest that the bats have different requirements or preferences for the fruits they were feeding on in late summer; however movements for various social and

other interactions cannot be discounted. A significant difference in home range size was found between the sexes; with males occupying a smaller home range than females.

### **Key words**

Wahlberg's epauletted fruit bat; urban environment; roost sites

### **Introduction**

The movement of organisms is considered a complex process that depends on the individual's ability to perform tasks, as well as the nature of the landscape on which it moves (Getz & Saltz, 2008). Recently a great interest has been shown in better understanding the movements of a variety of animal and plant taxa, this interest has even been called a new movement ecology paradigm (Nathan, 2008). Understanding movement ecology is important for a number of reasons; most importantly it is seen as a crucial component of climate change, habitat fragmentation, biological invasions and the spread of pests and diseases (Nathan, 2008). Foraging movements are important as they influence the spatial distribution as well as genetic structure of plant populations (Heithaus & Fleming, 1978). By understanding the movements of organisms in and around human populations, we may be in a better position to understand the effect humans have on wildlife populations.

Human modification of ecosystems is generally considered to reduce biological diversity, by replacing vegetation with a monoculture grown for food (Williams *et al.*, 2006). However, urbanisation may introduce many new organisms and species into towns and cities (McDonnell & Pickett, 1990), which often coexist with the natural biota (Williams *et al.*, 2006). Some of these introduced organisms often negatively affect biodiversity and are then known as alien invasive species. However, some urban environments may provide suitable habitat for various indigenous species, for example bats of the order Chiroptera (Hourigan, Catterall & Jones, 2010). Different species react differently to urbanisation and may be classed as urban avoiders, urban adapters or urban exploiters (McKinney, 2002). Urbanisation brings organisms into closer contact with humans which may mean that some human-borne diseases are passed on to these organisms, such as certain bat species (Hayman *et al.*, 2010, Smith & Gehrt, 2010).

Urbanisation is generally considered to negatively affect bats, however within some urban environments patches of woodland or forest remnants are thought to be important areas for bats (Smith & Gehrt, 2010) and in some cases man-made structures may serve as roosting sites for certain species. Many species of bats, especially from the suborder Megachiroptera can often be seen roosting in urban areas and in many cases the bats are moving into these areas probably as a response to loss of suitable forest habitat (Birt *et al.*, 1998), however these bats may have moved into urban areas to benefit from suitable food and roosting resources (McDonald-Madden *et al.*, 2005). Due to the differences of urban climate compared with surrounding rural areas, some bat species have been able to move into urban areas where the climate suits them, where previously the bats would not be able to live (Parris & Hazell, 2005). There are however many negative effects of bats living in urban environments, some of these include; fragmentation and loss of habitat (Berthinussen & Altringham, 2012), the emergence of certain viruses and diseases (Plowright *et al.*, 2011), toxic levels of lead in urban dwelling bat species (Hariono, Ng & Sutton, 1993) and light pollution (Stone, Jones & Harris, 2009).

Foraging movements of various frugivorous flying fox species in urban environments, especially in areas throughout Australia, have been extensively investigated (Markus & Hall, 2004; McDonald-Madden *et al.*, 2005; Parris & Hazell, 2005; Schmelitschek, French & Parry-Jones, 2009). By studying a number of different flying fox species in urban environments, it has become clear that they are feeding on a number different fruiting tree species, both indigenous and exotic. The flying foxes often flew considerable distances to reach fruiting trees during night-time foraging.

Some insectivorous bat species are also thought to thrive in some urban environments and are generally less affected by urbanisation as they can cover large distances per night, move fast between habitat patches and are able to quickly react to resource fluctuations and roost availability (Jung & Kalko, 2010). Jung and Kalko (2010) observed a number of insectivorous bat species in South America across different environments; forest and town. They found that foraging activity was highest around streetlights in town, intermediate in the dark areas of town and lowest in the forested areas. Another reason for these insectivorous bat species being able to live in urbanised habitats, is because of the abundance of suitable roosting sites such as in houses and

under bridges (Keeley & Keeley, 2004). This again shows how many bat species have been able to adjust to urban environments and in many cases they have been able to thrive as if in a natural environment.

Throughout Africa, Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) are known to forage singularly or in small groups (Monadjem *et al.*, 2011), removing fruits from the plants and then consuming the fruit 5-100 m away in small trees or vine tangles (Taylor, 2005). The areas where the fruit is consumed are known as feeding roosts (Taylor, 2005). In a night's foraging, an individual bat may easily consume more than its body weight in fruit and can harvest 10-80 fruits (Taylor, 2005). During the nights foraging the bats commute between daytime roosts, feeding roosts and one or more resource patches (Taylor, 2005). Occasionally scouting flights are taken when the bats will fly over the home range on the look out for any ripening fruit; these scouting flights are often done on darker moonless nights when predatory risks are reduced (Taylor, 2005). After the night's feeding the bats will return to their daytime roost sites, which change regularly (Taylor, 2005). *Epomophorus wahlbergi* will hang from the canopy of evergreen trees as well as in man-made structures, such as roof eaves and the underside of thatched roofs, in colonies of up to a hundred individuals. These bats are often found in eastern seaboard towns and will regularly roost along busy streets in trees such as in Durban and Pietermaritzburg (Pers. obs.), and various cities in Mozambique (Taylor, 2005).

Fenton *et al.* (1985) followed the movements of *E. wahlbergi* in the Kruger National Park, South Africa. They found that *E. wahlbergi* would constantly change roost sites (possibly due to predatory pressures) and roost sites did not appear to be located close to foraging sites. There appeared to be a difference in movement between males and females, with females generally making major movements from daytime roosts to feeding areas (up to 4 km) while males tended to make short movements at dusk and then only a major feeding movement later in the evening (Fenton *et al.*, 1985). Most activity occurred within the first couple hours after sunset and thereafter reduced dramatically to almost half the activity for the remainder of the night (Fenton *et al.*, 1985). Shortly after sunset the bats would proceed to trees, pluck the fruit while hovering and then move to a nearby site where the fruit was eaten (Fenton *et al.*, 1985).



Currently little is known of the movements and roosting sites of *E. wahlbergi* in an urban environment. Consequently, this pilot study investigated the foraging movements of *E. wahlbergi* in an urban environment of Pietermaritzburg, South Africa, during late summer. Home range size was also determined. It was predicted that there would be differences in home range size between the sexes and, that bats would use a range of roost sites and feed on both exotic and indigenous fruit species. Individual bats were also expected to have different foraging movements and home ranges. It is important to understand the foraging movements of urban-living species so as to better understand the positive and negative effects of encroaching human populations on wildlife.

## **Methods**

### **Study area and bat capture**

*Epomophorus wahlbergi* was identified by the presence of a single post-dental palatal ridge, a diagnostic feature in the subregion (Taylor 2005; Monadjem *et al.*, 2011). Bats were mist-netted around fruiting *Ficus sur* trees in February 2011 on the Agricultural and Life Sciences campus of the University of KwaZulu-Natal, Pietermaritzburg, (660 msl, GPS -29.62522 S, 30.40358 E), South Africa.

Captured *E. wahlbergi* (male = 3, female = 5) were immediately fitted with radio-transmitters (BD-2CT Transmitters, Holohil Systems Ltd. Ontario), weighed, measured (forearm length), sexed, and then released within 30 min of capture. Radio-transmitters were attached to the bats backs with the use of collars and a cyanoacrylate adhesive (Alcon, Chempet). The transmitters were attached behind the neck of the bat with the antenna running along the length of the back in such a way that they could not be removed by the bat or hinder movement. Transmitters weighed 1.15 g and so were below the recommended mass of less than 5 % of body weight. No immature or pregnant individuals were used for this study. Males were heard calling in the immediate vicinity throughout this study and so it is likely that some of the bats used in this study were in fact breeding.

### **Radio-tracking in the urban environment**

Bats were radio-tracked by using radio receivers (R-1000 Telemetry Receiver, Communications Specialists, Inc. California) between the frequencies of 151.042 MHz and 151.319 MHz. The receiver operated with the use of a hand-held collapsible antenna which was used to pick up signal from the transmitter. The bats geographical location was determined by homing in on the signal produced by the radio-transmitter with a global positioning system (GPS, Garmin, eTrex, Olathe) (White & Garrot, 1990); a visual fix was attained where possible. Eight bats fitted with transmitters were tracked for 12 days. Their movements were followed from sunset (roughly 18h30) until 00h00. To avoid autocorrelation, we allowed a 1 h interval between location fixes for individual bats. If the bats spent large amounts of time in a certain area (roughly 1 h), it was assumed that they were feeding at feeding roosts or fruiting trees. Thereafter fruiting trees or feeding spats were searched for in the immediate vicinity to determine what fruit the bats were feeding on. Unfortunately there were some occasions where an accurate GPS fix could not be attained, in these circumstances the GPS data were not used until an accurate/visual fix was made. Bats were tracked once a day to determine the location of their daytime roosts. Bats averaged 2.5 GPS fixes per night during the radio-tracking period, although this figure is low, the total number of fixes per individual was acceptable. Those bats, for which a minimum of 30 GPS fixes could not be obtained, were not used in this study, as it would not give an accurate prediction of home range size (Seaman *et al.*, 1999). Foraging/feeding distance was calculated as the straight line distance from daytime roost to a feeding site, or from one feeding site to another feeding site in a single night. Unfortunately one of the eight bats could not be used in this study, as a minimum of 30 GPS fixes could not be obtained.

### **Home range estimation**

The different GPS positions which bats were recorded at were placed in a Geographical Information System (GIS) using the program ArcMap 9.3 (ESRI, Redlands, California, USA). In ArcMap, Hawth's Tools (Beyer, 2004), was used to create minimum convex polygons (MCP). The MCP method was used as it is the most commonly used method in the analysis of animal home range studies (Harris *et al.*, 1990), and thus makes this study

comparable to other animal home range studies. All fixes were used to calculate MCP as this would give the maximal coverage. Fixed kernel density estimates were not used for this study as our number of GPS fixes was too low and so fixed kernel density estimates would produce disjunct home range estimations.

### **Statistical analyses**

Descriptive analyses were conducted using the Statistica 7 package (Statsoft Inc., Tulsa, OK, USA).

## **Results**

### **Body mass and measurements**

Body masses of the eight *E. wahlbergi* caught and radio-tagged ranged from 87 – 123 g (Table 1). Five of the bats were females, with masses ranging from 87 - 102 g, the remaining three males masses ranged from 111 – 123 g (Table 1). Transmitters thus ranged from 0.9 - 1.3 % of the bats body mass. These masses indicate all were mature individuals.

### **Foraging movements**

There was a large amount of heterogeneity in the local movements of the radio-tracked *E. wahlbergi* (Fig. 1a). A number of the bats flew relatively large distances from their daytime roosts to forage at night, while others would generally forage in the vicinity of their roosts without flying large distances (Fig. 1a and 1b). One of the bats flew over five km to a different area of town in a single nights foraging. Of the five female bats that were caught and fitted with radio-transmitters, two of these were found to be flying distances of over two km to different areas of town in a single nights foraging. One of the other females foraged in different areas over three km apart; however this was not recorded in the same night's foraging. Of the three males that were fitted with radio-transmitters only two were refound during foraging hours. The third male was only recorded once at a day-roost and was not recorded foraging at night. The furthest distance either of the two male bats travelled in an evening's foraging was two km.

It was difficult to determine what plant species *E. wahlbergi* were feeding on as an accurate enough GPS fix could not always be attained; however we were able to identify a number of exotic tree species (either by direct observation or the presence of feeding spats). Fruit species observed being utilised by *E. wahlbergi* in this study included exotics such as Syringa (*Melia azedarach*), Guavas (*Psidium* sp.), and Loquat (*Eriobotrya japonica*) along with indigenous species such as Cape Wild Fig (*Ficus sur*) and Natal Fig (*Ficus natalensis*).

### **Roost dynamics**

All bats changed their day-roosts during the study, although some bats did show fidelity to specific roosts (Table 2). The movements between day roosts varied from approximately 200 m to over 1000 m (Table 2). Two bats were found roosting at the same day roosts for 66 and 75 % of the days, while the most time any of the three other bats spent at a single roost was 33 % (Table 2). The roost sites for all of the bats could not be found, however for those bats whose roost sites could be found, they were recorded to have changed their roost sites on average 1.6 times during the radio-tracking period.

### **Home range estimation and movements**

There was much variation between home range size of male and female *E. wahlbergi* measured using MCP (Fig. 1). Average male home range sizes were smaller (0.46 km<sup>2</sup>) than average female home range sizes (0.78 km<sup>2</sup>). Many of the females would make large flights across Pietermaritzburg to feeding areas, while males tended to stay in a single area throughout, without making significant foraging flights. This would account for the large difference in home range size.

### **Discussion**

Healthy adult male *E. wahlbergi* from KwaZulu-Natal weighed between 70-124 g while healthy adult females ranged between 50-104 g (Taylor, 2005). As all bats caught in this study were between these ranges, it would suggest that all the bats were of sufficient maturity to be carrying the transmitters.

Although the bats roosted in similar areas most of them flew to different parts of town to forage, suggesting that individuals have individual preferences and sources for feeding. A number of the bats flew relatively large distances in an evenings foraging; locating certain fruiting plants in different parts of town. This is similar to results of a study in Kruger National park, where most *E. wahlbergi* made large movements to foraging areas (Fenton et al., 1985). However, many were feeding on *F. sur* fruits near to their roosting site when initially caught, but then fed in different parts of town thereafter.

Many Pteropodid species including *E. wahlbergi* are known to change their daytime roosts frequently (Fenton et al., 1985). Most of the *E. wahlbergi* in this study were recorded to have regularly changed their roosts, however others did not change roost sites as frequently. Fenton et al. (1985) found that numbers at roosts changed constantly, with roost numbers varying on most days suggesting very little roost fidelity. Predator avoidance has been suggested as a reason for roost switching. It could be possible that *E. wahlbergi* in the urban environment may change their day-roosts due to the disturbing activities of humans which could essentially be seen as predators. Other possible reasons for roost switching may include changing microclimate conditions and distances to food resources (Fleming, 1988). *Epomophorus wahlbergi* were found to be using natural (trees) and man-made structures (roof eaves), indicating the ability to be able to adjust to urban environments. Fenton et al. (1985) showed that roost location of *E. wahlbergi*, in the natural environment, was not strongly influenced by commuting costs but rather by the microclimate of the roost and exposure to risk of predation.

In Australia a number of flying fox species have lost a considerable amount of potential habitat and resources due to development since European settlement (Markus & Hall, 2004). A number of native and exotic fruit-bearing plants have been identified as food substitutes to those plants that would traditionally make up large components of flying foxes diets (Markus & Hall, 2004). Some of these exotic fruiting trees include stone fruit (*Prunus* sp.), bananas (*Musa acuminata*), paw-paws (*Asimonia* spp.) and mangoes (*Mangifera indica*) which are more readily available to flying-foxes as they are cultivated in orchards (Tidemann, 1997). Gardens have also been identified as a source of leguminous foliage which is sometimes used as a protein supplement (Richards, 1995). In some urban environments there is likely to be an increase in potential roosting

resources as well as foraging resources, as fruit and floral resources may increase in abundance, detectability and reliability, possibly due to the watering of plants in gardens (Markus & Hall, 2004). In contrast forest remnants are generally found on nutrient-poor soil and so resource yield is dramatically reduced (Braithwaite, Turner & Kelly, 1984).

Markus and Hall (2004) followed the foraging movements of the frugivorous black flying fox (*Pteropus alecto*) in the urban environment of Brisbane, Australia. They found that individuals would only visit two to three foraging sites per night and that they would return to these foraging sites a few times a night. A number of bats were found to return to the same foraging sites for weeks and even months, suggesting a large degree of foraging fidelity, during both winter and summer months (Markus & Hall, 2004). Depending upon which roost the bats used, they would average between 2.9 and 7.5 km to specific foraging sites (Markus & Hall, 2004). Bats would take fruit from a number of different native and exotic trees during summer. During winter the diversity of fruits taken was reduced, however fruits from both native and exotic trees were still eaten (Markus & Hall, 2004). These results are similar to the results of this study, as individual bats would show foraging fidelity to certain areas and plant species, often returning to the same area on many consecutive nights.

The presence of grey-headed flying foxes (*P. poliocephalus*) in Melbourne can be attributed to anthropogenic climate change, as the rise in temperature can be attributed to human activities while the watering of gardens could possibly be seen as increased precipitation, which all suit *P. poliocephalus* (Parris & Hazell, 2005). They found that due to an increase in temperature of the urban environment of Melbourne it now falls within the required climatic conditions for the survival of *P. poliocephalus*. Climate change appears to be shifting distributions of species, as some expand into new areas while many others are shrinking (Pearson & Dawson, 2003). Williams *et al.* (2006) found that the number of species which comprised the diet of *P. poliocephalus* in the Melbourne area prior to European colonisation consisted of 13 species, while an additional 87 tree species were included in their diet in 2003. A number of these tree species are considered exotic to Australia but are however regularly cultivated commercially for their fruit (Williams *et al.*, 2006). These food trees are generally found in greater densities in residential areas when compared to industrial areas (Williams *et*

*al.*, 2006). Schmelitschek *et al.*, (2009) found that *P. poliocephalus* relied heavily on fig (*Ficus*) species throughout the year, emphasising the importance of both indigenous and exotic tree species.

The difference in home range size of male and female *E. wahlbergi* in this study indicates that different sexes may have dietary preferences/requirements. These findings are different to those of Barclay & Jacobs (2011), who investigated differences in home range sizes of male and female Egyptian fruit bats (*Rousettus aegypticus*) and found that there were no notable differences in home range sizes between the sexes. Although there were some differences in the areas in which the different sexes foraged. It is important to note, that as male bats were calling throughout the study period, some of the bats' movements may have been influenced by this and were in fact not foraging flights but rather breeding opportunities.

A great deal has been learnt from this pilot study and will be useful for designing the remaining components of the study. It is important that radio transmitters with a greater battery life are used in future as this could greatly increase the number of GPS fixes per bat and thus further enhance the effectiveness of the study. The pilot study revealed that individual bats regularly change their daytime roost locations, and hence a study to understand the reasons for these regular roost changes would be important. Vital radio-tracking techniques were further fine-tuned in this study and were useful for the remaining radio-tracking components of the project. This pilot study also highlighted the difficulties of determining what plant species *E. wahlbergi* were feeding on, however it did become easier to determine the plant species being utilised with more practise. These new skills proved useful in Chapter 3 where more emphasis was placed on locating the plant species being utilised.

The present study has shown how individual bats of the same species show great variability in the areas in which they forage. Many of the bats foraged in the same area throughout the length of the study while other bats would choose to fly large distances to other parts of Pietermaritzburg which shows that individuals may have different dietary preferences. This study has also shown the variability in roost sites as bats have changed their roosts regularly. Possible reasons for roost switching will be looked at in more detail in Chapter 4. Further research is required to understand how frequently *E. wahlbergi* feed

on exotic/alien invasive species and what effect they are having on the spread of these species.

### **Acknowledgements**

The authors would like to thank; the Pietermaritzburg public for information on the whereabouts of bat roosts and feeding areas, UKZN students for the help in data collection, especially to Minke Witteveen who helped with many aspects of the project and to those people who helped with the GIS work. Information on the whereabouts of roosting and feeding *E. wahlbergi* from the Pietermaritzburg public is also greatly appreciated.

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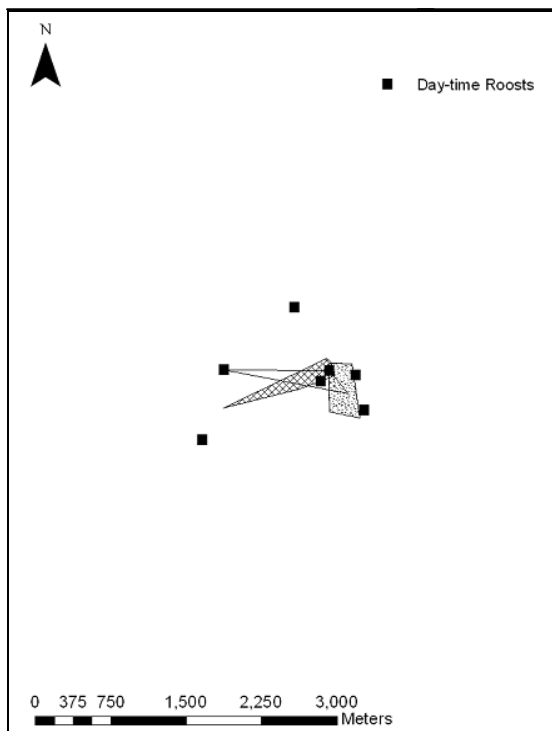
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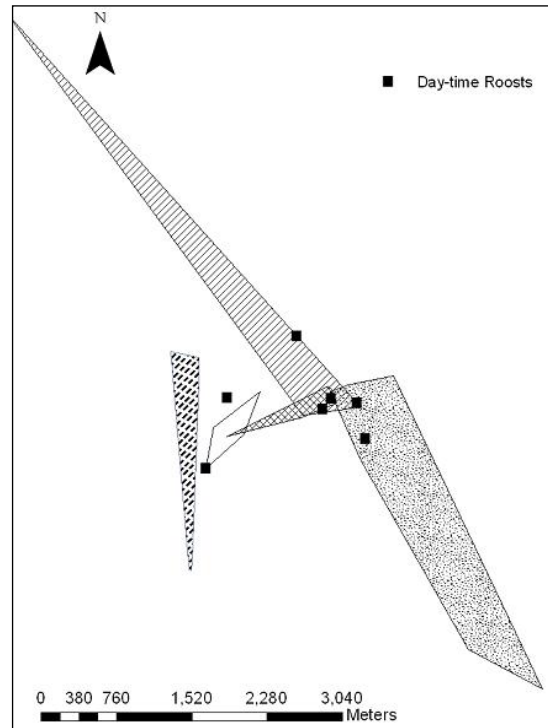
**Legend for Figure**

**Figure 1** Minimum convex polygons of (a) male and (b) female of *E. wahlbergi* in Pietermaritzburg during late summer 2011. Closed squares indicate daytime roosts used by all radio-tracked *E. wahlbergi*.

(a)



(b)



**Figure 1** Minimum convex polygons of (a) male and (b) female of *E. wahlbergi* in Pietermaritzburg during late summer 2011. Closed squares indicate daytime roosts used by all radio-tracked *E. wahlbergi*.

**Table 1** Body mass and forearm measurements of Wahlberg's epauletted fruit bats used for this urban study during late summer. \* = individual bat not used in study as could not be refound after initial release.

<u>Individual</u>	<u>Sex</u>	<u>Body Mass (g)</u>	<u>Forearm Length (mm)</u>
<u>1</u>	Female	91	77
<u>2</u>	Female	87	83
<u>3</u>	Female	93	84
<u>4</u>	Male	116	83
<u>5</u>	Female	90	82.5
<u>6</u>	Male	12	83
<u>7</u> *	Male	111	83
<u>8</u>	Female	102	75
<u>Mean + SE</u>		101.8 $\pm$ 4.77	81.3 $\pm$ 1.1.8

**Table 2** Summary of roost movements and roost switches, including days spent at different *E. wahlbergi* roosts in the urban environment of Pietermaritzburg during summer. \* = roosting sites could not be found.

<u>Individual</u>	<u>No. of Roost Sites</u>	<u>No. of days spent at roost site 1</u>	<u>No. of days spent at roost site 2</u>	<u>No of days spent at roost site 3</u>	<u>No. of days spent at unknown roosts</u>	<u>Maximum Distance between Roosts (km)</u>
<u>1</u>	*	*	*	*	12/12	*
<u>2</u>	2	4/12	0	0	8/12	0.42
<u>3</u>	*	*	*	*	12/12	*
<u>4</u>	2	9/12	2/12	0	5/12	0.80
<u>5</u>	2	8/12	1/12	0	7/12	1.0
<u>6</u>	2	1/12	1/12	0	10/12	1.05
<u>7</u>	3	1/12	1/12	1/12	11/12	0.57

## Chapter 3

### **Seasonal differences in foraging dynamics, habitat use and home range size of Wahlberg's epauletted fruit bat in an urban environment.**

**D. P. Rollinson<sup>1</sup>, J.C. Coleman & C. T. Downs<sup>1,2</sup>**

<sup>1</sup> School of Life Sciences, University of KwaZulu-Natal,  
Private Bag X01, Pietermaritzburg, 3209, South Africa

<sup>2</sup> Tel: 033 260 5127

Fax: 033 260 5105

Email: [downs@ukzn.ac.za](mailto:downs@ukzn.ac.za)

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#### **Abstract**

Urbanisation through the process of habitat loss and fragmentation has caused drastic changes in the ecosystems. Many species can no longer survive in these urban areas; however there are species that have been able to survive and in fact thrive in these newly created habitats. One such species is Wahlberg's epauletted fruit bat which has adjusted to this new environment by changing its diet and possibly foraging movements. We studied the seasonal variation in home range size and foraging dynamics of Wahlberg's epauletted fruit bats in the urban environment of Pietermaritzburg. Ten adult fruit bats were caught and fitted with radio-transmitters. Movements were followed for 3 weeks during winter and spring, and plant species comprising their diet were noted. A difference in home range size was found between winter and spring, with home range sizes being larger in winter. During winter the bats fed mostly on *Syringa* fruits while the diet in spring was more varied and included other species of indigenous and exotic fruits. This seasonal variation in home range size can possibly be explained by a reduced amount of fruiting species during winter resulting in bats having to move greater distances to search for food. The reduced variety in fruit eaten may be explained by a reduction in fruiting plant species in winter, and so they may become reliant on a few species to meet their dietary requirements. Further research is needed to assess the role played by exotic and alien plant species in the continued success of urban wildlife.



**Key words**

Wahlberg's epauletted fruit bat; urban environment; roost sites; seasonal differences.

**Introduction**

Urbanisation is seen as one of the most important threats to local and global biodiversity (Wilcox & Murphy, 1985). It drastically changes the ecosystem through the processes of fragmentation and habitat loss (Lizee *et al.*, 2011). Although both of these processes are very often detrimental to wildlife (Jung & Kalko, 2011), for some species urbanisation does have a positive effect and these species thrive in the newly created environment (DeStefano and DeGraaf, 2003). This differential effect of urbanisation on different species has led to a classification of animal species into three different classes; urban avoiders, urban adapters and urban exploiters (McKinney, 2002).

Urban avoiders are those species that typically do not occur in anthropologically modified environments or urban landscapes, while urban adapters are the species that are able to adapt to anthropogenic landscapes and profit from the additional resources (Jung & Kalko, 2011). Urban exploiters are those species that depend largely on the resources provided by humans in the urban landscape (Jung & Kalko, 2011). Many exotic species, often known as alien invaders, are classed as urban exploiters (van Rensburg, Peacock & Robertson, 2009).

The order Chiroptera contains representatives from all three categories (Jung & Kalko, 2011). Certain species of insectivorous bats are able to take advantage of anthropogenically modified habitats by using buildings as roosting sites as well as by exploiting insects around street lights (Jung & Kalko, 2011). While some bat species are able to exploit human modified landscapes, others are known to avoid these areas (Gaisler *et al.*, 1998). This suggests that the ability of insectivorous bats to survive in anthropogenic environments may be species-specific (Jung & Kalko, 2011).

Frugivorous bats are also known to exploit human modified landscapes, particularly in suburbia across Australia (Markus & Hall, 2004; McDonald-Madden *et al.*, 2005). The creation of parks and treed gardens, containing both indigenous and exotic flora is thought to have benefited frugivorous bats as it has provided additional food resources as well as roosting habitat (McDonald-Madden *et al.*, 2005). Although spacious

roosting sites may be scarce, the detectability, abundance and reliability of floral and fruit yields is generally higher in urban areas, possibly due to regular watering (Jung & Kalko, 2011).

Many species of frugivorous bats have been recorded feeding on the fruit and leaves of exotic tree species (Corlett, 2005; Tsoar, Shohami & Nathan, 2011), especially cultivated plants (Markus & Hall, 2004; McDonald-Madden *et al.*, 2005; Parris & Hazell, 2005) or even tree species that are considered alien invasives in some countries (Gosper & Vivian-Smith, 2010). Fruit bats are thus considered to contribute to the dispersal of exotic invasive plants in the urban environment (Corlett, 2005; Jordaan, Johnson & Downs, 2011; Tsoar *et al.*, 2011), and are known to have a positive effect on germination (Jordaan *et al.*, 2011).

Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) feeds on the fruit of a variety of indigenous and cultivated tree species (Monadjem *et al.*, 2011). In South Africa it has been documented feeding regularly on the fruits of alien invasive species, such as the fruits of *Syringa* (*Melia azedarach*) (Voigt, Farwig & Johnson, 2011). Although *E. wahlbergi* regularly feed on the fruit of *M. azedarach* it does not significantly contribute to long distance seed dispersal, as the seed is not swallowed but rather spat out under the canopy of another tree, 20 - 60 m from the parent tree (Voigt *et al.*, 2011). Jordaan *et al.* (2011) found that *E. wahlbergi* would consume more than their body weight in fruit in a single night foraging particularly of alien invasive fruits, and an average of 40 seeds were dispersed per night.

*Epomophorus wahlbergi* is commonly found in the urban environment, provided there are adequate woody areas (Taylor, 2005; Monadjem *et al.*, 2011). As with most species, *E. wahlbergi* adjustments to the urban environment may include changes in feeding habits and feeding ecology. These changes include variation in the fruits it feeds on and distances it flies to forage (McDonald-Madden *et al.*, 2005).

Very little work has been done on understanding the foraging movements of *E. wahlbergi* in the urban environment; however research has been done on better understanding foraging movements in the natural environment (Fenton *et al.*, 1985). Fenton *et al.*, (1985) radio-tracked *E. wahlbergi* in the natural environment of Kruger National Park, South Africa. It was found that females made larger initial movements to

feeding areas than males who made short initial movements. Roost locations were regularly changed, for no apparent reason, and roost location was not dependent on foraging area (Fenton *et al.*, 1985).

*Epomophorus wahlbergi* is known to breed throughout the year, with peaks during July (winter) and summer months (Monadjem *et al.*, 2011). Males will call from traditional calling sites to attract females (Monadjem *et al.*, 2011), which can be described as a loud „pinging’ sound.

Many bat species (both insectivorous and frugivorous) change their foraging behaviour depending on the changes in seasons (Fleming & Heithaus, 1986). In tropical bat species, seasonal changes are known to result in some of the following foraging changes; patterns of habitat use, diet breadth and type of food chosen, defence of feeding area, size of foraging group as well as both local and long-distance migratory movements (Fleming & Heithaus, 1986). The frugivore *Carollia perspicillata* exhibits seasonal changes in feeding ecology. In particular during the dry season they foraged further away from their day roost, concentrating feeding activity on a narrower range of habitats and changed feeding area locations more frequently, although the number of feeding areas did not change with the changing seasons (Fleming & Heithaus, 1986). Home range as defined by Burt (1943) is „that area traversed by the individual in its normal activities of food gathering, mating and caring for young.’

Movement and thus home range size of Chiroptera is determined by the availability and dispersion of both food and daytime roost resources (Winkelmann, Bonaccorso & Strickler, 2000). Many move because of changing food availability, especially frugivores and nectarivores. Some species migrate large distances e.g. straw-coloured fruit bat (*Eidolon helvum*) (Richter & Cumming, 2008). Other species remain in the same areas throughout the year, however must change their foraging patterns, such as foraging distances and dietary choice (McDonald-Madden *et al.*, 2005). Those bats which roost in large assemblages appear to commute longer distances to reach foraging areas than those species which roost in small numbers or solitarily (Bonaccorso *et al.*, 2002). Colonial roosting species such as gray-headed flying foxes (*Pteropus poliocephalus*) will often commute distances between 15 and 50 km to foraging areas (Spencer *et al.*, 1991).

We compared the seasonal foraging movements as well as home ranges and habitat use of *E. wahlbergi* during winter and spring in the urban environment of Pietermaritzburg, KwaZulu-Natal. A pilot study was carried out in this urban environment during summer (Chapter 2). We hypothesised that home range size and habitat use would vary between seasons and predicted that home ranges would be larger in winter than spring. This would most likely be due to reduced food availability and diversity during winter and so bats need to commute greater distances to foraging areas.

## **Methods**

### **Study area and bat capture**

*Epomophorus wahlbergi* were caught in June 2011 on the Agricultural and Life Sciences campus of the University of KwaZulu-Natal, Pietermaritzburg (660 msl, GPS -29.62522 S, 30.40358 E), using mist nets around fruiting trees or close to the bats' daytime roosts. These individuals were all different from those bats caught and radio-tracked in the pilot study. Bats were identified by the presence of a single post-dental palatal ridge which is characteristic of this species in the subregion (Monadjem *et al.*, 2011). Ten adult individuals (male = 6, female = 4) were caught and fitted with radio-transmitters (BD-2C Transmitters, Holohil Systems Ltd. Ontario) broadcasting at frequencies of 151.418 – 151.599 Mhz. Bats were weighed in cloth bags using a 500 g Pesola scale (Pesola, Baar, accurate to 5 g), measured (forearm length), and sexed, all within 30 min of capture, after which they were released at their capture site. The radio-transmitters were attached to the bats backs with small collars and a cyanocrylate adhesive (Alcon, Chempet). Transmitters were attached behind the neck of the bat with collars and the antenna running down the length of the back in such a way that they could not be removed by the bat nor hinder movement. In order to ensure movement of an organism is not restricted it is recommended that the transmitters weigh less than 5 % of the animal's body mass (Aldridge & Brigham, 1998). Transmitters weighed 1.15 g, which is less than 5 % body mass. Only individuals considered healthy were used for this study. No immature or pregnant bats were used in this study. Some of the bats used in this study may have been breeding as males were heard displaying in the immediate vicinity during the study and breeding is known to occur throughout the year in this species.

### **Radio-tracking in the urban environment**

The bats were tracked with a vehicle and on foot using a hand-held collapsible antenna with a radio receiver (R-1000 Telemetry Receiver, Communications Specialists, Inc. California). The geographical location of the bats was determined by homing in on the signal produced by the transmitter (White & Garrot, 1990). The geographical location was determined by varying signal strength; a visual fix was attained where possible. In some circumstances an accurate GPS fix could not be attained, mostly due to problems with accessing properties. On these occasions the GPS data were not used until a more accurate/visual fix was made. Eight of the ten bats fitted with transmitters were tracked for up to 21 nights from sunset to sunrise over winter and spring. Two of the bats fitted with radio-transmitters were not refound and so were not used in this study. Bats were also tracked once a day during daytime hours, to find the location of their daytime roosts. Bats were tracked by using two teams of observers (comprising 3 people each) who tracked from sunset (Winter approximately 17:00; Spring approximately 18:00) till midnight and then midnight till sunrise (winter approximately 06:00; spring approximately 05:00), to ensure the entire nights foraging was monitored. We allowed a 1 h interval between location fixes for the individual bats to avoid autocorrelation. Bats positions were recorded using a hand-held global positioning system (GPS, Garmin, eTrex, Olathe). The bats were tracked for 3 weeks in June/July 2011 and then in September/October 2011 respectively. During the winter tracking individual bats averaged 5 GPS fixes per night, while during the spring tracking the bats averaged 4 GPS fixes per night. Although these figures are low, they are similar to the number of fixes per night in a study by Bonaccorso *et al.* (2002). Any bats with less than 30 GPS fixes were not used in this; as 30 is considered the minimum number of fixes to accurately predict home range size (Seaman, *et al.* 1999).

### **Home range estimation**

Data were imported from Excel (Microsoft Office, 2003). Home range of *E. wahlbergi* was estimated using the home range extension, Hawth's Tools (Beyer, 2004) within the program ArcMap 9.3 (ESRI, Redlands, California, USA). All fixes were used for the home range, as it is important to include the organism's entire nightly foraging

movements (Harris *et al.*, 1990). Firstly 100 % minimum convex polygons (MCP) were calculated for each individual bat, to determine home range. In addition we calculated Fixed Kernel (FK) density estimates using 95%, 90% and 50% of locations for each individual in each season. FK estimates were used as they have been shown to be less sensitive to auto-correlated data (Millspaugh & Marzluff, 2001), and produce a less biased home range use and size calculation (Seaman *et al.*, 1999). The smoothing factor was obtained by visually comparing home range polygons using different smoothing factors. The smoothing factor which best linked up the home range polygons was chosen. For this study the h value was set to 150 m for all the individual bats.

### **Foraging**

Bats that spent large amounts of time (1 h or more) in a certain area were presumed to be feeding at feeding roosts, and so fruiting trees were searched for in the immediate vicinity which the bats were likely to be feeding on. Feeding spats were also searched for, which would identify what the bats were feeding on. Percentages of fruits fed on by bats was calculated by only using those GPS fixes where we were confident what the bats were feeding on, however for many GPS fixes the fruit the bats were feeding on could not be identified. Foraging/feeding distance was calculated as the straight line distance between daytime roosts and feeding sites, as well as the straight line distance between different feeding sites during the same night. Social and reproductive interactions were not taken into account during this study, however this may have influenced individual bats movements.

### **Statistical analyses**

Descriptive statistics were used for most of the parameters measured while generalised linear model repeated measures analysis of variance analyses (GLM RMANOVA) were used to compare home range estimates, and movement distances between seasons. These were followed by Tukey post-hoc tests when necessary. All tests were performed using the Statistica 7 package (Statsoft Inc., Tulsa, OK, USA).

## Results

### Body mass and measurements

Body mass of *E. wahlbergi* (n = 10) ranged from 81 - 127 g with a mean body mass of  $97.4 \pm 4.31$  g. Female (n = 4) body mass ranged from 88 – 105 g while males (n = 6) body mass ranged from 81 - 127 g (Table 1). Transmitter mass ranged from 0.9 - 1.4 % of bats' body mass.

### Home range and habitat use in winter versus spring

Home range size of *E. wahlbergi* measured using the respective methods (MCP and FK) was significantly different in winter (GLM RMANOVA  $F_{(3, 21)} = 48.036$ ,  $P = 0.00002$ , (Fig. 1) and in spring (GLM RMANOVA  $F_{(3, 24)} = 130.06$ ,  $P = 0.00002$ , (Fig. 1). In winter 95 % and 90 % FK density estimates were significantly greater than 50 % FK density and MCP estimates while in spring 95 % Fixed Kernel Density estimates were greater than the other estimates (Post-hoc Tukey,  $P < 0.05$ , Fig. 1). Although MCP is the most reflective of the home range definition (Burt, 1943), it predicted a significantly smaller home range size than the 95 % FK density estimator in both seasons. Calculation of home range size using MCP usually over estimates home range size and FK predicts a smaller home range size or habitat use. However, in this study MCP calculated a smaller home range size than FK irrespective of season. A possible reason for this would be that our sample size and home range sizes were small, and so it would mean that the FK method would produce a larger home range size than MCP. There was also more variation in home range size during winter than spring (Fig. 1). As expected winter estimates were significantly greater than spring estimates (GLM RMANOVA  $F_{(3, 21)} = 43.082$ ,  $P = 0.00002$ , Fig. 1 and 2). Every individual bat showed large differences in home range size between seasons, with a greater home range size during winter than spring (Fig. 3).

There was also a difference in average home range size between the sexes. During winter, average home range size for males (using MCP estimates) was  $0.607 \text{ km}^2$  while females averaged slightly smaller at  $0.541 \text{ km}^2$ . During spring the differences in home range estimates (using MCP estimates) were less pronounced; with females occupying a slightly larger ( $0.177 \text{ km}^2$ ) home range than males ( $0.130 \text{ km}^2$ ).

### Foraging movements

Maximum foraging distance of *E. wahlbergi* from their daytime roost varied between seasons (GLM RMANOVA  $F_{(1, 7)} = 13.13$ ,  $P = 0.00847$ ). Mean maximum foraging distance of the bats from their daytime roost during winter was  $1.45 \pm 0.2$  km while in spring it was  $0.88 \pm 0.08$  km. The maximum foraging distance of any single bat during winter was 2.0 km while in spring it was 1.3 km.

### Habitat use

In both seasons radio-tracked *E. wahlbergi* used the urban habitat of Pietermaritzburg, particularly the suburbs of Scottsville and Hayfields which are dominated by residential properties with treed gardens (Fig. 2, pers. obs.). They generally avoided the more built up central business district. They were not observed leaving the urban area of Pietermaritzburg and were found to be foraging relatively close to their roost sites in both seasons. Bats used a range of natural and man-made roosts and changed roosts in the seasons (see details in Chapter 4). Some of the individuals ( $n = 6$ ) would occasionally use the same daytime roost, however would not necessarily forage in the same area.

### Foraging

As *E. wahlbergi* fed on fruit in residential gardens it was not always possible to determine exactly what the bats were feeding on, as most properties were secured with fences and it was difficult to gain access. They predominantly fed on a range of exotic fruits in gardens including syringa (*Melia azedarach*, 50 % winter observations, 30 % spring observations, winter fruiting), loquat (*Eriobotrya japonica*, 10% winter observations, winter fruiting), guavas (*Psidium guajava*, 10 % spring observations, spring fruiting), and the Chinese scrambling fig (*Ficus pumila*, 10 % of spring observations, spring fruiting) (Fig. 4). They also fed on indigenous fruits such as; *Ficus* species (20 % winter observations, 30 % spring observations, fruiting throughout the year) (Fig. 4). Fruiting trees visited were not homogeneously distributed (pers. obs.). During the winter months, *E. wahlbergi* fed extensively on the invasive *M. azedarach* (50 % observations), and a number of individuals would often return to the same group of *M. azedarach* on consecutive nights to feed.



## Discussion

Home range size varied between seasons, and was greater in winter than in spring as predicted. This seasonal variation appears to be a consequence of change in food availability both temporally and spatially. Many indigenous trees cultivated in the Pietermaritzburg region produce fruit in the wetter months of the year (spring/summer/autumn), while in the drier months (winter) there is a reduced amount and diversity of fruit to be used as a food source (Boon, 2010; Wilson & Downs, 2011; pers. obs.). Similarly, several of the exotic fruits, most of which are invasive aliens were available to bats in spring (Jordaan *et al.*, 2011). The exception was *M. azedarach* which fruits during winter (Jordaan *et al.*, 2011; Voigt *et al.*, 2011). Consequently with reduced food availability in winter, bats had to forage further from their daytime roosts and hence have a larger home range because of the increased foraging range. Although fruiting *M. azedarach* occurs in large densities throughout Pietermaritzburg in winter (meaning reduced foraging flights), it is unlikely that *E. wahlbergi* can attain all its dietary requirements from this species and thus will need to supplement its diet with other fruit species. Individual dietary requirements were also evident as individual bats (from the same daytime roost) would forage in different areas and show particular preference for certain areas. As these fruiting species are found in lower densities during winter it is likely *E. wahlbergi* will need to make larger foraging flights and hence occupy a larger home range during winter.

These results are similar to those of Fleming and Heithaus (1986) for seasonal foraging patterns of the frugivorous Phyllostomid bat, *C. perspicillata*. They found that *C. perspicillata* foraged further away from daytime roosts, and commuted longer distances to foraging areas during the dry season than during the wet season. However they found some aspects of the bats foraging remained consistent through the season including number of foraging areas, number of individual visits per night and consistency that bats visited the same foraging areas.

In contrast seasonal variation in foraging ecology of the nectar and pollen eating Queensland blossom bat (*Sycnycteris australis*) differed (Law, 1993) as the bats reduced their commuting distance during winter, possibly as a way to cut down on energy costs. Similarly the insectivorous greater mouse-eared bat (*Myotis myotis*) reduced commuting

distance during winter (Audet, 1990). Law (1993) suggested that some bat species commute greater distances during the warmer months as this it is advantageous for adult males who are searching for females.

In a study on lesser bare-backed bats (*Dobsonia minor* [Pteropodidae]) home range size did not differ between wet and dry seasons or between sexes (Bonaccorso *et al.*, 2002). Many individuals would commute between daytime roosts and multiple foraging areas, which would result in disjunct core use areas and home ranges. Fruit from an exotic plant species was identified as a staple food item (Bonaccorso *et al.*, 2002).

Barclay & Jacobs (2011) specifically looked at differences in home range size and foraging movements between sexes of Egyptian fruit bats (*Rousettus aegypticus*) during reproduction. Home range size and diet did not differ between the sexes; however there was a difference in the areas in which the sexes would forage, as females foraged in native forest more than males did (Barclay & Jacobs, 2011).

The current study was undertaken in an urban environment, which has a very different plant composition compared with *E. wahlbergi* native woodland habitat (pers. obs.). Previously the area was mainly classified as a savanna bioregion dominated by grassland with Acacia species (Mucina & Rutherford, 2006). The greatest difference in the plant composition of a natural versus urban environment is the large percentage of exotic plants in the urban environment (Smith *et al.*, 2006). Although these exotic plants may cause various environmental problems they also serve as an important food source for many indigenous frugivores, and in some cases they may even prefer exotic fruits (Fraser, 1990). In this urban environment fruits *E. wahlbergi* fed on were mostly from exotic plants and in many cases alien invasive plants (Jordaan *et al.*, 2011). This highlights the fact that there is sometimes a greater abundance of food availability in urban areas, which can be used as alternative food sources especially during winter months when indigenous plant species are generally not fruiting. Urban roosting *E. wahlbergi* regularly feed on the fruits of alien invasive species, such as *M. azedarach*, *P. guajava*, *E. japonica* and *Morus alba*, and have even been recognised as important seed dispersers (Jordaan *et al.*, 2011).

The foraging movements *E. wahlbergi* in this urban study (max winter: 2.2 km, max spring: 1.3 km) were much shorter than those noted by Fenton *et al.*, (1985) in the

natural environment of the Kruger National Park (max: > 4 km). A likely explanation for this large difference in foraging movements is that there is often a greater abundance and diversity of available food sources in some urban environments compared with the natural environment (McKinney, 2002). The prevalence of many exotic tree species in the urban environment has increased the amount of food available for *E. wahlbergi*, and thus this may mean that shorter foraging flights are undertaken to reach food sources. Furthermore the urban environment provides several natural and man-made roost sites for this species that are in relatively close proximity to fruiting trees in residential areas.

Access to private property and land was a limitation in this urban study and meant that in some instances the accuracy of our GPS fixes was reduced. The use of GPS transmitters was not an option in this project due to the small size of the studied bats; however with advances in technology it may be possible to use GPS transmitters in the future which will give more accurate results for the various movements of the bats.

In conclusion *E. wahlbergi* shows a marked difference in home range size and foraging ecology between winter and summer. It is also evident that this species may have become reliant on exotic and alien invasive plant species to meet their daily energy requirements. Further research is required to assess the role played by alien and exotic plant species in the continued success of urban wildlife.

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**Legends for Figures**

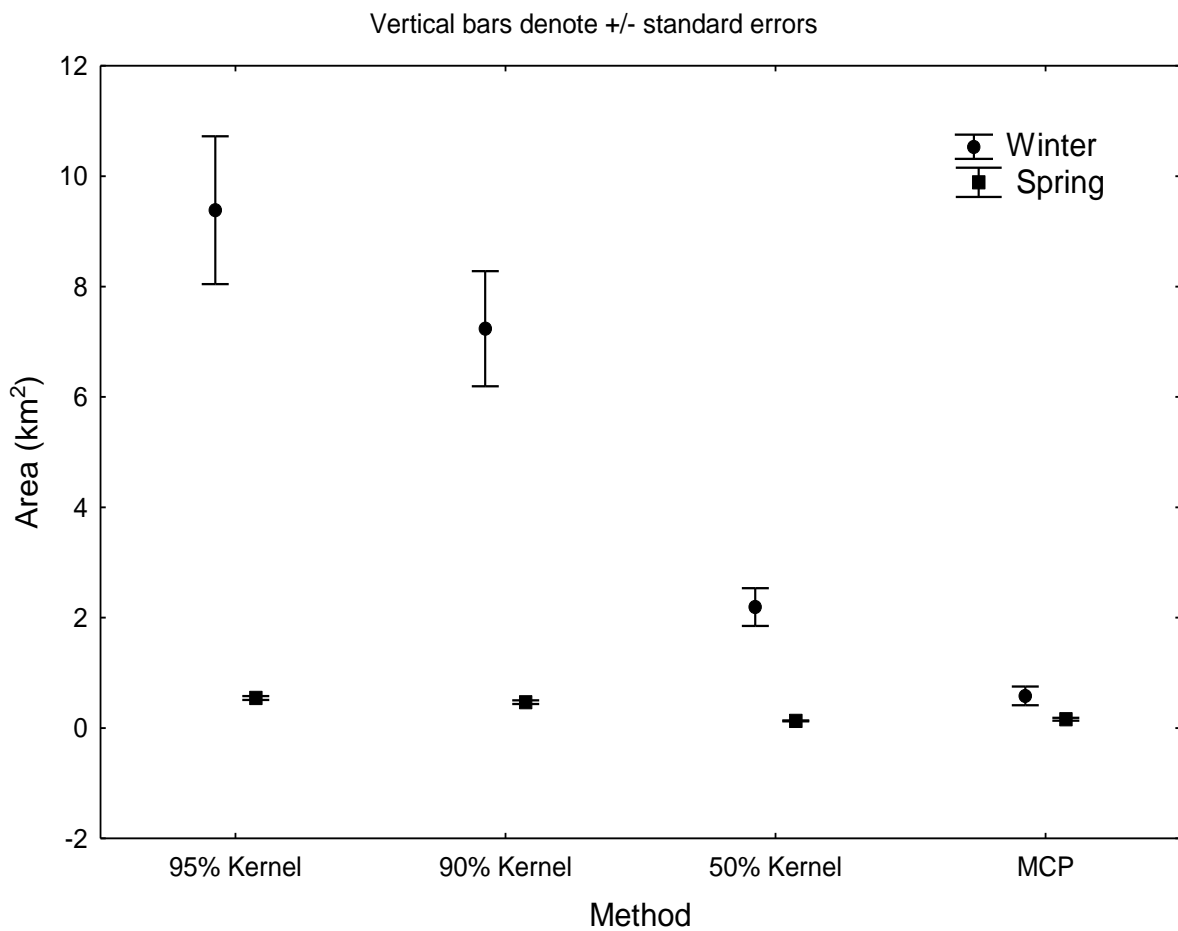
**Figure 1** Mean home range sizes of *E. wahlbergi* in winter and summer 2011, using the estimates FK 95 %, FK 90 %, FK 50 % and MCP. Values represent means  $\pm$  standard error.

**Figure 2** Combined home range of all radio-tracked *E. wahlbergi* (n = 8) in Pietermaritzburg, South Africa during a. winter and b. spring 2011.

**Figure 3** Individual home range sizes of *E. wahlbergi* of (a) males during winter, (b) females during winter, (c) males during spring, and (d) females during spring, with all daytime roosts included.

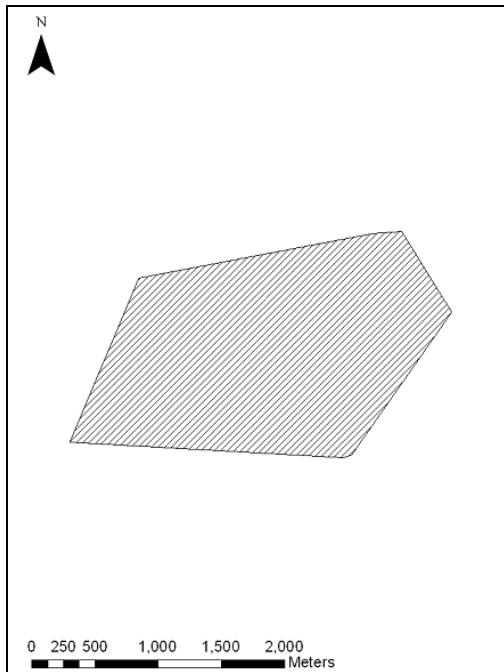
**Figure 4** Observed dietary component of tracked *E. wahlbergi* during (a) winter and (b) spring.



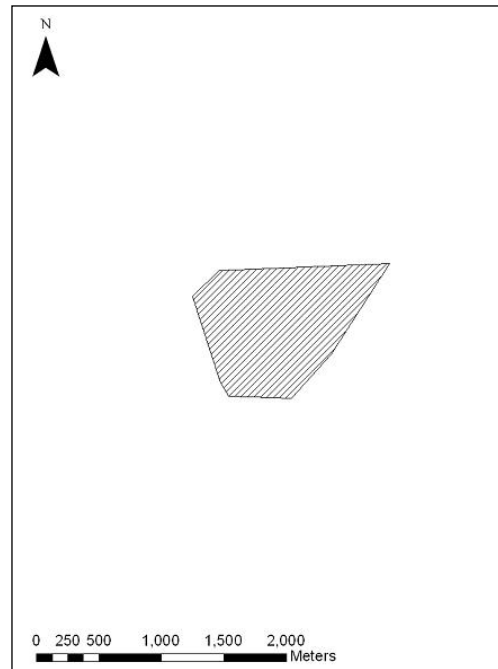


**Figure 1** Mean home range sizes of *E. wahlbergi* in winter and summer 2011, using the estimates FK 95 %, FK 90 %, FK 50 % and MCP. Values represent means  $\pm$  standard error.

(a)

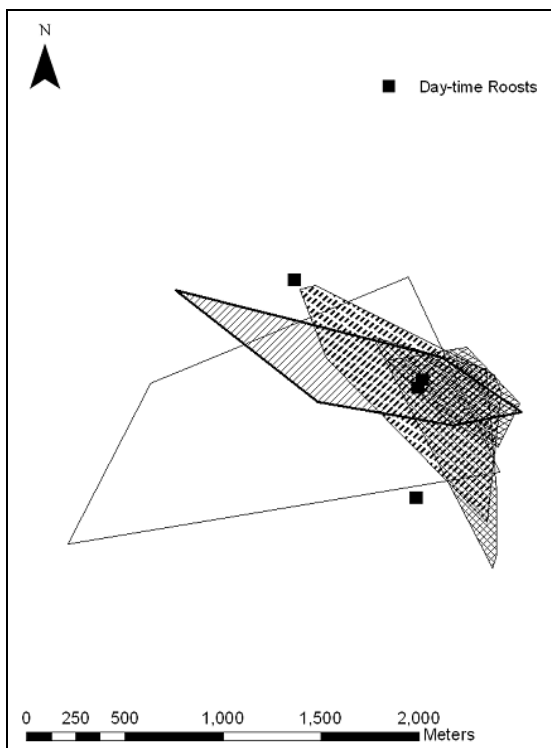


(b)

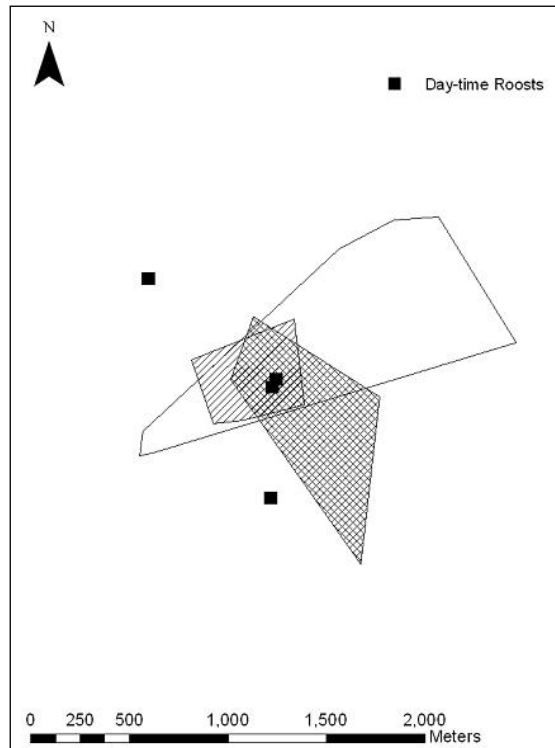


**Figure 2** Combined home range of all radio-tracked *E. wahlbergi* ( $n = 8$ ) in Pietermaritzburg, South Africa during a. winter and b. spring 2011.

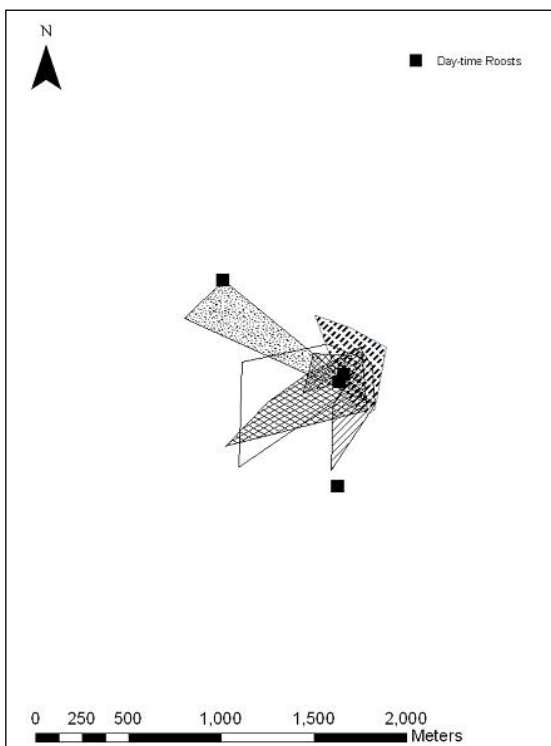
(a)



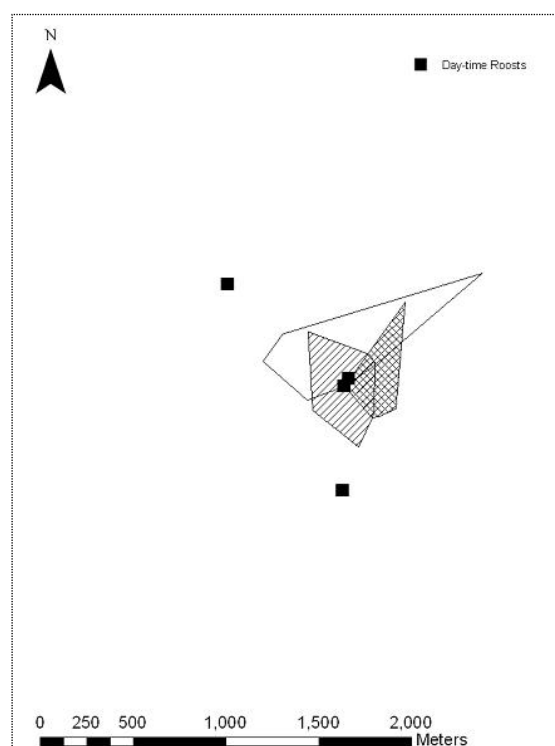
(b)



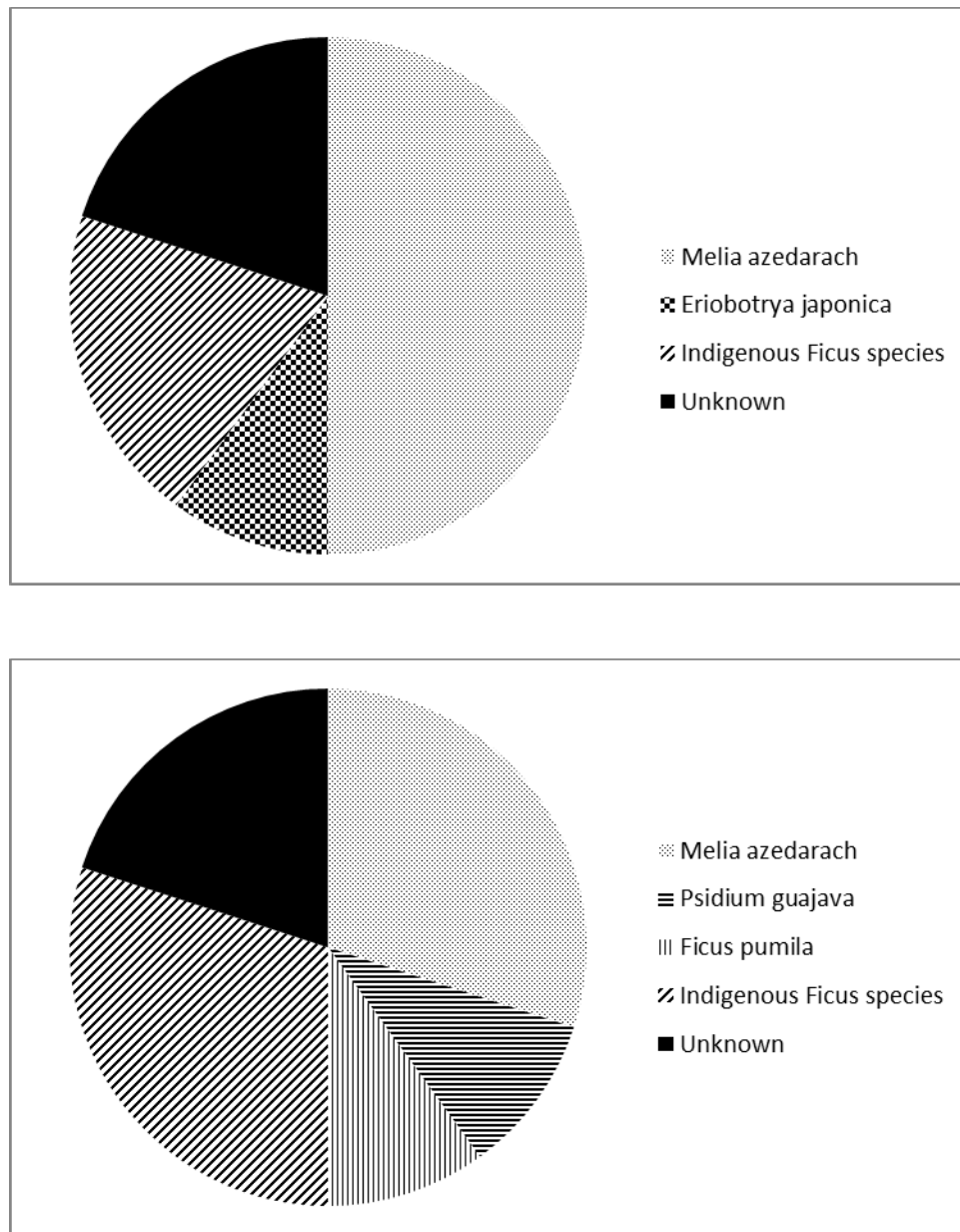
(c)



(d)



**Figure 3** Individual home range sizes of *E. wahlbergi* of (a) males during winter, (b) females during winter, (c) males during spring, and (d) females during spring, with all daytime roosts included.



**Figure 4** Observed dietary composition of tracked *E. wahlbergi* during (a) winter and (b) spring.

**Table 1** Body mass and forearm measurements of *E. wahlbergi* used in this study from the urban environment of Pietermaritzburg during winter. \* = not used in study as could not be refound after initial release.

<b>Individual</b>	<b>Sex</b>	<b>Body mass (g)</b>	<b>Forearm length (mm)</b>
<u>1</u>	Female	105	79.5
<u>2</u>	Male	127	82
<u>3</u>	Female	88	79
<u>4</u>	Female	87	76
<u>5</u>	Male	93	76
<u>6</u>	Male	106	79
<u>7</u> *	Female	91	84
<u>8</u> *	Male	81	81
<u>9</u>	Male	105	81
<u>10</u>	Male	89	80
Mean $\pm$ SE		97.4 $\pm$ 4.31	80 $\pm$ 0.77

## Chapter 4

### **Roost temperature and fidelity of Wahlberg's epauletted fruit bat in an urban environment.**

**D. P. Rollinson<sup>1</sup>, J.C. Coleman & C. T. Downs<sup>1,2</sup>**

<sup>1</sup> School of Life Sciences, University of KwaZulu-Natal,  
Private Bag X01, Pietermaritzburg, 3209, South Africa

<sup>2</sup> Tel: 033 260 5127

Fax: 033 260 5105

Email: [downs@ukzn.ac.za](mailto:downs@ukzn.ac.za)

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#### **Abstract**

With increasing urbanisation it is important that animals are able to adjust to a life in close association with humans. Some species have been able to thrive in this newly created environment while others avoid it altogether. One species which has been able to adjust to urbanisation is Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*); as these areas often provide additional food and roosting resources. This study investigated the roosting dynamics of *E. wahlbergi* in the urban environment of Pietermaritzburg, South Africa. To determine roost fidelity bats were radio-tracked to their daytime roosts. Bats were found to have changed their daytime roosts regularly, and would change more frequently during winter than spring. Roost temperatures were measured by placing *i-Button*<sup>®</sup> temperature loggers at known roosts, either in man-made structures or vegetation. Temperatures varied across different roosts however, roost temperatures were higher than ambient temperatures. Roosts in man-made structures had higher temperatures than those in natural vegetation. This study iterates the importance of temperature of *E. wahlbergi* daytime roosts, however other factors such as reproduction and social interactions, predator avoidance and proximity to food resources are almost certainly considered in daytime roosts.

**Key words**

Roost fidelity; Wahlberg's epauletted fruit bat; urban environment; roost temperature

**Introduction**

Increased urbanisation has meant that many species worldwide have been forced to live in close association with humans which has resulted in a dramatic loss of biological diversity (Jung & Kalko, 2011; Lizee *et al.*, 2011). However there are those species that are able to live in this newly created environment. These species are able to survive due to certain biological traits, such as whether the species are specialist or generalist feeders (Lizee *et al.*, 2011) or because they are able to adapt to their new environment by changing aspects of their ecology (Williams *et al.*, 2006). There are however many groups of organisms that have not been able to adapt or adjust to urbanisation and hence no longer occur in urbanised areas (Lizee *et al.*, 2011). Within the order Chiroptera many species of the suborder Microchiroptera have been unable to adapt to urbanisation (Jung & Kalko, 2011), possibly due to increased light pollution (Stone, Jones & Harris, 2009).

Conversely, many species within the suborder Megachiroptera have been able to withstand increased urbanisation and appear to have flourished in these areas (Williams *et al.* 2006). These bats include fruit bats of Africa and flying foxes from Asia, the South Pacific and Australasia. Flying foxes have fared particularly well in cities across Australia, where huge roosts have appeared in some urban areas (Markus & Hall, 2004; McDonald-Madden *et al.*, 2005; Schmelitschek, French & Parry-Jones, 2009). These huge flying fox roosts are thought to have been established in urban areas due to the increased quantity and diversity of food in urban areas, as well as the abundance of suitable roosting sites such as large trees (Markus & Hall, 2004).

Bats may be described as either generalists or specialists in their choice of roosts, this is based on the number of different structures the bat is able to roost in (Swier, 2003). Specialists select only one type of roost while generalists do not consistently select any particular roost type (Swier, 2003). Within both suborders of Chiroptera; Mega- and Microchiroptera there are roost generalists and specialists (Swier, 2003; Monadjem *et al.*, 2011)



Pteropodidae are a family within Megachiroptera which is comprised of fruit bats, including flying foxes. Most Pteropodidae hang to trees or shrubs in fairly exposed areas, they hang to the underside of leaves or branches and cling on using their hind claws (Monadjem *et al.*, 2011), however some African species such as Egyptian Rousette (*Rousettus aegypticus*) roost exclusively in caves (Monadjem *et al.*, 2011). Some Pteropodidae species such as Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) will roost in a number of different habitats; such as dense foliage of tall trees, man-made structures, and in caves (Monadjem *et al.*, 2011) and so may be considered to be roost generalists.

In Kruger National Park, South Africa, *E. wahlbergi* generally roost in riverine forest, often in trees overhanging the river; roosts are generally between 8 - 15 m up in trees of thick foliage (Fenton *et al.*, 1985). One individual was found to be roosting in a nearby cave which is unusual for this Pteropodidae species. *Epomophorus wahlbergi* would regularly change roost sites (Fenton *et al.*, 1985). These changes in roost sites could not be attributed to changes in food sources and hence reducing traveling distances from roost site to feeding sites (Fenton *et al.*, 1985).

Roost fidelity is described as the need to return to the same roost, which varies greatly between different species (Lewis, 1995). In a review by Lewis (1995) it was found that 25 of 43 species would regularly change their roosting sites and that roost fidelity was based on the type of roost occupied: as high fidelity is directly related to roost permanency while inversely related to roost availability. Some species will use the same roost for years while other species change their roosts almost daily (Lewis, 1995). Humphrey (1975) suggested that bats benefited from roost fidelity when they are well suited for reproduction or hibernation. Bats appear to change roosts for some of the following reasons; in response to disturbance by humans or predators (Kunz, 1982), minimising commuting distances between roost and foraging sites (Fleming, 1988), to avoid build up of ectoparasites within roost sites such as caves (Fleming, 1988), and to avoid unfavourable microclimate or structural changes within the roost (Fleming, 1988). Many bat species seem to be opportunistic in roosting habits (Kunz, 1982), however some species are highly selective in their choice of roost sites (Vaughan & O'Shea, 1976;

Monadjem *et al.*, 2011) which are chosen because of a combination of microclimate conditions, exposure to predators and other factors.

Roosts are not only important to bats for protection from predators and inclement weather but are also critical in balancing the energy budget, as bats are considered restrained energetically (Moussy, 2011). Correct roost temperatures are important as if temperatures are too low some bat species may go into torpor (Audet & Fenton, 1988), while low temperatures at a maternity roost may cause slowed growth of offspring (Moussy, 2011). Maternity roosts thus often have higher temperatures, which minimises energy expenditure, meaning there is more available energy to sustain pregnancy and lactation, and the growth of young (Moussy, 2011). *E. wahlbergi* is known to breed throughout the year, with peaks during July (winter) and summer months (Monadjem *et al.*, 2011). Males will call from traditional calling sites to attract females (Monadjem *et al.*, 2011), which can be described as a loud ‚pinging’ sound.

We investigated roosting dynamics of *E. wahlbergi* in the urban environment of Pietermaritzburg, KwaZulu-Natal. Specifically we investigated roost temperatures and roost fidelity. We predicted that *E. wahlbergi* would regularly change daytime roost locations and that these daytime roost switches might occur for a number of reasons; some which we tested for and others which we were unable to test. We hypothesised that roosts in/under man-made structures would have higher temperatures than roosts in vegetation, and that temperature extremes would affect bat roost numbers.

## **Methods**

### **Study area and bat capture**

*Epomophorus wahlbergi* were caught on the Agricultural and Life Sciences campus of the University of KwaZulu-Natal, Pietermaritzburg (GPS -29.62522 S, 30.40358 E, 660 msl) in June 2011. Bats were mist-netted either around fruiting trees or in close proximity to daytime roosts (Chapter 3). The individual bats used in this study were different to those used in Chapter 2. Bats were identified by the presence of a single post-dental palatal ridge which is unique to *E. wahlbergi* in the subregion (Monadjem *et al.*, 2011). Ten individual *E. wahlbergi* (male = 6, female = 4) were caught and fitted with transmitters (BD-2C Transmitters, Holohil Systems Ltd. Ontario) broadcasting at

frequencies between 151.418 Mhz and 151.599 Mhz. Two bats were not refound after capture and so were not used in this study. Bats were weighed using a Pesola scale (Pesola, Baar, accurate to 5 g), measured (forearm length), sexed and released within 30 min of capture. Radio-transmitters were attached to the bats backs with small collars and a cyanocrylate adhesive (Alcon, Chempet). The transmitters were attached behind the bats neck with the use of a collar and the antennae running down along the bats back in such a way that they could not be removed by the bat or hinder movement. Aldridge & Brigham (1998) recommend that transmitters should weigh less than 5 % of the animal's body mass to ensure movement is not restricted. The transmitters in this study weighed 1.15 g, which is less than 5 % body mass. Immature or pregnant individuals were released and not used in this study. It is likely that some of the bats used in this study were breeding, as a number of males were heard calling in the immediate vicinity.

### **Radio-tracking in the urban environment**

Bats were radio-tracked with the use of a vehicle and on foot, using a hand-held collapsible antenna with a radio receiver (R-1000 Telemetry Receiver, Communications Specialists, Inc. California). The geographical location of the bats was determined by homing in on the signal produced by the transmitter (White & Garrot, 1990). The geographical location was determined by varying signal strength; a visual fix was attained where possible. Eight of the ten bats fitted with transmitters were tracked for up to 21 nights from sunset to sunrise over winter and spring. Two of the bats fitted with radio-transmitters were not refound and so were not used in this study. Bats were also tracked once a day during daytime hours, to find the location of their daytime roosts. Bats were tracked by using two teams of observers (comprising 3 people each) who tracked from sunset (Winter approximately 17:00; Spring approximately 18:00) till midnight and then midnight till sunrise (winter approximately 06:00; spring approximately 05:00), to ensure the entire nights foraging was monitored. We allowed a 1 h interval between location fixes for the individual bats. Bats positions were recorded using a hand-held global positioning system (GPS, Garmin, eTrex, Olathe). The bats were tracked for 3 weeks in June/July 2011 and then in September/October 2011 respectively.

### **Roost fidelity**

The locations of the radio-tagged bats were determined by tracking the bats with the use of a radio receiver (R-1000 Telemetry Receiver, Communications Specialists, Inc. California) in a vehicle and on foot. Bats' Global Positioning System (GPS) location was determined by homing in on the signal produced by the transmitter. Bats' roost locations were recorded using a hand-held global positioning system (GPS, Garmin, eTrex, Olathe). It was not always possible to determine the location of the daytime roosts as the bats changed regularly. Known roosts were visited daily and presence or absence of individual bats was noted. Bats were tracked to their roost locations during June - July 2011, and August – October 2011.

Bat numbers were counted between March and October 2011 at the palm tree roost (UVeg) on the Agricultural and Life Sciences campus of the University of KwaZulu-Natal, Pietermaritzburg.

### **Roost temperatures**

Roost temperatures were recorded by calibrated data logger *i-Buttons*<sup>®</sup> (Model DS 1922L  $\pm 0.06^{\circ}\text{C}$ , Dallas semiconductor, Sunnyvale, CA) at seven *E. wahlbergi* roosts around the greater Pietermaritzburg area. A single *i-Button* was placed at each roost, programmed to record ambient temperature at 15 min intervals. Four *i-Buttons* were placed in roosts in man-made structures and three *i-Buttons* in roosts in vegetation. Of the four roosts in man-made structures, three were under roof eaves (CBuild, FBuild, SBuild) and the third was under a thatched roof (HBuild). Of the three vegetation roosts one was in a palm tree (*Borassus* sp.) between two buildings (UVeg), the second in a bougainvillea bush (*Bougainvillea* sp.) (FVeg) and the third in a pigeonwood tree (*Trema orientalis*) (SVeg). Heights of the different roosts varied, with most (FBuild, SBuild, HBuild, SVeg, UVeg) roosts between 5 – 10 m high while the other two roosts (CBuild and FVeg) were approximately 3 m high. The *i-Buttons*<sup>®</sup> were placed as close to the roosting bats as possible to attain accurate temperatures for the roosts. All roosts which were fitted with *i-Buttons* contained roosting bats except for CBuild which did not contain any roosting bats throughout, however bats have been known to roost there previously. Roost temperatures were recorded from March – September 2011 after which *i-Buttons*<sup>®</sup> were

removed and data downloaded using ColdChain Thermodynamics software (Fairbridge Technologies, Pretoria). Ambient temperature data were obtained from the South African Weather Service for the Pietermaritzburg weather station (-29.6330 S, 30.4000 E; 673 m asl) during the period March – September 2011.

### **Statistical analyses**

Descriptive statistics and Analysis of variance (ANOVA) were used for most of the parameters measured. Where necessary post-hoc Tukey tests were conducted. Minimum and maximum mean temperatures for each month were calculated by averaging daily min/max temperatures over the month. All were performed using the Statistica 7 package (Statsoft Inc., Tulsa, OK, USA).

## **Results**

### **Roost temperatures**

There was great variation in the roost temperatures between the seven different roosts around Pietermaritzburg. Roost temperatures were lowest during winter and warmest during spring (Fig. 1). Maximum recorded temperatures of the respective roosts differed significantly (ANOVA,  $F_{(6)} = 6.105$ ,  $P < 0.05$ ) and these maximum roost temperatures were higher than maximum ambient temperature for Pietermaritzburg for all months except September (Fig. 2a). Minimum roost temperatures differed significantly between the roosts (ANOVA,  $F_{(6)} = 5.508$ ,  $P < 0.05$ ) and were generally lower than minimum ambient temperature for Pietermaritzburg (Fig. 2b). Temperatures of those roosts in man-made structures (under roof eaves and thatched roofs) were warmer than those in natural areas (post-hoc Tukey,  $P < 0.05$ , Fig 3a, b). One particular roost CBuild had much higher maximum temperatures than all other roosts, except for the month of September (post-hoc Tukey,  $P < 0.05$ ). CBuild minimum temperatures were higher than all other minimum temperatures for the winter months (June-August) (post-hoc Tukey,  $P < 0.05$ ).

The number of bats at the roost UVEg generally increased during the warmer months and decreased during the cooler winter months (Fig. 4). Roost numbers at UVEg changed regularly and so individual bats appear to regularly change roost sites (Fig. 4).

The minimum number of *E. wahlbergi* at this roost was two on a day in April 2011 and a maximum of 33 on a day in October 2011. Roost numbers may be influenced by roost temperatures, however a number of different factors also influence roost choice, so it is difficult to be certain of the underlying factor which caused bats to change roosts.

### **Roost fidelity**

Bats (n = 8) all changed their daytime roosts at least once during the study. The daytime roost where an individual bat spent the greatest percentage of its days was identified as Roost 1. Average percentage of days spent at Roost 1 ranged from 59 % during winter to 72 % during spring. During the winter tracking period individual bats changed their roost an average of 4.6 times while during spring they only averaged 1 change per bat, and averaged 1.6 changes per bat in summer (Chapter 2). The largest distance between alternate daytime roosts used by the same individual was 0.85 km (during spring) while the shortest distance between daytime roosts was 0.04 km (both seasons). On some occasions the daytime roosts of individual bats could not be found, however we could determine that they were not present at roosting sites they had previously been using. These results are similar to those from Chapter 2, with some bats spending the majority of time at a single roost; however roost switching did happen regularly amongst the other individual bats.

### **Discussion**

Within the order Chiroptera there is a large amount of heterogeneity in roosting habits, particularly roost fidelity. Some species will use the same roost for years, while some species will change roosts daily (Lewis, 1995). *Epomophorus wahlbergi* switches roosts regularly; however it may spend a number of days at a particular roost before changing to another (Fenton et al., 1985). No individual bat was found to be roosting at the same roost throughout the tracking period; some bats would change roosts more frequently than others.

It appears to be temperature which causes the bats to change roosts, as no other discernable changes were noted at the UKZN roost, where roost numbers were regularly counted. Maximum temperature appeared to be the factor which caused bats to change

roosts, as there were more bats during the cooler winter months compared to the warmer months. As one would expect the minimum temperature dropped during winter, while bat numbers increased. It is likely that maximum temperature rather than minimum temperature would determine bat numbers as minimum roost temperatures would be attained during the night when bats were foraging and hence generating their own heat.

Maximum temperatures would be attained during the daytime hours which are when the bats would be present at the roost. However minimum temperatures during winter are certainly important as *E. wahlbergi* resting and basal metabolic rates are significantly higher during winter than in spring (Downs *et al.*, 2012). It is thus important that daytime roost temperatures are not too low as this would mean increased metabolic rates which are difficult to sustain. Individual bats did show fidelity to a preferred roost (Roost 1), which is similar to what previous research has revealed (Fenton *et al.*, 1985).

*Epomophorus wahlbergi* changed their roosting sites more regularly during winter than during spring and summer. A possible explanation for this could be that temperatures at certain roost were too low and that other roost sites were sought out with more suitable microclimate conditions. Another possible reason for this is that there is a reduced diversity of fruiting plants available during winter and so bats would need to change their roost sites more regularly, to be closer to food sources. However previous studies on *E. wahlbergi* have found that roost switching was not influenced by proximity to food resources; during a study in Kruger National Park, South Africa, Fenton *et al.* (1985) found that *E. wahlbergi* would regularly change roosts, alternating between a number of different roosts in an unpredictable manner. Roost temperatures were not recorded during this study; however Fenton *et al.* (1985) could conclude that roost location was not influenced by proximity to food resources. Fenton and colleagues (1985) suggested that it could be predator avoidance or microclimatic conditions (affecting thermoregulatory properties of bats) which were causing bats to change roosts.

The roosting fidelity of the musky fruit bat (*Ptenochirus jagori*) was investigated in the Philippines. Both males and females regularly changed their daytime roosts at varying intervals (Reiter & Curio, 2001). Spatial changes in availability of food resources and hence minimising of commuting costs to food resources were suggested reasons for regular roost switching (Reiter & Curio, 2001).

Snoyman & Brown (2010) suggested that thermoregulatory properties of certain roosts are a key driving force behind roost selection. Microclimatic conditions, particularly temperature, did vary across different *Pteropus poliocephalus* roosts, as well as a great amount of temperature variation within the roosts. As there are temperature differences between roosts, it means that the bats have different options to make with regards to roost microclimate, which could mean that on particularly hot days bats would avoid certain roosts and use others.

In this study roost maximum temperatures were found to be higher than ambient maximum temperature. This would suggest that *E. wahlbergi* prefer higher temperatures at a roost as bats expend very little energy during roosting. However as temperature loggers were not placed at other known roosts, it is not possible to compare different roost temperatures and thus temperature can only be speculated as the reason for roost changes. Data from this study were similar to results from Snoyman & Brown (2010) who found that temperatures at *P. poliocephalus* camps were higher than surrounding bushland.

Unfortunately not all the possible reasons for roost changing were investigated in this study. Kunz (1982) suggested that ectoparasite build-up at roosts may be a factor for roost changing; however ectoparasite build-up may be more of a problem for bats roosting in larger numbers or in more confined spaces such as caves. For this reason ectoparasite build up was not considered in this study, however it could still be a factor. Fleming (1988) suggests that predator and human disturbance may cause bats to change roosts. This may be a limitation to this study, however human and predator avoidance was very difficult to monitor at the roosts and in some cases not possible at all, and so was not included in this study.

### **Acknowledgements**

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to those who allowed us to place the *i-Button*<sup>®</sup> temperature loggers in their gardens or roof eaves.

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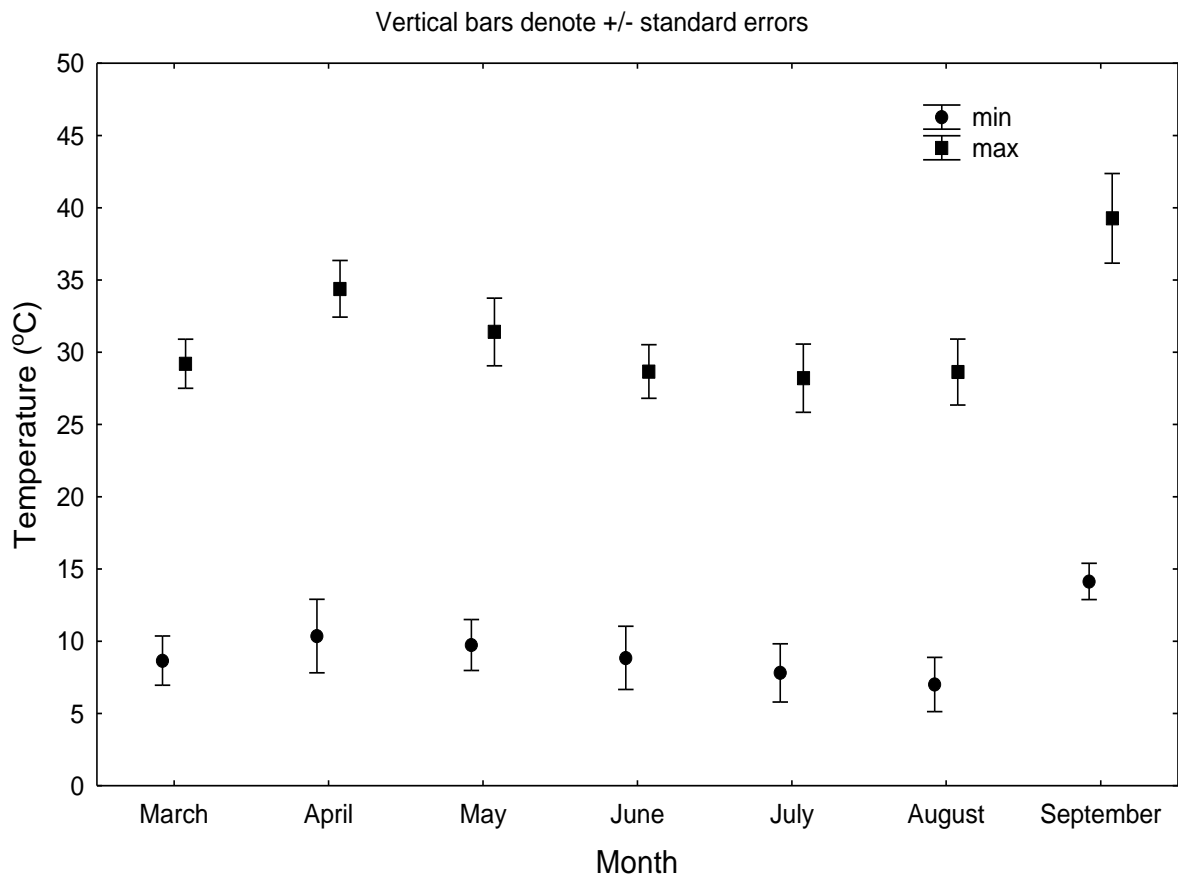
### Legends for Figures

**Figure 1** Mean minimum and maximum monthly temperatures of all *E. wahlbergi* roosts combined over the observed months. Values represent means  $\pm$  standard error.

**Figure 2** Monthly maximum (a) and minimum (b) temperatures at *E. wahlbergi* roosts across Pietermaritzburg.

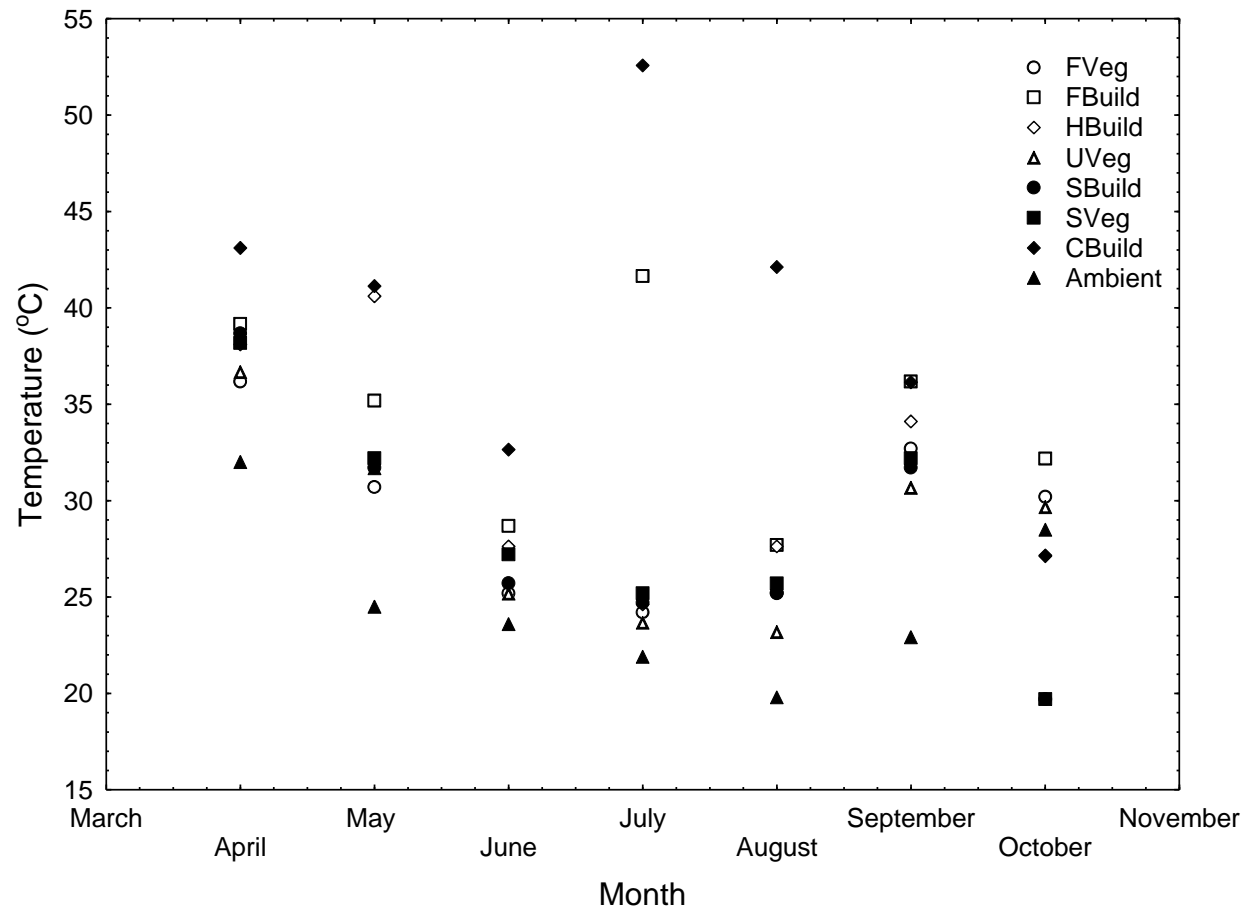
**Figure 3** Maximum (a) and minimum (b) mean temperatures over observed months at all *E. wahlbergi* roosts sites. FVeg = Ashburton Farm roost in vegetation; FBuilding = Roost under roof eaves; HBuilding = Roost under thatched roof; UVeg = Roost in vegetation; SBuilding = Roost under roof eaves; SVeg = Roost in vegetation; CBuilding = Roost under roof eaves. Values represent means  $\pm$  standard error.

**Figure 4** Minimum and maximum temperature, and daily roost counts at the UVeg roost (between buildings).

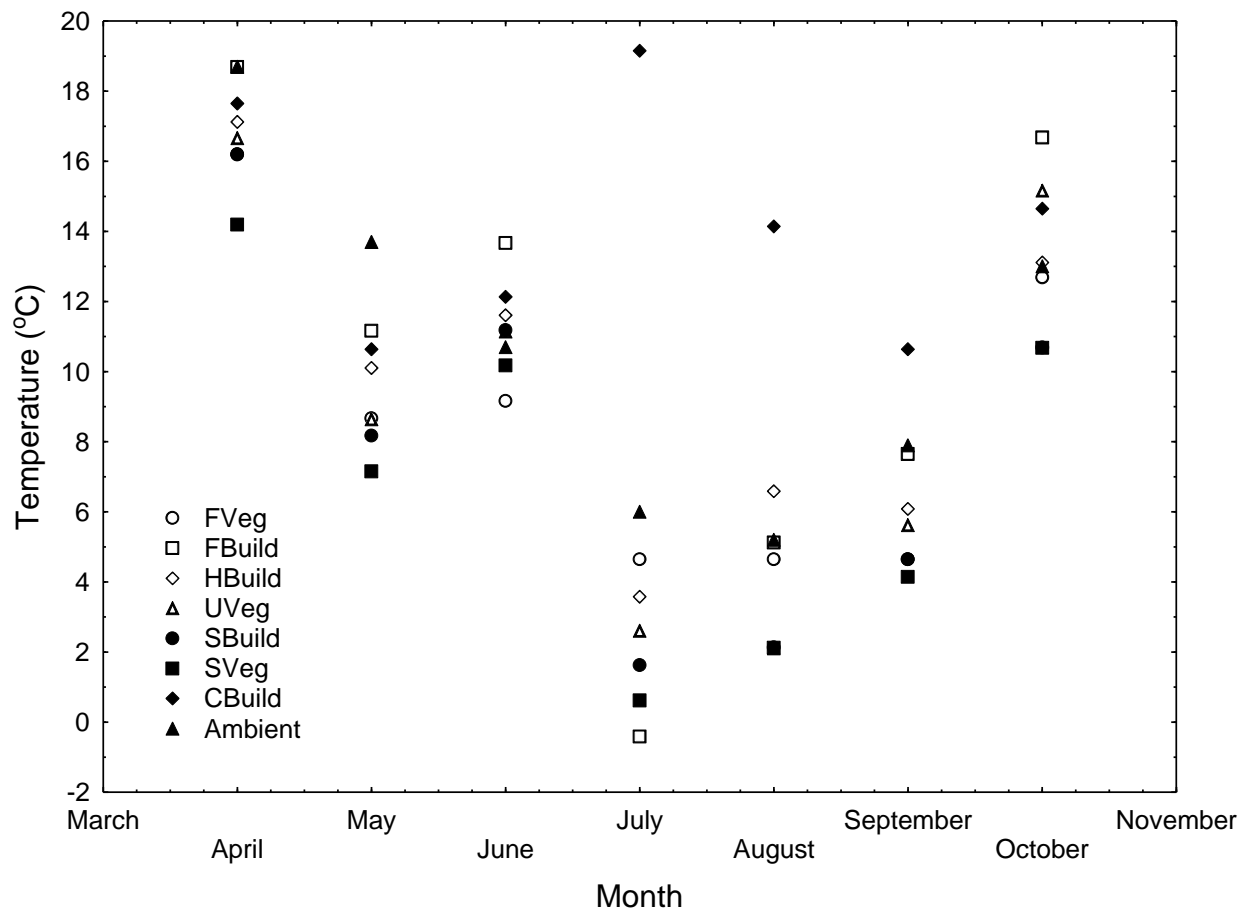


**Figure 1** Mean minimum and maximum monthly temperatures of all *E. wahlbergi* roosts combined over the observed months. Values represent means  $\pm$  standard error.

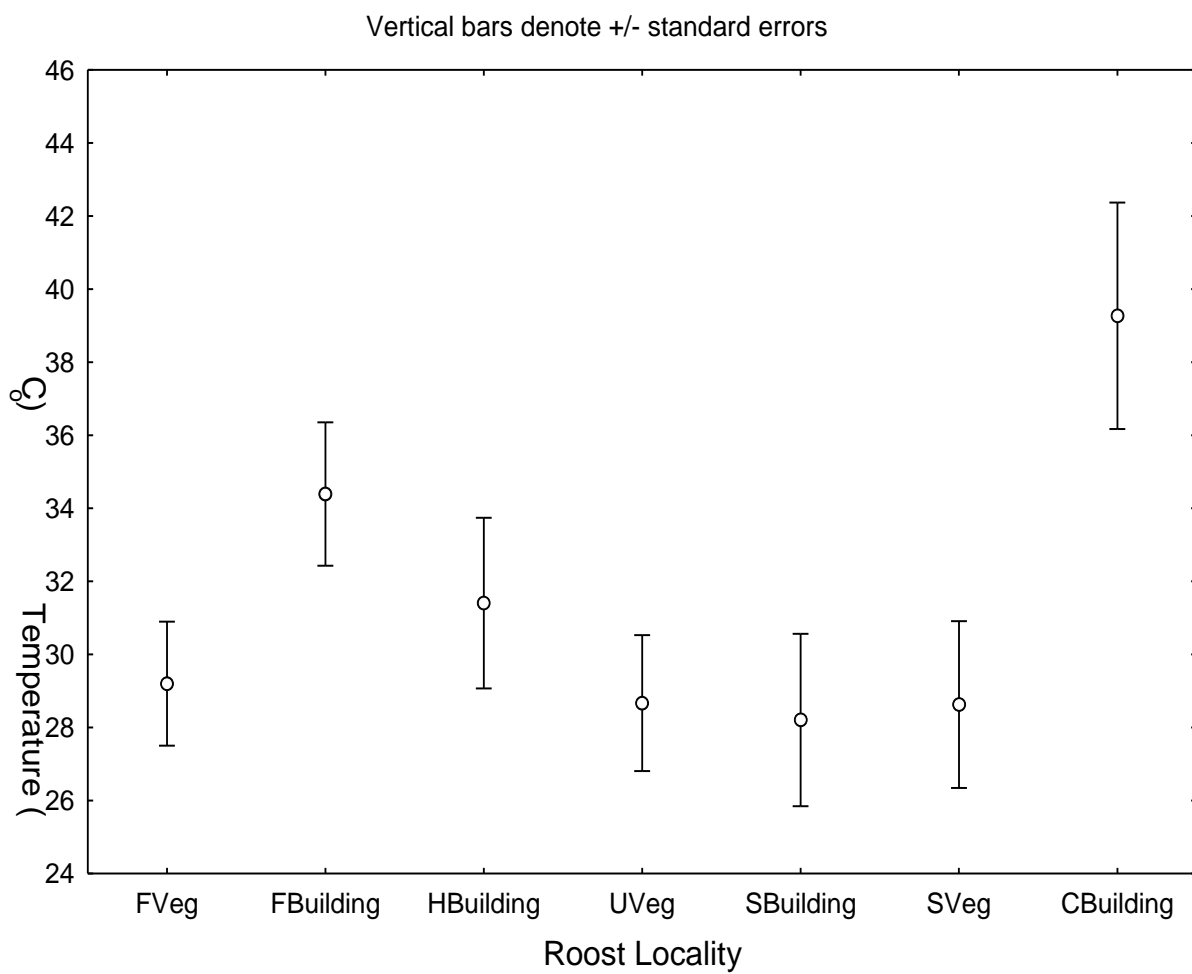
(a)



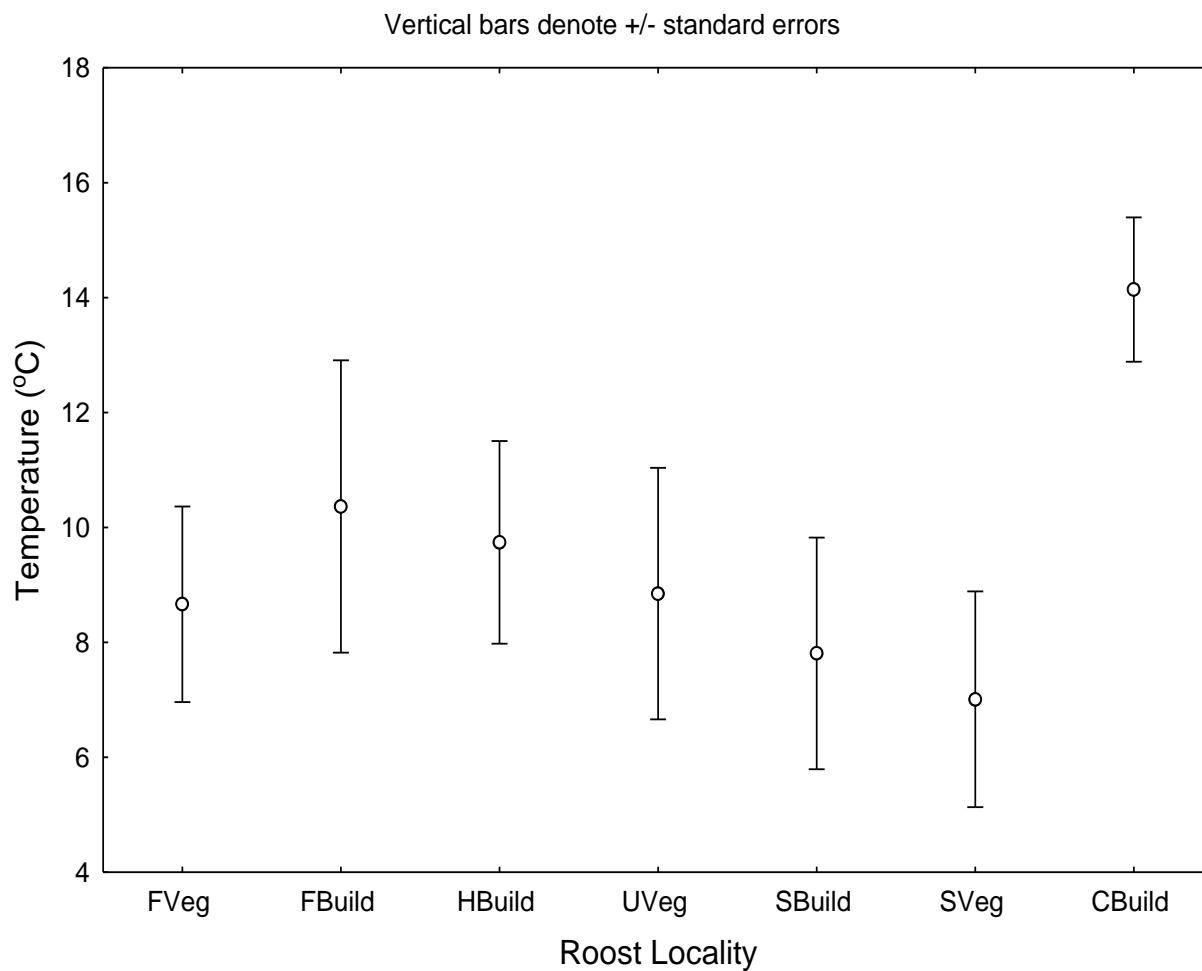
(b)



**Figure 2** Monthly maximum (a) and minimum (b) temperatures at *E. wahlbergi* roosts across Pietermaritzburg.

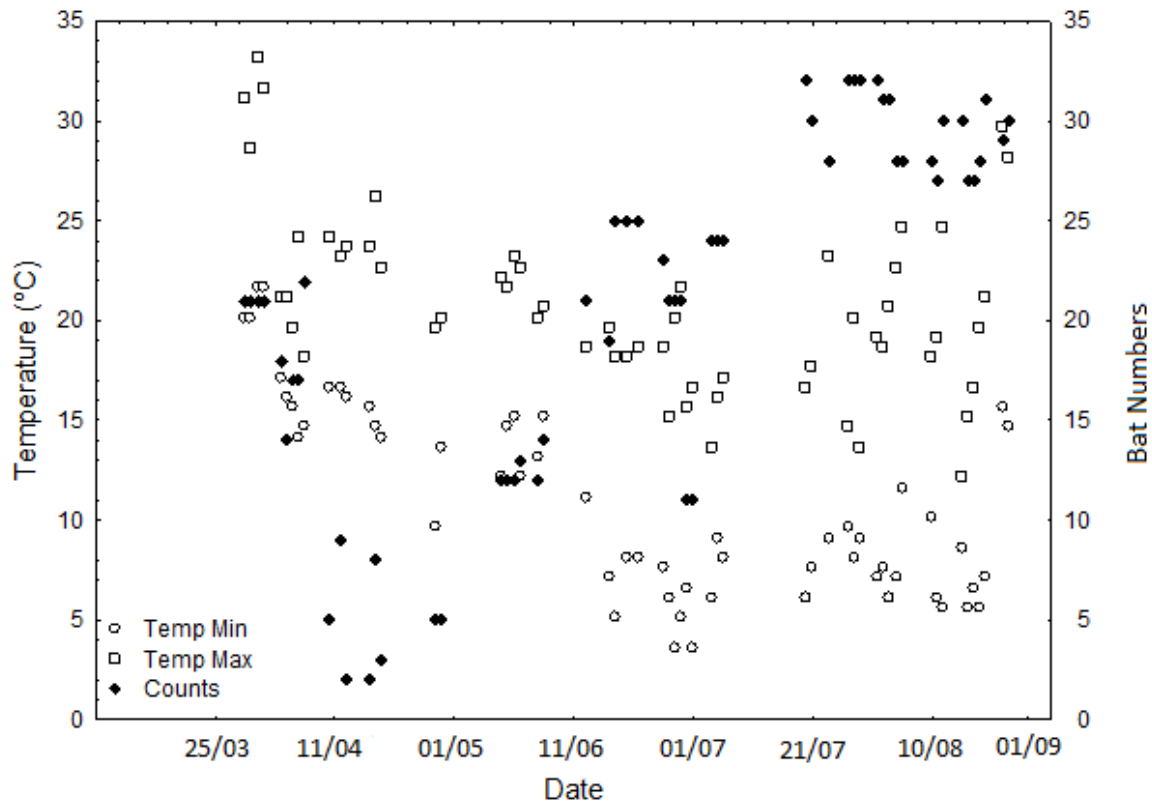


(b)



**Figure 3** Maximum (a) and minimum (b) mean temperatures over observed months at all *E. wahlbergi* roosts sites. FVeg = Ashburton Farm roost in vegetation; FBuilding = Roost under roof eaves; HBuilding = Roost under thatched roof; UVeg = Roost in vegetation; SBuilding = Roost under roof eaves; SVeg = Roost in vegetation; CBuilding = Roost under roof eaves. Values represent means  $\pm$  standard error.





**Figure 4** Minimum and maximum temperature, and daily roost counts at the UVeg roost (between buildings).

## Chapter 5

### Conclusion

With increasing urbanisation it is important to understand why and how many species are negatively affected, however it is also important to understand the reasons why other species are not negatively affected and are in fact flourishing in some urban environments. Many species have been able to adjust to the urban environment by changing certain aspects of their ecology. Some species of Chiroptera (particularly the suborder Megachiroptera) have adapted well to urban life. By roosting in man-made structures, such as roof eaves, many bat species have been able to flourish in urban environments. There is also a greater abundance of food resources in some urban environments for certain bat species (Jung & Kalko, 2011), as many exotic fruiting tree species have been introduced both purposely and accidentally. Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) is one of these species which has been able to adjust to some urban areas and appears to thrive in this new environment. These adjustments are able to occur because of plasticity in many aspects of this species ecology.

The present study has revealed much about home range size as well as foraging and roosting dynamics of *E. wahlbergi* in the urban environment. Previously research has been done on the foraging and roosting dynamics of *E. wahlbergi* in the natural environment, however very little has been done on *E. wahlbergi* in the urban environment. Fenton and colleagues (1985) found that *E. wahlbergi* were commuting large distances to foraging areas; much greater distances than those bats in this current study were commuting. A possible explanation for this may be that the urban environment (with the introduction of exotic species) now has greater food resources than in the natural environment (McDonald-Madden *et al.*, 2005; Jung & Kalko, 2011) and so it is not necessary for bats to travel large distances in search of food.

It was found that there was great variation in the distances *E. wahlbergi* would fly while foraging, as well as variation in the areas used for foraging. Some bats would fly large distances to other parts of Pietermaritzburg to forage while most other bats would forage in the same general area on consecutive nights. Some individual bats would return to the same fruiting trees on consecutive nights to forage during late summer (Chapter 2).

Home range size did differ between the sexes, with females occupying a much larger home range than males. This would suggest that individual bats have dietary preferences based on a number of factors such as age, sex as well as reproductive and social interactions.

There were significant differences in home range sizes of bats during winter and spring as well as differences in habitat use (Chapter 3). Home range sizes were found to be significantly larger during winter than during spring. A likely explanation for this difference in home range size, is that due to a reduction in food resources during winter, bats need to travel greater distances to find food resources. The bats were found to be feeding extensively on exotic plant species, very often alien invasive species, particularly fruits of *Syringa* trees (*Melia azedarach*). The bats were found to be utilizing very similar home ranges, and many individual bats would return to the same fruiting trees for consecutive nights for feeding, sometimes for consecutive weeks. This study has shown that alien invasive plants form an important component of *E. wahlbergi* diet. As urban areas very often have high levels of alien invasive plant species it may mean that *E. wahlbergi* will respond positively to urbanisation, unlike many other species around the world.

Roost temperatures were found to be higher than ambient temperature and it appears bats can tolerate high roost temperatures, however it was found that roost numbers did increase as roost temperatures lowered, i.e. during winter months (Chapter 4). Those roosts which were located in man-made structures had higher temperatures than those roosts in natural vegetation. Although *E. wahlbergi* changed their roosts regularly, some bats did show some roost fidelity and returned to the same roosts for a number of consecutive days during the radio-tracking period. These results are similar to the results Fenton *et al.* (1985) obtained from the natural environment of Kruger National Park. Unfortunately, some potential factors for daytime roost switching were not investigated in this study, such as human and predator disturbance as well as ectoparasite build-up at daytime roosts.

It is not only important to understand what impact the urban environment has had on these species, but it is important to understand what impact urban species have had on the urban environment. Most importantly, by using alien invasive and exotic plant species

as a food source, are urban species aiding in the spread of these exotic species? It is well known that birds contribute significantly to dispersal of alien invasive plants (Debussche & Isenmann, 1994; Carlo & Morales, 2008) however Jordaan *et al.* (2011) found that *E. wahlbergi* should also be considered an important disperser of alien invasive plants in the urban environment. It is important to draw upon research of this nature to make future environmental decisions, such as those decisions regarding alien invasive species.

Future research on *E. wahlbergi* is still needed, perhaps tracking the bats with global positioning system (GPS) transmitters. Using GPS transmitters, the bats entire movements may be followed, and excursions away from urban areas can still be tracked. A problem with the research conducted in this thesis, is that at times the bats could not be located and so their movements were unknown until a GPS fix could be attained, similar research conducted with GPS transmitters would give more detailed results, as the bats movements would be known throughout the tracking period. A limitation to this study is the small sample size of radio-tracked bats. The home range size and foraging movements of *E. wahlbergi* could be better understood if future studies used a larger sample size. Another limitation to this study is that bat roost numbers were only recorded from one daytime roost. Greater conclusions could have been drawn had there been bat roosting data from a number of daytime roosts.

Much research still needs to be conducted on urban species, particularly species from the order Chiroptera. Many species from the suborder Microchiroptera have not responded well to urbanisation (Gaisler *et al.*, 1998), however certain Microchiroptera species have thrived in some urban areas (Lesinski *et al.*, 2000) and are now more common in urban areas than in natural areas. It is thus important to understand the reasons behind this decline in urban Microchiroptera diversity as well as the reasons why some bat species have been able to thrive in this environment.

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