

DEVELOPING AN UNDERSTANDING OF THE
DRIVERS OF BAT ACTIVITY PATTERNS RELEVANT
TO WIND TURBINES

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DRIVERS OF BAT ACTIVITY PATTERNS RELEVANT
TO WIND TURBINES

By

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PREFACE

Declaration

I, Tiffany Edan Thwaites (s209025810), hereby declare that the dissertation for degree of Master of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.



Tiffany Edan Thwaites

All procedures adhered to the Code of Animal Experimentation adopted by the Nelson Mandela Metropolitan University (NMMU). Animal ethics clearance was granted by the NMMU ethics committee (A12-SCI-ZOO-005). Permits for live animal capture and transport were issued by the Eastern Cape Department of Economic Affairs, Environment and Tourism (CRO 85/12CR, CRO 86/12CR, CRO 97/12CR, CRO 100/13CR, CRO 101/13CR and CRO 102/13CR).

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Every creature is better alive than dead, men and moose and pine trees, and he who understands it aright will rather preserve its life than destroy it.

Henry David Thoreau, from 'Chesuncook', the Maine Woods, 1848

GENERAL ABSTRACT

The increasing number of proposed wind farm developments in South Africa provides an immediate reason to assess bat activity and diversity, with the expectation of developing measures to mitigate for negative impacts. The overall aim of this thesis was contribute to an understanding of the drivers of bat activity, relevant to wind turbines, and to determine what factors (exogenous – environmental, or endogenous – intrinsic physiological processes) contributed to observed bat activity patterns, at the Metrowind Van Stadens Wind Farm in the Eastern Cape of South Africa.

A combination of active (mist netting) and passive (acoustic) bat monitoring techniques were used to determine free-ranging bat activity patterns (Chapter 3). A total of 889 bat passes were recorded over 323 detector nights from the beginning of May 2012 to the end of December 2012. The Cape serotine bat (82%) and the Egyptian free-tailed bat (97%) made up the majority of all bat passes recorded on site. Large variations in bat activity per month and per hour were apparent, with bat activity peaking in May 2012 and during the first few hours after sunset (18:00-23:00). Patterns in nightly, free-ranging bat activity at the site were modelled against various environmental conditions. Month, temperature, wind speed and an interaction between month and rainfall were the most significant predictors of bat activity, explaining 80% of the variation observed on free-ranging bat activity patterns.

A total of eight Cape serotine bats (Table 4.1.) were caught in mist nets on site and changes in the resting metabolic rate (RMR) of torpid ($n = 6$), and normothermic ($n = 2$) bats, over a 24 hr period, were measured and used to predict free-ranging Cape serotine bat activity (Chapter 4). Cape serotine bats showed a high proclivity for torpor in the laboratory and peaks in RMR were observed at 18:00 ($0.89 \pm 0.95 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$) and again from 20:00-21:00 ($0.89 \pm 0.91 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$). Peaks in RMR of torpid individuals coincided with peaks in the average hourly free-ranging activity of the Cape serotine bat, and RMR explained 33% of the variation and was a good predictor of free-ranging bat activity ($R^2 = 0.2914$).

This study showed that both exogenous (Chapter 3) and endogenous (Chapter 4) factors drive bat activity in the wild. Although this dissertation was not intended for wind turbine management, the information presented on the biology and activity of bats is important for managing interactions between bats and wind turbines. By determining what factors influence bat activity, we are able to predict when bats will be most active and thus can develop mitigation measures to reduce the potential impacts that wind turbines will have on the bat community. In order to conserve bats and reduce potential bat fatalities from occurring at the site, mitigation measures should be concentrated to those times when bats are most active (May and during the first few hours after sunset – 18:00 to 22:00).

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CHAPTER 1

GENERAL INTRODUCTION

The increasing development of wind farms (Department of Minerals & Energy 2003; International Energy Agency (IEA) 2013) is posing a new and growing threat to bats. Numerous studies are starting to show that bats are particularly vulnerable to be killed by wind turbines (Erickson *et al.* 2003, Kerns & Kerlinger 2004, Arnett *et al.* 2008, Brinkman 2006). This is a matter of considerable concern given the importance of conserving biodiversity (Hooper *et al.* 2005, Bastian 2013), of which the bats are unique element (Mendellin *et al.* 2000), as well as in terms of the need to maintain the ecosystem services provided by bats (Kunz *et al.* 2011). It is also clear that the growth of alternative energy sources is a global priority (IEA 2006) and currently, wind-generation of electricity is an important part of this (Department of Mineral & Energy 2003, Kaldellis & Zafirakis 2011, IEA 2013). Accordingly, there is a need to better understand the interaction between bats and wind farms, ideally with the expectation of developing measures to mitigate these impacts (Sowler & Stoffberg 2012). This is however a relatively new field of study in South Africa (Sowler & Stoffberg 2012) and this project therefore represents an initial attempt to contribute to this area, in the form of a pilot study of factors that may lead to the prediction of bat vulnerability to wind turbines.

1.1. GENERAL ECOLOGY OF BATS

Bats are nocturnal mammals which belong to the order Chiroptera and are the only mammals capable of powered flight (Fenton & Ratcliffe 2010). There are approximately 1115 bat species worldwide, with 116 species of bat found in the Southern African sub-region (Monadjem *et al.* 2010). Four species; the Angolan fruit bat (*Lissonycteris goliath*), the East African little collared fruit bat (*Myonycteris relicta*), Percival's short-eared trident bat (*Cloeotis percivali*), and the Lesueur's hairy bat (*Cistugo lesueurii*), have a global Red List status of Vulnerable and 17 are classified as Near Threatened (IUCN 2013).

A variety of day roosts are used by bats, ranging from roosting in trees and foliage (Taylor 2000), to hollow roosting sites such as caves, mines and old mine shafts (Kunz & Lumsden 2003), roofs and basements of houses (Entwistle *et al.* 1997; Law & Chidel 2007), and in the hollow of trees (Fenton *et al.* 1985). Cave-dwelling bat colonies form some of the largest aggregations of bats than any other roosting sites (McDonald *et al.* 1990). Bats are also known to roost in crevices in buildings or bridges (Adams & Hayes 2000; Skinner & Chimimba 2005, Jacobs & Barclay 2009).

Some bats migrate seasonally, either in response to changing climatic conditions, changes in food availability, or for mating and reproduction (Popa-Lisseau & Voigt 2009). Temperate zone bats such as the little brown bat (*Myotis lucifugus*) migrate from summer roosts to winter roosts to avoid the cold (Norquay *et al.* 2013). Tropical or subtropical migratory bats, such as the Mexican long-nosed bat (*Leptonycteris nivalis*, Moreno-Valdez *et al.* 2000) and straw-coloured fruit bat (*Eidolon helvum*, Richter & Cumming 2006), migrate when fruit abundance changes. In South Africa, Natal long-fingered (*Miniopterus natalensis*) bats migrate up to 260 km between maternal roosts in summer and winter hibernacula (van der Merwe 1975)

Frugivorous and nectivorous bats are from the family Pteropodidae (fruit bats) with soft-fleshed fruits, flowers and nectar being part of their diet (Monadjem *et al.* 2010; Fleming *et al.* 2009). These bats do not echolocate as they rely mostly on eye sight and scent to locate food (Monadjem *et al.* 2010). However, the genus *Rousettus* has been shown to use a primitive form of echolocation such as repetitive tongue clicks used by *R. aegypticus* (the Egyptian rousette fruit bat, Neuweiler 1990).

Insectivores make up over 70% of the world's bat population (Jones & Rydell 2004). Different species of insectivorous bats feed on different groups of insects depending on factors such as habitat, foraging behaviour and echolocation (Section 1.2). Those bats that hunt flying insects are known as aerial feeders (Aldridge & Rauntenbach 1987) and most

belong to the Vespertilionidae (plain-faced bats), Emballonuridae (sheath-tailed bats) and Molossidae (free-tailed bats) bat families. Bats that snatch prey from branches or the ground are known as gleaning bats (Aldridge & Rauntenbach 1987; Faure & Barclay 1994) and belong to the Hipposideridae (trident & leaf-nosed bats), Nycteridae (slit-faced bats) and Rhinolophidae (Horseshoe bats) families.

1.2. ECHOLOCATION AND FORAGING

1.2.1. Echolocation systems and types of bat echolocation

Sophisticated echolocation systems are found only in cetaceans and Vespertilioniformes (Whitlow 1997; Whitlow & Simmons 2007; Monadjem *et al.* 2010). Insectivorous bats make use of echolocation as a means to navigate, as well as to hunt prey (Jakobsen & Surlykke 2010), and have evolved and adapted to different habitats by altering their call features, becoming effective nocturnal foragers (Jones & Holdereid 2007). Most bat species use ultrasonic calls (Surlykke *et al.* 2009) that vary in intensity, frequency, duration and pulse intervals (collectively referred to as call features), and are the most sophisticated vocalisations made by animals (Jones & Holderied 2007).

Two different echolocation systems are present in bats; high duty (HD) and low duty (LD) cycle systems (Eick *et al.* 2005). Low duty cycle echolocation signals are characterized by both narrow or broadband pulses, and long inter-pulse intervals (Schnitzer & Kalko 2001). High duty echolocation signals are characterized by narrowband pulses and short intervals between each pulse (Schnitzer & Kalko 2001). Echolocation calls that are short, and sweep down across a range of frequencies are known as broadband, low duty (LD), frequency modulated (FM) echolocation pulses (LD-FM), which are primarily used by open air foragers (Moss & Surlykke 2010). Short echolocation calls with changes in frequency of a few 100 kHz are known as narrowband, low duty, constant frequency (LD-CF) echolocation calls and if only a single note of long durations is held, it is then referred to as a narrowband, low duty, quasi-constant frequency (LD-QCF) echolocation call (Moss & Surlykke 2010). Both LD-CF

and LD-QCF echolocation calls are primarily used by dense foliage or clutter edge foragers (Moss & Surlykke 2010).

1.2.2. Echolocation and foraging

Call features differ with habitat type, foraging mode and diet, and the returning echoes contain information about their position in space and the position of objects such as prey (Schnitzler & Kalko 2001). Bats are able to detect prey, classify the returning echo and locate prey in various cluttered (dense vegetation, thicket, obstacles) and uncluttered spaces (open spaces, less vegetation) (Schnitzler & Kalko 2001; Moss & Surlykke 2010). Based on echolocation call features and the influence that habitat has on foraging, bats can be separated into three functional, habitat-specific foraging groups: open, clutter-edge and clutter foragers (Kunz *et al.* 2011). Open air foragers have to be able to locate a small target, i.e. prey item, in a large volume of space. As a result, such bat species emit narrowband search signals characterised by long call durations (8-75 ms), low frequencies (<30 kHz), low repetition rates and long pulse intervals (Schnitzler & Kalko 2001). Species that forage in forests edges and gaps (clutter-edge foragers) must be able to track and navigate successfully and will tend to emit broadband medium frequencies (30-60 kHz) with shorter pulse intervals (70-150 ms). These foraging adaptations are species specific and allow us to predict where specific bat species will forage based on knowing their echolocation calls, and allow us to identify bat species using equipment that can detect and characterise their echolocation calls.

1.3. INTERACTIONS BETWEEN BATS AND WIND TURBINES

1.3.1. History of wind energy

With increasing demands for energy by a growing human population, alternate energy resources are being sought after by the energy industry. Wind energy has been used for thousands of years; with the first small scale wind turbines (wind mills) used to pump water

or to grind grain (Fleming & Probert 1984, Ackermann & Söder 2002). The harnessing of wind energy for electricity generation began in Ohio in 1888, where small wind turbines were used to produce electricity (12 kW) for domestic and agricultural use (Kaldellis & Zafirakis 2011). Following this, large scale wind turbines were developed from 1935 to 1970 in Denmark, France, Germany and the UK (Ackermann & Söder 2002, Kaldellis & Zafirakis 2011), and after the oil crisis in the USA in 1973 (Carmoy 1978, Gipe 1991), larger commercial wind turbines were developed in the United States (50-600 kW), in order to substitute the use of fossil fuels in power generation (Kaldellis & Zafirakis 2011). The first large-scale wind turbine facility was built in California where 16000 wind turbines were erected from 1981 to 1990 (Richter 1996). Since then, the use of wind turbines for power-generation has increased globally (IEA 2013).

1.3.2. Bat fatalities at wind farms

Wind energy is showcased as being a clean and renewable energy resource (Hein *et al.* 2011). Carbon emissions and other greenhouse gases associated with climate change are almost non-existent in wind energy development, as compared to other fossil fuels (Saidur *et al.* 2011; Leung & Yang 2012). However, wind energy is not as “green” as it claims to be, having many negative impacts on wildlife (Arnett *et al.* 2005; Brinkman 2006, Carrete *et al.* 2011; Carrete *et al.* 2012).

Many monitoring programs have focussed on the impact between birds and wind turbines (Drewitt & Langston 2006, Fielding *et al.* 2006, Bright *et al.* 2008, Strickland *et al.* 2011, Pearce-Higgins *et al.* 2012, Herrera-Alsina *et al.* 2013). Recent literature on the effect of wind turbines on bats reveals that bats are significantly more vulnerable to wind farm impacts as compared to birds (Kerns & Kerlinger 2004; Arnett *et al.* 2005; Grodsky & Drake 2011). The majority of literature regarding the interactions between bats and wind turbines are from American and European case studies (Kunz *et al.* 2007a). Kerns & Kerlinger (2004) were among the first to report on the impacts that wind turbines had on a bat community in

the USA. Between 1400 and 4000 bats were killed by wind turbines at the Mountaineer Wind Energy Centre in West Virginia over a two year period versus only 174 bird fatalities (Kerns & Kerlinger 2004). Since then, bat fatalities studies at wind farm facilities have been progressively studied within USA, Canada and Europe (Table 1.1.). In 2007, it was estimated that between 33,000 and 111,000 bats will be killed by 2020 as a result of wind turbine associated mortality in the mid-Atlantic highlands in the United States alone (Kunz *et al.* 2007a), highlighting the need to investigate wind turbines and bat interactions, so that bat populations, and the ecosystem services they provide (Section 1.4), can be properly managed.

Table 1.1. Examples of the number of bat fatalities recorded during post-construction surveys at wind farms in the USA, Europe, Canada and South Africa.

Where	Period	Number of fatalities	Reference
Mountaineer Wind Energy Centre (West Virginia, USA)	2002-2003	2092	Kerns & Kerlinger (2004)
Casselman Eind Project (South-central Pennsylvania, USA)	2008	784	Arnett <i>et al.</i> (2009)
Coega Test Turbine (Eastern Cape, South Africa)	2011	17	Doty & Martin (2012)
Buffalo Ridge Wind Farm (Minnisotat, USA)	2002	151	Johnson <i>et al.</i> (2004)
Forward Wind Energy Centre (South-western Wisconsin, USA)	2010	122	Grodsky & Drake (2011)
Nine Canyon Wind Power Project (Washington, USA)	2002-2003	119	Erickson <i>et al.</i> (2003)
Wind facilities in Southern Germany	2004	335	Brinkman (2006)
St. Leon Wind Energy Project (South-western Manitoba, Canada)	2007	98	Jameson & Willis (2012)

Species that are most affected by wind farms, and the bat species that are most often killed by wind turbines in the USA, are migratory and tree-roosting species such as hoary bats, (*Lasiurus cinereu*), eastern red bats (*Lasiurus borealis*), and silver-haired bats (*Lasionycteris noctivagans*) (Erickson *et al.* 2003; Kerns & Kerlinger 2004; Arnett *et al.* 2008). These bats

are typically open-air foragers and fly high above the tree canopy (Arnett *et al.* 2008). In addition, resident species of bats are also killed by wind turbines. High fatalities of non-migrating, resident common pipstrelle bats (*Pipstrellus pipstrellus*), have been found at wind farms in Southern Germany (Brinkman 2006) and Cape Serotine bats (*Neoromica capensis*) have been killed by wind turbines in the Western Cape (Aronson *et al.* 2013) and Eastern Cape (Doty & Martin 2012) of South Africa.

Information on South African wind farms and bat fatalities is scarce and only two studies have been published (Doty & Martin 2012, Aronson *et al.* 2013). A single pilot wind turbine was erected in June 2010 in the Coega Industrial Development Zone in Port Elizabeth (Doty & Martin 2012). Over one year, 17 bat fatalities were recorded with the majority of casualties recorded during mid-December to mid-March. Only two species were involved; the Cape serotine bat and the Egyptian free-tailed bat (*Tadarida aegyptiaca*). Both are slow-reproducing bats; the Egyptian free-tailed bat produces only one pup per year (Herselman 1980; Bernard & Tsita 1980), whereas the Cape serotine bat produces 1-2 pups a year (Lynch 1989; van der Merwe 1994). According to South African good practice guidelines for surveying bats in wind farm developments and based on their general ecology (Sowler & Stoffberg 2012), the Cape serotine bat has a medium to high likelihood of risk of fatality due to the fact that it is a clutter-edge forager, and the Egyptian free-tailed bat has a higher risk of fatality due to the fact that it is an open-air forager. These results highlighted the need for extensive bat monitoring programs to be conducted in wind farm developments in South Africa, prior to construction (to get baseline estimates of the bat community) and after construction (to monitor actual bat mortality and mitigate where necessary) (Sowler & Stoffberg 2012).

1.3.3. Why do bat fatalities occur?

Bat fatalities occur due to direct collisions with turbine blades or towers (Kunz *et al.* 2007b; Cryan & Barclay 2009; Strickland *et al.* 2011), or indirectly via barotrauma (Baerwald *et al.*

2008; Strickland *et al.* 2011). Death results from physical injuries caused by collisions (Cryan & Barclay 2009) and barotrauma results in the sudden decompression of bat lungs (Baerwald *et al.* 2008), due to low pressure air pockets created by turbine blades as they cut into the air (Kunz *et al.* 2007a).

Wind turbines may be attractive to bats as potential night roosts, especially those of tree-roosting, migratory species (Kunz *et al.* 2007a; Cryan & Barclay 2009), making them susceptible to collisions. Using thermal imaging, bats could be seen repeatedly flying by rotating and non-rotating parts of turbines indicating that bats are inquisitive of new structures and were possibly scouting turbines as potential roosts (Horn *et al.* 2008a). In doing so, bats were often trapped in blade-tip vortices and directly struck by moving turbine blades (Horn *et al.* 2008a).

Other factors influencing bat collisions are those factors which attract bats to the vicinity of wind turbines in the first place (Cryan & Barclay 2009). In the USA, many wind turbine farms are built along forested ridges (Young *et al.* 2007; Arnett *et al.* 2009; Hein *et al.* 2010), which are used by bats during migration and while commuting and foraging (Kunz *et al.* 2007b). Lights at the top of wind turbines and the heat produced by nacelles attract insects to them, which then attract foraging bats (Ahlén 2002; Kunz *et al.* 2007b; Horn *et al.* 2008a). Seasonal changes in insect density and activity influence bat abundance in an area (Cryan & Barclay 2009), and thus bats run the risk of being struck by rotating turbine blades in the pursuit of prey.

1.3.4. Why are bats vulnerable?

Small mammals typically have short life spans and produce large litters, which grow and mature rapidly (Promislow & Harvey 1990; Kraus *et al.* 2005). Bats are unlike other small mammals in that they are long-lived species and produce small litters, which grow and develop slowly (Barclay *et al.* 2004). Gestation periods in South African bats range from 60 days to 8 months (van der Merwe *et al.* 2006; van der Merwe & Stirnemann 2007; Le

Grange *et al.* 2011) and typically only 1 pup is produced per year per female and females reach sexual maturity at an average age of 2-3 years (Taylor 2000). This coupled with high infant mortality (Hayman *et al.* 2012), an estimated 70% of newborn bats die in their 1st year of life (Taylor 2000), making any mortality an issue of concern for conservation, as their ability to recover from major population declines is limited (Fenton 2013).

1. 4. ROLE OF BATS IN THE ECOSYSTEM

Bats provide a number of ecosystem services that either directly or in-directly affect humans (Kunz *et al.* 2011). They are important pollinators of fruiting trees (Fujita & Tuttle 1991), aid in seed dispersal (Fleming *et al.* 2001, Hodgekins *et al.* 2003) and suppress insect populations (Kalka *et al.* 2008), many of which are agricultural pests (García-Morales *et al.* 2013).

Insectivorous bats seek out areas where insects are concentrated (Kunz *et al.* 2011; Noer *et al.* 2012; McCracken *et al.* 2012). For example, seasonal occurrences of insectivorous bats were correlated with seasonal occurrences of the Macadamia nut borer moths (*Cryptophlebia ombrodelta*) and the twin spotted (*Bathyo-coelia natalicola*) and green (*Nezara spp*) stinkbugs, both common pests in Macadamia orchards (Taylor *et al.* 2013). Seasonal foraging on these insects by bats, over summer and autumn (Bohmann *et al.* 2011), resulted in reduction of crop losses by the industry (Taylor *et al.* 2013). Molossid bats act as potential pest controlling agents over sugar cane fields in the Swaziland Lowveld area (Noer *et al.* 2012), and a general trend of higher bat activity was observed at sites with higher insect activity at two tomatoe farms in the Moolcetsi and Secrabie regions of Limpopo, South Africa (Marais 2009). Brazilian free-tailed bats (*Tadarida brasiliensis*) will opportunistically prey on cotton earworm moths (*Helicoverpa zea*, a common cotton crop pest) during seasonal migrations in Texas, USA (McCracken *et al.* 2012). The economic value of pest control services to the cotton industry was estimated to be between \$121 000 and \$1 725 000 versus the annual cotton harvest of between \$4.6 and 6.4 million (Cleveland *et al.* 2006). In

2011, the economic value of bats in the USA agricultural industry was estimated to be from \$3.7 billion/yr up to \$53 billion/yr (Boyles *et al.* 2011). This represents what it would cost the USA agricultural industry to buy pesticides to mimic the same environmental service that these bats provide. A loss of \$750 per ha per year (31% decrease in crop yields) in the Indonesian agroforest industry resulted from the removal of pest services provided by both birds and birds (Maas *et al.* 2013). No such studies have been done in South Africa, but much information is needed in order to predict what the economic value of different bat species to the South African economy is.

1. 5. THESIS MOTIVATION AND OUTLINE

Impacts that wind turbines will have on bat populations remain poorly understood, both internationally (Arnett *et al.* 2005) and especially in southern Africa (MacEwan 2011; Sowler & Stoffberg 2012). How South African bat populations will be affected by wind turbines and how these populations will respond to wind energy developments remains unknown. The increasing number of proposed wind farm developments (Department of Minerals and Energy 2003) provides an immediate reason to assess bat activity and diversity (Fenton 2013), with the expectation of developing measures to mitigate these impacts. Bats are slow to recover from any adverse effects due to their slow reproduction rates (Fenton 2013) and any bat fatality is a cause for concern in terms of conserving biodiversity (Mendellin *et al.* 2000; Hooper *et al.* 2005, Bastian 2013) and the valuable ecosystem services that bats provide (Kunz *et al.* 2011). This is however a relatively new field of study in South Africa (Sowler & Stoffberg 2012) and this project therefore represents an initial attempt to contribute to this area, in the form of a pilot study of factors that may lead to the prediction of bat vulnerability to wind turbines.

The overall aim of this thesis is contribute to an understanding of the drivers of South African bat activity, relevant to wind turbines, thereby contributing to the body of literature on bat activity and diversity in South Africa. This study aims to determine what factors (exogenous

– environmental, or endogenous – intrinsic physiological processes) contribute to observed bat activity patterns at a wind farm facility in the Eastern Cape of South Africa, with the objectives of 1) identifying the temporal patterns of bat activity, and identifying 2) when bat activity is the highest. If we can identify what factors are responsible for observed bat activity patterns, we can develop mitigation measures in order to mitigate against potential negative impacts of wind turbines.

This thesis is constructed from two data chapters, written as individual papers, and so some repetition should be expected. The outline of this thesis is as follows:

- Chapter 1: General introduction
- Chapter 2: Study site and species
- Chapter 3: Effect of environmental factors on bat presence and activity, at the Metrowind Van Stadens Wind Farm – A pilot study
- Chapter 4: Endogenous rhythms of resting metabolic rate of an insectivorous bat and its uses in predicting wild bat activity
- Chapter 5: General discussion

CHAPTER 2

STUDY SITE AND SPECIES

2.1. STUDY SITE

2.1.1. Locality

This study was conducted at the site of the Metrowind Van Stadens Wind Farm, Eastern Cape, South Africa (35°57'S, 25°14'E). The site is located approximately 30 km west of Port Elizabeth and is approximately 2.8 km long and 1.7 km wide (Figure 2.1.). Most of the area within a 20 km radius is farmland, with few settlements. Two protected areas are found near the site: the Maitland Nature Reserve and The Island Nature Reserve.

2.1.2. Vegetation & topography & climate

Regional vegetation: The vegetation site is dominated by the Albany Coastal Belt and the Southern Coastal Forest (Mucina & Rutherford 2006), both of which are considered as least threatened in terms of conservation status (Rouget *et al.* 2004; Driver *et al.* 2011). The Albany Coastal Belt is characterized by the Albany Thicket Biome and vegetation type (Rouget *et al.* 2004). The Southern Coastal Forest is characterised by low trees and shrub land as is found in coastal plains between Alexandria and the Van Stadens River (Mucina & Rutherford 2006).

Local vegetation & topography: The site is located on the crest of a ridge, behind the Blue Horizon Bay suburb and alongside the Van Stadens River. Due to constant grazing by cattle, the site is mostly comprised of transformed open grassland, surrounded by forested patches (Figures 2.1. & 2.2.).

2.1.3. Habitat suitable for bats

Riparian zones (Grindal *et al.* 1999, Monadjem & Reside 2008) may be important landscape features used by bats. Bat diversity is typically higher in forested versus open areas (Ford *et al.* 2005, Adams *et al.* 2009) and many bats are clutter-edge (foraging at the edges of forests) foragers (Table 2.2.), indicating that the forest patches within the site are suitable foraging areas for bats. Ridges are also important landscape features which bats use to navigate during migrations (Cryan & Diehl 2009; Furmankiewicz & Kucharska 2009). In addition to vegetation, the site has two farm buildings which are used as roosts by the Cape Serotine (Figure 2.1.).

2.2. STUDY SPECIES

No studies on the bat community have been done on this site. One study on the physiology of four, cave-dwelling Rhinolophid bats (Doty 2012) was conducted at Sleep Hollow (approximately 3 km from the current study site). Using broad distribution maps from Monadjem *et al.* (2010), 23 bat species are likely to occur at the Metrowind Van Stadens Wind Farm site (Table 2.1.), all of which are echolocating bats, with the exception of two fruit bats: the Egyptian rousette bat and Wahlberg's epauletted fruit bat. Species likely to be found on site include both open-air foragers as well as clutter and clutter-edge foragers (Table. 2.2.). All of these species are currently of least concern, according to the International Union for Conservation of Nature (IUCN) Red data list (IUCN 2013), with no species of high conservation risk.

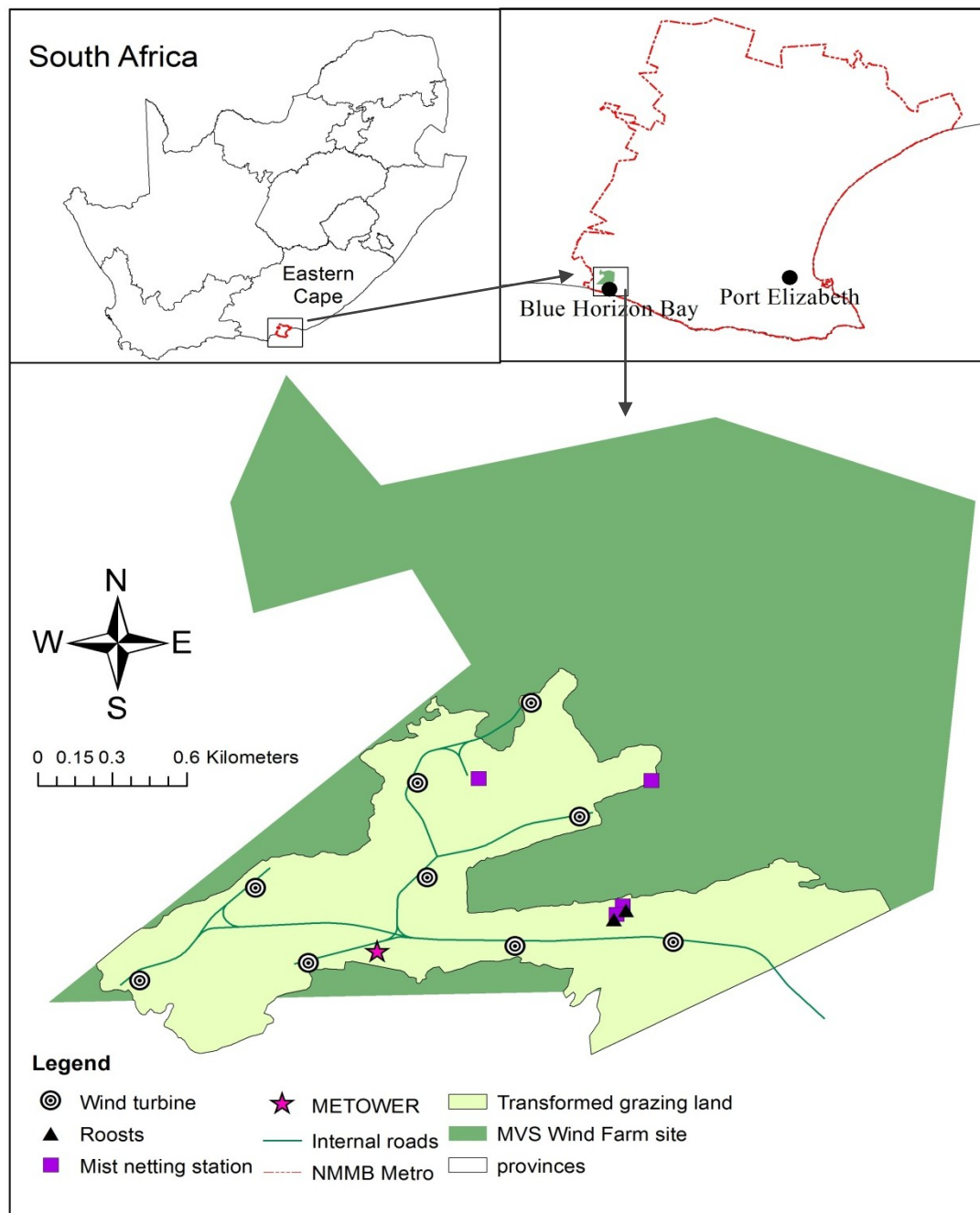


Figure 2. 1. Location of the study site at the Metrowind Van Stadens Wind Farm (MVS), Eastern Cape, South Africa. NMMB = the Nelson Mandela Metropolitan Bay district. METOWER = wind farm's meteorological tower.

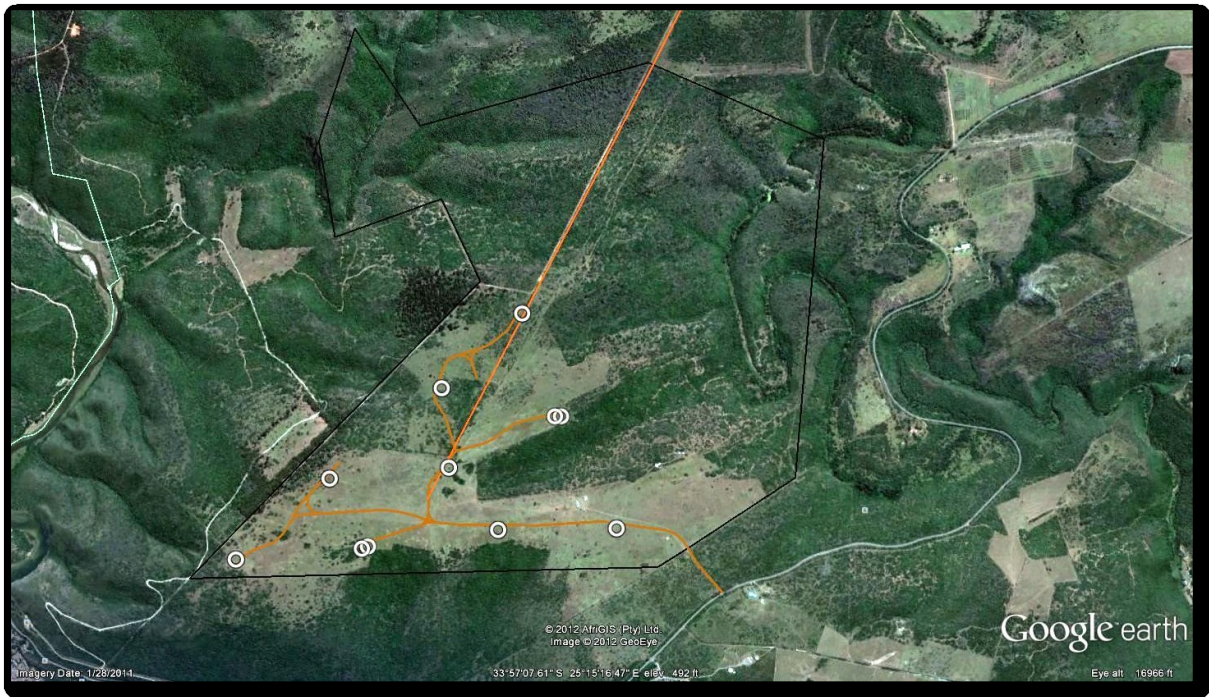


Figure 2. 2. Aerial image of the Metrowind Van Stadens Wind Farm site. Open circles indicate turbine locations. Orange lines indicate internal roads. (Imagery ©2011 GeoEye; Map Data ©2011 Tele Atlas, AfriGIS (Pty) Ltd., Google, Europa Technologies, Data SIO, NOAA, U.S. Navy, NGA, GEBCO).

Table 2. 1. Bat species likely to be present, based on broad distributions maps in Monadjem *et al.* (2010), and conservation status (IUCN Red data list) for the Metrowind Van Stadens Wind Farm. Dominant call frequencies (kHz) and echolocation types are also given (Monadjem *et al.* 2010). LC = least concern, HD = high duty cycle, LD = low duty cycle, CF = constant frequency, FM = frequency modulated, QCF = quasi-constant frequency.

Family	Species	Common name	Conservation status	Dominant call frequency (kHz)	Echolocation type
Pteropodidae	<i>Epomorphus wahlbergi</i>	Wahlberg's epauletted fruit bat	LC	none	none
	<i>Rousettus aegyptiacus</i>	Egyptian rousette fruit bat	LC	Tongue clicks	none
Hipposideridae	<i>Hipposideros caffer</i>	Sundevall's leaf-nosed bat	LC	142.3 ± 0.6	HD-CF
Rhinolophidae	<i>Rhinolophus capensis</i>	Cape horseshoe bat	LC	83.9 ± 0.6	HD-CF
	<i>Rhinolophus clivus</i>	Geoffroy's horseshoe bat	LC	91.7 ± 1.0	HD-CF
	<i>Rhinolophus simulator</i>	Bushveld horseshoe bat	LC	80.1 ± 1.2	HD-CF
	<i>Rhinolophus swinnyi</i>	Swinnyi's horseshoe bat	LC	106.6 ± 0.4	HD-CF
Emballonuridae	<i>Taphozous mauritanus</i>	Mauritian tomb bat	LC	25.9 ± 0.9	HD-CF
Nycteridae	<i>Nycteris thebaica</i>	Egyptian slit-faced bat	LC	90.0 ± 1.3	LD-FM
Molossidae	<i>Tadarida aegyptiaca</i>	Egyptian free-tailed bat	LC	22.7 ± 2.2	LD-QCF
Miniopteridae	<i>Miniopterus natalensis</i>	Natal long-fingered bat	LC	49.7 ± 1.0	LD-FM
	<i>Miniopterus fraterculus</i>	Lesser long-fingered bat	LC	62.3 ± 1.9	LD-FM
Vespertilionidae	<i>Eptesicus hottentotus</i>	Long-tailed Serotine bat	LC	30.6 ± 1.7	LD-FM & LD-QCF
	<i>Hypsugo anchietae</i>	Anchieta's pipistrelle bat	LC	55.7	LD-FM
	<i>Kerivoula argentata</i>	Damara woolly bat	LC	90 - 118	LD-FM
	<i>Kerivoula lanosa</i>	Lesser woolly bat	LC	85 - 140	LD-FM
	<i>Myotis tricolor</i>	Temminck's hairy bat	LC	47.8 ± 3.1	LD-FM
	<i>Neoromicia capensis</i>	Cape Serotine bat	LC	39.4 ± 1.6	LD-FM
	<i>Pipistrellus hesperidus</i>	Dusky pipistrelle bat	LC	50.1 ± 1.5	LD-FM
	<i>Scotophilus dinganii</i>	Yellow-bellied house bat	LC	33.6 ± 1.3	LD-FM

Table 2. 2. Habitat and foraging types of bat species expected to occur at the Metrowind Van Stadens Wind Farm site.

Species	Habitat	Foraging type / habitat	Source
<i>Epomorphus wahlbergi</i>	Dense foliage of large, leafy trees, forests	Hover or perch	Fenton <i>et al.</i> (1985)
<i>Rousettus aegyptiacus</i>	Caves	Hover or perch	Monadjem <i>et al.</i> (2010)
<i>Hipposideros caffer</i>	Caves, sink holes & mines	Clutter	Cotteril (2001)
<i>Rhinolophus capensis</i>	Caves and mines	Clutter	Herselman & Norton (1985)
<i>Rhinolophus clivosus</i>	Caves and mines	Clutter	Smithers (1983)
<i>Rhinolophus simulator</i>	Caves and mines	Clutter	Rautenbach (1982)
<i>Rhinolophus swinnyi</i>	Caves and mines	Clutter	Cotteril (1996)
<i>Taphozous mauritanus</i>	Rock faces, tree trunks and walls	Open-air	Monadjem <i>et al.</i> (2010)
<i>Nycteris thebaica</i>	Caves, aardvark burrows and tree trunks	Clutter	Monadjem <i>et al.</i> (2010)
<i>Tadarida aegyptiaca</i>	Caves, rock crevices and hollow trees	Open-air	Herselman & Norton (1985)
<i>Miniopterus natalensis</i>	Caves	Clutter-edge	Monadjem <i>et al.</i> (2010)
<i>Miniopterus fraterculus</i>	Caves	Clutter	Monadjem <i>et al.</i> (2010)
<i>Eptesicus hottentotus</i>	Rock crevices and caves	Clutter-edge	Kerney & Taylor (1997)
<i>Hypsugo anchietae</i>	Riparian forest	Clutter-edge	Monadjem <i>et al.</i> (2010)
<i>Kerivoula argentata</i>	Unkown	Clutter-edge	Monadjem <i>et al.</i> (2010)
<i>Kerivoula lanosa</i>	Unkown	Clutter-edge	Monadjem <i>et al.</i> (2010)
<i>Myotis tricolor</i>	Caves	Clutter-edge	Monadjem <i>et al.</i> (2010)
<i>Neoromicia capensis</i>	Under bark of trees, base of aloe leaves an roofs	Clutter-edge	Taylor <i>et al.</i> (2000)
<i>Pipistrellus hesperidus</i>	Narrow cracks in rocks, loose bark in dead trees, forests	Clutter-edge	Skinner & Chimimba 2005
<i>Scotophilus dinganii</i>	Sheltered holes in tree & roofs	Clutter-edge	Jacobs <i>et al.</i> 2007b

CHAPTER 3

EFFECT OF ENVIRONMENTAL FACTORS ON BAT PRESENCE AND ACTIVITY AT THE METROWIND VAN STADENS WIND FARM – A PILOT STUDY

3.1. INTRODUCTION

Patterns in bat activity can be observed on different spatial and temporal scales. On the spatial scale, bats are typically more active in forested areas (Ford *et al.* 2005; Adams *et al.* 2009; Presley *et al.* 2009; Estrada-Villegas *et al.* 2012; Scrimgeour *et al.* 2013) and riparian habitats (Grindal *et al.* 1999; Monadjem & Reside 2008) and use mountain ridges, passes and valleys to navigate during migrations (Cryan & Diehl 2009; Furmankiewicz & Kucharska 2009). Bat activity also differs according to height (Adams *et al.* 2009; Collins & Jones 2009; Staton & Poulton 2012; Scrimgeour *et al.* 2013). Flight height ranges from between 24-43 cm for trawling pond bats (*Myotis dasycneme*, van de Sijpe 2008) to between 200-3000 m for Mexican free-tailed bats (*Tadarida brasiliensis*, Williams *et al.* 1973; McCracken 1996), and more than 500 m for echolocating bats in Zambia (Fenton & Griffin 1997).

Temporal pattern in bat activity can be at different time scales (Milne *et al.* 2005). On a nightly scale, bat activity is strongly correlated with the timing of sunset and sunrise (Erkert 1978; Taylor & Oneill 1988; Griffiths 2007), with bat activity being highest during the first two hours following sunset (Milne *et al.* 2005; Esberard & Bergallo 2010). Insectivorous bats restrict their activity to periods of high insect activity (O'Donnell 2000; Wickramasinghe *et al.* 2004; Payne & Walter 2011; McCracken *et al.* 2012; Taylor *et al.* 2013), which is typically higher during dusk and dawn (Rautenbach *et al.* 1988), in order to maximise foraging success and energy gain over a short period of time (Taylor & Oneill 1988).

Nightly activity also changes seasonally with changes in food availability or in response to changing weather conditions. Seasonal increases in bat activity may be as a result of increased foraging activity in preparation for mating (Kuenzi & Morrison 2003; Van der

Merwe *et al.* 2006; Cryan & Barclay 2009) or when food availability changes (Popa-Lisseanu & Voigt 2009). In Germany, male Daubenton's bat (*Myotis daubentonii*), activity increases as they try and fatten up for the mating period, because there is a high demand for energy for sperm production (Encarnação *et al.* 2006). Fluctuating food supplies trigger the mass migration of straw-coloured fruit bats (*Eidolon helvum*) in Zambia (Richter & Cumming 2006) and of the Mexican long-nosed bat (*Leptonycteris nivalis*) in Northern Mexico (Moreno-Valdez *et al.* 2000). Migrations to winter hibernacula in response to changing weather conditions can also lead to seasonal differences in bat activity (Speakman & Thomas 2003, Geiser & Stawski 2010).

Weather variables are important factors influencing bat activity in the short term. Bat activity and wind speed is negatively correlated (Kerns & Kerlinger 2004; Arnett *et al.* 2011; Rydell *et al.* 2010b; Hein *et al.* 2011). Bats suppress their activity during strong winds (O'Farrell 2010), especially when wind speeds exceed 6 m.s^{-1} (Hein *et al.* 2011). Temperature has been positively associated with bat activity (Erickson & West 2002; Christie & Simpson 2010), and bats will hibernate when temperature declines below certain temperature thresholds, as it becomes energetically costly to maintain a constant body temperature (Anthony *et al.* 1981; Burles *et al.* 2009). Bat activity has been shown to decrease during rainy nights (Erickson & West 2003; Johnson *et al.* 2011; Geluso & Geluso 2012), as well as when humidity is high (Milne *et al.* 2005). Prey is difficult to detect during rainfall (Burles *et al.* 2009), and it is more energetically costly for bats to fly when it rains and their fur gets wet (Voigt *et al.* 2011).

Moonlight has been shown to affect the foraging activity of bats so that bats reduce their activity during periods of increased moon light (Lang *et al.* 2006). The evidence in support of lunar phobia is contradictory (Saldaña-Vázquez & Munguía-Rosas 2012) as some bats reduced their activity (Börk 2006; Lang *et al.* 2006) while activity in other bat species shows no relationship to moonlight (Gannon & Willig 1997; Karlsson *et al.* 2002; Thies *et al.* 2006; Holland *et al.* 2011). Lunar phobia is more prevalent in tropical bat species than temperate

bat species (Saldaña-Vázquez & Munguía-Rosas 2012) and may have evolved as a way to avoid predation, by visual predators during full moon periods (Meyer *et al.* 2004; Börk 2006). In addition, activity of insectivorous bats is also indirectly affected by moonlight because their prey (insects) is less active during fully lit nights (Lang *et al.* 2006).

Information on South African bat species is scarce, and the impacts that wind turbines will have on bat populations remains poorly understood, both internationally (Arnett *et al.* 2005) and especially in southern Africa (MacEwan 2011; Sowler & Stoffberg 2012). How South African bat populations will be affected by wind turbines and how these populations respond to wind energy developments remains unknown. The growth of alternative energy sources is a global priority (Hara 2006) and currently, wind-generation of electricity is an important part of this (Department of Minerals & Energy 2003). There is a need to better understand bat activity patterns in relation to wind energy development with the purpose of developing measures to mitigate for potential impacts (Arnett *et al.* 2013a). This study aimed to analyze the temporal patterns in bat activity, using active (mist netting) and passive (acoustic) monitoring techniques and to test the relationship between bat activity patterns and prevailing weather conditions with the aim of determining what extrinsic variables contribute to free-ranging bat activity at the site.

3.2. MATERIAL AND METHODS

This project forms part of a pilot study conducted at the Metrowind Van Stadens Wind Farm site, Eastern Cape, South Africa (35°57'S, 25°14'E). The site is located approximately 30 km west south west of Port Elizabeth and is approximately 2.8 km long and 1.7 km wide (Figure 2.1). The proposed wind farm site is primarily composed of open grassland, and is surrounded by forested patches.

4.2.1. Data collection

Bat monitoring began in April 2012. Recommendations for conducting bat monitoring studies at wind energy facilities were followed as described by Sowler & Stoffberg (2012). A

combination of both active (mist netting) and passive (acoustic) bat monitoring techniques were used and the details are provided below.

Active monitoring: Roost surveys were conducted in April 2012. The site was walked to search for features which may support bats such as trees, buildings, and vegetation cover (Sowler & Stoffberg 2012). Two roosts were identified, both being old farm buildings (Figure 2.1). Mist nets (Denier: 0.08 mm; mesh: 20 mm; shelves: 4; dimensions: 12 m; M-20/12 ECOTONE) were set up on the edges and within the forested patches and roosts (Figure 2.1, Sowler & Stoffberg 2012). Mist nets were set to 3 m from the ground, 30 min prior to sunset and remained set for two hours after sunset. Once caught, bats were identified to species level (Monadjem *et al.* 2010) and sexed, and the location recorded. Bats captured using mist nets were used to corroborate echolocating species recorded using acoustic detectors, as well as to capture and record any non-echolocating bats. Permits for live animal capture were issued by the Department of Economic Development, Environmental Affairs and Tourism, permit no's: CRO 85/12CR, CRO86/12CR, CRO 87/12CR, CRO 100/13CR, CRO 101/13CR, and CRO 10/13CR.

Passive monitoring: Acoustic monitoring began on the 3rd May 2012 and continued until the end of May 2013. Bats were continuously recorded using a Song Meter SM2BAT+ acoustic monitor (Version 2.2.0, Wildlife Acoustics Inc. 2012). The SM2BAT+ was mounted onto the existing meteorological tower (METOWER) on site. An omnidirectional ultrasonic microphone (SMX-II, sensitivity -36 ± 4 dB, frequency response 20 Hz -200 kHz, Wildlife Acoustics Inc. 2012) was positioned at 10 m above the ground, a minimum height as proposed by Sowler & Stoffberg (2012). In order to determine bat activity within the turbine rotor swept area, a second ultrasonic microphone was acquired in August 2012 and positioned at 55 m above the ground, on the same METOWER. The vertical arrangement of ultrasonic microphones allowed for concurrent monitoring of high flying and low flying bats within the air space between the ground and the turbine rotor swept area (Weller & Zabel 2002; Menzel *et al.* 2005).

3.2.2. Data analysis

The SM2BAT+ acoustic detector was pre-set to automatically record bat activity from 30 min before sunset to 30 min after sunrise (Sowler & Stoffberg 2012). Bat activity was recorded in stereo, and detected bats which use echolocation signals up to 194 kHz. It was assumed that bat activity was independently recorded from both microphones. All bat activity was recorded with a date (day/month/year) and time (hour/min/sec) stamp. Data recorded by the SM2BAT+ as .WAC files were converted to zero-crossing files using Wildlife Acoustics' Kaleidoscope programme (1.1.20.exe, Wildlife Acoustics Inc. 2012). Zero-crossing files (a format used by the program AnaLookW (Version 3.8s, Titley Electronics), which simplifies complex acoustic recordings so that bat calls can be identified) were visually scanned for bat passes using AnaLookW (Version 3.8s, Titley Electronics). A bat pass was defined as a series of more than two echolocation calls (Hayes 2000; Hein *et al.* 2011) having less than one second separating each call (Redell *et al.* 2006, Whitlow & Simmons 2007). The number of bat passes per unit time was used as an index of bat activity. It was assumed that 1) a bat pass was a discrete event, 2) a bat call remained consistent within each species or phonic group, and 3) each bat pass recorded was a proxy of the relative use of the area by bats and did not reflect actual bat abundance (Hein *et al.* 2011). For example; 10 bat passes could represent either 10 individual bats passing a recorder or one individual being recorded 10 times. Where possible, bat species were identified by examining various call characteristics (Table 2.1, Mondjem *et al.* 2010). These included the dominant frequency of the call, call duration, slope of the call and the time between call pulses (Jones & Holderied 2007). Where bat species could not be positively identified from echolocation calls, the recording was either classified as a high frequency bat pass (>35 kHz) or low frequency bat pass (<35 kHz).

Construction on the Metrowind Van Stadens Wind Farm began at the end of December 2012. Anthropogenic disturbance has been shown to influence animal behaviour (Barber *et al.* 2009; Berthussen & Aldringham 2012) and reduce populations (Mallard *et al.* 2007). In

addition, bats tend to avoid areas with loud background noises (Schaub *et al.* 2008). For these reasons, bat activity data collected from the beginning of April 2012 until the end of December 2012 were analyzed, so as to avoid bias associated with the construction process and to give an unbiased representation of bat activity patterns in the absence of anthropogenic disturbances.

3.2.3. Statistical analysis

Nightly activity: Bats use different echolocation calls depending on the habitat that they forage in (Schnitzer & Kalko 2001; Moss & Surlykke 2010). Open air foragers are able to locate small prey items in a large volume of space, and as such, emit narrowband search signals characterised by low frequencies (<35 kHz; Schnitzer & Kalko 2001; Jung *et al.* 2007). Species that forage along forested edges and in forest gaps tend to emit broadband search signals characterised by high frequencies (>35 kHz, Monadjem & Reside 2008; Adams *et al.* 2009). For this reason, bat passes per night were separated into two phonic groups (high and low-frequency calling bats), with 35 kHz representing an appropriate threshold that could be used to distinguish between them (Hein *et al.* 2011). The average number of bat passes per phonic group per hour (from 17:00 to 08:00) was determined to establish how bat activity varied during the night from sunset to sunrise.

Bat passes were also divided into bat passes at 10 m and bat passes at 55 m per night. Chi-squared goodness of fit tests were used to determine differences in the number of bat passes recorded at 10 m and 55 m, as well as to determine whether more high-frequency or low-frequency bat passes were recorded at each height. Only bat passes from August 17th 2012 to 31st December 2012 was used to determine differences in the total number of bat passes at height, as the second microphone at 55 m was only installed on the 17th of August 2012.

Activity, weather and lunar cycles: Details for moon phase and percentage illumination were obtained from Time and Date AS (1999-2013, www.timeanddate.com/worldclock/

astronomy). Data for relative humidity, barometric air pressure and rainfall, recorded every hour at the Port Elizabeth Airport, were obtained from the South African Weather Service. A meteorological station associated with the wind farm's wind resource program was positioned at 33°57'45.22"S and 25°14'37.52"E. Air temperature and wind speed was sampled every 10 min. Wind speed was measured at 30 m and 50 m heights and air temperature was measured at 5.5 m. Only wind speed at 30 m was used to calculate hourly average wind speed as it represented the midpoint between both microphones. Meteorological data was averaged for every hour, starting from 16:00 to 08:00 the next morning, to give hourly averages of all weather variables per sampling night.

Generalized linear modelling was used to determine which weather variables (predictors) best explained the variation in bat activity (response). The total numbers of bat passes per night were used for modelling. The distribution of bat passes per night displayed a strong Poisson distribution with a large number of zero counts and observed bat pass rates had much more variation than expected from a Poisson distribution. Consequently, data were modelled as an over-dispersed Poisson distribution using a generalised linear model with the quasi-likelihood link function (ver Hoef & Boveng 2007) in the statistical program R (Package *stats*: version 2.15.3, R core development team, version 3.0.1, 2013).

Five weather variables (air temperature, wind speed, barometric air pressure, amount of rainfall, and relative humidity), together with month, moon phase and percentage of the moon illuminated and interactions between the weather variables were initially treated as potential predictors of bat activity and incorporated into a global model. The log-likelihood ratio test (Package *stats*: version 2.15.3, R core development team, version 3.0.1, 2013) was used to test for the significance of all predictor variables, by removing one variable at a time from the global model, whilst leaving all others in place (Milne *et al.* 2005). For quasi-Poisson distributions, Akaike information criterion (AIC scores) cannot be used to compare various models (Ver Hoef & Boveng 2007) and so backward stepwise selection, using model p-values, was used to select the best model.

3.3. RESULTS

3.3.1. Active monitoring

Only one species of bat, the Cape serotine bat (*Neoromicia capensis*; n = 8), was successfully caught in mist nets whilst exiting two known roosts (Figure 2.1.), suggesting that this species is resident on site. Cape serotine bats were caught in mist nets in autumn (May 2012 & April 2013), spring (September 2013) and summer February 2013). In addition, the Egyptian Rousette fruit bat (*Rousettus aegyptiacus*) was observed as being present on site by its distinctive repetitive tongue clicks in the range of 10 – 60 kHz, with the lower part of its range audible to the human ear (Neuweiler 1990), on the 13th of April 2012 at 19:05 and again on the 23rd of April 2012 at 19:17.

3.3.2. Passive monitoring

A total of 889 bat passes were recorded over 323 detector nights from the beginning of May 2012 to the end of December 2012. The Egyptian Rousette bat was not recorded acoustically during the study period. Only four species of bat were positively identified as being present on site from acoustic recordings. These included high-frequency calling bats (n = 459): the Cape serotine bat (*Neoromicia capensis*), Anchieta's pipstrelle bat (*Hypsugo anchietae*), the Long-tailed serotine bat (*Eptesicus hottentotus*) and low-frequency calling bats (n = 391): the Egyptian free-tailed bat (*Tadarida aegyptica*). The Cape serotine bat and the Egyptian free-tailed bat were the dominant species recorded on site. The Cape serotine bat made up 82% (n = 376) of all high-frequency bat passes and the Egyptian free-tailed bat accounted for 97% (n = 386) of all low-frequency bat passes. Twenty six high-frequency and five low-frequency bat passes could not be identified down to species levels.

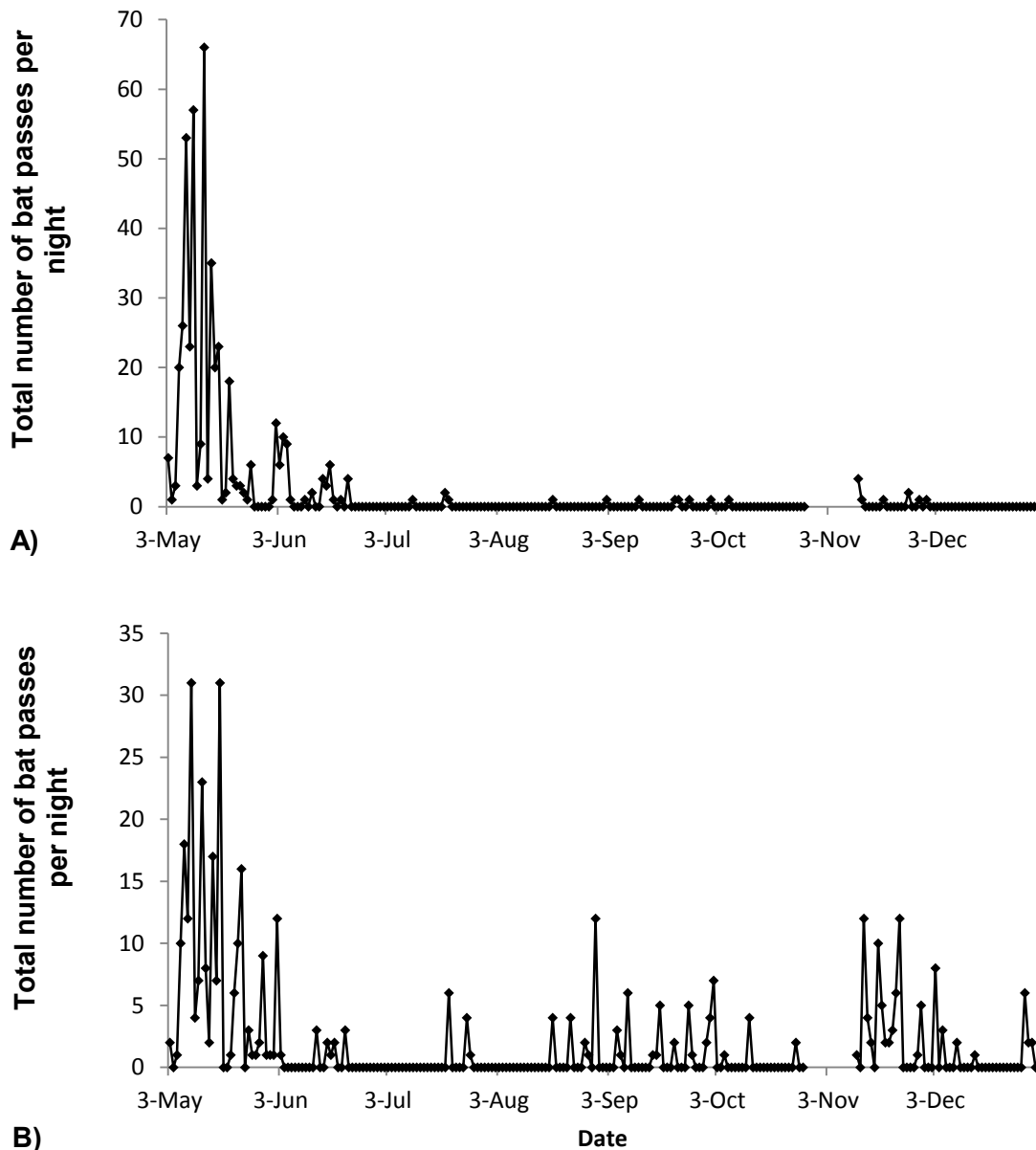


Figure 3.1. Total number of bat passes recorded during each night on site from 3rd May 2012 to 31st December 2012, for A) high-frequency calling bats (>35 kHz) and B) low-frequency calling bats (<35 kHz).

Large fluctuations in the number of bat passes per night were observed, with many nights having no recorded bat activity (Figure 3.1). No bat activity was recorded between 28 October and 10 November due to equipment failure. Over 80% of high-frequency bat passes were recorded during May 2012, with an average (\pm SE) of 13.6 ± 3.24 bat passes recorded per night. In subsequent months, the number of high-frequency bat passes declined to just 4 bat passes per night in July and none in December. Similarly, more than 55% of all low-

frequency calling bat passes were recorded in May 2012 with an average (\pm SE) of 8.1 ± 1.74 bat passes recorded per night, thereafter, bat activity declined. Low-frequency bats remained active throughout the year with activity increasing from 24 bat passes in September to 55 bat passes in November.

Bat activity per night was higher at 55 m than 10 m (Figure 3.2, $\chi^2 = 147.393$, $df = 1$, $p < 0.001$), with 98% of all bat passes recorded at 55 m. The majority of all bat passes recorded from mid-August to December were of low-frequency calling bats (89%) and low-frequency bat passes were recorded significantly more at 55 m as compared to 10 m ($\chi^2 = 104.660$, $df = 1$, $p < 0.001$). In comparison, high-frequency calling bats made up only 11% of all bat passes

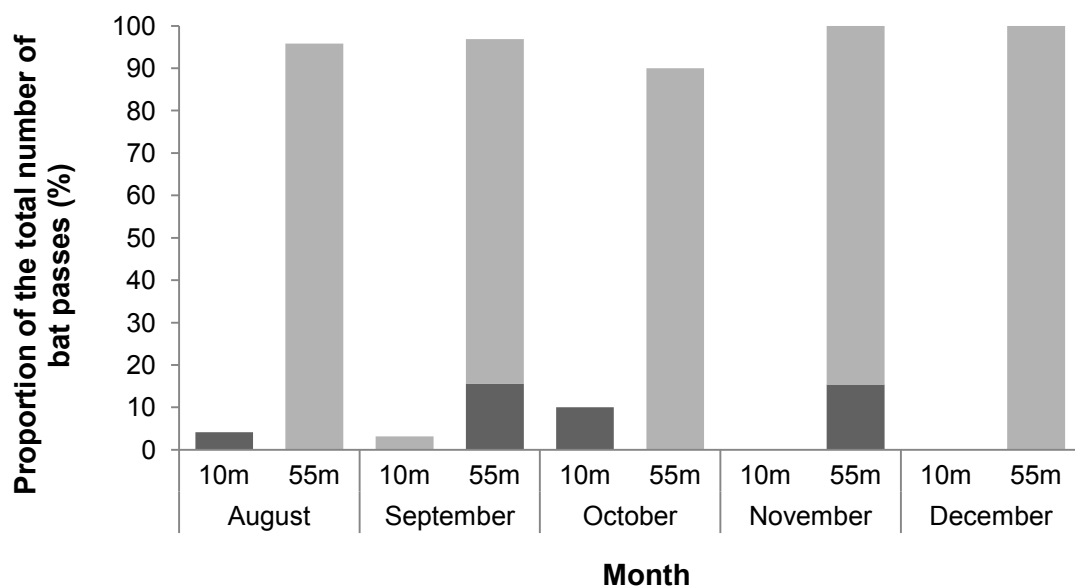


Figure 3. 2. Total number of bat passes recorded by month and detector height (10 m and 55 m). Light bars represent low-frequency calling bats and dark bars represent high-frequency calling bats. August recordings began on the 17th of August.

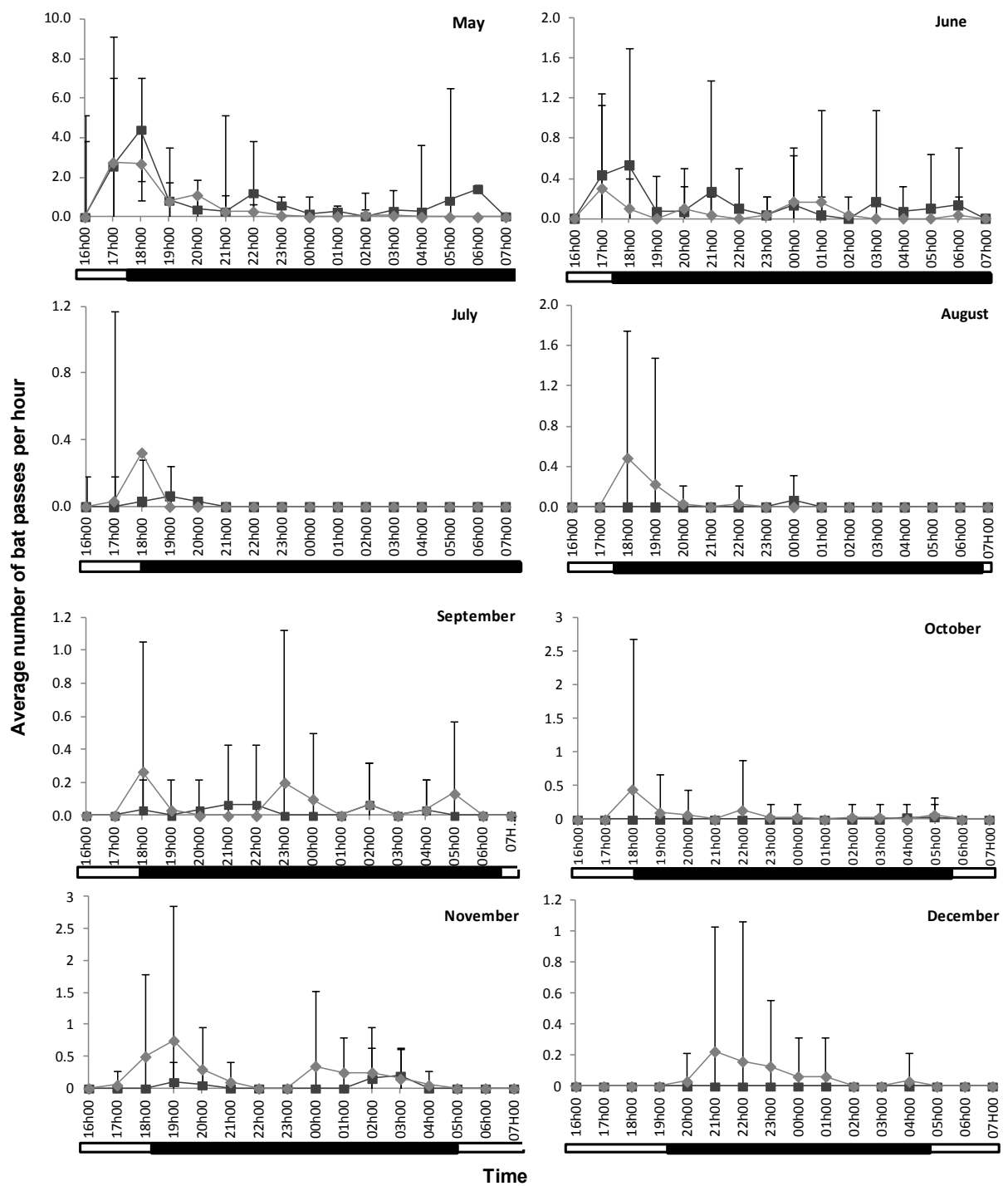


Figure 3.3. Mean number of bat passes per hour (\pm SE), at both heights collectively, for high-frequency calling bats (>35 kHz, squares) and low-frequency calling bats (<35 kHz, diamonds), per month from May 2012 to December 2012. Dark bars indicate time between average sunset and sunrise.

Large variation in the hourly rates of bat passes for each month and each phonic group was evident with the highest hourly bat pass rates observed in May (Figure 3.3). Total bat activity was highest for the first few hours after sunset with a gradual decline in activity throughout the night. For all months, except July and to a lesser extent August and October, bats remained active throughout the night, with activity periods interspersed with periods of inactivity. The duration of bat activity decreased during July, August and October, where activity was concentrated in the early evening (between 18:00 and 19:00 in July and August and between 18:00 and 22:00 in October).

3.3.3. Activity and weather

Out of 17 tested predictor variables and interactions, eight variables contributed significantly to the explanatory power of the global model, accounting for 84% of the variation observed in bat activity on a nightly basis (Table 3.2). Using backwards stepwise selection, five variables were chosen as the most significant predictors in the final model (Table 3.3). The final model explained 80% of the variation observed in nightly bat activity and strong relationships between bat activity and the five predictor variables were evident ($p < 0.001$, Table 3.3.).

The odds of bats being active or not on a given night would be 1.3 times greater for every 1°C increase in overnight average temperature and between 0.53 (July) to 6.79 (May) times greater depending on which month it was (Table 3.4.). For every $1 \text{ m}\cdot\text{s}^{-1}$ increase in wind speed, bat activity decreased by a factor of 0.77. The probability of bats being active was higher during the full moon, 3rd quarter moon and the new moon. Bat activity was negatively related to the average amount of rainfall received in a particular month, resulting in little or no bats activity when it was raining.

Table 3. 2. Log-likelihood ratio test, χ^2 statistics and significance levels from the global model of bat activity in relation to weather variables. 84% of the variation in bat activity was explained by the global model.

Predictor variable / intercept	χ^2	df	p	
Variables:				
Month	373.79	7	< 0.0001	****
Temperature	43.24	1	< 0.0001	****
Wind speed	9.45	1	0.0021	***
Pressure	2.2	1	0.1382	
Rainfall	0.47	1	0.4912	
Humidity	2.2	1	0.1382	
Moon phase	11.32	3	0.0101	*
Illumination	0.31	1	0.5770	
Interactions:				
Month:Temperature	6.42	7	0.4919	
Month:Wind speed	15.18	7	0.0338	*
Month:Rainfall	20.28	7	0.0050	***
Temperature:Wind speed	0	1	0.9442	
Temperature:Pressure	0.04	1	0.8407	
Pressure:Humidity	2.32	1	0.1275	
Temperature:Humidity	5.53	1	0.0186	*
Moon phase:Illumination	9.49	3	0.0234	*
Temperature:Pressure:Humidity	0.93	1	0.3355	

**** p < 0.0001 *** p < 0.001 ** p < 0.01 * p < 0.05

Table 3. 3. Log-likelihood ratio test χ^2 statistics and significance levels from the final model. 80% of the variation in bat activity was explained by final model.

Predictor variable	χ^2	df	p	
Variables				
Month	383.99	7	< 0.0001	****
Average nightly temperature	49.98	1	< 0.0001	****
Average nightly wind speed	22.38	1	< 0.0001	****
Moon phase	18.63	3	0.0003	***
Interactions				
Month:Rainfall	28.01	8	0.0005	***

**** p < 0.0001 *** p < 0.001

Table 3.4. Best fit logistic regression model describing the relationship between weather conditions and bat activity. SE=standard error of coefficients, OR=odds ratio, CI=confidence intervals. The odds ratio gives the change in odds for an increase in one unit of the predictor variable (Hosmer & Lemeshow 2000).

Predictor variable	Coefficient	SE	OR	CI lower	CI upper
Intercept	-2.6900	0.6914	0.0679	0.0175	0.2633
Month (May)	1.9170	0.4314	6.7975	2.9186	15.8315
Month (June)	0.4406	0.4705	1.5537	0.6179	3.9069
Month (July)	-0.6380	0.6508	0.5284	0.1476	1.8918
Month (September)	-0.0810	0.5403	0.9222	0.3198	2.6589
Month (October)	-0.4527	0.6012	0.6359	0.1957	2.0658
Month (November)	0.0446	0.5190	1.0456	0.3781	2.8918
Month (December)	-2.0850	0.6508	0.1243	0.0347	0.4450
Temperature	0.2814	0.0400	1.3249	1.2252	1.4328
Wind speed	-0.2591	0.0571	0.7717	0.6900	0.8631
Moon phase (3rd Quarter)	0.7580	0.2462	2.1341	1.3172	3.4575
Moon phase (Full moon)	0.9147	0.2437	2.4960	1.5480	4.0245
Moon phase (New moon)	0.3619	0.2660	1.4360	0.8527	2.4185
Month (May):Rainfall	12.1600	2.4210	1.90 ⁺⁰⁵	1.65 ⁺⁰³	2.19 ⁺⁰⁷
Month (June):Rainfall	-0.6516	1.0280	0.5212	0.0695	3.9062
Month (July):Rainfall	-1.02 ⁺⁰³	1.01 ⁺⁰⁵	0.0000	0.0000	∞
Month (August):Rainfall	-1.23 ⁺⁰²	1.03 ⁺⁰⁵	0.0000	0.0000	∞
Month (September):Rainfall	-3.6510	7.0660	0.0260	0.0000	26849.2300
Month (October):Rainfall	-32.6500	44.1900	0.0000	0.0000	2.74 ⁺²³
Month (November):Rainfall	1.7620	2.0310	5.8258	0.1088	311.8464
Month (December):Rainfall	-0.5777	5.6800	0.5612	0.0000	3.84 ⁺⁰⁴

Despite being identified as strong predictors of bat activity in the final model (Table 3.3.), the relationship between bat activity and temperature ($R^2 = 0.0496$) as well as bat activity and wind speed ($R^2 = 0.0404$), remained weak (Figure 3.4.). Average wind speed was less than 6 m.s^{-1} on 66% of the nights and the highest average wind speed recorded for a night was 12.86 m.s^{-1} (Figure 3.4.). Even at wind speeds greater than 12 m.s^{-1} , some bat activity was observed (Figure 3.4.).

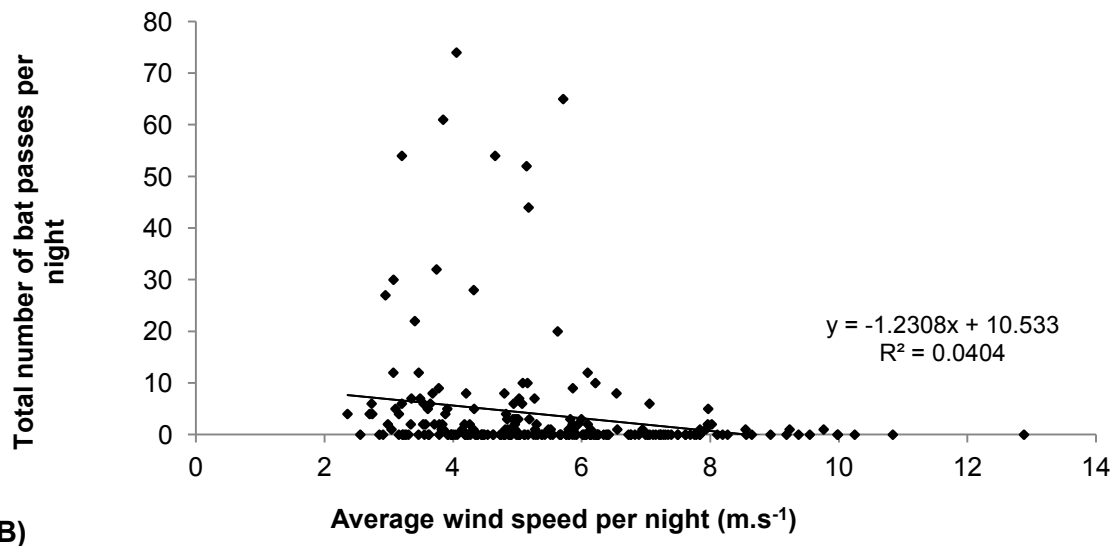
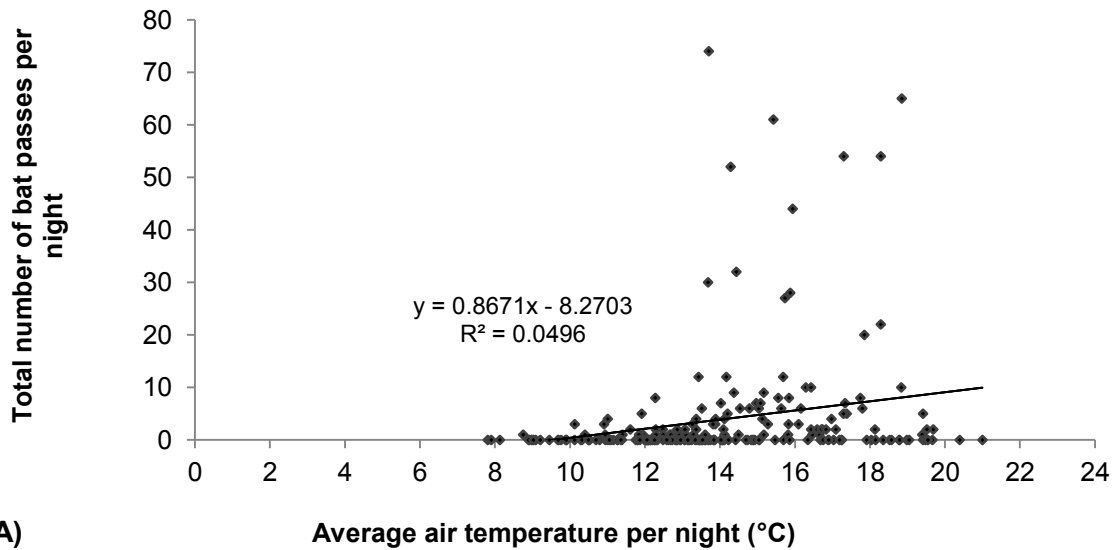


Figure 3. 4. The relationship between bat activity and two weather variables, average overnight temperature (°C) and average overnight wind speed (m.s⁻¹). Trend lines are presented as solid lines and R² values are displayed.

Significant differences in bat activity were evident across all moon phases (Table 3.3.), and in bat activity at 10 m ($\chi^2 = 281.91$, $df = 3$, $p < 0.0001$), 55 m ($\chi^2 = 10.887$, $df = 3$, $p = 0.0124$) and between low-frequency calling bats ($\chi^2 = 227.68$, $df = 3$, $p < 0.0001$) were significantly different across all moon phases (Figure 3.5.). Bat activity of high-frequency calling bats was significantly more ($W = 1183.5$, $p = 0.008$) than low-frequency calling bat activity during the full moon phase (Figure 3.5.). Low-frequency calling bat activity was significantly higher than

high-frequency calling bat activity during the 1st quarter ($W = 1215$, $p = 0.0018$) and new moon phases ($W = 1088$, $p = 0.0029$).

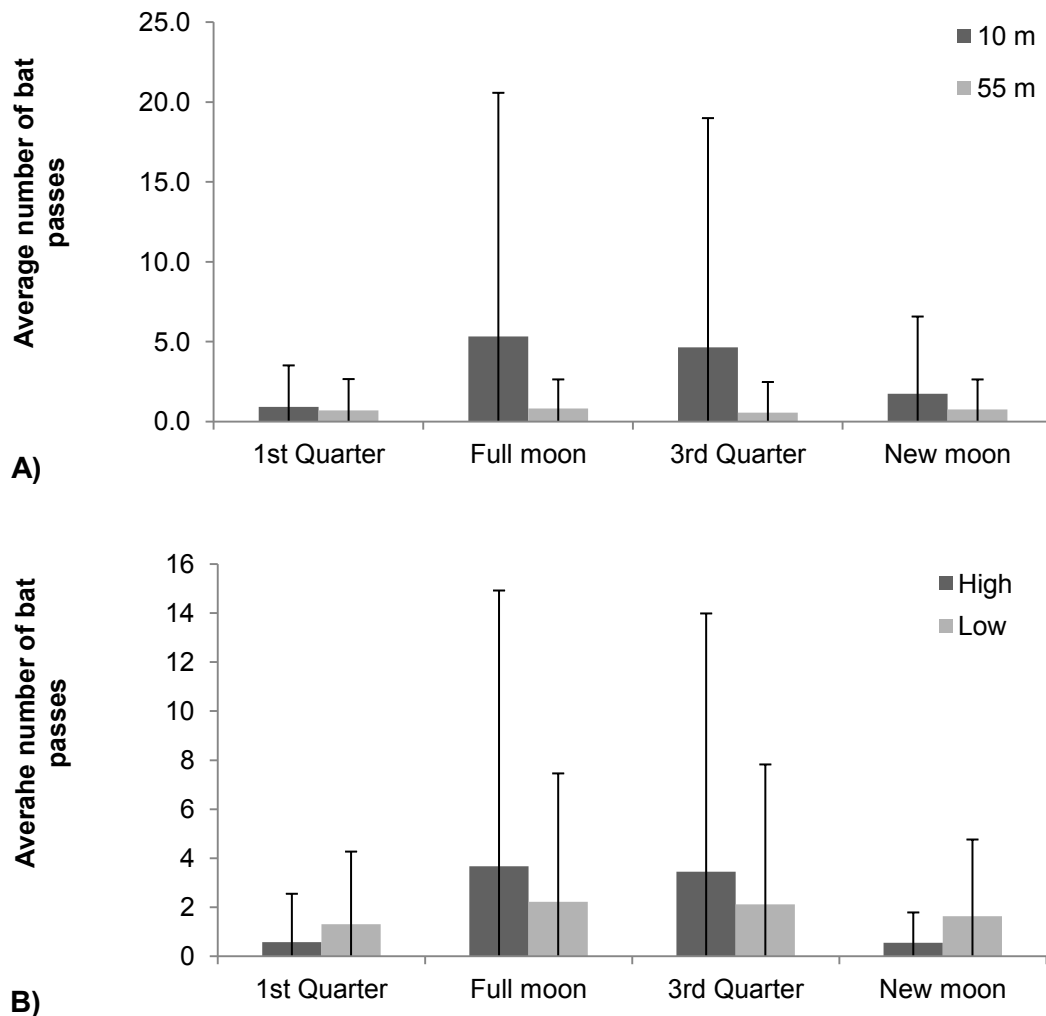


Figure 3. 5. The average number of bat passes A) at different heights (10 m and 55 m) and B) of the two phonic groups (High and low-frequency calling bats), during different phases of the moon.

3.4. DISCUSSION

This study illustrates that bat activity is highly variable both between months as well as between nights and provides a baseline measure of bat activity for the site. It is important to remember that bat activity data by no means is an estimate of actual bat abundance but is rather a measure of relative bat abundance, bat presence and use of the study area (Barclay 1999).

The potential bat community on site included three high-frequency calling bat species (the Cape serotine bat, Anchieta's pipstrelle and the long-tailed serotine bat), one low-frequency calling bat species (Egyptian free-tailed bat) and one fruit bat (the Egyptian Rousette bat). The Cape serotine bat was the only bat species that was successfully identified using both active (mist netting) and passive (acoustic detectors) methods. The use of mist nets was limited in corroborating the presence of other acoustically recorded bat species. The Egyptian Rousette fruit bat was heard calling twice and was neither caught in mist nets, nor was it recorded acoustically, despite the fact that its echolocation calls range from 10 kHz to 60 kHz (Neuweiler 1990).

A high degree of variation in bat activity was found between months. Similar levels of variation in bat activity have also been identified in other studies (Hayes 1997; O'Donnell 2000; Milne *et al.* 2005; O'Farrell 2010; Taylor *et al.* 2013). Bat activity was significantly higher in May as compared to all other months. In Southern Africa, the month of May falls within autumn and South African bat studies have shown that bat activity is highest in autumn and summer (Taylor *et al.* 2013). Changes in bat activity are influenced by migrations (Popa-Lisseanu & Voigt 2009), hibernation (Geiser & Stawski 2010), and mating (van der Merwe *et al.* 2006; Le Grange *et al.* 2011). High-frequency calling bats, such as the Cape serotine bat, begin mating in autumn (van der Merwe 1994). Migrations and mating for most bat species in South Africa occur in the autumn months between March and May (Monadjem *et al.* 2010), with the exception of the Egyptian free-tailed bat, which begin mating in August (Bernard & Tsita 1980) and establish maternity colonies in November and December (Herselman 1980). This may explain why high-frequency calling bat species were more frequently recorded in May 2012 and why low-frequency calling bat species were recorded more frequently in November and December.

Vertical separation between different phonic groups is a common phenomenon (Hecker & Brigham 1999; Arnett *et al.* 2005; Scrimgeour *et al.* 2013), and reports on bat activity have indicated that total bat activity is typically higher at ground level than at height (10 m and

higher; Arnett *et al.* 2005; Hein *et al.* 2011). High flying species are often under-represented in monitoring studies due to the fact that sampling effort at heights of 10 m and above, and within rotor swept areas, is not done high enough to capture high flyers (Collins & Jones 2009). Thus the addition of a second ultrasonic microphone at 55 m (within the rotor swept area) proved useful, as over 98% of the total number bat passes recorded, between August and December, were from 55 m above ground. High bat fatalities are as a result of increased bat activity in the rotor swept area at a certain point in time (Cryan & Barclay 2009). Monitoring bat activity within rotor swept areas of turbines is critical, as bats are often struck by turbine blades and suffer from barotrauma (Cryan & Barclay 2009). Low-frequency calling bat species, such as the Egyptian free-tailed bat, are generally high flyers and foragers (Monadjem *et al.* 2010), putting these species at particular risk of being struck by wind turbines (Sowler & Stoffberg 2012).

Reports from the USA and Europe indicate the majority of bat species killed by wind turbines are migratory species (Kerns & Kerlinger 2004), and that 98% of all bat fatalities are of high-flying bats species (Rydell *et al.* 2010b). However in a recent South African study, both a migratory bat species and low flying bat species were killed by a single wind turbine in the Coega Industrial Development Zone (Doty & Martin 2012). Over one year, 17 bat fatalities were recorded at this turbine, with the majority of casualties recorded during mid-December to mid-March. Two species were involved; the Cape serotine bat and the Egyptian free-tailed. Both are widespread throughout Southern Africa, occupy a wide range of habitats and are the two most abundant species in South Africa (Monadjem *et al.* 2010) and both were the dominant species recorded in this study.

At this site, it is highly likely that the same species of bats will be impacted by wind turbines. In contrast to other small mammals, they are slow to reproduce, producing only one pup per year (Bernard & Tsita 1980), in the case of the Egyptian free-tailed bat, and one to two pups a year (Lynch 1989, van der Merwe 1994), in the case of the Cape serotine bat. Low reproduction rates means that recovery from any adverse effect is slow; making any

anthropogenic cause of fatality for these bats a cause for concern for the conservation of biodiversity. Both species have been rated as having a medium-high (Cape serotine bat) and a high (Egyptian free-tailed bat) likelihood of risk of wind turbine associated fatalities, based on broad ecological features (Sowler & Stoffberg 2012). While they are listed as species of Least Concern according to the IUCN red data list (www.iucnredlist.org), based on high abundance alone, these two species provide important ecosystems services which are critical in maintaining a healthy, functional ecosystem (Lereau *et al.* 2001; Hooper *et al.* 2005).

Activity in both phonic groups was highest within the first few hours following sunset, a trend which is observed in other studies of bat activity (Erkert 1978; Milne *et al.* 2005; Redell *et al.* 2006; Esberard & Bergallo 2010). Changes in hourly bat activity patterns are most often associated with changes in insect abundance and availability (O'Donnell 2000; Burles *et al.* 2009; McCracken *et al.* 2012; Taylor *et al.* 2013), and so observed patterns in overnight bat activity may reflect higher insect activity at dusk and dawn (Rautenbach *et al.* 1988, Hein *et al.* 2011). In this way, bats are able to gain the necessary energy from their food in a shorter amount of time thereby maximising their foraging potential (Taylor & Oneill 1988). In addition, bats often return to roosts throughout the night (Anthony *et al.* 1981; Holland *et al.* 2011), resulting in a drop in activity during the middle of the night. Bats which are still out foraging will return to their roost shortly before sunrise (Milne *et al.* 2005), resulting in a smaller, second peak in activity just before dawn. These second peaks have been reported in many other studies (Arnett *et al.* 2005, Hayes 1997; Esberard & Bergallo 2010; Holland *et al.* 2011).

Temperature was one of the most significant predictors of bat activity on site and bat activity was shown to increase as temperature increased. Bat activity will only increase with temperature, up until a certain point. Where ambient temperature exceeds the animal's thermal neutral zone, activity will decline as it becomes too energetically costly to remain active at very high temperatures (Boyles *et al.* 2006). In addition, insect abundance is

positively linked with ambient temperature (Raimondo *et al.* 2004; Kasper *et al.* 2008), and when temperature decreases, insects become less active. Reductions in bat activity from June to September may be as a direct result of colder temperatures, as well as reduced food availability (Christie & Simpson 2006). Bats remain inactive for long periods of time and use torpor to save energy during such unfavourable conditions (Christian & Geiser 2007; Wojciechowski *et al.* 2007). Arousal from torpor is energetically expensive (Christie & Simpson 2006), particularly in winter, thus it may be too energetically expensive for bats to forage below certain temperature thresholds, despite food being available (Geiser *et al.* 2011). Tree and foliage roosting bats are more likely to be active during colder temperatures than cave dwelling bats as they can detect changes in ambient temperature (Boyles *et al.* 2006) and can exploit brief warm periods. These opportunistic activity bouts are short and dependent on temperature. The greater horseshoe bat (Park *et al.* 2010) and the Natterer's bat (Hope & Jones 2012) remain torpid for up to 12 and 20 days respectively, after which they arouse spontaneously to feed. Arousal will only occur when temperatures are above a threshold level (Park *et al.* 2010; Hope & Jones 2012). However, winter arousals are not entirely for foraging only, but also for drinking and mating (Boyles *et al.* 2006).

The influence of wind speed on bat activity levels was a significant predictor of activity in the final model. The majority of bat activity was concentrated in wind speeds that were less than 6 m.s⁻¹. Most studies have found a negative relationship between strong winds and bat activity (Erickson & West 2002; Kerns & Kerlinger 2004; Arnett *et al.* 2011; Rydell *et al.* 2010b; Hein *et al.* 2011). Bats often remain inactive or return to roosts during strong winds (O'Farrell 2010) as flying becomes increasingly difficult and more energetically costly (O'Farrell *et al.* 1967). In addition, the probability of finding food in strong winds is limited, as insects are not active during windy nights (Briers *et al.* 2003).

Most bats reduce their activity during periods of increased moon light (Meyer *et al.* 2004; Lang *et al.* 2006; Saldaña-Vázquez & Munguía-Rosas 2012). In contrast, bat activity in this study was higher during brightly lit nights, more so for high-frequency calling bats. High-

frequency calling bats are generally low flyers and are both clutter or clutter-edge foragers (Schnitzer & Kalko 2001), and so are able to reduce predation risk by changing where they forage (Hecker & Brigham 1999). Many studies have argued that in the absence of any predators (Karlsson *et al.* 2002) or where the benefit of foraging during the full moon outweighs the risk of potential predation (Thies *et al.* 2006; Holland *et al.* 2011); bats may remain active during full moon periods. No bat predators are known to occupy the site, and it is therefore plausible that bats remain active during full moon periods due to the lack of natural predators.

Surveys at wind farm developments, in the USA and Europe, have indicated that bat activity, and hence bat fatalities, are linked to calm winds, high temperatures and no rainfall and during the new moon phase (Kerns & Kerlinger 2004; Kunz *et al.* 2007a; Kunz *et al.* 2011; Payne & Walter 2011; Amorim *et al.* 2012). Results on the timing of bat activity in response to weather conditions, coupled with the fact that on a nightly basis, activity is highest for the first few hours following sunset, allows us to predict when bats are most active on site and thus allows us to develop mitigation measures in order to reduced the potential impacts of wind turbines on the local bat community. Mitigation measures will be discussed in detail in the general discussion chapter (Chapter 5). In order to conserve bats and reduce potential bat fatalities from occurring at the site, mitigation measures should be concentrated at those times when bats are most active (May and during the first few hours after sunset – 18:00 to 22:00), however, the demand for electricity is highest from 18:00 to 20:00 (Eskom 2013), a time when power generated from wind turbines would need to be integrated into the electricity grid, to supplement coal-fuelled power generation. Thus, there needs to be a trade-off between the conservation of bats, mitigating for potential bat fatalities and operating turbines during peak demand times for electricity generation in South Africa.

CHAPTER 4

ENDOGENOUS RHYTHMS OF RESTING METABOLIC RATE OF AN INSECTIVOROUS BAT AND ITS USE IN PREDICTING WILD BAT ACTIVITY

4.1. INTRODUCTION

Diel rhythmicity in animal behaviour (Shepard *et al.* 2006), physiology (Gachon *et al.* 2004; Refinetti 2004) and biochemistry (Pavlidis *et al.* 1999) has been well described in all organisms, ranging from bacteria (Golden *et al.* 2003), and plants (Johnson *et al.* 1995; Harmer 2009), to fish (Reebs 2002), reptiles (Winnie & Keck 2004), birds (Gwinner 1996; Underwood *et al.* 2001) and mammals (Voute *et al.* 1974; Reppert & Weaver 2002). In a review by Kronfeld-Schor & Dayan (2003), activity rhythms are primarily governed by: 1) endogenous circadian rhythms; 2) direct responses to external stimuli and 3) entrainment of endogenous circadian clocks by the environment.

Endogenous circadian rhythms are adaptable to changes in the environment (Daan & Aschoff 2001), and are controlled by intrinsic, inflexible internal biological clocks (Daan 1981), in the absence of external time or environmental cues (Marimuthu *et al.* 1981; Daan & Aschoff 1982; Gachon *et al.* 2004). Under constant conditions, many animals do not become disorientated with regards to time, but continue operating on a free-running internal clock typically over a period of 24 hrs (Aschoff 1965; Daan 1981; Gerkema 1992). Internal biological clocks allow animals to anticipate changes in the environment so that they can respond in the right way at the right time (Gerkema 1992; Aronson *et al.* 1993; Levy *et al.* 2012), thereby increasing their fitness (Bennet 1987; Daan & Aschoff 1982).

Direct responses to environmental conditions can mask underlying endogenous circadian rhythms (Waterhouse *et al.* 1996). One of the most important environmental cues that exists in nature is light (Daan & Aschoff 2001; Kronfeld-Schor & Dayan 2003), and most circadian rhythms are synchronized to the day/night cycle (Voute *et al.* 1974; Gerkema 1992).

Changes in sunset and sunrise times are gradual and result in seasonal changes in day length. As day length increases, the internal clocks of nocturnal animals are adjusted, thus the timing of activity is also adjusted (Park *et al.* 2000). In deep caves, bats, even in the absence of any light stimuli, wake up and fly to the entrance of the cave to sample light conditions (DeCoursey & DeCoursey 1964). They will only exit the cave and begin foraging if light conditions are favourable.

Endogenous patterns of metabolism and activity are tightly linked in endotherms, such that animals exhibit the highest body temperature and metabolic rates during their active phase, and lower metabolic rates during their natural rest phase (Geiser 2004; Refinetti *et al.* 2004). For example, at the end of the rest phase, the tube-nosed bat (*Nyctimene robinsoni*) exhibits the lowest body temperatures just after sunset and the highest body temperatures at the end of the active phase, just before sunrise (Riek *et al.* 2010). Resting metabolic rate (RMR) represents the basic cost of important physiological processes (Speakman & Selman 2003) and is defined as the metabolism of a post-absorptive animal, measured during the rest phase (Becker *et al.* 2012). Body mass (Bennett & Harvey 1987; Clarke *et al.* 2010), life-history traits (Bielby *et al.* 2007), food (Selman *et al.* 2001), and climate (Lovegrove 2003; Rezende *et al.* 2004) can influence RMR. Larger mammals typically have lower mass-specific metabolic rates than smaller mammals (Speakman 2005), whereas in both large and small animals, RMR is increased during reproductive periods (Johnson *et al.* 2001). Lovegrove (2003) showed that higher mass-specific RMRs are associated with small mammals living in high latitudes, where ambient temperatures significantly influence RMR. Resting metabolic rates will be higher in animals whose diets are higher in nutritional value and lower in animals whose diets contain little nutritional value (McNab 2003). This is evident in bats, where the RMR of insectivorous and frugivorous bats are generally lower than bats which feed on vertebrates (Cruz-Neto *et al.* 2001).

Some mammals employ energy-saving measures to reduce energetic demands during unfavourable conditions and changes in food availability. Bats are endotherms that make

use of heterothermy as a way to conserve energy (Geiser *et al.* 2011). Endotherms maintain a constant body temperature, a strategy which becomes energetically costly when environmental conditions become unfavourable (Geiser *et al.* 2010). Heterothermy involves the suppression of the metabolic rate which leads to a decreased body temperature and results in animals becoming inactive (Toussaint *et al.* 2009; McKechnie & Mzilikazi 2011). During unfavourable conditions, heterothermic endotherms make use of either daily torpor (Wojciechowski *et al.* 2007) or hibernate (Heldmaier *et al.* 2004) to conserve energy. The main difference between hibernation and torpor is that daily torpor bouts last for less than 24 hours, whereas hibernation involves extended periods of reduced body temperature, typically over many days (Geiser & Ruf 1995).

Arousal from torpor is pre-determined by circadian rhythms (Park *et al.* 2000; Turbill *et al.* 2003), allowing bats to keep activity patterns synchronised with the photoperiod so that when conditions become favourable, foraging activity is maximised (Geiser 2004; Turbill *et al.* 2008; Hope & Jones 2013). Patterns of torpor and activity in the free-living greater horseshoe bat (*Rhinolophus ferrumequinum*) during winter, showed that arousal from torpor was strongly synchronized with the timing of sunset, particularly between 2 hrs before and 2 hrs after sunset (Park *et al.* 2000). By examining the changes in metabolism over 24 hrs, at a constant ambient temperature and light or dark cycle, periods of rest or activity can be identified in the metabolic rate of an animal, even when animals are torpid (Körtner & Geiser 2000; Geiser 2004).

The relationship between free-ranging bat activity and extrinsic weather variables was tested in Chapter 3; however, bat activity is not only influenced by exogenous stimuli but timing of activity is also constrained by intrinsic rhythms in metabolism. This chapter has two main points of focus. The first part of this chapter deals with bat physiology (metabolic rates) and the second part deals with the use of bat physiology to predict free-ranging bat activity. The first aim of this study was to measure changes in the resting metabolic rate (RMR) of Cape serotine bats, over a 24 hr period. The Cape serotine bat was chosen because it was the

most abundant, resident species found at the Metrowind Van Stadens Wind Farm site (Chapter 3), and it was easy to capture in mist nets set up outside known roosts (Figure 2.1). Secondly, this study aimed to test whether the RMR of the Cape serotine bat could be used to predict free-ranging bat activity levels on site. To my knowledge, no studies have been done on the metabolic rates of the Cape serotine bat, nor has metabolic rates of captive bats been used to predict free-ranging bat activity levels.

4.2. MATERIAL AND METHODS

4.2.1. Bat capture and handling

Bat capture: Mist nets (Denier: 0.08 mm; mesh: 20 mm; shelves: 4; dimensions: 12 m; M-20/12 ECOTONE) were erected at two known roosts (Figure 2.1) at the Metrowind Van Stadens Wind Farm site, and set to 3 m from the ground, 30 min prior to sunset and remained set for two hours after sunset. A total of eight Cape serotine bats (Table 4.1.) were caught in mist nets and used in respirometry studies. Permits for live animal capture were issued by the Department of Economic Development, Environmental Affairs and Tourism, permit no's: CRO 85/12CR, CRO86/12CR, CRO 87/12CR, CRO 100/13CR, CRO 101/13CR, and CRO 102/13CR.

Bat handling and housing: After capture, each bat was placed in a cloth bag and transported to the animal physiology unit of the Zoology Department at the Nelson Mandela Metropolitan University. Bats were handfed mealworms (*Tenebrio molitor*) and water before being kept overnight in roost boxes at room temperature (22 - 25°C). Roost boxes (54 cm x 29 cm x 31 cm) were made out of plywood with the inside and lid covered with shade cloth, to create a rough surface for bats to cling on to. After the 24 hr respirometry trials, bats were kept in roost boxes before being transported in cloth bags and released at the exact point of capture, after sunset.

Table 4.1: Cape serotine bats (n = 8) caught in mist nets, at two known roosts on the Metrowind Van Stadens Wind Farm site. Location of mist nets and roosts are given in decimal degrees. F = female, M = male.

Bat	Year	Month	Day	Latitude	Longitude	Roost	Time of capture	Sex	Weight (g)
1	2013	Feb	25	-33.960894	25.253648	1	18:51	F	6.1
2	2013	Feb	25	-33.960894	25.253648	1	18:51	F	6.2
3	2013	April	5	-33.960894	25.253648	1	19:00	F	5.7
4	2013	Sept	7	-33.961244	25.253216	2	18:45	F	6.5
5	2013	Sept	17	-33.961244	25.253216	2	19:10	M	5.4
6	2013	Sept	17	-33.961244	25.253216	2	19:10	M	5.3
7	2013	Sept	18	-33.961244	25.253216	2	19:12	F	6.7
8	2013	Sept	18	-33.961244	25.253216	2	19:12	F	5.8

4.2.2. *Respirometry*

Animal ethics clearance was granted by the Research Ethics Committee: Animal, of the Nelson Mandela Metropolitan University (reference number: A12-SCI-ZOO-005). Animal respirometry chambers were constructed using 1.2 l air tight Perspex containers with three small holes at the base of the container to allow the inflow of air (Figure 4.1.). Opposite to this, near the top of the container was a large outflow port which was fitted with a tube so that air could be pulled through the chamber by Mass Flow System pumps (MFS-2, Sable Systems International, USA). Mesh netting was placed on the side and lid of the container to give bats something to cling onto and maintain normal roosting positions.

Resting metabolic rate (RMR), of post-absorptive bats, was indirectly measured as oxygen consumption (VO_2), using an open-flow respirometry system with a pull-through configuration (Hill 1972), over 24 hrs. Body temperature was not measured to avoid disturbing animals during recordings (Willis *et al.* 2005). Bats are not active after sunrise (Chapter 4) and so bats were put into respirometry chambers early in the morning (07:00-08:00) and placed in a darkened Humidity Incubator Cabinet; model FSIE-RH 20 (Labcon Laboratory Marketing Services (Pty) Ltd, South Africa). Ambient temperature (T_a) was kept between 22°C and 25°C, using a water bath (Labsec Scientific Equipment Company, South

Africa), which pumped water through aluminium coils within the incubator. Air was pulled through respirometry chambers at a flow rate of $400 \text{ mL}\cdot\text{min}^{-1}$ using Mass Flow System pumps (MFS-2, Sable Systems International, USA) to ensure that less than one percent of oxygen was depleted between incurrent and excurrent air.

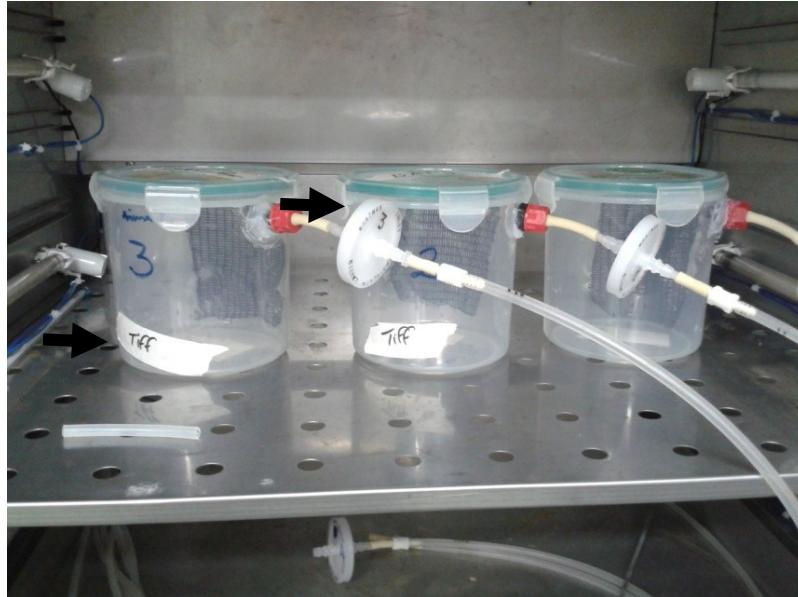


Figure 4.1. Animal respiratory chambers set up for use in open-flow respirometry experiments. Arrows indicate the flow of air through the respirometry chamber to humidity and gas analyzers.

Excurrent air passed through Whatman dust filters and through a RM-8 Intelligent Multiplexer V3 (Sable Systems International, USA) to remove debris and for gas stream selection between animal and reference chambers. Thereafter, the excurrent air passed through a RH-300 Relative Humidity / Dew Point hygrometer (Sable Systems International, USA) to determine relative humidity, and then through silica gel scrubbers to remove excess water vapour, before passing through a carbon dioxide analyzer (Model CA-10A, Sable Systems International, USA). Excess carbon dioxide and moisture was scrubbed from the air stream, through the use of soda lime granules and silica gel granules before being analyzed by an oxygen analyzer (Model FC-10A, Sable Systems International, USA). Each bat and reference chamber was sub-sampled at 10 min intervals at a sampling rate of 1 sample of excurrent air per second. Outputs from analyzers were digitized using a Universal Interface 2

and data acquisition software (EXPEDATA version 1.1.18, Sable Systems International, USA) (Lighton & Halsey 2011).

4.2.3. Free-ranging bat activity

Free-ranging Cape serotine bat (as opposed to all species reported in the previous chapter) activity was determined using an acoustic monitor (SM2BAT+, version 2.2.0, Wildlife Acoustics Inc. 2012), at the Metrowind Van Stadens Wind Farm Site (Chapter 3).

4.2.3. Data analysis

Respirometry: Data acquisition was performed using Sable Systems International EXPEDATA (1.1.18). Flow rate was corrected for the presence of water vapour using the following equation: $FR_{(corrected)} = FR_{(measured)} \times ((BP - WVP) / BP)$, where FR = flow rate, BP = barometric pressure and WVP = water vapour pressure (Melanson *et al.* 2010). The volume of oxygen consumed per hour was calculated using the following equation from Brown *et al.* (1984): $VO_2 = (FR_{(corrected)} \times 60 \times (F_iO_2 - F_eO_2)) / (1 - F_iO_2)$, where FR = flow rate in $mL \cdot min^{-1}$ after WVP correction, F_iO_2 = fractional concentration of oxygen entering the metabolic chamber and F_eO_2 = fractional concentration of oxygen leaving the metabolic chamber. Mass specific VO_2 was calculated as $VO_2 \text{ mL} \cdot g^{-1} \cdot hr^{-1}$, so that metabolic rates could be compared to other species of bats. The average hourly rate of oxygen consumption was used as a measure of metabolic rate.

Free-ranging bat activity: Nightly Cape serotine bat activity data was analysed in the program AnaLookW and the average hourly number of bat passes recorded per night was used as an index of relative bat activity (Chapter 3).

4.2.4. Statistical analysis

Individual metabolic rate over 24 hrs: Bats were considered normothermic when metabolic rate was within the range of normothermic rates of similarly sized insectivorous bats.

Normothermic metabolic rates of similarly sized bats range between $1.55 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ (*Pipstrellus pipstrellus*, 4.9 g, Genoud & Christie 2011) and $3.0 \pm 0.6 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ (*Nyctophilus geoffroyi*, 7.13 ± 0.7 g, Turbill *et al.* 2008). Bats were considered torpid when measured metabolic rates matched or were lower than the torpid metabolic rates (TMR) of similarly sized bats and where metabolic rate fell rapidly to a reduced steady-state level (Willis *et al.* 2005). For example, the little Australian forest bat (*Vespadelus vulturnus*) weighs 4.0 ± 0.5 g and has an average TMR of $0.25 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ at 25°C (Willis *et al.* 2005). Lesser long-eared bat (*Nyctophilus geoffroyi*) has a M_b of 7.13 ± 0.7 g and an average torpid metabolic rate (TMR) of $0.53 \pm 0.12 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ at 26°C (Turbill *et al.* 2008). The mean oxygen consumption rate ($\text{VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$) was determined by taking the mean oxygen consumption rate in each 10 min interval, for each animal, within each hour and averaging them to get an hourly rate. Means are expressed \pm standard deviation (SD).

Free-ranging bat activity: Average hourly bat activity over a 24 hr period was determined by averaging the number of Cape serotine bat passes recorded every hour over the study period. The average metabolic rate and number of bat passes, across the entire 24 hr period, was calculated and used as a baseline measurement to identify any peaks. Peaks were identified when oxygen consumption or the number of bat passes increased above average levels over the 24 hr period.

Using RMR to predict free-ranging bat activity: Generalized linear models, using the Gaussian family, were constructed (3.0.1, R core development team 2013), to determine the relationship between average resting metabolic rate of only the torpid bats ($n = 6$) over 24 hrs and average hourly, free-ranging bat activity patterns. The first model included the average number of bat passes per hour over a 24 hour period and the second model looked only at night time bat activity patterns, representing 15 hours out of the 24 hr sampling period. Models were compared using R^2 values, where a higher R^2 value represented the best fitted model. Predictions and standard errors of those predictions, from the best fitted model, were determined using the predict function in the statistics program R (Package

stats: version 2.15.3, R core development team 2013). Predicted relative number of free-ranging hourly bat activity, was presented with standard errors of the model estimates.

4.3. RESULTS

4.3.1. Metabolic rate over 24 hrs

Under laboratory conditions, only two bats remained normothermic throughout the 24 hr sampling period (Figure 4.2.A). The majority of Cape serotine bats ($n = 6$) showed a high proclivity for torpor in the laboratory (Figure 4.2.B). For normothermic bats ($n = 2$), average daytime (07:00-17:00) and average night-time (18:00-06:00) metabolic rate was $1.14 \pm 0.3 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ and $1.18 \pm 0.25 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$, respectively. The maximum metabolic rate recorded for normothermic individuals was $2.53 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ at 18:00. No distinct patterns in metabolic rate over the 24 hr sampling period were apparent, and bats maintained metabolic rates between 1-2 $\text{VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$.

Bats which remained torpid (Figure 4.2.B) for most of the recording had average daytime (07:00-17:00) and average night-time metabolic rates (18:00-06:00) of $0.47 \pm 0.09 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ and $0.58 \pm 0.28 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ respectively. Torpid metabolic rates (TMR) were recorded 61% of the time, during both day-time and night-time hours, with the lowest average metabolic rate recorded as $0.34 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$, at 04:00. For all torpid bats, metabolic rates were higher at the start of recordings when bats were placed in respirometry chambers. Thereafter, metabolic rates slowly decreased. The highest metabolic rates were observed between 18:00 and 22:00. Abrupt changes in metabolic rate were observed for 3 bats, where metabolic rate ranged from $2.5 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ to $2.8 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ during the bats' active phase. These peaks were greater than the average highest metabolic rate recorded for all 6 torpid bats collectively ($1.2 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$).

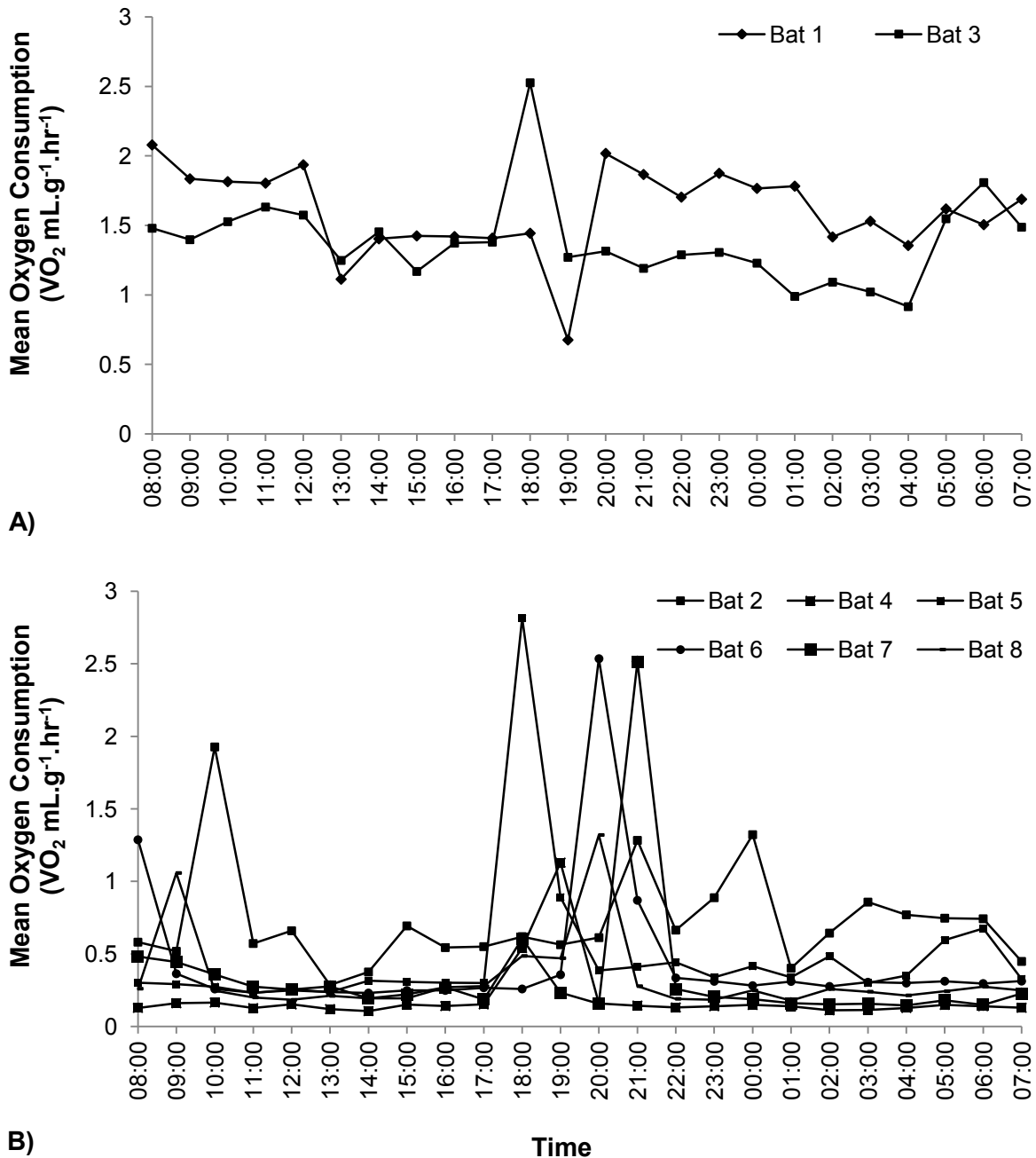


Figure 4.2. Time courses of average resting metabolic rate (RMR) measured, as $\text{VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ of A) normothermic ($n = 2$) and B) torpid ($n = 6$) Cape serotine bats (*Neoromicia capensis*), under constant darkness and at a constant ambient temperature of $22 \pm 3^\circ\text{C}$.

3.3.2. Using RMR to predict free-ranging bat activity

Cape serotine bats showed RMR suggestive of activity after sunset, even when torpid. Average metabolic rate of torpid Cape serotine bats ($n = 8$) were higher during the first 4 hrs of the recording trial, thereafter, metabolic rates declined. A definite peak in average

metabolic rate occurred at 18:00 ($0.89 \pm 0.95 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$) and again from 20:00-21:00 ($0.89 \pm 0.91 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$). These peaks in metabolic rate exceeded the average metabolic rate of $0.42 \pm 0.21 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$ across all 24 hrs. After the initial peak at 18:00, the metabolic rate dropped to average metabolic rate of $0.60 \pm 0.34 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$.

Large amounts of variation were present in the hourly activity patterns of bats in the wild (Chapter 3). Cape serotine bat were active from just before sunset (17:00) to just before sunrise (06:00). A definite peak in average hourly free-ranging Cape serotine bat activity occurred at 18:00 (5.8 ± 7.6 bat passes per hour) and a smaller peak occurred at 06:00 (1.52 ± 6.83 bat passes per hour). Cape serotine bat activity declined from 19:00 (1.39 ± 3.35 bat passes per hour) to 20:00 (0.29 ± 3.35 bat passes per hour). Thereafter, average hourly bat activity of the Cape serotine bat remained low throughout the remainder of the evening, with the little or no bats being active from 00:00 to 05:00, and after 06:00.

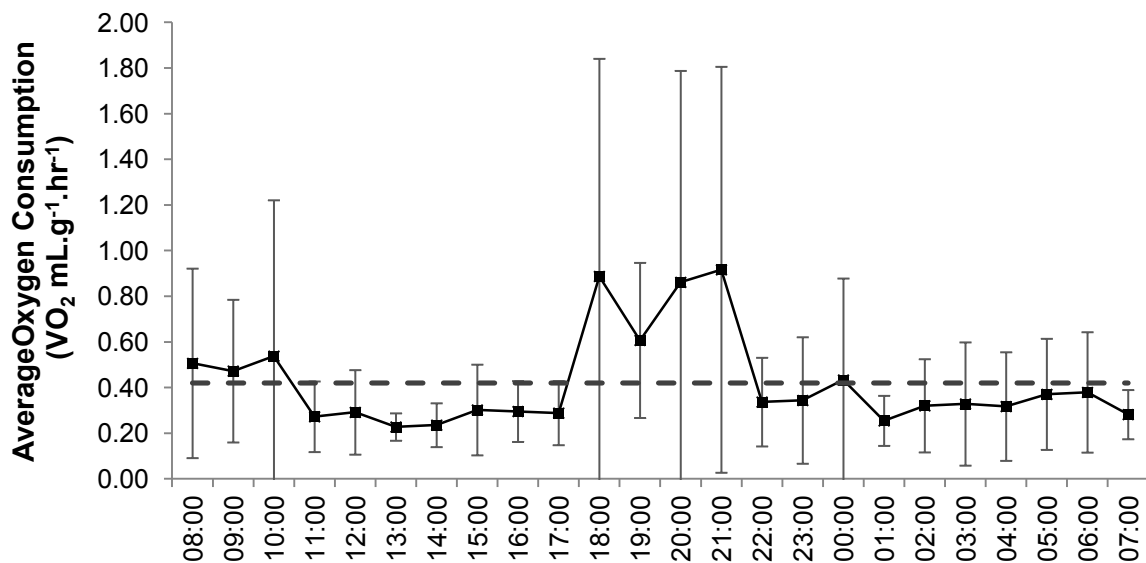


Figure 4.3. Time courses of average resting metabolic rate (RMR) measured, as $\text{VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$, for torpid individuals ($n = 6$), over a 24 hr period (Mean \pm SD). Horizontal dotted line represents the average metabolic rate = $0.69 \pm 0.18 \text{ VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$, across all hours.

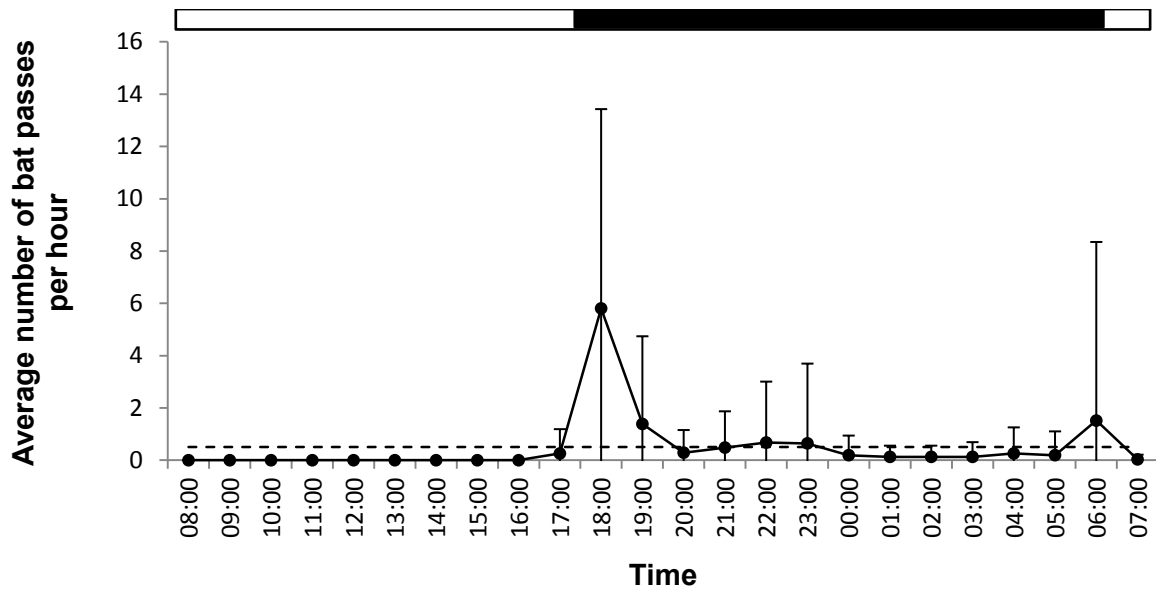
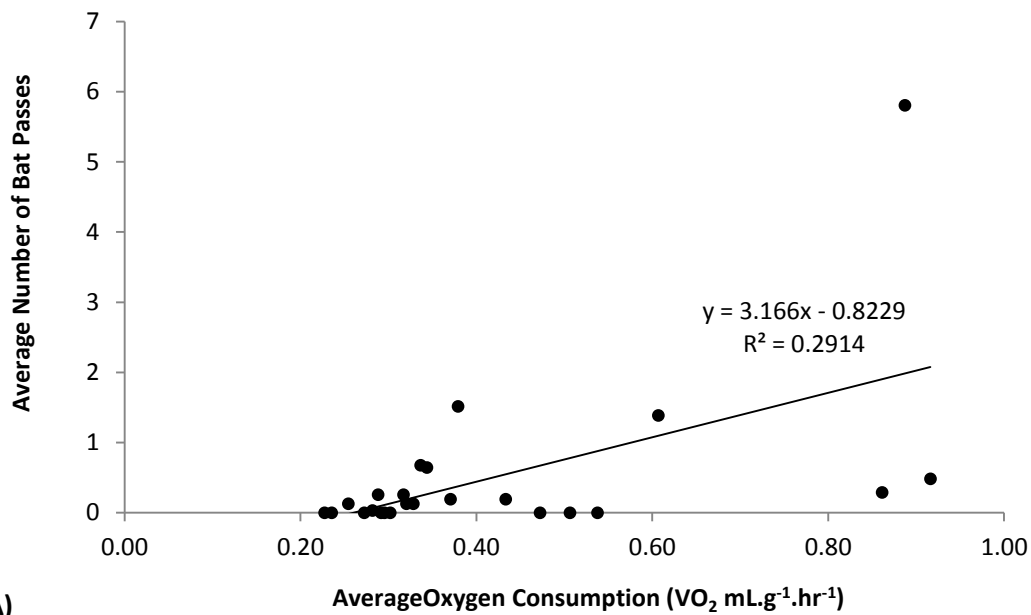


Figure 4.4. Average hourly free-ranging bat activity of Cape serotine bats, at the Metrowind Van Stadens Wind Farm, over a 24 hour period starting at 08:00. Horizontal dashed lines represent the average number of bat passes per hour (0.51 ± 1.22 bat passes per hour), across 24 hrs. Black and white bars represent the dark and light period, respectively.

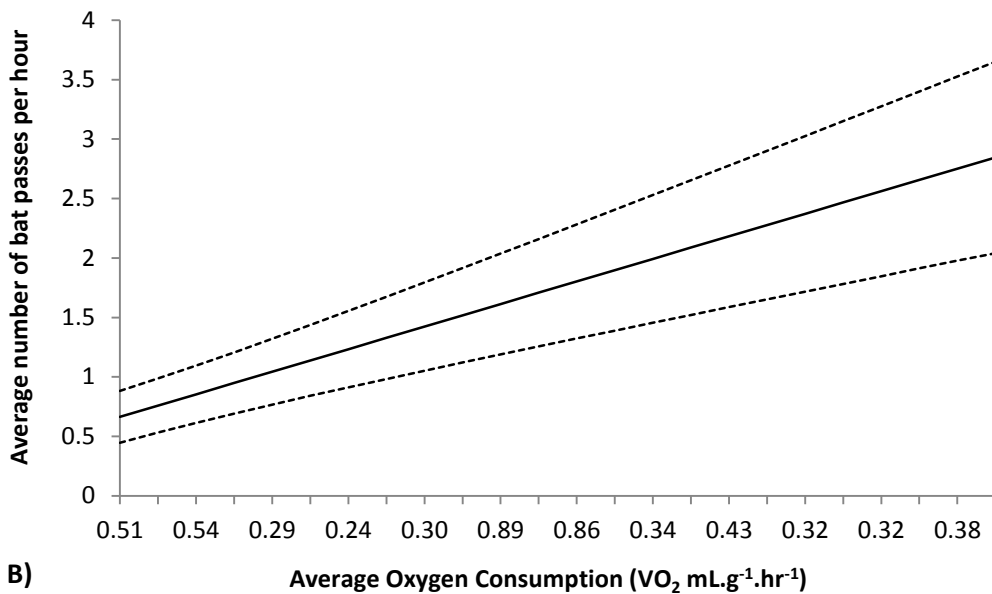
Significant relationships between average resting metabolic rates of torpid and field-observed bat activity of free-ranging Cape serotine bats were evident (Table 4.2.). The first model included the relationship between the two variables across the full 24 hr period and explained 33% of the variation in the data. The second model included nightly activity only and explained 30% of the variation in the data.

Table 4.2. Summary of the results from generalised linear modelling of hourly, free-ranging Cape serotine bat activity ($n = 376$) using average resting metabolic rates (RMR, $n = 6$) of torpid bats, over 24 hrs ($VO_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$). Percentage of deviance explained and r^2 values for each model is given.

Model	Description	Variable	Estimate	SE	p	R ²	
1	24 hr activity	<i>(Deviance 33.316, deviance captured = 33%)</i>					
		Intercept	-0.8226	0.4889	0.1066		
		Average VO_2	3.1628	1.0498	0.0064	0.29	
2	15 hr nightly activity	<i>(Deviance 29.632, deviance explained = 30%)</i>					
		Intercept	-0.7021	0.7438	0.3624		
		Average VO_2	3.2715	1.4428	0.0411	0.28	



A)



B)

Figure 4.5. A) The best generalized linear model (Model 1), illustrating the relationship between resting metabolic rate ($\text{VO}_2 \text{ mL.g}^{-1}.\text{hr}^{-1}$) and hourly, free-ranging bat activity over 24 hrs and B) predicted relative number of bat passes (solid line) based on the best generalised linear model. Dashed lines represent the standard error of the model estimates.

Cape serotine bat activity was positively associated with average resting metabolic rate (Figure 4.5.A), and the overall fit of the model (Model 1, Table 4.2.) was strong ($R^2 = 0.2914$), explaining 33% of observed hourly bat activity. Average metabolic rate of the Cape

serotine bat was used to predict free-ranging Cape serotine bat activity (Figure 4.5.B). The highest number of bat passes per hour predicted by the best fit model ranged between 2.04 and 3.65 bat passes per hour (Figure 4.5.B), whereas the highest number of bat passes per hour recorded in the field for Cape serotine bats was 5.81 ± 7.62 bat passes per hour (Figure 4.4.), and so the best fit model tended to underestimate high numbers of bat passes.

4.4. DISCUSSION

4.4.1. Patterns in metabolic rate of Cape serotine bats

This study showed that in the absence of any light stimuli and at a constant ambient temperature, activity in the Cape serotine bat is governed by endogenous rhythms in resting metabolic rate and that these free-running patterns in resting metabolic rate are good predictors of when free-ranging bats may be active.

Lower metabolic rates are expected for bats which inhabit lower latitudes, such as the subtropics and temperate zones (Lovegrove 2003), and are common features of bats from the Vespertilionidae family (insectivorous bats, Speakman & Thomas 2003; Riek *et al.* 2010). Resting metabolic rates in the Cape serotine bat were very low, even for normothermic individuals. When compared to other bats of similar size, resting metabolic rates of the Cape serotine bat ($0.47 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ to $1.16 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$) were much lower than the Californian leaf-nosed bat (*Macrotubs californicus*, 11.7 g, $1.28 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$, Rodriguez-Duran 1995) and the common pipstrelle bat (*Pipstrellus pipstrellus*, 4.9 g, $1.55 \text{ VO}_2 \text{ mL}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$, Genoud & Christie 2011). Insectivorous bats typically have metabolic rates that are 58 – 77% lower than those predicted using body mass mammalian standards (Bonaccorso & McNab 2003; Willis *et al.* 2005; Genoud & Christie 2011), and this has been largely attributed to the fact that a diet containing insects has less calorific value than a diet containing fruit or nectar (Cruz-Neto *et al.* 2001, Speakman & Thomas 2003).

When bats were taken out of overnight roost boxes and put into respiratory chambers, they were observed breathing heavily as they had been woken up. High metabolic rates during the morning (08:00-11:00) were most likely as a result of bats not being acclimated to respirometry chamber conditions after handling, prior to resting metabolic rate being measured, and so this data should be treated with caution, as it may not be a true representation of the resting metabolic rate of the Cape serotine bat during the morning (08:-11:00). Metabolic rate declined at 19:00 after the initial peak in metabolic rate at 18:00. The most plausible explanation for reduced metabolic rates at 19:00 is that bats lowered their metabolic rates in order to conserve energy as they were unable to leave the respiratory chambers.

Gradual increases in the RMR of Cape serotine bats prior to arousal at sunset were to be expected, as bats typically begin to re-warm and raise body temperatures in preparation for flight and foraging (Kurta & Kunz 1988; Turbill *et al.* 2003). In general, bats are able to balance the increased energetic cost of flight during foraging trips (Voigt *et al.* 2010) while maximising foraging success when food is readily available (Taylor & Oneill 1988), by arousing from torpor in the late afternoon and emerging from roosts at sunset (Turbill *et al.* 2003). In summer, the lesser long-fingered bat, *Nyctophilus geoffroyi*, begins to re-warm in the late afternoon before arousal at sunset (Turbill *et al.* 2003) and the timing of emergence of Leschenault's Rousette fruit bat (*Rousettus leschenaulti*) from roosts is controlled by the timing of sunset (Vanlalngaka & Joshi 2005). The timing of peak activity in Natterer's bats (*Myotis nattereri*) changed as day length changed during winter, however, activity remained entrained to the timing of sunset and sunrise i.e. the photoperiod (Hope & Jones 2012; Hope & Jones 2013). This enables bats to continuously track dusk so that when food becomes available in summer months, the circadian rhythm of bats will already be entrained to the photoperiod so that foraging opportunities are not missed.

Flying is the most energetically costly form of locomotion (Nudds & Bryant 2000; Voigt *et al.* 2010; MacAyeal *et al.* 2011), and flight metabolism can be 6 – 10 times higher than basal

metabolic rates (BMR) of endotherms and 7 – 12 times the BMR for bats (Speakman & Racey 1991; Norberg *et al.* 1993; Winter & von Helversen 1998). When bats emerge from roosts, metabolic rates are expected to increase substantially due to the energetic costs of flight, as opposed to their rest phase (Bartholomew *et al.* 1964; Maina 2000).

In this study, the majority of the bats were torpid during daylight hours and after initial peaks in metabolic rate at 18:00 and 20:00-21:00. Peaks in RMR in torpid bats suggested peaks in activity, even after sunset. This was arousal followed by a return to torpor after 21:00. To counteract the trade-off between maintaining a constant body temperature and conserving energy, bats enter into daily torpor, which allows them to lower their body temperature and metabolic rate and then arouse when conditions become favourable (Wojciechowski *et al.* 2007). Endogenous rhythms persist even during torpor (Park *et al.* 2000; Hope & Jones 2013) and torpor in bats has been well documented in both summer (Kurta & Kunz 1988; Turbill *et al.* 2003) and winter (Turbill & Geiser 2008; Liu & Karasov 2012), and throughout the year in some subtropical bat species (Stawski & Geiser 2010; Vivier & van der Merwe 2007). Thus the ecological significance of having an entrained endogenous rhythm lies in the fact that an opportunity to forage and get energy is never missed. This study showed that torpid Cape serotine bats arouse from torpor at a time that coincided with sunset, suggesting that the metabolic rate of the Cape serotine bat is entrained to the photoperiod, so that bats wake up at a time when light conditions are favourable for foraging.

4.4.2. Using metabolic rate to predict free-ranging bat activity

Bats are known to synchronise their activity with sunset (Erkert 1978; Griffiths 2007), a time when insect activity is also high (O'Donnell 2000; Payne & Walter 2011; Taylor *et al.* 2013). Patterns in free-ranging bat activity were significantly linked to average metabolic rate, both of which peaked at sunset. Studies that have examined daily rhythms in the metabolism of reptiles (Winnie & Keck 2004), birds (Bennet & Harvey 1987; Dawson *et al.* 2001; Al-Mansour 2004), mammals (Selman *et al.* 2001; Gattermann *et al.* 2008), and bats (Kurta &

Kunz 1988; Turbill *et al.* 2003, Vanlalngaka & Joshi 2005) all show that peaks in metabolic rate, together with body temperature, coincide with the active phase of the rest-activity cycle. Therefore, this can serve as a useful tool to predict activity patterns in free-ranging bats (Chapter 5).

Comparing the RMR of captive bats, under constant laboratory conditions, to wild bat activity patterns, may not be a true representation of the complex mechanisms controlling bat activity in the wild (Geiser *et al.* 2000), because the environment in which an animal exists is not always constant. During laboratory studies, golden hamsters (*Mesocricetus auratus*) were nocturnal, whereas in nature, they are typically diurnal (Gattermann *et al.* 2008). Gattermann *et al.* (2008) reasoned that golden hamsters forego a nocturnal lifestyle for a diurnal lifestyle as a strategy to avoid predation and to ensure access to food. In this way, biotic factors such as predation, food and competition can entrain or mask the natural circadian rhythm of animals (Daan 1981; Daan & Aschoff 2001; Halle 2000; Levy *et al.* 2012). In addition, abiotic factors, such as temperature (Erickson & West 2002; Chirstie & Simpson 2010), wind (Kerns & Kerlinger 2004; Arnett *et al.* 2010), rainfall (Johnson *et al.* 2011; Geluso & Geluso 2012) and humidity (Milne *et al.* 2005) play an important role in determining when an animal chooses to be active, and so bat activity is not only controlled by endogenous rhythms in metabolic rate, but also by exogenous stimuli.

In Chapter 3, a number of exogenous factors were shown to be important in determining when bats were active and temperature was one of the most significant predictors of wild bat activity. In the wild, arousal from torpor in the early hours of the morning is due to passive re-warming when ambient temperature increases after sunrise (Körtner & Geiser 2000). Willis *et al.* (2005) measured RMR of little Australian forest bats, *Vespadelus vulturnus*, under constant ambient temperatures as well as during ambient temperatures that mimicked the change in ambient temperature in the wild. Results showed that under laboratory conditions, bats remained torpid for the majority of the time with one spike in RMR at sunset (Willis *et al.* 2005). When ambient temperature mimicked a natural temperature cycle, metabolic rates of

the little Australian forest bats were lower and bats were torpid during daylight hours with a slight peak in the early hours of the morning (04:00) when ambient temperatures were at the lowest. At sunset, metabolic rates increased, despite ambient temperature decreasing. Thereafter, metabolic rates decreased back down to torpid levels after 20:00 (Willis *et al.* 2005).

A combination of endogenous and exogenous factors is responsible for observed activity patterns in free-ranging bats (Daan & Aschoff 2001; Levy *et al.* 2012). Endogenous rhythms in resting metabolic rate, and the entrainment of metabolic rates to the timing of sunset, work together to ensure that bats wake up at a time when conditions are favourable, so that an opportunity to forage, either in summer or winter, is never missed. This study showed that 37% of the variation in observed free-ranging Cape serotine bat activity was explained by endogenous patterns in resting metabolic rate of the Cape serotine bat. Exogenous factors such as air temperature, wind speed, the amount of rainfall (all of which changed on a nightly and monthly basis, Chapter 3), and moon phase were shown to explain 80% of observed activity of all free-ranging bat species at the site (Chapter 3), and so, bats will only exit roosts when conditions are favourable. Thus endogenous rhythms in resting metabolic rates are important for the initiation of bat activity and changes in weather conditions (exogenous stimuli) are responsible for the cessation of bat activity (Winnie & Keck 2004). In the future, the combination of resting metabolic rates and factors contributing to free-ranging activity patterns of the Cape serotine bat should be included into one model, to determine how much of the variation in free-ranging bat activity patterns of the Cape serotine bat is explained by a combination of both endogenous and exogenous factors.

CHAPTER 5

GENERAL DISCUSSION

This dissertation is based on a pilot study that aimed to contribute to the understanding of bat activity and what factors are responsible in determining bat activity, with respect to wind turbine interactions. Bat activity was significantly associated with air temperature, wind speed and moon phase and the probability of bats being active increased or decreased depending on the time of year (Chapter 3). Environmental stimuli exert a masking effect on underlying circadian clocks by either increasing or decreasing activity (Underwood 1992). Once these factors were removed under constant laboratory conditions, the underlying circadian rhythms in resting metabolic rate (RMR) of the Cape serotine bat become apparent (Chapter 4). Daily rhythms in RMR were significantly linked to periods when bats were most active in the wild and could be used to predict wild bat activity (Chapter 4). Together, these two chapters show that both exogenous and endogenous factors drive bat activity in the wild, a trend which has been observed in other bat populations (Thies *et al.* 2006) and mammals (Rezende *et al.* 2004), as well in ectotherms such as lizards (Winnie & Keck 2004). By determining what factors influence bat activity, we are able to predict when bats will be most active and thus can develop mitigation measures to reduce the potential impacts that wind turbines will have on the bat community.

Bats were mostly torpid during the day and both activity and RMR peaked at sunset, indicating that even in constant darkness and at a constant temperature, intrinsic and extrinsic activity was entrained by the photoperiod. Bats are known to track dusk (Erkert 1978; Milne *et al.* 2005; Redell *et al.* 2006; Esberard & Bergallo 2010) and are sensitive to seasonal changes in day length (Hope & Jones 2013). During winter, the sun sets earlier than in summer and bats are sensitive to the gradual changes in the timing of sunset across the seasons. This was evident in that bat activity was always highest at sunset for all months as compared to other times of the night.

Bat activity decreases with increasing wind speed, and temperature plays an important role, both in influencing bat activity patterns (Erickson & West 2002; Christie & Simpson 2010) and in determining when bats choose to enter torpor (Christian & Geiser 2007; Wojciechowski *et al.* 2007). Although bat activity was positively associated with air temperature and wind speed in this study, the relationship remained weak, and so bats may have been responding to other factors not tested in this study.

The timing of both free-ranging bat activity and metabolic rates were synchronised, so that bats were most active at sunset, which coincides with the time that insect biomass and density is the typically highest (Rautenbach *et al.* 1988; Lang *et al.* 2006). Bats are known to track insect movements and congregate in areas where insect density is high (de Jong & Ahlén 1991), and so the availability of food (not investigated in this study) is an additional factor contributing to nightly free-ranging bat activity (Thies *et al.* 2006; Popa-Lisseanu & Voigt 2009). However different insect orders have been found to be most active when temperature and humidity (Briers *et al.* 2003; Raimondo *et al.* 2004) are high, and when wind speeds (Briers *et al.* 2003) and precipitation are low (Kasper *et al.* 2008), and so both insect activity (food availability) and bat activity are governed by the same controlling weather variables. Thus the ecological significance of having an entrained internal clock lies in the fact that an opportunity to forage and get energy is never missed.

Bat fatalities have been shown to occur at South African wind farms, both in the Western (Aronson *et al.* 2013) and Eastern Cape (Doty & Martin 2012). Both studies indicated that the Cape serotine bat, a low flying bat species (Monadjem *et al.* 2010) has been killed by wind turbines. Although samples sizes were small, they provide evidence that both high-flying (Cape serotine bat) and low-flying (Egyptian free-tailed, Doty & Martin 2012) bat are killed by wind turbines in South Africa. This study showed that the majority of all high-frequency calling bats at this study site were Cape serotine bats (82% of the total number of bat passes) and the majority of all low-frequency calling bats were Egyptian free-tailed bats (97% of the total number of bat passes). As a result, both bat species are most likely to be

negatively affected by wind turbines at this site, due to their abundance on site alone. In addition, the Egyptian free-tailed bat is a high-flying bat and forages in open-air spaces (Monadjem *et al.* 2010), putting it at particular risk of being struck by rotating turbines blades (Cryan & Barclay 2009).

This study is important in that it provides baseline information on what species were present on the site, as well as when bats were most active (both on a monthly and nightly basis). Although this dissertation was not intended for wind turbine management, the information presented on the biology and activity of bats is important for managing interactions between bats and wind turbines. Current mitigation measures being used at wind farm facilities in the USA include curtailment (stopping blades by cutting out generators or angling blades parallel to wind), altering cut-in speeds of turbine blades (either increasing or decreasing the speed at which turbines rotate to produce electricity), and the use of acoustic deterrents to prevent bats from coming near turbines (NWCC 2007; Szewczak & Arnett 2006; Arnett *et al.* 2013b).

Curtailment involves the shutting down of wind turbines during periods when bat activity is highest or during important seasonal migrations of bats, thereby reducing bat mortality at wind farms (Fink *et al.* 2009). Studies on the use of curtailment at time of anticipated high bat activity indicate significant nightly reductions in bat fatalities of between 44% and 93%, with minimal annual power losses to operational mitigation (Arnett *et al.* 2010). The use of increasing cut-in speeds of turbines blades at ten wind farms in North America was reviewed by Arnett *et al.* (2013). Modern day wind turbines have cut-in speeds of between 3 - 4 m.s⁻¹ (standard manufacturer settings, Arnett *et al.* 2013a). In a review of 10 wind farm facilities in the USA by Arnett *et al.* (2013a), most wind farm facilities reported significant reductions in nightly bat fatalities of at least 50%, when cut-in speeds of turbine blades were increased between 1.5 m.s⁻¹ - 3 m.s⁻¹ above standard manufacture settings (Arnett *et al.* 2013a). At the Casselman Wind Project in Pennsylvania, USA, significant nightly reductions (53-87%) in bat fatalities were reported at turbines where cut-in speeds of turbine blades were increased by

1 – 2 m.s⁻¹ above manufacturer settings, and total bat fatalities were 5.4 times greater at normally operated turbines (Arnett *et al.* 2009).

The use of acoustic deterrents, such as radar, is a relatively new technique use to discourage bats from turbine areas (Spanjer 2006; Szewczak & Arnett 2006; Nicholls & Racey 2009). Deterrents emit randomised, broadband ultrasonic noise which is hypothesised to interfere with echolocation calls of insectivorous bats, thereby discouraging bat activity around treated turbines (Horn *et al.* 2008b). At a wind energy facility in Pennsylvania, USA, 21-51% (2009), and up to 64% (2010) fewer bats were killed at turbines with acoustic deterrents than those without acoustic deterrents (Arnett *et al.* 2013b), however responses to acoustic deterrents were species specific as some bat species showed no reduction in fatality rates (Johnson *et al.* 2012). Such studies are scarce, both locally as well as internationally, and the possible negative impacts of using acoustic deterrents on bat behaviour is not fully understood (Horn *et al.* 2008b, Johnson *et al.* 2012).

In light of this, the use of curtailment or changing cut-in speeds, at the Metrowind Van Stadens Wind Farm site, represents the most viable option for mitigation. Bat activity in this study was highest during months where temperature was higher and was concentrated in the few hours following sunset, patterns which were apparent in both free-ranging hourly bat activity as well as in the metabolic rate of the Cape Serotine bat. Thus mitigation should be focused during these periods of high bat activity so as to reduce the impact that wind turbines will have on the local bat community. In order to conserve bats and reduce potential bat fatalities from occurring at the site, mitigation measures should be concentrated to those times when bats are most active (May and during the first few hours after sunset – 18:00 to 22:00), however, the demand for electricity is highest from 18:00 to 20:00 (Eskom 2013), a time when power generated from wind turbines would need to be integrated into the electricity grid, to supplement coal-fuelled power generation. Thus, there is a trade-off between the conservation of bats, mitigating for potential bat fatalities and operating turbines during peak demand times for electricity generation in South Africa.

5.1. Study limitations

The benefits of active bat monitoring (mist netting and roost surveys) allows one to determine species diversity, locations of important roosts and determining population demographics, in addition to corroborating bat species presence of non-echolocating bats, which would otherwise be missed if only acoustic monitoring techniques were used (Kunz *et al.* 2007a). However, this technique is invasive and requires specialised equipment and some species of bats tend to avoid mist nets, thanks to their use of highly specialised echolocation calls (Moss & Surlykke 2010). This technique was only effective when nets were erected outside known roosts and is biased to those species that are low flyers, and so this technique is limited in corroborating the presence of other high-flying species, such as the Egyptian free-tailed bat, unless erected outside of known roosts.

Acoustic monitors are non-invasive and can be deployed in remote areas for extended periods of time (Kunz *et al.* 2007b). In addition, real-time activity and presence as well as species diversity can be determined from analysis of bat echolocation calls (Barclay 1999, Britzke *et al.* 2013). The use of acoustic monitors to study bat activity inherently includes some degree of pseudo-replication (the same individual is recorded more than once, even on the same night), because passes of individual bats cannot be distinguished from other individuals flying around the microphones at the same time (Hein *et al.* 2011). This represents an over-estimation of relative bat abundance as there is no way to determine if 10 individual bat passes were recorded or whether that same bat was recorded 10 times (Hein *et al.* 2011). In addition, acoustic detectors have restricted ranges and population dynamics cannot be determined. It is believed that pseudo-replication was limited in this study due to the large sample size of bat passes recorded ($n = 881$).

The sensitivity of the ultrasonic microphones changes in different weather conditions (Adams *et al.* 2012), and so bat activity may be under-represented during rainy or windy nights. When the protective foam covering of the acoustic microphone gets wet during rainy nights,

sound is attenuated; especially those echolocation calls that are greater than 30 kHz (Lawrence & Simmons 1982), and high winds can result in the microphones picking up wind noises, which masks fainter bat calls (Fenton 2013). Nonetheless, acoustic bat monitoring is a widely used tool in monitoring programs (Ford *et al.* 2005, Celuch & Zahn 2008, Furey *et al.* 2009) and enables one to detect and record various calls of echolocating bats, as a means of investigating relative bat activity and aids in identifying bat species or species groups (Kunz *et al.* 2007b, Gorresen *et al.* 2009, Hughes *et al.* 2010, Brtízke *et al.* 2013). This provides insight into nightly/seasonal activity patterns of bats (Hein *et al.* 2011), and is useful in identifying key times when bats are active.

Patterns observed in the resting metabolic rate of the Cape serotine bat, may not be representative of other bat species on site. The Cape Serotine bat does not fly at heights associated with the rotor swept area. However, because it was one of the most abundant species (82% of all bat activity) recorded, using its RMR to predict general bat activity is warranted. In addition, bats were not given sufficient time to settle in respirometry chambers before measurements on metabolic rates were made. This may have led to bats RMR being higher in the morning hours when bats were first placed into chambers and so in future, bats should be allowed to acclimatise to respiratory chamber conditions before commencement of respirometry measures or metabolic rates can be measured over 28 hours, thereby ensuring that metabolic rates recorded between 08:00 and 11:00 are of resting individuals.

Mist netting sampling was ineffective in capturing large numbers of bats and so, due to small samples sizes ($n = 8$), torpid ($n = 6$) and normothermic ($n = 2$) Cape serotine bats' resting metabolic rates, over 24 hours, were averaged and compared to free-ranging bat activity of Cape serotine bats. However, grouping torpid and normothermic individuals provides a bias, in that torpor and normothermy are distinct physiological states and torpor involves metabolic depression (Turbill *et al.* 2003; Geiser 2004; Wojciechoski *et al.* 2007), and so results from Chapter 4 should be interpreted with caution. In future, sampling effort should

be increased so that larger sample numbers of both torpid and normothermic bats can be obtained and the model re-run for separately for torpid and normothermic individuals.

5.2. Recommendations for future research

This pilot study identifies future research options, some of which are explored here.

The influence that insect abundance and movement has on bat activity needs to be tested in order to determine if bats are only active when food is available on site. This will become increasingly important because once turbines on site begin spinning; heat generated around the nacelle will most likely attract insects (Ahlén 2002; Kunz *et al.* 2007b) and thereby attract bats to the vicinity of the turbines themselves, putting these bats at risk of being struck by turbine blades (Horn *et al.* 2008a; Cryan & Barclay 2009). Changes in insect abundance and diversity across seasons can be determined by using light traps and mist netting (Pinheiro *et al.* 2002; Wickramasinghe *et al.* 2004). Insect abundance data as well as other environmental factors can be included in one model to determine if insect abundance on site results in higher bat activity (Lang *et al.* 2006; Horn *et al.* 2008a) and whether the interaction between insect abundance and bat activity changes seasonally. In addition, the proportion of feeding-buzzes (rapid echolocation calls used to hone onto the location and capture of prey) can be calculated from acoustic recordings of bat echolocation calls (Jones *et al.* 2007; Schnitzler & Kalko 2001). The detection of more feeding-buzzes recorded around a turbine indicates that bats are concentrating foraging attempts around turbines, putting them at increased risk of being struck by turbine blades (Cryan & Barclay 2009).

Free-ranging bat activity patterns were compared to RMR of captive bats, however, free-ranging animals respond differently in the field (Geiser *et al.* 2000). In addition, free-ranging bat activity changes on a seasonal basis due to bats either migrating (Moreno-Valdez *et al.* 2000, Richter *et al.* 2006) or hibernating (Park *et al.* 2000, Turbill & Geiser 2008, Geiser & Stawski 2010) to avoid adverse weather conditions. In the future, metabolic rates measured during field studies on bats need to be investigated and compared to real-time bat activity

during different seasons in order to determine if seasonal differences in metabolism are responsible for seasonal differences in bat activity on site or whether seasonal differences in bat activity are as a result of changing weather conditions. In addition, future studies on endogenous rhythms in metabolic rate during different lunar cycles should be investigated to determine if the effect of moon phase on bat activity may be as a result of a natural free-running ultradian (lunar) cycles.

The current stance on global climate change is that temperature is increasing (Hughes 2000) and currently there are trade-offs between generating energy from wind turbines to meet a growing demand for energy worldwide (and other renewable resources, IEA 2013) and the conservation of bats (Mendellin *et al.* 2000; Hooper *et al.* 2005, Bastian 2013). This study and many other studies show that bat activity increases with ambient air temperature (Erickson & West 2002; Christis & Simpson 2010; Hein *et al.* 2011), however many bats are physiologically constrained to certain habitats (Lovegrove 2000; Lovegrove 2003). Future research into how bats will respond to increasing mean temperature associated with global climate change is needed so that predictions can be made as to whether bat activity patterns and the distribution of bats will change.

As previously mentioned there are trade-offs between the conservation of bats through mitigation measures and ensuring power-generation when demand for electricity is highest in South Africa. Unfortunately, bat activity is highest when demand for electricity is highest (18:00-20:00). The next step, in terms of research, would be to test whether the peaks in energy demand coincide statistically with peaks in bat activity and whether this changes seasonally, with the demand for power supply increase in winter (Eskom 2013). In addition, we need to test the value of mitigation through curtailment or changing the cut-in speeds of turbine blades. Only then can the negative impacts associated with energy be properly mitigated for whilst still ensuring sufficient power supply when demand is highest.

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