The effects of artificial lighting on activity of Namib Desert bats (Mammalia: Chiroptera)

by

Angela Lesley Curtis

submitted in accordance with the requirements
for the degree of

MASTER OF SCIENCE

in the subject

NATURE CONSERVATION

at the

UNIVERSITY OF SOUTH AFRICA

SUPERVISOR: DR M KEITH

CO-SUPERVISOR: MR E SEAMARK

DR W M STRAUSS

JANUARY 2019

Declaration

UNISA | university of south africa

Declaration

I, Angela Curtis, hereby declare that the dissertation/thesis, which I hereby submit for the degree of Master of Science in Nature Conservation at the University of South Africa, is my own work and has not previously been submitted by me for a degree at this or any other institution.

I declare that the dissertation/thesis does not contain any written work presented by other persons whether written, pictures, graphs or data or any other information without acknowledging the source.

I declare that where words from a written source have been used the words have been paraphrased and referenced and where exact words from a source have been used the words have been placed inside quotation marks and referenced.

I declare that I have not copied and pasted any information from the internet, without specifically acknowledging the source and have inserted appropriate references to these sources in the reference section of the dissertation or thesis.

I declare that during my study I adhered to the Research Ethics Policy of the University of South Africa, received ethics approval for the duration of my study prior to the commencement of data gathering, and have not acted outside the approval conditions.

I declare that the content of my dissertation/thesis has been submitted through an electronic plagiarism detection program before the final submission for examination.

Student signature: Date: 18 January 2019

Acknowledgements

Table of Contents

List of figures

List of Tables

Abstract

The large-scale use of artificial light throughout the night has occurred in the last 100 years and continues to increase globally. Artificial light impacts many animal and plant taxa. The effects of artificial light on bats is species specific. The Namib Desert in Namibia is still relatively dark but subject to the same drivers of increasing development and urbanization that have increased the spread of artificial light globally. This study investigated the effects of the introduction of ultraviolet, yellow and white artificial light on the activity of bats in a rural environment with minimal development in the Namib Desert. Four sites, 100 m apart, had one light and one bat detector each. The fourth light was a dark control. Each site was sampled four times by each light type. Bat activity was recorded by the bat detectors. Eight bat species were recorded during the experiment. Activity increased for open air and clutter-edge foraging species analysed. Broadband white light caused the highest increases in activity followed by yellow light when compared with the dark control site. Ultraviolet light caused the lowest increases in activity contrary to expectations.

Key terms:

Artificial light; light wavelengths; bats; Namib Desert; bat activity; ultraviolet light; yellow light; white light; compact fluorescent light bulbs; undeveloped habitat

Isifinyezo esiqukethe umongo wocwaningo

Iminyaka engu 100 edlule ibonise ukusetshenziswa kakhulu kwezikhanyisi ezenziwe kubo bonke ubusuku. Le mvamisa iya ngokuya isetshenziswa kuwo wonke umhlaba, kanti futhi lokhu kuchaphazela izilwane eziningi kanye nezinhlobo zezitshalo Ugwadule lwe-Namib eNamibia lusemnyama, kodwa nalo lulandela imithelela eya ngokukhula kanye nokwenziwa kwamadolobha, osekubangele ukuthi kusetshenziswe izikhanyisi ezenziwayo zokukhanyisa kuwo wonke umhlaba. Imiphumela yalokhu kukhanyisa okwenziwa ngamabomu kwizinhlobo zamalulwane ezithile. Lolu cwaningo luphenyisisa ngomphumela wokusungulwa kwama-ultraviolet, izikhanyisi eziphuzi (yellow) kanye nezikhanyisi ezimhlophe kokwenziwa ngamalulwane endaweni yasemakhaya kanye nomphumela wakho kugwadule lwase-Namib. Kwafakelwa isikhanyisi esisodwa kanye ne-detector eyodwa yamalulwane kwizindawo ezine, ezihlukaniswe ngebanga lamamitha angu 100. Isikhanyisi sesine sasingesimnyama sokulawula. Indawo nendawo kwenziwa amasampuli amane ngayo ngohlobo lwesikhanyisi. Okwenziwa ngamalulwane kwakurekhodwa ngama-detector amalulwane. Izinhlobo zamalulwane eziyishagalombili zarekhodwa ngesikhathi se-experiment. Okwenziwa ngamalulwane endaweni evulekile, yezinhlobo zamalulwane kwahlaziywa ngokungezelelekile. Isikhanyisi esibanzi se-broadband esimhlophe sabangela ukwanda kakhulu kokwenziwa ngamalulwane, ngokulandelwa yisikhanyisi esiphuzi, uma kuqhathaniswa nesikhanyisi esimnyama esasetshenziselwa ukulawula. Kunalokho okwakulindelwe, isikhanyisi se-ultraviolet sabangela ukunyakaza okuncane ngokwenziwa ngamalulwane.

Khutsofatšo

Mengwaga ye 100 ya go feta go bile le koketšego ye kgolo ya tšhomišo ya seetša sa maitirelo bošego ka moka. Setlwaedi se se ata kudu lefaseng ka moka go feta pele, gomme se ama diphoofolo tše ntši le mehuta ya dimela. Leganata la Namib go la Namibia gabotse le sa ntše le swiswetše, eupša le ka fase ga dikgontšhi tša go oketša tlhabollo le toropofatšo tšeo di hlotšego koketšego tšhomišong ya seetša sa maitirelo lefaseng ka bophara. Dikhuetšo tša seetša sa maitirelo go memankgagane di fapana go ya ka mohuta. Nyakišišo ye e nyakišišitše dikhuetšo tša tsebagatšo ya seetša sa maitirelo sa go phadima, serolwane le se sešweu go modiro wa memankgagane ka tikologong ya nagaselegae ya go ba le tlhabollo ye nyane ka Leganateng la Namib. Seetša se setee le tithekethara e tee ya mankgagane di hlomilwe go le lengwe le le lengwe la mafelo a mane, a go arogantšhwa ka 100 m. Seetša sa bone se be se le taolo ya leswiswi. Lefelo le lengwe le le lengwe le dirilwe mohlala makga a mane ka mohuta wo mongwe le wo mongwe wa seetša. Modiro wa mankgagane e rekotilwe ka ditithekethara tša mankgagane. Mehuta ya mankgagane ye seswai e rekotilwe nakong ya eksperimente. Modiro wa mehuta ya sebakabakeng le ya go sela thobekgeng ye e sekasekilwego e oketšegile. Seetša se sešweu sa porotepente se hlotše dikoketšego tša modiro, sa latelwa ke seetša se se serolwane, ge se bapetšwa le lefelo la taolo ya leswiswi. Go fapana le ditetelo, seetša sa go phadima se hlotše dikoketšego tša fasefase modirong.

Chapter 1 Introduction and Literature Review

1.1 Introduction

Bats occur on all continents except Antarctica. Due to their diversity, distribution, abundance and high trophic level, bats are effective bio-indicators, reflecting changes in the ecosystems in which they occur (Jones *et al.*, 2009; Park, 2015).

The phenomenon of large scale artificial lighting throughout the night is a recent development in human history. The Northern Hemisphere has seen an unprecedented increase in artificial lighting throughout the night over a relatively short timeframe of 100 years (Gaston, Visser and Hölker, 2015; Falchi *et al.*, 2016). In contrast, the Southern Hemisphere, particularly sub-Saharan Africa, is still relatively dark (Falchi *et al.*, 2016).

Artificial lighting can have far reaching environmental repercussions on both diurnal and nocturnal organisms (Rich and Longcore, 2006). Bats are one such taxon of mammals found to be impacted by artificial lighting (Rydell, 2006; Stone, Jones and Harris, 2009; Stone, Harris and Jones, 2015; Rowse *et al.*, 2016).

Urbanization is increasing in Namibia at an unprecedented rate (Namibia Statistics Agency, 2011a) and an increase in urbanization is linked to increasing levels of artificial lighting (Kyba *et al.*, 2017).

This current study was designed to investigate changes in bat activity associated with different colours and wavelengths of commercially available, popular, energy-saving lighting in a minimally developed setting in the Central Namib Desert. These results could be used to anticipate potential changes caused by artificial lighting so that mitigating measures can be taken to reduce the impact.

1.2 An introduction to bats

Bats are nocturnal, flying mammals in the order Chiroptera. Chiroptera is the second most species-rich order of mammals contributing considerably towards worldwide biodiversity (Simmons, 2005).

As a diverse order, bats fill many ecological niches. About 70 percent of bat species are mainly insectivorous (Monadjem *et al.*, 2010). Other species are frugivorous, nectivorous or sanguinivorous and some are generalists. Fish, frogs, arachnids, rodents, birds and other bats have been found in the diets of various species of bats (Monadjem *et al.*, 2010; ACR, 2018).

1.2.1 Ecosystem services and the use of bats as bio-indicators

In addition, bats provide valuable ecosystem services. Insectivorous bats reduce arthropod crop pests, which could potentially limit the use of insecticides with economic benefits to farmers and health benefits to the general public (Cleveland *et al.*, 2006; Federico *et al.*, 2008; Kalka, Smith and Kalko, 2008; Williams-Guillén, Perfecto and Vandermeer, 2008). In South Africa, bats have been shown to reduce crop pests in macadamia orchards (Taylor *et al.*, 2013, 2017, 2018). Bat guano collected from underneath bat roosts can be used as a valuable organic fertilizer (Kunz *et al.*, 2011). Nectivorous and frugivorous bats pollinate plants and disperse seeds (Kunz *et al.*, 2011).

Changes in the activity, abundance and diversity of insectivorous bat populations can reflect natural or anthropogenic changes to the environment, affecting organisms over a wide range of trophic levels. Equally, changes in bat assemblage species composition and prey selection will cascade down to affect lower trophic levels (Jones *et al.*, 2009).

Most insectivorous bats echolocate (Altringham and Fenton, 2003). Echolocation calls can be recorded using ultrasonic recording equipment, which enables non-invasive monitoring of bat populations in sensitive areas. As a result bats could serve as bio-indicators of the status of a range of taxa in many ecosystems (Jones *et al.*, 2009).

1.2.2 Bat echolocation

Insectivorous bats use echolocation for prey detection (Altringham and Fenton, 2003). When using echolocation, a foraging insectivorous bat will produce a series of short, high frequency sounds in its larynx. The sounds are projected forward through the mouth or nose depending on the species (Monadjem *et al.*, 2010). Any object in the path of the soundwave will reflect an echo back to the listening bat. The bat is able to interpret the returning echoes into spatial information about its environment.

Echolocation calls are often species specific and related to habitat structure and foraging techniques (Monadjem *et al.*, 2010). Higher frequency sounds attenuate quickly in the atmosphere but provide more detailed spatial information in their echoes and are used in cluttered habitats. Lower frequency sounds travel much further but provide less detailed spatial information in their echoes and are generally used in open environments (Parsons and Szewczak, 2009).

An echolocation call consists of a series of individual sound pulses. Low duty cycle echolocation calls are characterised by long interpulse intervals in relation to pulse duration, while high duty cycle echolocation calls have short interpulse intervals and a relatively long pulse duration (Monadjem *et al.*, 2010). In addition, echolocation call pulses can be broadband, sweeping through a range of frequencies, or narrowband, limited to a narrow range of frequencies. Calls with broadband pulses are termed frequency modulated calls (FM) while calls with narrowband pulses are termed quasi constant frequency calls (QCF) or constant frequency calls (CF). Each pulse of an FM echolocation call usually starts at a higher frequency and sweeps down to a lower frequency. Quasi constant frequency calls are similar to frequency modulated calls but cover a far narrower range of frequencies and appear almost constant. Constant frequency calls have long pulses dominated by a single frequency (Monadjem *et al.*, 2010).

Echolocation calls of Southern African bats can be low duty cycle, frequency modulated or low duty cycle, constant frequency or low duty cycle, quasi constant frequency or high duty cycle, constant frequency (Monadjem *et al.*, 2010) (Figure 1.1).

A high duty cycle, constant frequency call
(*Rhinolophus damarensis*)

A low duty cycle, frequency modulated call
(*Sauromys petrophilus*) above a low duty cycle,
quasi constant frequency call.
(*Tadarida aegyptiaca*)

A low duty cycle, constant frequency call
(*Tadarida aegyptiaca*)
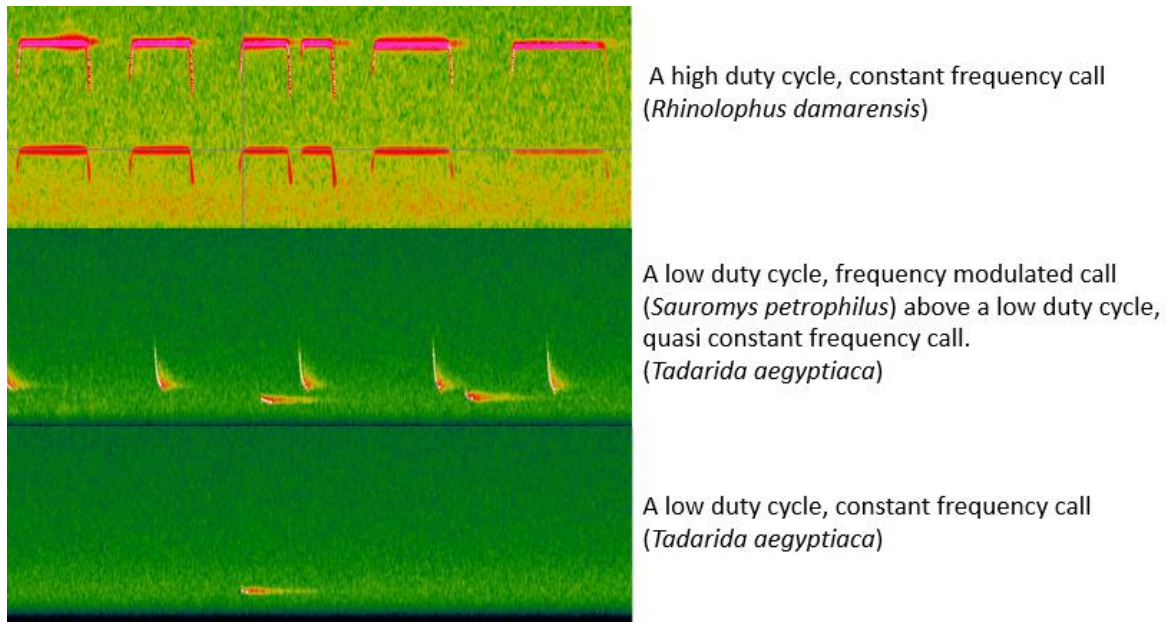
Figure 1.1: Four different types of echolocation calls. At the top is a pass from *Rhinolophus damarensis* (Damara horseshoe bat). It has a high duty, constant frequency echolocation call similar to those used by other bats in the families Rhinolophidae and Hipposideridae that forage in cluttered habitats. In the middle are examples of a low duty low frequency modulated call above a quasi constant frequency call below. These calls are made by two species, *Sauromys petrophilus* (Robert's flat-headed bat) and *Tadarida aegyptiaca* (Egyptian free-tailed bat) respectively, foraging in the open air bordered by vegetation. At the bottom is a low duty cycle constant frequency call made by *Tadarida aegyptiaca* (Egyptian free-tailed bat) flying in an open unobstructed environment.

1.2.3 Bat foraging guilds

Insectivorous bats will forage in a variety of habitats in different situations, however species specific, physical limitations result in the primary use of one habitat or foraging method over others. Bats are often placed into three different foraging guilds related to foraging method and habitat, echolocation call and wing morphology (Neuweiler, 1981; Aldridge and Rautenbach, 1987). These foraging guilds are closely linked to three different types of foraging habitat. These habitats are: open air, clutter-edge and cluttered (Figure 1.2).

Open air foraging habitat has no obstacles and bats often fly high above vegetation or geographical features. Clutter-edge foraging habitat is the open air along the

Figure 1.2: An example of the different foraging habitats available along the Kuiseb River in the Central Namib Desert, Namibia (20 October 2018).

edges of vegetation, buildings or geographical features. Cluttered foraging habitat refers to small clearings and paths surrounded by thick vegetation or other obstacles (Monadjem *et al.*, 2010).

The first bat foraging guild is the aerial hawking or open air foraging guild. Bats belonging to this guild forage in open air, usually above obstacles or clutter on the ground and catch prey on the wing. These bats are fast flying but not very "manoeuvrable". They have long, narrow wings and long, intense, low frequency, low duty cycle QCF or CF echolocation calls. *Tadarida aegyptiaca* (Egyptian free-tailed bat) and *Sauromys petrophilus* (Robert's flat-headed bat) are examples of bats in this guild (Monadjem *et al.*, 2010).

Bats belonging to the clutter-edge foraging guild tend to forage in the open along the edge of vegetation or prominent geographical features, sometimes close to the ground. These bats fly more slowly than the aerial hawking bats but are also more "manoeuvrable" with shorter, broader wings and low duty cycle FM echolocation calls of intermediate frequencies. *Neoromicia zuluensis* (Zulu serotine) and *Eptesicus hottentotus* (long-tailed serotine) are examples of bats in this guild (Monadjem *et al.*, 2010).

The third guild is the clutter feeding and gleaning guild. These bats forage in dense vegetation, catching flying insects on the wing or plucking stationary prey from the ground or surfaces of vegetation. Bats in this guild are highly "manoeuvrable" but slow flying. They have short broad wings and high duty cycle CF echolocation calls or low duty cycle FM echolocation calls at high frequencies. Some gleaning bats

5

have large ears and rely on prey created sound for detection rather than echolocation (Aldridge and Rautenbach, 1987; Jones and Rydell, 2003). *Rhinolophus damarensis* (Damara horseshoe bat) is an example of bat in this guild using a high duty cycle, constant frequency echolocation call, while *Nycteris thebaica* (Egyptian slit-faced bat) is an example of a bat using a low duty cycle, frequency modulated echolocation call (Monadjem *et al.*, 2010).

Bats in these different foraging guilds have been found to react differently to changes in the environment (Rydell, 1992a, 2006; Stone, Jones and Harris, 2009). One such change has been the global increase in artificial lighting (Jones *et al.*, 2009; Falchi *et al.*, 2016).

1.3 Global use of artificial lighting

For millennia humans have used fire for heating, cooking, security and illumination. Remnants of fat burning lamps have been found in Europe and dated as early as 40 000 BCE (Nordhaus, 1996). Wicked oil lamps and candles were developed during the Greco-Roman period around 700 BCE (Nordhaus, 1996) but there were very few advances in lighting until the industrial revolution in the 19th century (Nordhaus, 1996).

The industrial revolution saw the development of gas lighting followed quickly by the development of the incandescent electrical light bulb in the late 19th Century. The commercialization of the incandescent light bulb and supporting electrical grid in the United States of America in 1882, allowed the large-scale implementation of artificial lighting in factories, businesses and homes in developed areas (Nordhaus, 1996).

Currently it is estimated 20% of the world is under light polluted skies and that artificial lighting is increasing worldwide at an annual rate of 6%, in line with development and increased urbanization (Hölker, Moss, *et al.*, 2010; Falchi *et al.*, 2016). New lighting technology has lowered costs and increased access to lighting to a greater number of people (Hölker, Moss, *et al.*, 2010; Hölker, Wolter, *et al.*, 2010; Gaston *et al.*, 2013; Kyba *et al.*, 2017). Up until the 1960s light was provided by incandescent light bulbs. These were replaced by low pressure sodium (LPS) lights (Jackle, 2001). LPS lights emit a near monochromatic orange light under which colour distinction is difficult for humans. These lights were replaced in turn by

high pressure sodium lights which emit a slightly more broadband, yellow light and mercury vapour lights which emit a broadband white light (Jackle, 2001; Dusquene Light, 2013; Gaston *et al.*, 2013). A demand for more energy efficient lighting has led to the development of metal halide lights, a refinement of mercury vapour lights, also emitting a broadband white light, followed by compact fluorescent lamps (CFL) and light emitting diode (LED) lamps. Both CFL and LED lighting is highly energy efficient and can be custom made to emit different light spectra (Dusquene Light, 2013; Gaston *et al.*, 2013). CFL lighting tends to be used more for domestic use while LED lighting in slowly replacing older street lighting types. This is especially true in Europe where greenhouse gas emissions need to be reduced in line with the Kyoto Agreement (Gaston *et al.*, 2013).

An image of global distribution of artificial light at night was released by NASA in 2016 (Figure 1.3). The bright dots are areas with high densities of artificial lighting. Most of these are in the Northern Hemisphere in Europe, North America and Asia.

Figure 1.3: The Black Marble satellite map of the earth released by NASA during 2016 clearly indicating areas with most artificial lighting at night (available from https://svs.gsfc.nasa.gov/30876).

By contrast large areas in Africa, Australia and South America remain relatively dark. Increases in lighting are measured by comparing remote sensing images of a particular area over time (Hölker, Moss, *et al.*, 2010; Falchi *et al.*, 2016; Kyba *et al.*, 2017). Most countries in the Southern Hemisphere, particularly in Africa, recorded

increases in artificial lighting although there are countries where no data is available due to levels of light undetectable by remote sensing (Kyba *et al.*, 2017). There is a lack of research on the use or artificial lights in Africa (Coetzee, 2019), however most increases in lighting worldwide have been attributed to large scale urbanization (Kyba *et al.*, 2017; Coetzee, 2019). The global average annual increase in rate of urbanisation is 2.0% while in Africa the regional average increase is 4.1%, the highest worldwide (Saghir and Santora, 2018).
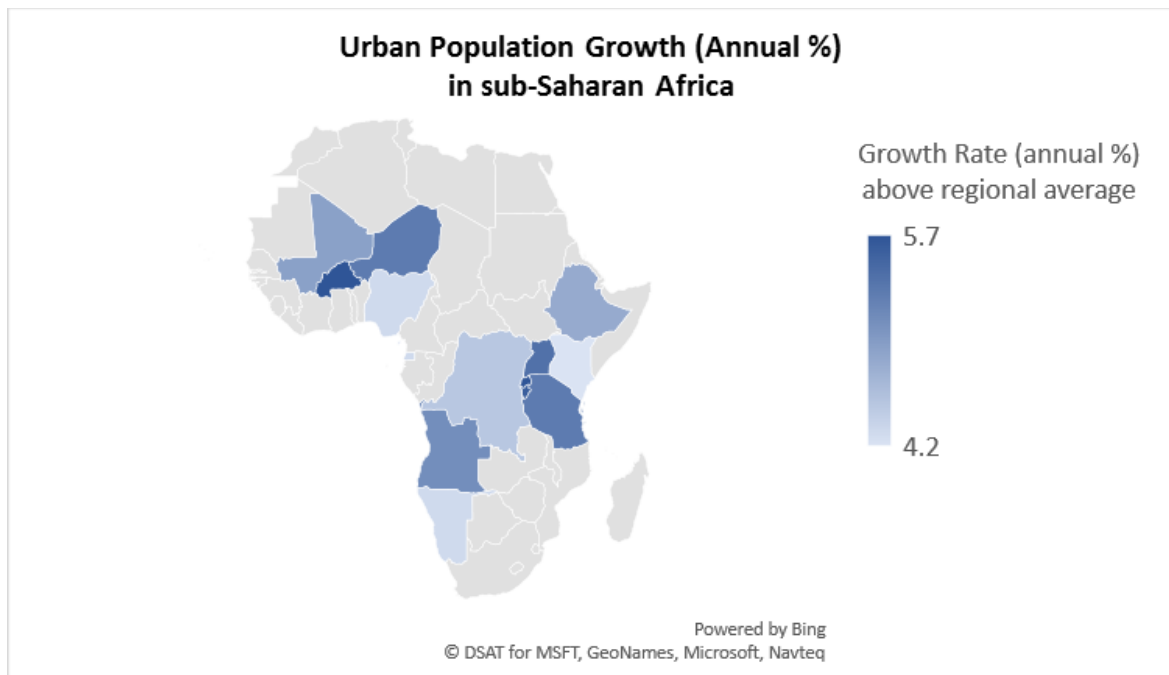
Figure 1.4: Annual percentage urbanisation in sub-Saharan Africa produced by the World Bank in 2017 (available from https://www.csis.org/analysis/urbanization-sub-saharan-africa). The map shows African countries with an annual urbanisation rate above the regional average of 4.1%.

With such high rates of urbanisation and the link between urbanisation and increase in artificial lighting, it is likely that Africa will experience large increases in light pollution in the near future (Coetzee, 2019).

1.4 Effects of artificial lighting on living organisms

The earth has been exposed to natural daily, monthly and seasonal cycles of light since the beginning of its existence. Many taxa have evolved to take advantage of these cycles for reproduction, migration, camouflage, the timing of natural processes, avoidance of competition and utilisation of specific food sources, all of

which can be disrupted by artificial lighting (Beier, 2006; Gauthreaux and Belser, 2006; Salmon, 2006; van Langevelde *et al.*, 2018).

Artificial lighting can affect living organisms through two pathways. The first is the direct effect from individual point sources of light and the second is an indirect effect through skyglow (Figure 1.5). Skyglow is caused by light from multiple light sources from urban areas being reflected back to earth by atmospheric particles causing a generalized increase in ambient light (Kyba *et al.*, 2011, 2017). When caused by large cities, skyglow can have effects at distances of over 100 kilometres from its source (Falchi *et al.*, 2016).

Figure 1.5: Skyglow over the town of Swakopmund on the Namibian west coast. The skyglow is caused by many point sources of light from individual streetlights reflected back to the earth by water particles in the low lying fog (17 October 2018).

Artificial light can benefit some species, be detrimental to others or have no noticeable effect depending on the organism involved (Gaston, Visser and Hölker, 2015). Artificial lighting has come with undeniable benefits for humans in increased security, lower accident rates (Plainis, Murray and Pallikaris, 2006) and increased

productivity due to an extended day. Other taxa benefit as well. Worldwide many species of geckos, bats, birds, spiders and beetles benefit from foraging on prey aggregations attracted to artificial lighting. Examples are: geckos; *Chondrodactylus bibronii* (Bibron's thick-toed gecko) and *Chondrodactylus turneri* (Turner's thick-toed gecko) in Namibia (Perry and Fisher, 2006), bats; *Tadarida aegyptiaca* (Egyptian free-tailed bat), and *Neoromicia capensis* (Cape serotine) in South Africa (Minnaar *et al.*, 2015; Schoeman, 2016), birds; *Sayornis phoebe* (Eastern phoebe) and *Vermivora ruficapilla* (Nashville warbler) in the USA (Lebbin *et al.*, 2007), spiders; *Eriophora biapicata* (Australian garden orb-web spiders) in Australia (Willmott *et al.*, 2019) and beetles; *Silpha* sp. (carrion beetle) in Germany (Manfrin *et al.*, 2017).

These animals may in turn be more vulnerable to predation by other predators (Jones and Rydell, 2003; Perry and Fisher, 2006; Rydell, 2006). For example a *Boaedon fuliginosus* (brown house snake) was recorded preying on a gecko preying on arthropods at an artificial light (Cunningham, 2002).

Exploitation of prey at light sources could increase reproductive success of predators as seen in urban populations of *Vespertilio murinus* (parti-coloured bat) (Zhigalin and Moskvitina, 2017) due to increased availability of high quality nutrition, which in turn could have a negative effect on population numbers of the prey species at lower trophic levels. As an example, insectivorous bats can consume between 25% and 70% of their body weight in one night depending on season and energy requirements (Kunz *et al.*, 2011). It has been estimated that a single colony of one million *Tadarida brasiliensis* (Brazilian free-tailed bats) could consume 8.4 tons of insects in one night. Most insectivorous bat species are opportunistic predators (Kunz *et al.*, 2011) . Minnaar *et al.* (2015) found that the diet of *Neoromicia capensis* (Cape serotine) included significantly more lepidopterans under lit conditions than under dark conditions and it is reasonable to assume that this will apply to other bat species foraging at lights. If prey at lights is opportunistically selected by foraging bats over other prey sources the large volume of arthropods consumed will affect the abundance of species attracted to lights.

A detrimental effect of artificial lighting is disruption of circadian rhythms due to altered periods of light and darkness. Light of sufficient intensity and duration reaching the retina acts as a zeitgeber for the entrainment circadian rhythms for all

vertebrates (Beier, 2006). Circadian rhythms control the timing of the release of a variety of hormones that affect sleep, stress, metabolism and reproduction among other things (Beier, 2006; Gaston and Bennie, 2014; Ouyang *et al.*, 2015; Gaston *et al.*, 2017; Ouyang, Davies and Dominoni, 2018) . Blind humans, with retinas unable to react to light as a zeitgeber, have abnormal sleep/wake cycles due to disruptions in melatonin secretion (Sack *et al.*, 1992). Human exposure to extended periods of artificial light has been linked to obesity in children (Pattinson *et al.*, 2016) and breast cancer in female shift workers (Stevens, 2006), thought to be caused by disrupted patterns of hormone release (Dominoni, Borniger and Nelson, 2016; Ouyang, Davies and Dominoni, 2018).

Disruptions in circadian rhythms due to extended exposure to artificial light have been shown in various free-living organisms as well and may be widespread across many taxa. *Turdus merula* (blackbird) reach reproductive maturity 19 days earlier in lit conditions than in dark conditions (Dominoni, Partecke and Partecke, 2015). *Parus major* (great tit) show disrupted sleep patterns in lit areas (Raap, Pinxten and Eens, 2015). *Perca fluviatilus* (European perch) show reduced levels of melatonin even when exposed to low levels of artificial lighting (Brüning *et al.*, 2015, 2016).

Reduced periods of darkness caused by artificial light at night can have other negative consequences. Artificial light can make nocturnal animals more visible to predators, fragment or reduce habitat, delay emergence times and cause roost or habitat abandonment for light aversive animals (Gaston *et al.*, 2013). *Tringa totanus* (common redshank) use increased visibility of prey under artificial lighting to increase capture success (Dwyer *et al.*, 2013). Some light aversive animals will avoid lit areas which act like barriers to movement and fragment habitat (Hale *et al.*, 2015; Azam *et al.*, 2018). The introduction of a row of lights disrupted commuting paths of *Rhinolophus hipposideros* (lesser horseshoe bat) and significantly delayed roost emergence time (Stone, Jones and Harris, 2009). The indiscriminate use of artificial lighting can even result in roost abandonment, as seen in Sweden where churches with *Plecotus auritus* (brown long-eared bats) roosts reduced from 61% to 38% following the installation of aesthetic night lighting (Rydell, Eklof and Sanchez-Navarro, 2017).

Some animals are attracted to lights. Many phototaxic flying insects are attracted to point sources of artificial light where they sit immobilized, fly around the light source until dying of exhaustion, are eaten by predators or burned by the hot bulb. If not killed at the light source their chance of survival may be reduced due to wasted foraging time or inappropriate reproductive behaviour triggered by the light (Eisenbeis, 2006; Eisenbeiss and Hanel, 2009; Barghini and De Medeiros, 2012; Degen *et al.*, 2016).

Some seabirds seem to be phototaxic. It is thought that they may be using lights for navigation (Montevecchi, 2006; Rodríguez *et al.*, 2017). Seabirds have been found circling bright lights until exhausted or colliding with solid structures. Juvenile petrels and shearwaters are often found grounded near sources of artificial light (Rodríguez *et al.*, 2017).

Adult female turtles and turtle hatchlings use the reflection of natural light on the ocean for orientation towards the water. On beaches with artificial lighting they have been found disorientated and moving inland towards the lights instead of towards the sea (Witherington and Bjorndal, 1991; Salmon, 2006).

Different animal taxa do not respond equally to all wavelengths of light (Davies *et al.*, 2013). Insects are significantly more attracted to light with shorter wavelengths towards the ultraviolet (UV) side of the spectrum (Eisenbeiss and Hanel, 2009; Barghini and De Medeiros, 2012; Justice and Justice, 2016; Wakefield *et al.*, 2016, 2018) while birds seem more affected by light with longer wavelengths towards the red side of the spectrum (Gauthreaux and Belser, 2006; Ouyang *et al.*, 2015). Mammals are affected most by medium to long wavelengths of light (Davies *et al.*, 2013). With new lighting technologies, white light has become more popular in urban areas as it is a combination of many wavelengths. This enables accurate colour perception in humans but affects the largest range of taxa due to its broadband nature (Davies *et al.*, 2013; Gaston *et al.*, 2013).

Most studies of the effects of artificial lighting on bats and the insects they prey upon, have taken place around streetlights in the Northern Hemisphere (Rydell, 1992b, 2006; Blake *et al.*, 1994; Acharya and Fenton, 1999; Jones and Rydell, 2003; Avila-Flores and Fenton, 2005; Stone, Jones and Harris, 2009, 2012; Stone *et al.*, 2015; Azam *et al.*, 2015, 2016; Russo and Ancillotto, 2015; Wakefield *et al.*,

2016; Rowse, Harris and Jones, 2016, 2018; Russo *et al.*, 2017; Voigt *et al.*, 2017; Lewanzik and Voigt, 2017). Traditionally, streetlights have been mercury vapour (MV) lamps, which emit a broadband white light with a large proportion in the UV spectrum (Lewanzik and Voigt, 2017). These have been replaced by low pressure sodium (LPS) lamps and high pressure sodium lamps (HPS) in many areas. LPS lamps emit a narrowband, almost monochromatic yellow/orange light with no ultraviolet component and HPS lamps emit a more broadband yellow light composed primarily of longer wavelengths of light with a small component of shorter wavelength light (Davies *et al.*, 2013). LPS and HPS streetlamps, in turn, are currently being replaced by metal halide (MH) and light emitting diode (LED) lamps (Stone, Harris and Jones, 2015; Lewanzik and Voigt, 2017). Both of these lamp types emit a broadband white light encompassing a range of wavelengths including a short wavelength component. MH lamps emit a larger UV component than LED lamps (Davies *et al.*, 2013; Gaston *et al.*, 2013; Stone *et al.*, 2015). Compact fluorescent (CFL) lamps have gained in popularity for private use due to energy efficiency and variety of available colours (Gaston *et al.*, 2013; Justice and Justice, 2016).

Responses of bats to lights are species specific but generally associated with their foraging guild. Insects are most strongly attracted to lamps that emit light with a large component of shorter wavelengths (Eisenbeis, 2006; Barghini and De Medeiros, 2012; Wakefield *et al.*, 2016, 2018). Species of light tolerant, insectivorous bats are attracted to aggregations of insects around these lamps, benefit from an abundant food source and increase in numbers like *Pipestrellus kuhlii* (Kuhl's pipistrelle) in southern Europe and *Vespertilio murinus* (parti-coloured bat) in Russia (Ancillotto *et al.*, 2016; Zhigalin and Moskvitina, 2017). These tend to be bats from the aerial hawking and clutter-edge foraging guilds used to hunting in open environments like *Eumops perotis* (western mastiff bat) in Mexico and *Pipestrellus pipestrellus* (common pipistrelle) in Europe (Blake *et al.*, 1994; Jones and Rydell, 2003; Avila-Flores and Fenton, 2005; Rydell, 2006; Schoeman, 2016).

In contrast, light avoiding bats are usually from the clutter feeding and gleaning foraging guild. These bat species are accustomed to foraging in darkness in dense vegetation like *Rhinolophus hipposideros* (lesser horseshoe bat) (Stone, Jones and Harris, 2009; Stone, Harris and Jones, 2015). They are slow flying and may avoid

artificial lighting to reduce chances of detection by predators (Stone, Jones and Harris, 2009).

The attraction of light tolerant bats to the various types of streetlights mirrors the attraction of insects to these lights, which in turn is dependent on the amount of short wavelength light emitted (Rydell, 2006; Wakefield *et al.*, 2015a, 2018). Based on the decreasing amount of short wavelength light that is emitted, MV lamps are most attractive to insects and therefore foraging bats, followed by MH. The attraction of insects to UV light to create prey patches to attract bats has been exploited for research purposes in a forest in Australia (Adams, Law and French, 2005) and in a desert in the United States of America (Bell, 1980).

The opposite effect occurs for light avoiding bat species. Artificial lighting causes delayed roost emergence, roost abandonment, altered commuting routes, reduced foraging time and fragmented foraging ranges for these bats as illuminated areas are avoided (Kuijper *et al.*, 2008; Stone, Jones and Harris, 2009, 2012; Threlfall, Law and Banks, 2013; Froidevaux *et al.*, 2017; Rydell, Eklof and Sanchez-Navarro, 2017). In addition, abundance of prey species in dark foraging areas bordering illuminated areas is reduced by what Eisenbeis (2006) terms "the vacuum cleaner effect". By "the vacuum cleaner effect" Eisenbeis (2006) refers to the fact that insects in dark areas are seemingly "sucked" out of the dark habitat, towards the lights. This could result in longer foraging flights and increased energy expenditure by these light avoidant bat species (Stone, Jones and Harris, 2009).

The reaction of bats to different wavelengths of light is also species specific and generally related to the foraging guild although there are some exceptions. Greater tolerance for long wavelength red lighting has recently be reported in some *Plecotus* and *Myotis* species in the clutter feeding guild in the Netherlands (Spoelstra *et al.*, 2017). These species still avoided broadband white lighting and shorter wavelength green lighting like other bats in the same foraging guild (Spoelstra *et al.*, 2017). In contrast, two species of *Rhinolophus*, a genus or clutter feeding bats adversely impacted by lights in Europe, have been observed foraging around lights in Australia (Rydell, 2006).

In addition to causing insects to aggregate around lights, exposure to light interferes with the predator avoidance behaviour of moths, causing them to be more easily

caught by predatory bats (Acharya and Fenton, 1999; Minnaar *et al.*, 2015; Wakefield *et al.*, 2015b). A comparison of the diet of *Neoromicia capensis* (Cape serotine), foraging in darkness and around streetlights, has found a larger proportion of phototaxic insects included in the diet under the lit conditions (Minnaar *et al.*, 2015). Many individuals of multiple bat species opportunistically preying on larger numbers of phototaxic insects at lights could have far reaching consequences at lower trophic levels in the ecosystem as many of these insects are nocturnal pollinators (van Langevelde *et al.*, 2011, 2018; Bennie *et al.*, 2016; Knop *et al.*, 2017).

Most studies on the effects of light pollution on bats have occurred in the Northern Hemisphere following large-scale illumination and the resultant environmental changes that accompany it (Lacoeuilhe *et al.*, 2014). Little work has been done on the effects of artificial lighting on bats in Africa. The researcher is aware of only two published studies from South Africa. The first study took place in the Rietvlei Nature Reserve in Gauteng (Minnaar *et al.*, 2015). Dietary analysis of *Neoromicia capensis* (Cape serotine) found that under lighted conditions the bulk of the diet consisted of lepidopterans compared to dark conditions, where the bulk of the diet consisted of coleopterans; *Neoromicia capensis* (Cape serotine) therefore feeds opportunistically on phototaxic insects at white lights. In addition this study found that eared moth defences in response to bat echolocation calls were compromised under white lighting, increasing their risk of predation (Minnaar *et al.*, 2015). The second study investigated the opportunistic exploitation of insects attracted to stadium lights by bats at stadiums in urban areas in central KwaZulu-Natal (Schoeman, 2016). As in Europe, the aerial hawking bat species and clutter-edge foraging bat species, which were tolerant of both light and urbanization, benefitted most from stadium lights. The slow flying clutter feeding bat, *Rhinolophus simulator* (bushveld horseshoe bat)*, was only recorded once in a dark stadium. Besides the avoidance of lights this may also be due to the fact that this species forages in a small home range in cluttered habitats and roosts in caves, both of which are limited in the area (Schoeman, 2016).

Due to the restricted nature of resources in deserts, desert organisms could be more vulnerable to both natural and anthropogenic changes to the environment than organisms in more mesic areas (Bell, 1980; Polak *et al.*, 2011). Large areas of the

Namib Desert in Namibia remain relatively dark. It is unknown how bats in these areas will respond to the introduction of artificial light. This knowledge could be used to limit the impact of artificial lighting accompanying development in the desert.

1.4 Development and the use of artificial lighting in the Central Namib Desert

The Namib Desert is a long, narrow desert lying on the west coast of Southern Africa. The Namib Desert is approximately 2 000 km long, running parallel to the coast from southern Angola to northern South Africa with its bulk lying in Namibia. It extends eastwards, 140 km at its widest, to the Great Western Escarpment (Lancaster, Lancaster and Seely, 1984; Warren-Rhodes *et al.*, 2013). There are five coastal towns. The largest two, Swakopmund and Walvis Bay, fall within the Central Namib Desert (Figure 1.5).

Figure 1.6: Southern Africa showing Namibia and the Namib Desert running along the west coast (28 March 2018, Google Earth).

While Namibia currently appears dark at night (Figure 1.3), it is subject to the same factors that facilitated the spread of artificial light in the Northern Hemisphere. Urbanisation in Namibia increased by 11.5% between 2007 and 2017 with the largest increases seen in Windhoek and Walvis Bay (Ottolenghi and Watson, 2010; Plecher, 2019). This trend is expected to increase as a rising population and poor economic circumstances compel people to move to towns and cities to look for work (Namibia Statistics Agency, 2011a). Development is increasing in the mining (Namibian Government, 2016; The Namibian, 2016), industrial (Walvis Bay Corridor Group, 2018), tourism (New Era, 2014, 2017) and real estate (New Era, 2016) sectors.

1.5 Bats in the Central Namib Desert

The coastal towns of Swakopmund and Walvis Bay are surrounded by two national parks, the Dorob National Park and the Namib-Naukluft National Park. These national parks protect some pristine desert areas which include rare endemic plants like *Welwitschia mirabilis* (welwitschia), endemic animals like *Onymacris ungucularis* (fog basking beetle) and the primary nesting areas of the vulnerable *Sternula balaenarum* (Damara tern) as well as extensive lichen fields (Seely and Pallet, 2012). The Dorob contains two Ramsar wetland sites and the Namib Sand Sea, a world heritage site, is housed entirely within the Namib-Naukluft National Park.

Desert ecosystems are fragile and extremely sensitive to anthropogenic disturbance (Seely and Pallet, 2012). This area was selected for the study because of its proximity to two towns undergoing a high rate of urbanization, because there is still very little light pollution in many areas and because very little is known about the bats in this area.

Twenty two species of bats reportedly occur in the Namib Desert (Table 1.1). All of these species are listed by the IUCN as Least Concern with the exception of *Eidolon helvum* (straw-coloured fruit bat) and *Cistugo seabrae* (Angolan wing-gland bat), which are listed as Near Threatened, and *Rhinolophus denti* (Dent's horseshoe bat), listed as Data Deficient (IUCN, 2016). Taylor (2000) questions the IUCN assessments of most species listed as Least Concern due to the limited data available. It may be more appropriate for some species, such as *Laephotis*

namibensis (Namibian long-eared bat), first described at Gobabeb and only known from a few museum specimens, to be listed as Data Deficient (Monadjem *et al.*, 2010). With the exception of *Eidolon helvum* (straw-coloured fruit bat) all these species are insectivorous (ACR, 2018).

Two species, *Sauromys petrophilus* (Robert's flat-headed bat) and *Neoromicia zuluensis* (Zulu serotine), are adapted to extremely arid conditions and able to survive long periods on water from of prey species alone (Roer, 1971). This may be true for other desert species as well.

Due to the lack research on bats in the Namib, the sensitive area and projected future large scale urbanization and light pollution it was decided to investigate the potential impacts of the introduction of artificial on the activity of bats in a relatively unaffected area of the Namib.

1.6 Research questions and hypotheses

The primary research question is: How does short-term artificial lighting affect the activity of the bat species in the Namib Desert?

Secondary research questions and associated hypotheses are:

1. Is the overall short-term activity of bats affected by different colours of artificial lighting?

The null hypothesis (H_0) is: Different colours of artificial lighting have no effect on overall bat activity.

The test hypothesis (H_1) is: Different colours of artificial lighting either increase or decrease overall bat activity.

2. Do different colours of artificial lighting cause species specific differences in activity?

The null hypothesis (H_0) is: Different colours of artificial lighting do not cause species specific differences in activity.

The test hypothesis (H_1) is: Different colours of artificial light cause species specific differences in activity.

3. Does bat species richness change between different colours of artificial light?

The null hypothesis (H_0) is: Bat species richness is unchanged by different colours of artificial light.

The test hypothesis (H_1) is: Bat species richness differs between different colours of artificial lighting.

Table 1.1: Summary of bat species reported to occur in the Central Namib Desert, Namibia (table composed using data obtained from ACR, 2018; Monadjem et al., 2010).

Family	Species	Common Name
Pteropodidae	*Eidolon helvum* (Kerr, 1792)	Straw-coloured fruit bat
Hipposideridae	*Hipposideros caffer* (Sundervall 1846)	Sundervall's leaf-nosed bat
	Macronycteris vittatus (Peters 1852)	Striped leaf-nosed bat
Rhinolophidae	*Rhinolophus damarensis* Roberts 1946	Damara horseshoe bat
	Rhinolophus clivosus Cretzschmar 1828	Geoffroy's horseshoe bat
	Rhinolophus denti Thomas 1904	Dent's horseshoe bat
	Rhinolophus fumigatus Rüppell 1842	Ruppell's horseshoe bat
Emballonuridae	*Taphozous mauritianus* E. Geoffroy Saint-Hilaire 1818	Mauritian tomb bat
Nycteridae	*Nycteris thebaica* E. Geoffroy St.-Hilaire, 1818	Egyptian slit-faced bat
Molossidae	*Sauromys petrophilus* (Roberts, 1917)	Robert's flat-headed bat
	Tadarida aegyptiaca (E. Geoffroy St-Hilaire 1818)	Egyptian free-tailed bat
Miniopteridae	*Miniopterus natalensis* (A. Smith, 1833)	Natal long-fingered bat
Cistugonidae	*Cistugo seabrae* Thomas 1912	Angolan wing-gland bat
Vespertilionidae	*Eptesicus hottentotus* (A. Smith, 1833)	Long-tailed serotine
	Laephotis namibensis Setzer, 1971	Namibian long-eared bat
	Neoromicia capensis (A. Smith, 1829)	Cape serotine
	Neoromicia nana (Peters, 1852)	Banana bat
	Neoromicia zuluensis (Roberts, 1924)	Zulu serotine
	Mimetillus thomasi Hinton 1920	Thomas's flat-headed bat
	Nycticeinops schliffeni (Peters 1859)	Schlieffen's twilight bat
	Pipistrellus rueppellii (Fisher 1829)	Ruppell's pipistrelle
	Pipistrellus rusticus (Tomes 1861)	Rusty pipistrelle
	Scotophilus dinganii (A. Smith 1833)	Yellow-bellied house bat

Chapter 2 Methodology

2.1 Introduction

An experiment was devised to investigate activity changes of bat species following the introduction of three different colours of commonly used energy-saver compact fluorescent lighting. This chapter opens with a brief overview of the study location followed by the description of the four sites used in the experiment. This leads to a detailed description of the experiment, equipment used, and deployment at each site. A description of the data format and the analyses performed is also provided. The chapter closes with a reference to the ethics clearance and research permits.

2.2 The Study Area

The research took place in Namibia along the Kuiseb River near the Gobabeb Namib Research Institute (Gobabeb) (23° 33.712' S; 015° 02.468' E) in the Namib-Naukluft National Park in Namibia (Figure 2.1). The Namib Desert borders the Atlantic Ocean and runs the entire length of Namibia extending into Angola in the north and South Africa in the south. An almost 50 000 km^2 portion of the Central Namib Desert has been incorporated into the Namib-Naukluft National Park (Figure 2.2), making it the largest conservation area in Namibia and third largest in Africa (Seely and Pallet, 2012). In addition, an area of 30 777 km^2 surrounded by a 8 995 km^2 buffer zone within the Namib-Naukluft National Park incorporating the Namib Sand Sea was designated a World Heritage Site by the United Nations Educational, Scientific and Cultural Organisation (UNESCO) in 2013 (UNESCO, 2013) The study site in the Kuiseb River falls within the buffer zone.

There are three small tourism areas within the national park but most of the national park is inaccessible to tourists and uninhabited with the exception of the park staff, researchers and a small population of 300 traditional Topnaar people living along the lower Kuiseb River (Seely and Pallet, 2012).

Figure 2.1: A satellite image of Namibia with the central area demarcated by the red rectangle expanded below to show the study site at Gobabeb during both the day (a) (Google Earth, 2018) and the night (b) (NASA Black Marble, 2016).

Figure 2.2: The Namib-Naukluft National Park in Namibia with the position of Gobabeb within the park. Main roads are presented on the map by alpha numeric, and major cities/towns (Ast Reisen, no date)

Gobabeb is situated on the northern bank of the Kuiseb River, 64 km east of the Atlantic Ocean (Figure 2.2). The Kuiseb River abruptly divides the sand dunes of the Namib Sand Sea in the South from the gravel plains in the North (Seely and Pallet, 2012). The flow of the Kuiseb River is highly variable and dependent on large rainfall in its catchment area in the interior. For most of the year it is a dry riverbed

(Jacobson, Jacobson and Seely, 1995). The Namib Desert is a hyper-arid desert with an annual rainfall at Gobabeb of 25 mm (Eckardt *et al.*, 2013). Fog occurs more frequently than rainfall due to the cold Benguela Current flowing up the West coast of Africa and prevailing South Westerly winds (Shanyengana *et al.*, 2002). Condensed water from fog is the most reliable and important source of water for many desert organisms (Seely and Pallet, 2012).

Gobabeb was selected as the study area due to its remote location within a national park in a desert and its available infrastructure. It was established as a research station in 1962 and has the infrastructure to run sophisticated scientific equipment while at the same time having less than 20 permanent staff with minimal impact on the surrounding environment.

2.3 Experimental Design

Four sites, 100 m apart, were selected along the Kuiseb River in the dry riverbed. The distance of 100 m between sites was selected to ensure that lights were independent of each other.

There are few studies quantifying distance of attraction and avoidance of lights by insects and bats however, Robinson and Robinson (1950), as cited by Frank (2006), found that the number of lepidopterans attracted to individual lights in a row of streetlights decreased as the distance separating lights dropped below 46 m. Avoidance of streetlights by *Myotis* spp. of bats in Paris was found up to 50 m away from the lights while attraction of *Pipestrellus* spp. to lights was significant at distances up to 10 m (Azam *et al.*, 2018). Vertical height of illumination was found more disruptive than horizontal illumination (Azam *et al.*, 2018). These distances were used as guidelines for distances between experimental lights.

While the height of the streetlights was not mentioned in either study, streetlights are set at standard heights depending on the width of the road to be illuminated starting ,with the lowest at 5 m (Razorlux Lighting, 2019). The higher the streetlight the larger the area illuminated (Razorlux Lighting, 2019). The spotlights used in the experiment were set at a height of 2 m so distances found at streetlights and used as guidelines are likely to be overestimations and thus have a greater margin for error. In addition the spotlights produced directed beams of light, which were

orientated perpendicular to the row of lights, to further reduce possible light interference. The sites were selected on the river bank close to the edge of vegetation to maximise the detection for bat species from all three foraging guilds.

The sites were designated Site 1, Site 2, Site 3 and Site 4 (Figure 2.3).
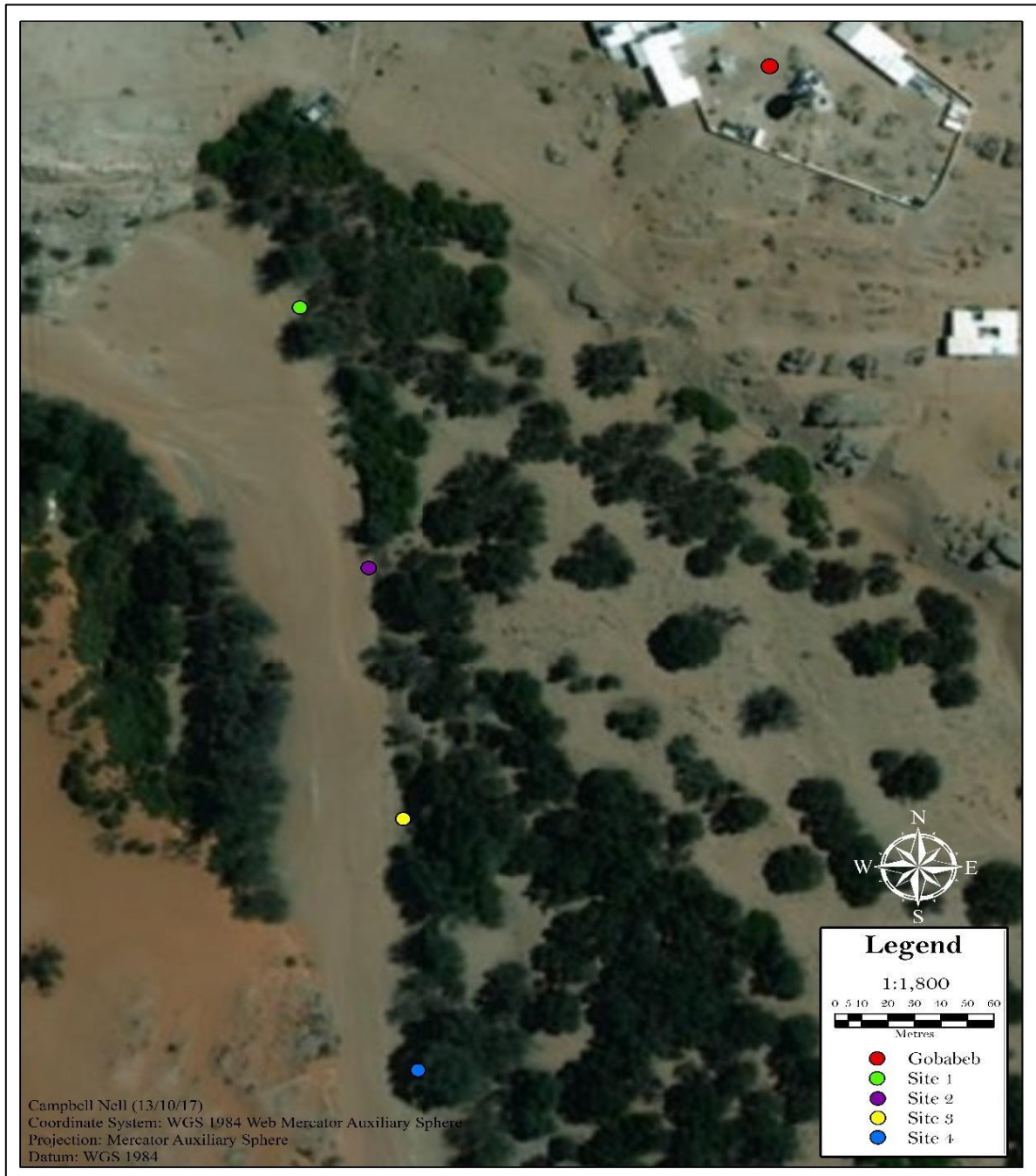
Figure 2.3: An aerial view of the Kuiseb River indicating the position of the 4 sites in relation to Gobabeb in the Central Namib Desert of Namibia.

At each site a spotlight was erected on a pole at a height of 2 m so that the beam was perpendicular to both the ground and the line of lights (Figure 2.4). A bat detector (SM4 BAT, Wildlife Acoustics Inc, Concord, Massachusetts, USA) was also placed at each site at the height of 2 m and a distance of 0.5 m from the light, with the microphone perpendicular to the direction of the light beam. The copper poles holding the lights were secured to a 0.6 m metal stake sunk 0.3 m into the ground.

Figure 2.4: Typical site setup along the Kuiseb River, Gobabeb, Namibia. The spotlight and bat detector microphone are at a height of 2 m. The microphone is 0.5 m away from the spotlight.

The copper poles holding the bat detectors were mounted on custom-made aluminium stands to provide support for the suspended bat detectors (see Figure 2.4 for light and detector set-up). At Site 4 a Hygrochron iButton temperature/humidity sensor (Model DS 1923; Maxim Integrated, San Jose, CA, USA), housed in an open plastic container, was suspended from the pole bearing the bat detector (Figure 2.5).

Figure 2.5: A hygrochron iButton temperature/humidity sensor suspended in an open plastic container. Photo (a) shows the suspended container from the side while (b) shows the hygrochron suspended within the container. Care was taken to ensure that the humidity sensor was not obstructed (20 September 2017).

The hygrochron iButton temperature sensor was calibrated against a high-accuracy thermometer (Quat, Heraeus, Germany) in a stable water bath while the relative humidity sensor was calibrated in the laboratory using reference saturated salt solutions.

Each spotlight was fitted with two bulbs of the same type and colour. A different colour of compact fluorescent light bulb was used for each of three individual spotlights. These were, white light (Osram 11201 m 60W compact fluorescent bulbs), ultra-violet light (Beamz 160.023 UV Black Light 25W E27 compact fluorescent bulbs) and yellow light (Eurolux G433Y 12W yellow compact fluorescent bulbs). An empty spotlight casing served as a control.

A light bulb of a particular colour emits a unique combination of wavelengths rather than a single wavelength (Gaston *et al.*, 2013). It is critical to know the combination of wavelengths emitted by each colour bulb when investigating the effects of the different light colours on the activity of bats. A light emission spectrum for each compact fluorescent light colour used in the experiment (Figure 2.6) was therefore measured in a darkroom in the Gobabeb laboratory using an Avantes AvaSpec – ULS 3648-USB2-RS portable spectrometer.

The UV light used in the experiment emitted light at two short wavelengths, 405.07 nm and 436.19 nm (Fig. 2.6). Strictly speaking this is in the near ultraviolet range rather than the ultraviolet range, which has wavelengths below 400 nm (Gaston *et al.*, 2013), however the light is sold as an ultraviolet light and will be referred to as such during the study.

The different lights were rotated around the four different sites (Figure 2.3) throughout the study period from the 11th September 2017 until the 24th of February 2018 as described in the following paragraphs. Details of the equipment used for this study are summarised in Table 2.1 while the bat detector settings are summarised in Table 2.2. Power from the Gobabeb hybrid power system was used to power the lights.

The white spotlight started the experiment at Site 1, the ultraviolet spotlight at Site 2, the yellow spotlight at Site 3 and the control set-up, with no light-bulb, at Site 4. The bat detectors at each site recorded bat echolocation calls throughout the night for 10 nights; five nights of darkness followed by five nights of light. The five nights under lighted conditions was termed one sample session. Five nights was chosen as the period for lighted conditions to allow for the possibility of a lag effect following the introduction of light. The five nights of darkness between sample sessions were to allow the environment to rest between sessions. Echolocation calls were recorded during the dark phases to establish a baseline of activity at each site without artificial lighting over the course of the experiment.

Following each five-night sample session, each light-type was moved one site to the South while the light at the last site (Site 4) was returned to the top (Site 1). Another 10 nights, five of darkness and five under lighted conditions were recorded. This process was repeated 16 times over a period of 160 nights.
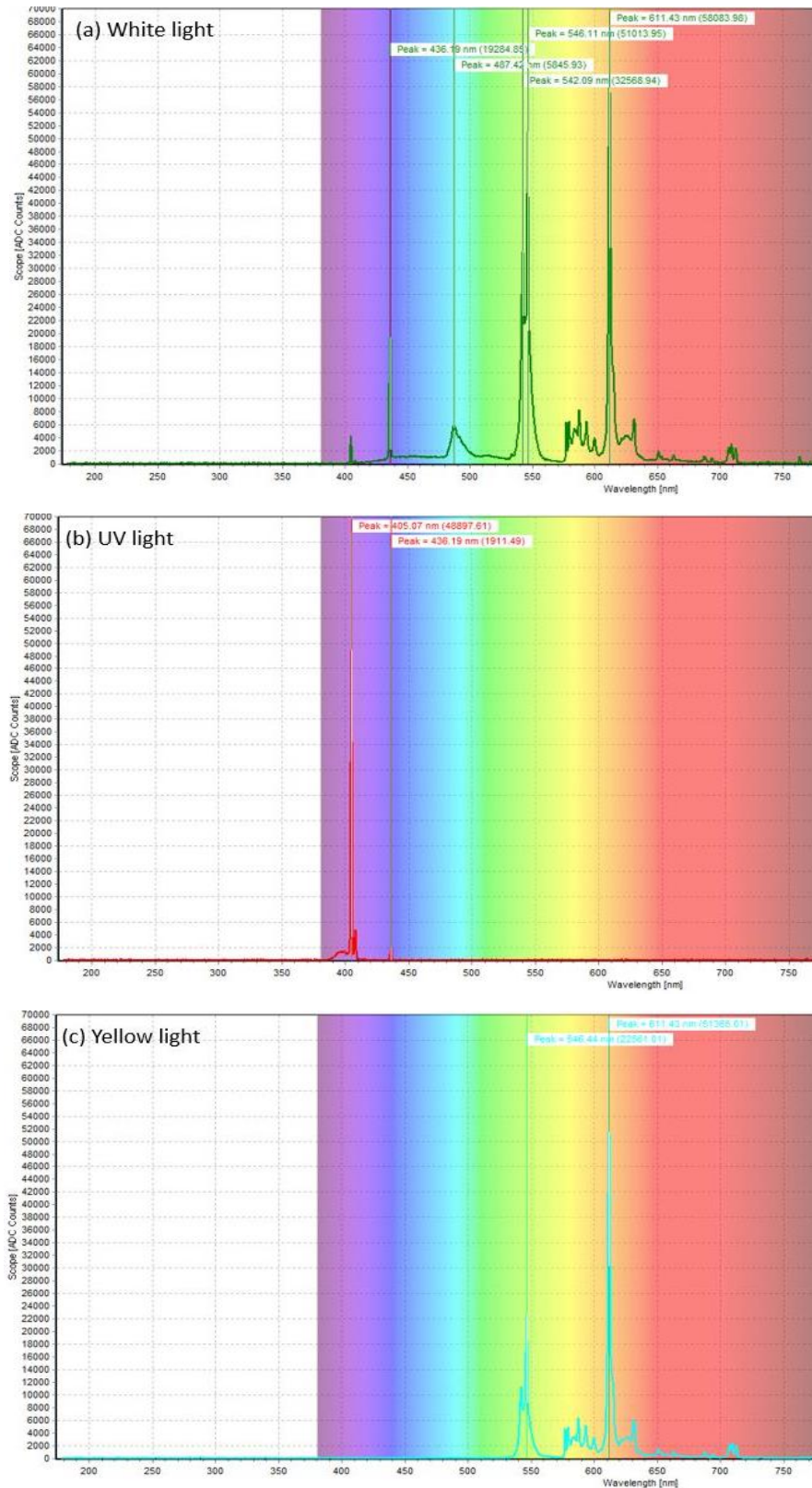
Figure 2.6: Light emission spectra for all three colours of Compact Fluorescent light bulbs used in the experiment. (a) White light, (b) UV light and (c) Yellow light. Wavelength is on the x axis and intensity on the y axis measured in Analogue to Digital Conversion units (ADC).

The lights were connected to a day/night switch during the five nights of lighted conditions which automatically switched them on at dusk and off at dawn. This was checked manually. During dark conditions power was disconnected. The bat detectors were set to record from sunset to sunrise during both light and dark conditions.

Table 2.1: Equipment used in the experiment assessing the effect of light on bat activity in the Kuiseb River, Central Namib Desert, Namibia.

Quantity	Equipment
4	Wildlife Acoustics SM4 BAT bat detectors
4	Eurolux FS35 spotlight fixtures
2	Beamz 160.023 UV black light 25W compact fluorescent light bulbs
2	Osram 11201m 60 W white compact fluorescent light bulbs
2	Eurolux G433Y yellow 12W compact fluorescent light bulbs
4	One hundred metre long extension cables
8	Two metre long copper poles for mounting lights and bat detectors
4	0.60 m long metal stakes for mounting copper pipes with lights
4	Custom aluminium stands for mounting copper pipes with bat detectors
1	Avantes AvaSpec – ULS 3648-USB2-RS portable spectrometer
1	DS 1923 Hygrochron iButton temperature/humidity sensor

Table 2.2: Wildlife Acoustics SM4 BAT detector settings used in the experiment assessing the effect of light on bat-activity along the Kuiseb River, Central Namib Desert, Namibia.

Variable	Setting
Gain	12 dB
16k filter	On
Sample rate	256 kHz
Min duration	1.5 ms
Max duration	None
Min trig freq	16 kHz
Trigger level	12 dB
Trigger window	1 s
Max length	15 s
Compression	None

2.4 Call Analysis

Echolocation calls were recorded as uncompressed WAV files. Each file typically contains a series of echolocation pulses as a bat flies past the bat detector microphone. This is termed a pass. Activity was measured by the number of passes recorded per species (Stone, Jones and Harris, 2009, 2012; Krauel and LeBuhn, 2016). Analysis of the recordings was done using specialist, commercially available software (Wildlife Acoustics Kaleidoscope Pro 4; Wildlife Acoustics Inc, Concord, Massachusetts, USA). Files with similar pulses were clustered together by the software. These were sorted according to cluster and distance from cluster centroid (Agranat, 2013). For large clusters the first and last 50 files were examined manually. If the pulses were representative of one species the cluster was assigned a manual identification. Some clusters contained files with more than one species in each file. In this case the cluster was given a manual identification of up to three species which were present in every file in the cluster. Species were limited to three in one file as full spectrum detectors are able to record multiple frequencies simultaneously. Calls and associated harmonics can overlap as the spectrogram becomes more cluttered with more species which can make identification of individual species difficult and potentially unreliable. Some clusters could not be assigned a single identification as they covered areas where species calls overlapped. All files in these clusters were examined manually and identified individually. Where identification was uncertain the individual file or the entire cluster was assigned no identification and excluded from the analysis. Clusters containing social calls were also excluded from the analysis.

Published echolocation call parameters of Southern African bats (Monadjem *et al.*, 2010; ACR, 2018) were used for the manual identification in conjunction with some unpublished local call parameters of known species (Curtis, 2016) as species calls can differ with habitat (Limpens, 2004) (Table 2.3).

Presence or absence of species in the recordings was used as a measure of species richness (Korine *et al.*, 2015).

Table 2.3: Call parameters used for the identification of the species detected in recordings during the experiment. Parameters were obtained from published call parameters (Monadjem *et al.*, 2010) in combination with unpublished local call parameter data as parameters are known to vary between populations and locality (Limpens, 2004; Parsons and Szewczak, 2009)

Species	Common name	Peak frequency (kHz)	Duration in ms (search phase)
Tadarida aegyptiaca	Egyptian free-tailed bat	22.5 ± 3.0	9.6 ± 3.4
Sauromys petrophilus	Robert's flat-headed bat	27.5 ± 2.5	5.3 ± 2.5
Neoromicia zuluensis	Zulu serotine	45.0 ± 2.5	2.7 ± 0.4
Eptesicus hottentotus	Long-tailed serotine	31.0 ± 1.5	5.5 ± 2.1
Neoromicia capensis	Cape serotine	39.4 ± 1.6	5.1 ± 1.3
Laephotis namibensis	Namibian long-eared bat	21.0 ± 1.0	2.6 ± 0.8
Rhinolophus damarensis	Damara horseshoe bat	84.0 ± 1.5	39.5 ± 10.6
Nycteris thebaica	Egyptian slit-faced bat	90.0 ± 3.0 (additional peaks at 50, 73 & 113)	1.7 ± 0.5

2.5 Statistical analyses

Overall activity and activity of individual species for each light type was compared to the activity at the control. The data were not normally distributed so a Kruskal-Wallis test was used followed by a focused multi-comparison post-hoc Kruskal test to detect significant differences between activity at each light type and the control for all species (Field, Miles and Field, 2012). The statistical program R (R Core Team, 2018) and packages, pgirmess (Giraudox, 2018) and ggplot2 (Wickam, 2016), were used for the analysis.

Generalised linear mixed effects models (GLMER) were run using lme4 packages (Bates *et al.*, 2019) in R (vs) and RStudio (vs), where the fixed factors were light type, temperature, and temperature at 20:00. To control for the possible variability introduced by samples undertaken across the various months, samples nested in month were set as random effect (samples |months) in the various models.

For data analyses lme4 packages (Bates *et al.*, 2019), sjPlot and sjPlot tutorial (Luedecke and Schwemmer, 2019) were used to create the Incidence Rate Ratio figures.

2.6 Ethics and permits

All research was carried out under a Ministry of Environment and Tourism Research Permit, Permit number 2284/2017.

Ethics clearance, reference number: 2017/CAES/121, was obtained from the University of South Africa following the acceptance of the proposal and renewed on the 1st of October 2018. All three documents can be found in the appendices.

Chapter 3 Results

3.1 Introduction

The experiment ran from the 11th of September 2017 until the 24th of February 2018. During this period a total of 160 nights of recordings of ultrasonic bat echolocation calls were made. Eighty nights were recorded under dark conditions and 80 nights were recorded under light conditions. Sixteen samples were recorded during the experiment. Each sample consisted of five nights of darkness followed by a five-night sample session under experimentally illuminated conditions. Recordings from the dark periods were used to establish a baseline of activity at each site without the effects of artificial lighting. Recordings from the 16 experimental sample sessions were used for the analysis into the effects of artificial lighting on bat activity.

Sample sessions 1 and 2 were recorded during September 2017, sample sessions 3, 4, and 5 during October 2017, sample sessions 6, 7 and 8 during November 2017, sample sessions 9, 10 and 11 during December 2017, sample sessions 12, 13 and 14 during January 2018 and sample sessions 15 and 16 during February 2018.

A total of 360 761 echolocation passes were recorded during both dark and light periods of the experiment. Of these 355 809 passes were identified and 4 952 were ignored. Of those passes ignored, 1 655 were social calls and 3 297 were unidentified. Under illuminated experimental conditions 278 979 echolocation passes were identified and used for analysis.

Eight species of bats from four families were identified from the recordings. Two species from the family Molossidae: *Tadarida aegyptiaca* (Egyptian free-tailed bat) and *Sauromys petrophilus* (Robert's flat-headed bat). Four species from the family Vespertilionidae: *Neoromicia zuluensis* (Zulu serotine), *Neoromicia capensis* (Cape serotine), *Eptesicus hottentotus* (long-tailed serotine) and *Laephotis namibensis* (Namibian long-eared bat), a single species from the family Rhinolophidae: *Rhinolophus damarensis* (Damara horseshoe bat) and a single species from the family Nycteridae: *Nycteris thebaica* (Egyptian slit-faced bat).

3.2 The effect of light spectra emitted by different coloured artificial lighting on the overall activity of bats

From the 16 sample sessions a total of 30 596 passes were recorded at the dark control site, a total of 45 775 passes were recorded at the UV light, a 50% difference in activity relative to the control, a total of 122 613 passes were recorded at the white light, a 300% difference in activity relative to the control, and a total of 79 995 passes were recorded at the yellow light, a 161% difference in activity relative to the control (Figure 3.1). The mean number of echolocation passes per sample session were 1 912.2 ± 328.5 passes at the dark control site, 2 860.9 ± 531.6 passes at the UV light, 7 663.3 ± 1 444.8 passes at the white light and 4 999.7 ± 944.6 passes at the yellow light.

Results from a Kruskal-Wallis test showed that overall bat activity was significantly influenced by artificial lighting (H (3) = 13.68, p = 0.003). Comparisons of each light type to the control using a focused, multi-comparison post-hoc Kruskal test at a significance level of p = 0.05, showed that overall bat activity at the white light differed significantly from activity at the control. No significant differences were found in overall bat activity at either the UV light compared to the control or at the yellow light compared to the control. As an indication of effect size, the critical difference from the post-hoc Kruskal test was 15.76, while the difference at the UV light was 7.81, the difference at the white light was 23.19 and the difference at the yellow light was 15.25, close to the critical difference. A general post hoc Kruskal test comparing light types to each other found no significant difference between light types.
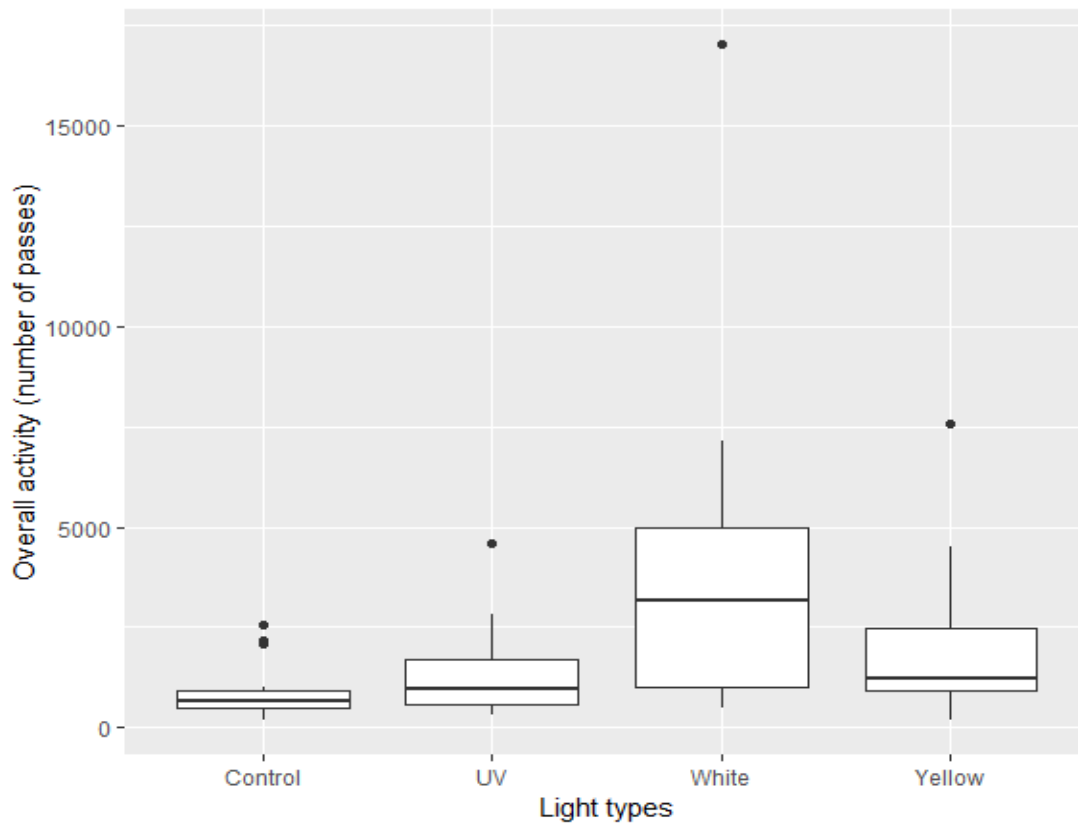
Figure 3.1: Overall activity of bats at different light types in the Kuiseb River, Central Namib Desert, Namibia showing the large increase in activity at the white light relative to the control. The sample size is 16 and the values for the median number of passes at each light type are: the dark control site, 1 433.5 passes, the UV light, 2323.0 passes, the white light, 5 424.5 passes and the yellow light, 2 859.5 passes.

Summary statistics of the overall bat activity for each sample session have been included in a table in Appendix 3. Standard deviations were large both within each five-night sample session and between sample sessions, with many outliers. Possible causes of the large standard deviations and outliers are discussed in section 3.3.9. Mean overall bat activity for each of the 16 sample sessions at each light type has been plotted in Figure 3.2 to show temporal differences in activity over the course of the experiment. Activity changes between sample sessions were frequent throughout the course of the experiment. These changes were probably due to external factors, possibly weather, location or insect emergences specific to that time period, as activity changes seemed similar at all light types. No consistent, long-term changes in activity are seen, either between light types or in general for all light types over time.
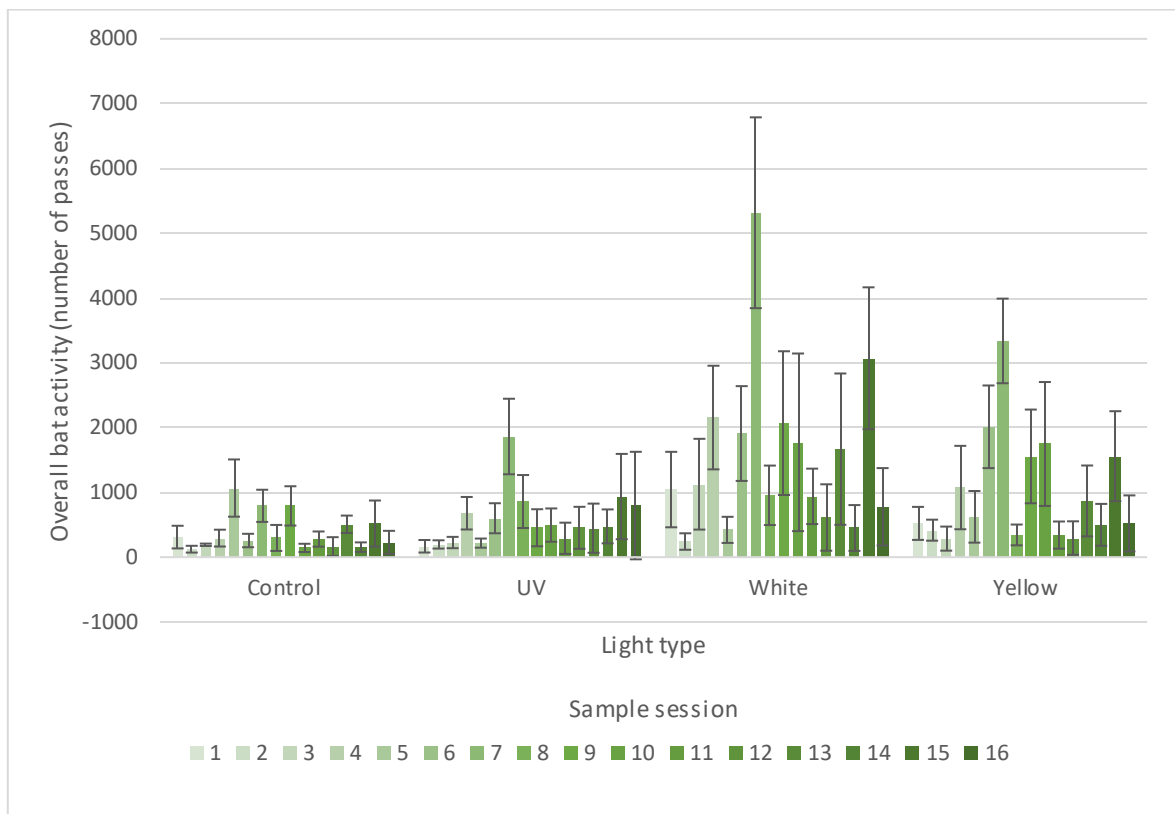
Figure 3.2: Mean overall bat activity for each of 16 five-night sample session at each light type recorded in the Kuiseb River, Central Namib Desert, Namibia from September 2017 to February 2018. Each sample session is depicted by a different shade of green in the legend below the graph. Activity peaked for all light types during sample session 7.

3.3 The effect of light spectra emitted by different colours of artificial lighting on the different bat species identified.

The results for the eight species identified (Figure 3.3) will be presented individually below and discussed together in Section 3.5.

Figure 3.3: The bat species identified from the recordings: (a) *Tadarida aegyptiaca* (Egyptian free-tailed bat) (Photo: Michelle Stange), (b) *Neoromicia zuluensis* (Zulu serotine) (Photo: Stretch Combrink), (c) *Sauromys petrophilus* (Robert's flat-headed bat) (Photo: Stretch Combrink), (d) *Eptesicus hottentotus* (long-tailed serotine) (Photo: Oliver Halsey, (e) *Neoromicia capensis* (Cape serotine) (Photo: Stretch Combrink), (f) *Laephotis namibensis* (Namibian long-eared bat) (Photo: Jessica Sack), (g) *Rhinolophus damarensis* (Damara horseshoe bat) (Photo: Oliver Halsey) and (h) *Nycteris thebaica* (Egyptian slit-faced bat) (Photo: Marcel Chaves).

The 278 979 bat passes used in the analysis were dominated by three species, *Neoromicia zuluensis*, *Tadarida aegyptiaca* and *Sauromys petrophilus*. The number of passes detected for each of the eight species in decreasing order are: *Neoromicia zuluensis* with 132 451 passes, *Tadarida aegyptiaca* with 93 970 passes, Sauromys petrophilus with 34 974 passes, *Neoromicia capensis* with 10 286 passes, *Eptesicus hottentotus* with 4 969 passes, *Laephotis namibensis* with 2 160 passes, *Rhinolophus damarensis* with 165 passes and lastly *Nycteris thebaica* with 4 passes.

Data for all species detected in the experiment contained many outliers which resulted in large standard deviations between sample sessions, with many outliers.

Although the cumulative totals over each five night sample session were used in the analysis, similar variation in data was also noted on a nightly basis within each sample session. Possible reasons for these outliers for all species will be discussed in section 3.3.9.

Summary statistics for the overall activity and activity of each species at each light type for each sample session have been included in a table in Appendix 3.

3.3.1 *Tadarida aegyptiaca* (Egyptian free-tailed bat)

From the 16 sample sessions a combined total number of 93 970 bat echolocation passes were recorded for *Tadarida aegyptiaca* during the artificially illuminated experimental period. Of these 10 717 passes were recorded in dark conditions at the control, 16 277 passes were recorded at the UV light, a 52% difference in activity relative to the control, 43 026 passes were recorded at the white light, a 301% difference in activity relative to the control and 23 950 passes were recorded at the yellow light, a 123% difference in activity relative to the control (Figure 3.4). The means per sample session were: 669.8 ± 538.2 passes at the control site, 1 017.3 ± 826.6 passes at the UV light, 2 689.1 ± 2 722.3 passes at the white light and 1 496.9 ± 1 458.7 passes at the yellow light.

Tadarida aegyptiaca activity was increased significantly by the artificial lighting treatment, (Kruskal-Wallis H (3) = 10.41, p = 0.015). A focused, multi-comparison post-hoc Kruskal test at a significance level of p = 0.05, showed that *Tadarida aegyptiaca* activity at white light differed significantly from activity at the control. No significant differences were found in *Tadarida aegyptiaca* activity at either the UV light compared to the control or at the yellow light compared to the control. As an indication of effect size the critical difference form the post-hoc Kruskal test was 15.76 while the difference at the UV light was 8.16, at the white light was 20.66 and at the yellow light 13.06. A general post hoc Kruskal test comparing light types to each other found no significant difference between light types other than the difference between the control and white light. Values are summarised in Appendix 4.
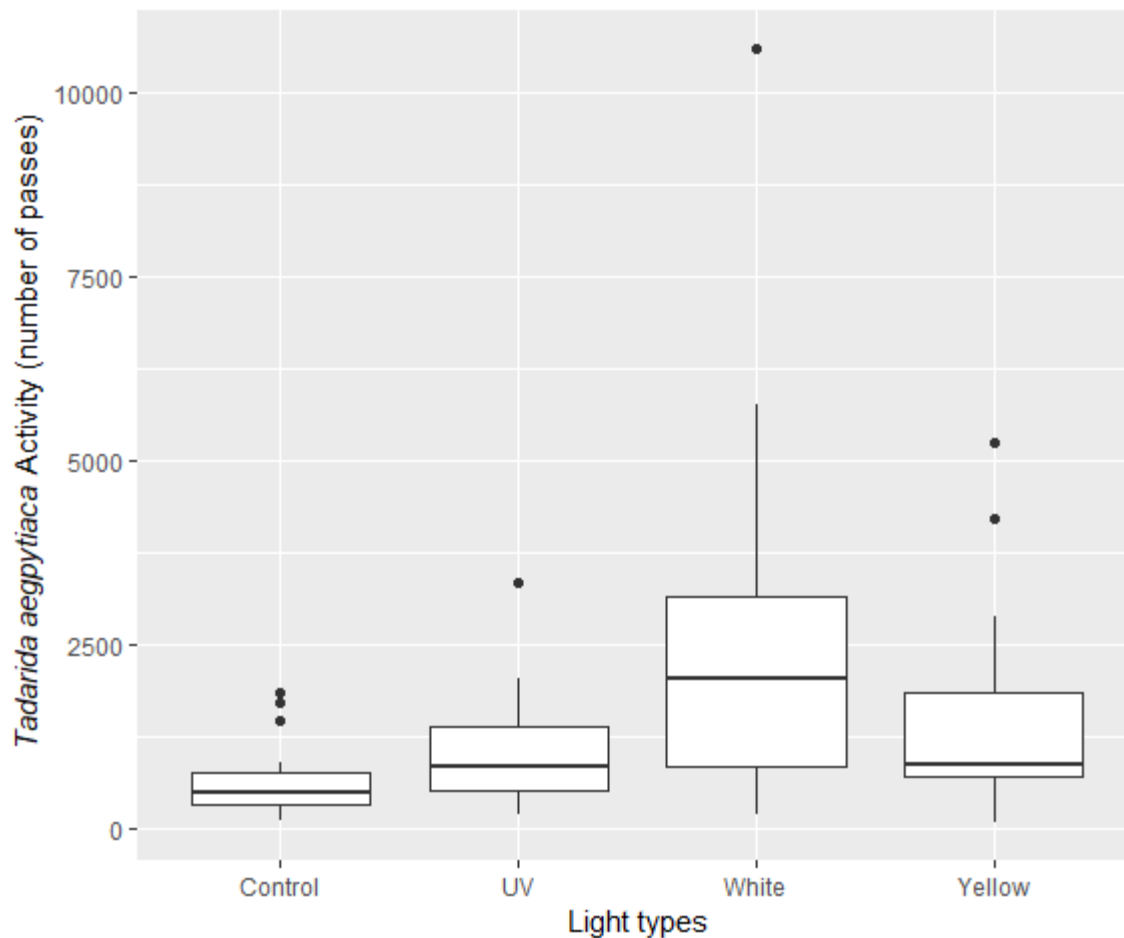
Figure 3.4: *Tadarida aegyptiaca* activity at each light type in the Kuiseb River, Central Namib Desert, Namibia. The large increase in activity at the white light is clearly seen. The sample size is 16 and the values for the median number of passes at each light type are: the dark control site, 472.5 passes, the UV light, 819.0 passes, the white light, 2 018.5 passes and the yellow light, 850.0 passes.

There were no discernible long-term, consistent changes in activity on a temporal scale. Mean *Tadarida aegyptiaca* activity for each of 16 five-night sample sessions at each light type has been plotted in Figure 3.5 to show the temporal changes in activity over the course of the experiment. Different sample sessions show changes in activity but these seem to be consistent across all light types. Similar trends in changes in activity were seen for some species during the same sample sessions. A peak in activity was seen for four species, *Tadarida aegyptiaca*, *Sauromys petrophilus*, *Neoromicia zuluensis* and *Eptesicus hottentotus*, during sample session 7. These changes in activity are probably related to external factors such as weather, site or insect emergences rather than the effect of artificial lighting.
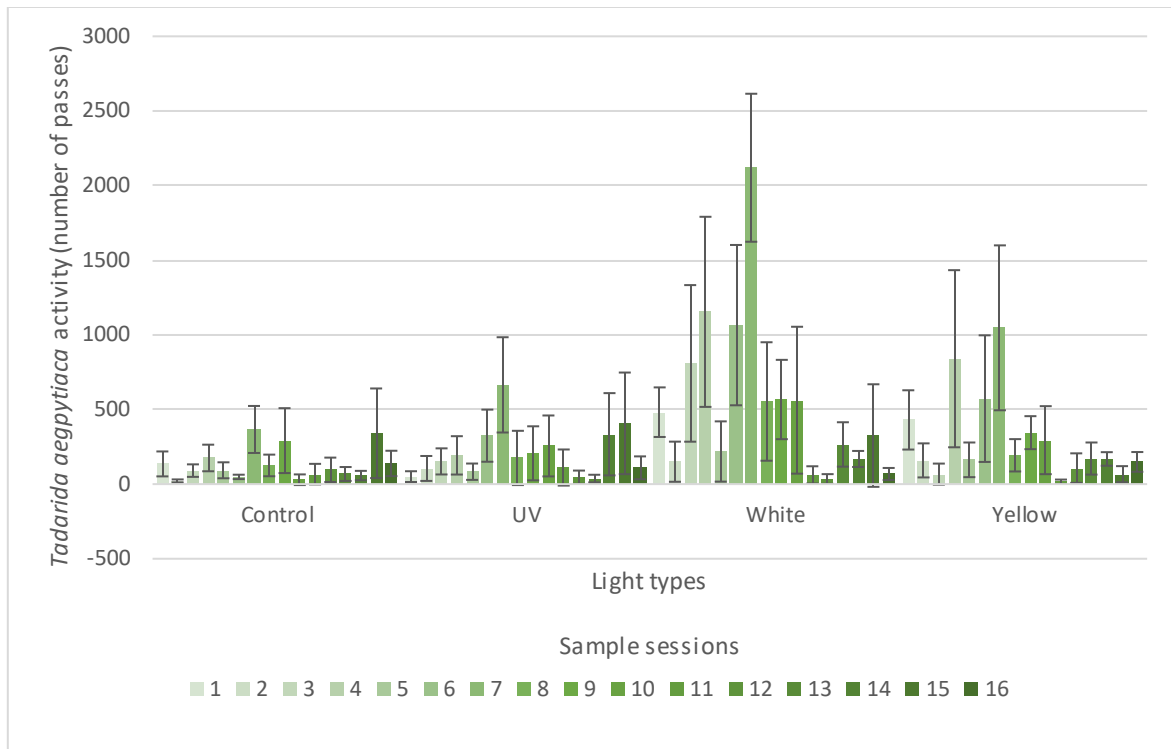
Figure 3.5: The mean *Tadarida aegyptiaca* activity for each light type for each of the 16 sample sessions in the Kuiseb River, Central Namib Desert, Namibia. Activity for four species peaked during sample session 7 which is clear for *Tadarida aegyptiaca* in this graph. No long-term trends in activity changes are discernible during the experimental period.

3.3.2 *Sauromys petrophilus* (Robert's flat-headed bat)

From the 16 sample sessions a combined total of 34 974 passes were recorded for *Sauromys petrophilus* during the artificially illuminated experimental period. Of these, 3 822 passes were recorded in dark conditions at the control, 4 850 passes were recorded at the UV light, a 26% change in activity relative to the control, 18 596 passes were recorded at the white light, a 386% change in activity relative to the control and 7 706 passes were recorded at the yellow light, a 102% change in activity relative to the control (Figure 3.6). The means per sample session were: 238.9 ± 202.6 passes at the control, 303.1 ± 316.1 passes at the UV light, 1 162.2 ± 1 613.9 passes at the white light and 481.6 ± 550.9 passes at the yellow light.

A Kruskal-Wallis test showed that *Sauromys petrophilus* activity increased significantly under artificial lighting, H (3) = 13.773, p = 0.003. A focused, multi-comparison post-hoc Kruskal test at a significance level of p = 0.05 showed that

Sauromys petrophilus activity at white light differed significantly from activity at the control. No significant differences were found in *Sauromys petrophilus* activity at either the UV light compared to the control or at the yellow light compared to the control. As an indication of effect size from the post-hoc Kruskal test, the critical difference was 15.76 while the difference at the UV light was 4.06, the difference at the white light was 21.97 and difference at the yellow light 14.47. A general post hoc Kruskal test comparing light types to each other found a significant difference between white light and UV light in addition to the difference between white light and the control at p = 0.05. Values are summarised in Appendix 4.
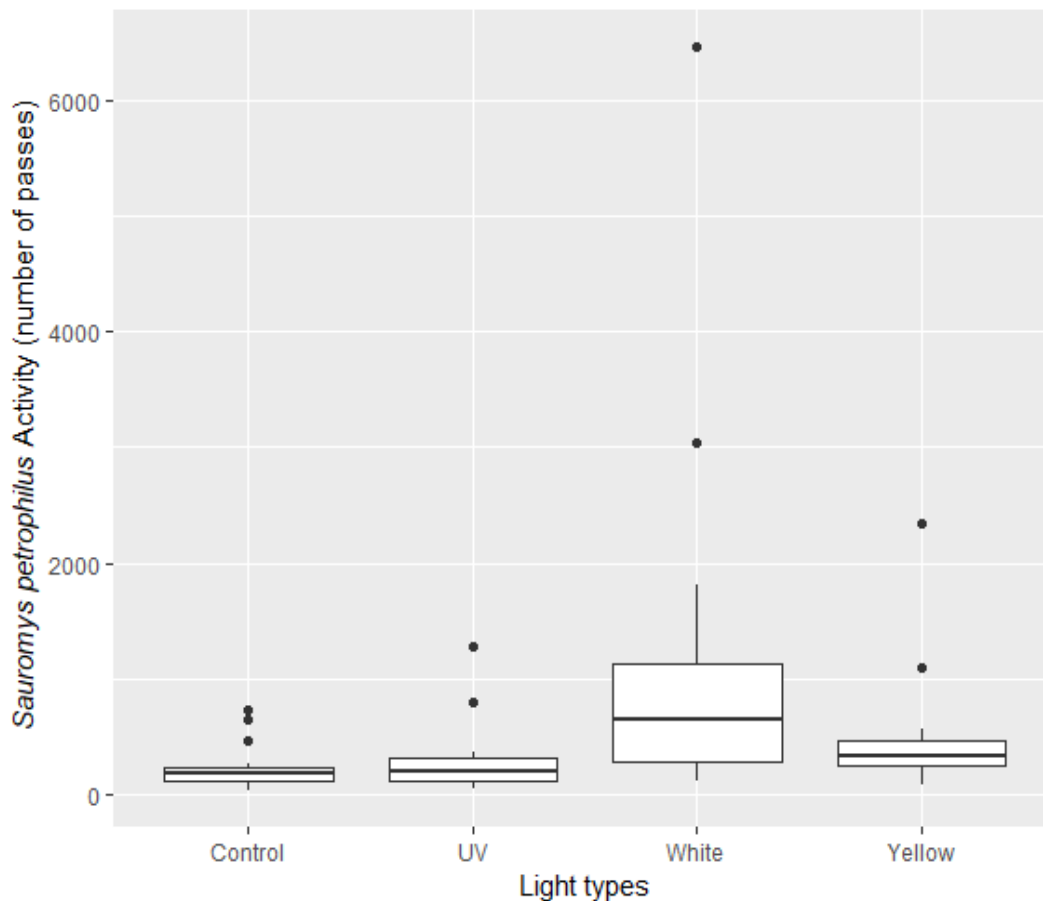
Figure 3.6: Activity of *Sauromys petrophilus* at different light types in the Kuiseb River, Central Namib Desert, Namibia. Activity at the white light shows a large increase relative to activity at the dark control site. The sample size was 16 and the median values at each light type are: at the dark control site, 185.5 passes, at the UV light, 199.5 passes, at the white light, 644.0 passes and at the yellow light, 325.0 passes.

Mean *Sauromys petrophilus* activity for each of 16 five-night sample sessions at each light type has been plotted in Figure 3.7 to show temporal changes in activity over the course of the experiment. As for *Tadarida aegyptiaca* above there seem to be no consistent, long-term changes in activity over the course of the experiment. Where changes in activity are seen for different sample sessions these changes seem to be similar at each light type and are probably due to the same external factors mentioned before. Activity also peaked during sample session 7.
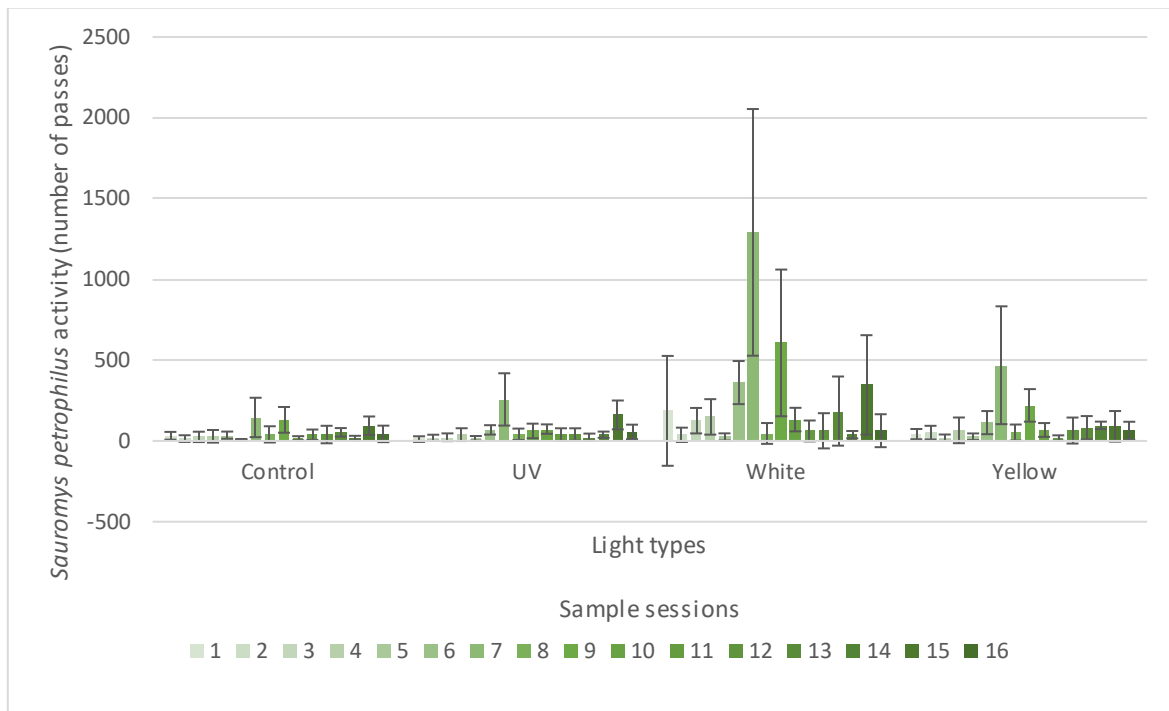
Figure 3.7: Mean *Sauromys petrophilus* activity at each light type for each of 16 sample sessions in the Kuiseb River, Central Namib Desert, Namibia. Changes in activity seem to affect activity at all light types during the same sample session and are probably due to external factors. There seems to be no consistent long-term changes in activity over the course of the experiment.

3.3.3 *Neoromicia zuluensis* (Zulu Serotine)

From the 16 sample sessions a combined total of 132 451 bat echolocation passes were recorded for *Neoromicia zuluensis* during the artificially illuminated experimental period. Of these 14 464 passes were recorded in darkness at the control, 23 202 passes were recorded at the UV light, a 60% change in activity relative to the control, 52 788 passes were recorded at the white light, a 265% change in activity relative to the control and 41 997 passes were recorded at the

yellow light, a 190% change in activity relative to the control (Figure 3.8). The means per sample session were: 904.0 ± 1 098.0 passes at the control, 1 450.1 ± 1 188.6 passes at the UV light, 3 299.2 ± 2 910.6 passes at the white light and 2 624.8 ± 2 515.5 passes at the yellow light.

A Kruskal-Wallis test found that *Neoromicia zuluensis* activity was significantly increased by artificial lighting, $H(3) = 14.69$, $p = 0.002$. A focused, multi-comparison post-hoc Kruskal test at a significance level of $p = 0.05$, showed that *Neoromicia zuluensis* activity at both the white light and the yellow light differed significantly from activity at the control. No significant difference was found between activity at the UV light and activity at the control. As an indication of effect size the critical difference from the post-hoc Kruskal test was 15.76 while the difference at the UV light was 9.88, the difference at the white light was 21.12 and the difference at the yellow light was 19.00. A general post hoc Kruskal test comparing light types to each other found no significant difference between each light type with the exception of the difference between white light and the control. Values summarised in Appendix 4.
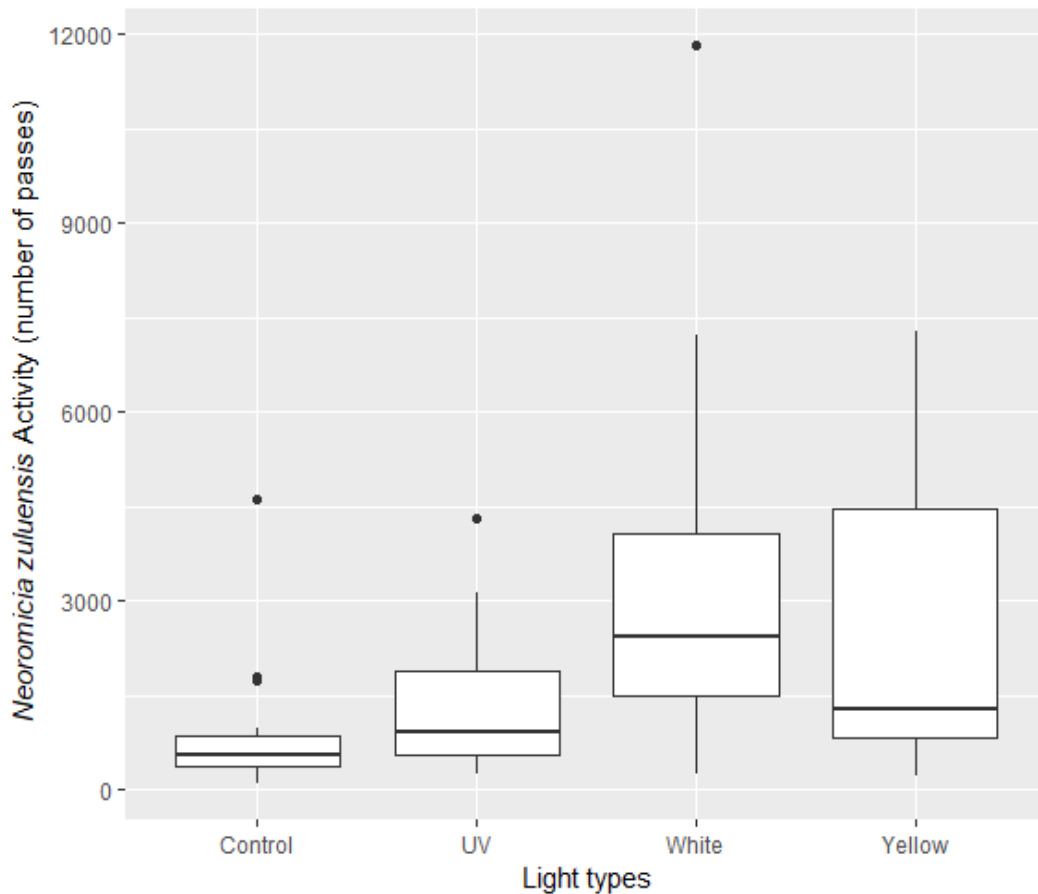
Figure 3.8: *Neoromicia zuluensis* activity at the different light types in the Namib Desert. Large increases in activity are clear at both the white and the yellow light relative to the dark control site. The sample size was 16 and the values for the median number of passes at each light type are: the control, 551.5 passes, the UV light, 921.0 passes, the white light, 2 417.0 passes and the yellow light, 1 281.0 passes

Mean *Neoromicia zuluensis* activity for each of 16 five night sample sessions at each light type has been plotted in Figure 3.9 to show temporal changes in activity over the course of the experiment. Once again there seemed to be no consistent, long-term changes over the course of the experiment. As with *Tadarida aegyptiaca*, *Sauromys petrophilus* and *Eptesicus hottentotus,* activity also peaked during sample session 7 for this species*,* however, there was a greater peak in activity at both the white light and to a lesser extent at the yellow light in sample session 15 which was not seen in the other species. Reasons for this are not clear. *Neoromicia zuluensis* was the smallest bat species identified weighing an average of 4.2 g

(Monadjem *et al.*, 2010). It may be possible that a particular prey item, more readily eaten by this species emerged during that sample session.
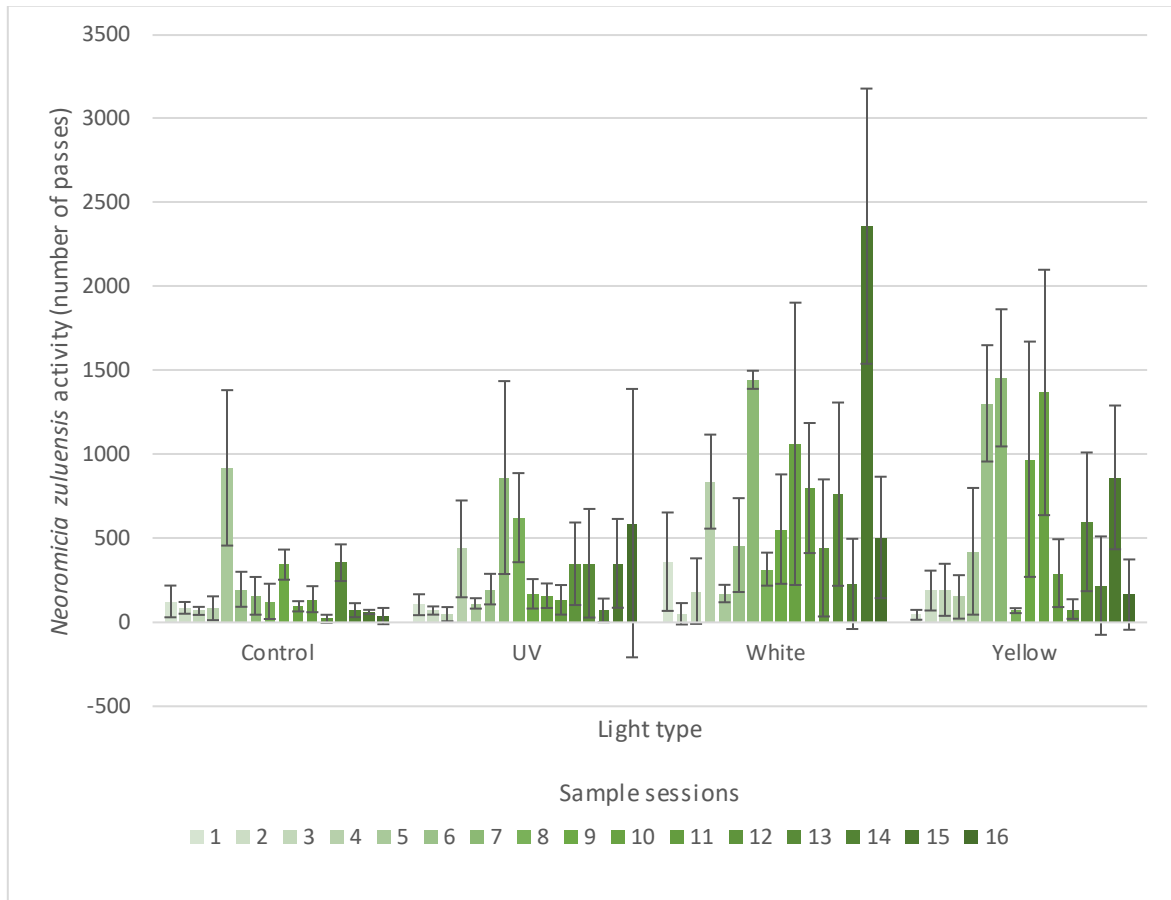
Figure 3.9: Mean *Neoromicia zuluensis* activity at each light type for each of the 16 sample sessions in the Kuiseb River, Central Namib Desert, Namibia. The spike in activity at sample session 7 seen in some of the other species is seen here too. Also clear, is the large spike in activity during sample session 15 not seen in the other species identified during the experiment.

3.3.4 *Eptesicus hottentotus* (Long-tailed serotine)

From the 16 sample sessions a total of 4 969 bat echolocation passes were recorded for *Eptesicus hottentotus* during experimental conditions. Of these 396 passes were recorded in darkness at the control, 437 passes were recorded at the UV light, a 10% change in activity relative to the control, 3 144 passes were recorded at the white light, a 694% change in activity relative to the control and 992 passes were recorded at the yellow light, a 150% change in activity relative to the control (Figure 3.10). The means per sample session were: 24.8 ± 63.3 passes at

the control, 27.3 ± 71.6 passes at the UV light, 196.5 ± 519.8 passes at the white light and 62.0 ± 185.2 at the yellow light.

A Kruskal-Wallis test found that *Eptesicus hottentotus* activity was significantly increased by artificial lighting, H(3) = 8.006, p = 0.046. A focused, multi-comparison post-hoc Kruskal test at a significance level of p = 0.05, showed that *Eptesicus hottentotus* activity at white light differed significantly from activity at the control. No significant differences were found in *Eptesicus hottentotus* activity at either the UV light compared to the control or at the yellow light compared to the control. As an indication of effect size from the critical difference from the post-hoc Kruskal test was 15.76 while the difference at the UV light was 1.06 while the difference at the white light was 15.88 and the difference yellow light was 10.19. A general post hoc Kruskal test comparing light types to each other found no significant difference between light types. Values are summarised in Appendix 4.
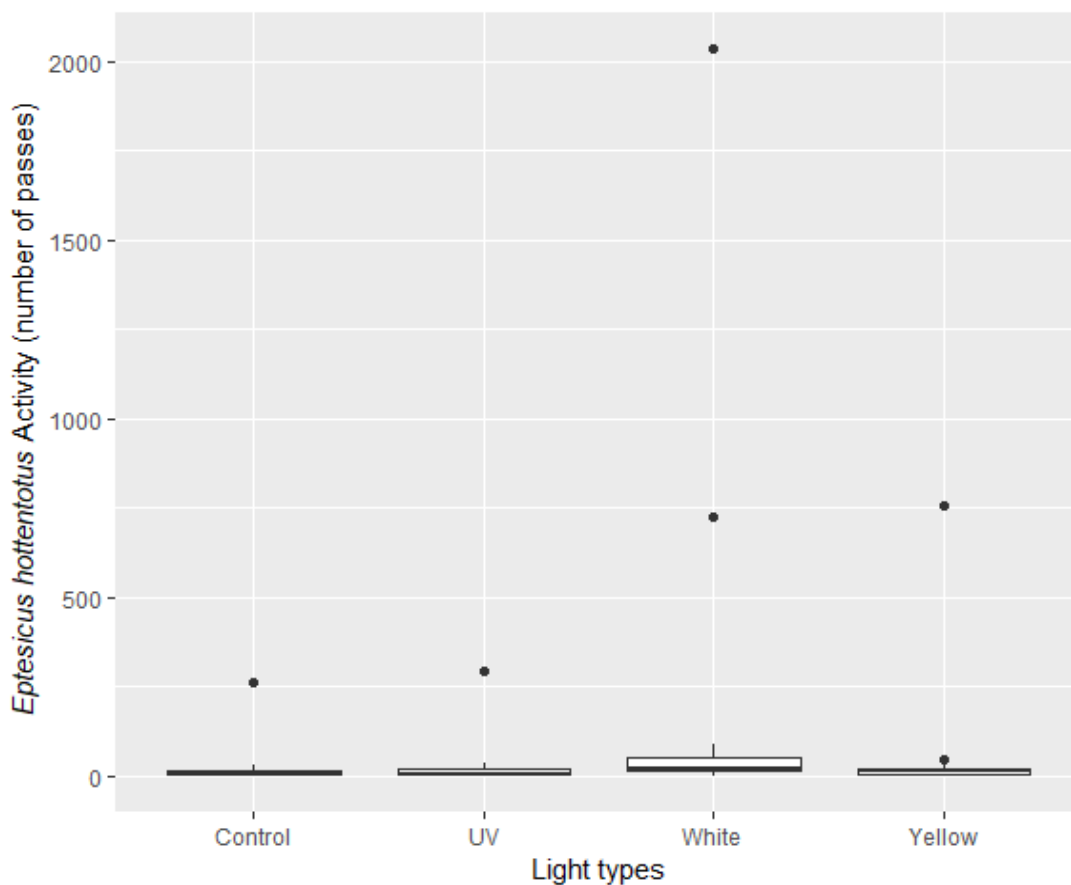
Figure 3.10: *Eptesicus hottentotus* activity for each light type in the Namib Desert. There are two high value outliers in activity at the white light and lower ones at the

other light types. The sample size is 16 and values for the median number of passes at each light type was: the control, 7.0 passes, the UV light, 6.0 passes, the white light, 21.5 passes and the yellow light, 13.5 passes.

Mean *Eptesicus hottentotus* activity for each of 16 five night sample sessions at each light type has been plotted in Figure 3.11 to show temporal changes in activity over the course of the experiment. As with *Tadarida aegyptiaca*, *Sauromys petrophilus* and *Neoromicia zuluensis* changes in activity varied between sample sessions with a peak in activity during sample session 7. Reasons for these changes have already been discussed in previous species accounts. Once again there seemed to be no consistent, long-term changes in activity over the course of the experiment.
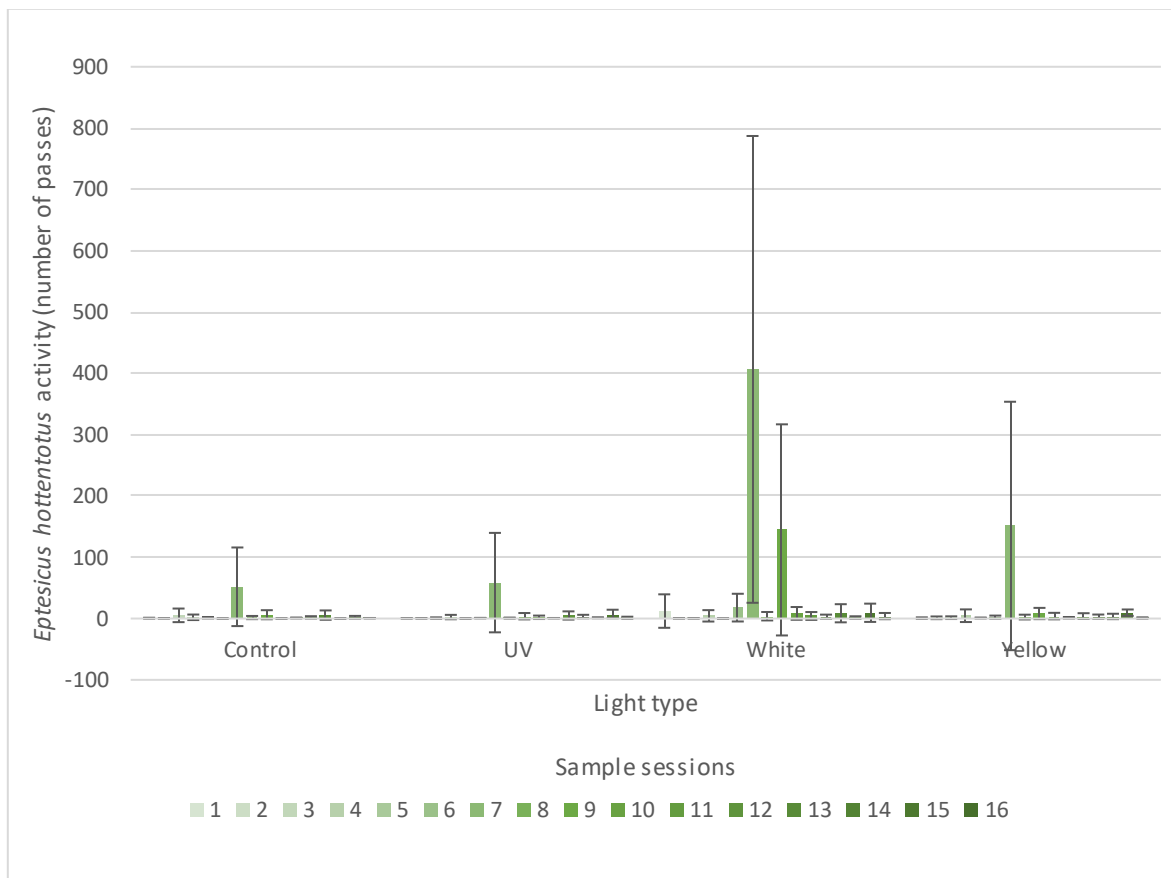
Figure 3.11: Mean *Eptesicus hottentotus* activity at each light type for each of the 16 sample sessions between September 2017 and February 2018 in the Kuiseb River, Central Namib Desert, Namibia showing the same trends in changes in activity seen in the species discussed previously.

3.3.5 *Neoromicia capensis* (Cape serotine)

From the 16 sample sessions, a combined total of 10 286 echolocation passes were recorded for *Neoromicia capensis* during the experiment. Of these 633 passes were recorded in darkness at the control, 518 passes were recorded at the UV light, a change of -18% in activity relative to the control, 4 437 passes were recorded at the white light, a 601% change in activity relative to the control and 4 698 passes were recorded at the yellow light, a 642% change in activity relative to the control (Figure 3.12). The means per sample session were: 39.6 ± 81.9 passes at the control, 32.4 ± 39.6 passes at the UV light, 277.3 ± 556.5 passes at the white light and 293.6 ± 675.4 passes at the yellow light.

A Kruskal-Wallis test found that *Neoromicia capensis* activity was not significantly affected by artificial lighting, H (3) = 3.226, p = 0.3581. As an indication of effect size comparisons of each light type to the control using a focused, multi-comparison post-hoc Kruskal test at a significance level of p = 0.05, the critical difference was 15.76 while the difference at the UV light was 5.59, the difference at the white light was 10.81 and the difference at the yellow light was 9.34. While not significant these results show the same trend in activity increases at white and yellow lights with a smaller increase at the UV light seen in the four species already presented. A general post hoc Kruskal test comparing light types to each other found no significant difference between light types. Values are summarised in Appendix 4.
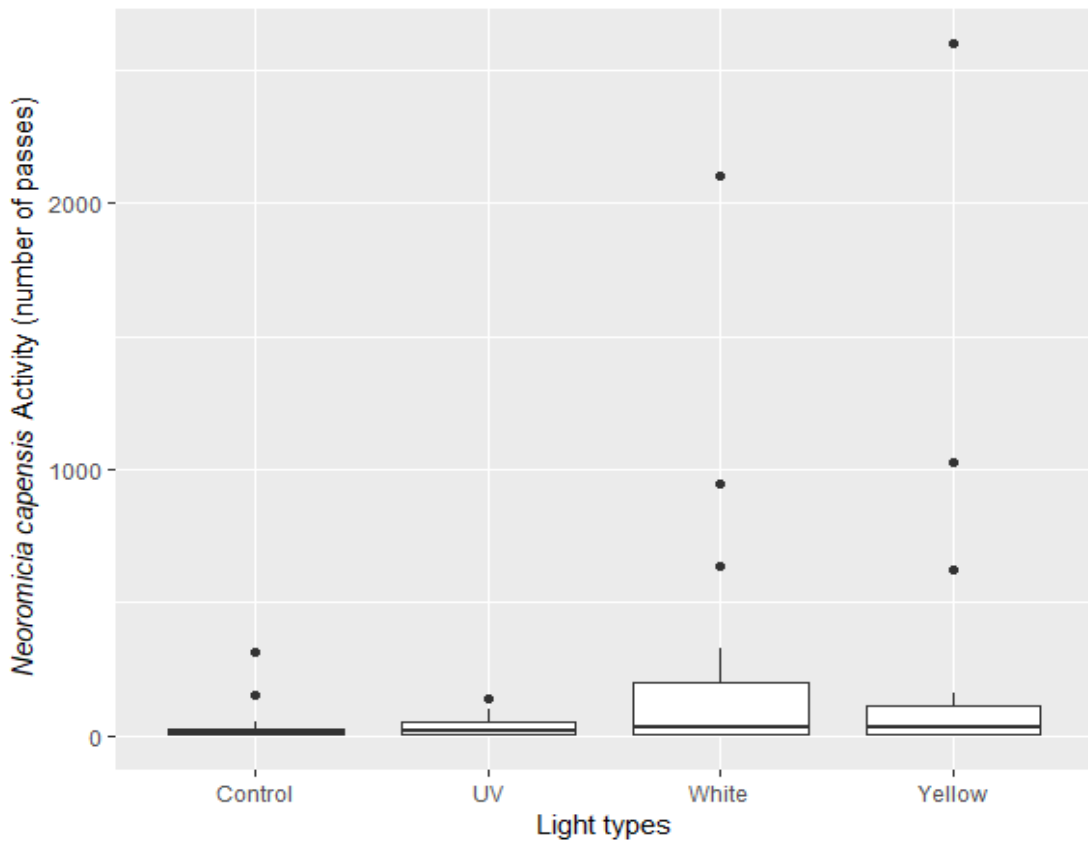
Figure 3.12: *Neoromicia capensis* activity per light type in the Namib Desert. There were no significant differences between activity at the UV, white or yellow lights and activity at the control although the differences in activity shown on the graph suggest the same trend seen in the four species above. The sample size was 16 and the median number of passes at each light type are: the control, 9.0 passes, the UV light, 14.5 passes, the white light, 34.0 passes and the yellow light 33.5 passes.

Mean *Neoromicia capensis* activity for each of 16 five night sample sessions at each light type has been plotted in Figure 3.13 to show temporal changes in activity over the course of the experiment. While *Neoromicia capensis* showed the same trend of increased activity at the white and yellow lights seen in the previous four species discussed and also showed changes in activity during different sample sessions this species did not show the same peak in activity during sample session 7. It may be that this is a transitory species which is not present in the area for long periods of time although this is not clear.
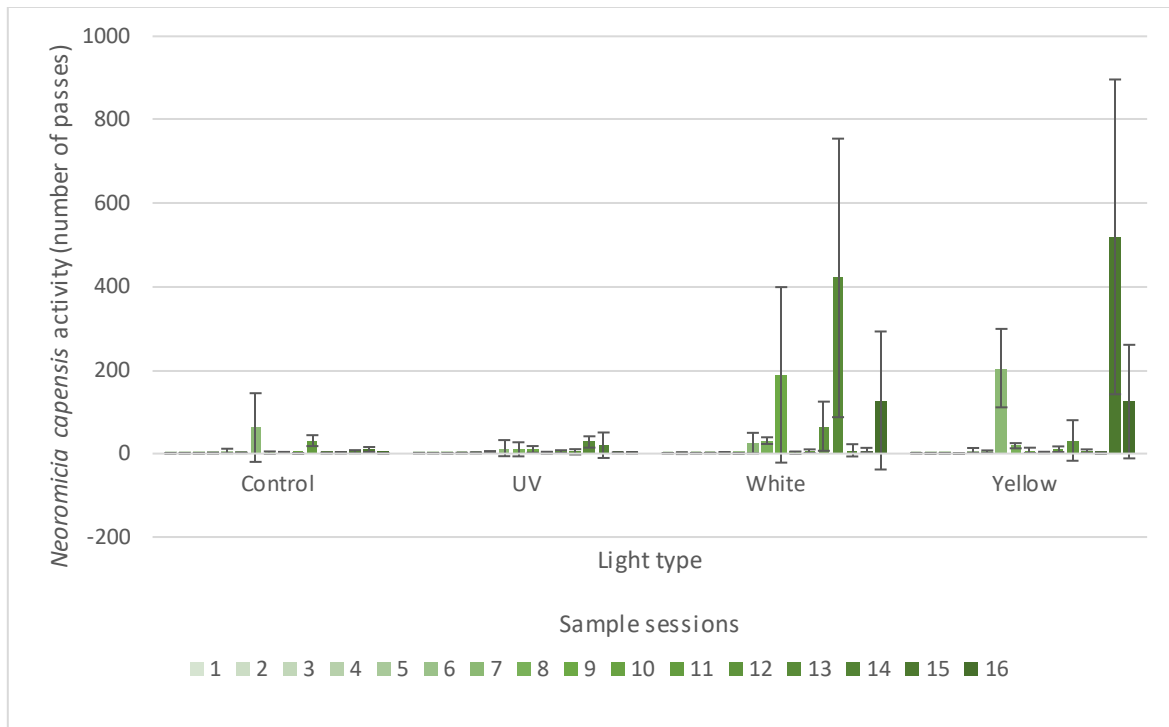
Figure 3.13: Mean *Neoromicia capensis* activity at each light type for each of 16 sample sessions recorded between September 2017 and February 2018 in the Kuiseb River, Central Namib Desert, Namibia. Unlike the trends in activity changes occurring during the same sample sessions seen in the previous four species discussed, none were seen in this species.

3.3.6 *Laephotis namibensis* (Namibian long-eared bat)

From the 16 sample sessions a total of 2 160 bat echolocation passes were recorded for *Laephotis namibensis* during the experiment. Of these 513 passes were recorded in darkness at the control, 449 passes were recorded at the UV light, a change of -12% in activity relative to the control, 594 passes were recorded at the white light, a 16% change in activity relative to the control and 604 passes were recorded at the yellow light, a 18% change in activity relative to the control (Figure 3.14). The means per sample session were: 32.1 ± 32.1 passes at the control, 28.1 ± 43.0 passes at the UV light, 37.1 ± 40.4 passes at the white light and 7.8 ± 25.6 passes at the yellow light.

A Kruskal-Wallis test found that *Laephotis namibensis* was not significantly affected by artificial lighting, H (3) = 3.124, p = 0.373. As an indication of effect size comparisons between each light type and the control using a focused, multi-comparison post-hoc Kruskal test showed that the critical difference was 15.76

while the difference at the UV light was 1.91, the difference at the white light was 4.41 and the difference at the yellow light was 6.66. A general post hoc Kruskal test comparing light types to each other found no significant difference between light types. Values are summarised in Appendix 4.
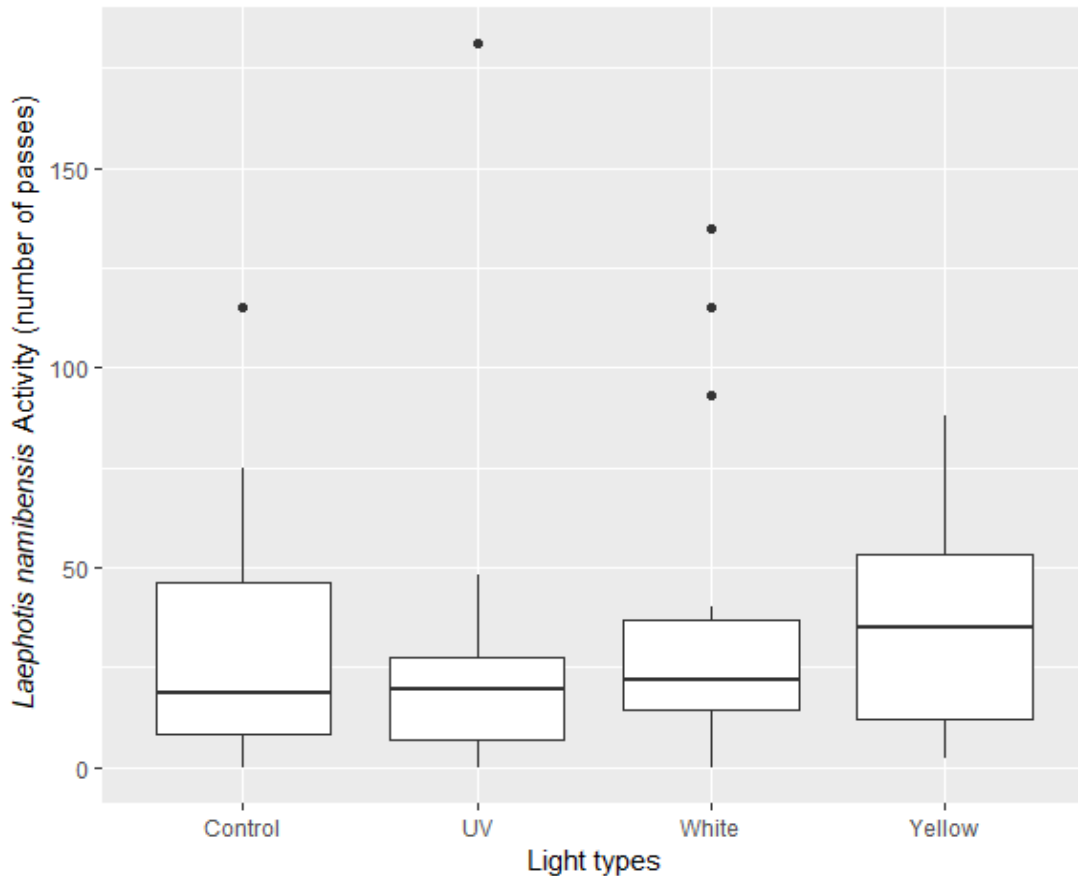
Figure 3.14: *Laephotis namibensis* activity for each light type in the Namib Desert. No significant differences were found between the UV light, the white light or the yellow light and the control. The sample size is 16 and values for the median number of passes at each light type are: the control, 18.5 passes, the UV light, 19.5 passes, the white light, 22.0 passes and the yellow light, 35.0 passes.

Mean *Laephotis namibensis* activity for each of 16 five-night sample sessions at each light type has been plotted in Figure 3.15 to show temporal changes in activity over the course of the experiment. Activity varied between sample sessions but peak in activity at all light types during sample session 7 seen for the first four species discussed did not occur. In addition changes in *Laephotis namibensis* activity during specific sample sessions were not seen consistently at all light types during the same period. This pattern of behaviour would be expected of a bat

species not preying on insect aggregations at artificial lights but also not avoiding lights.
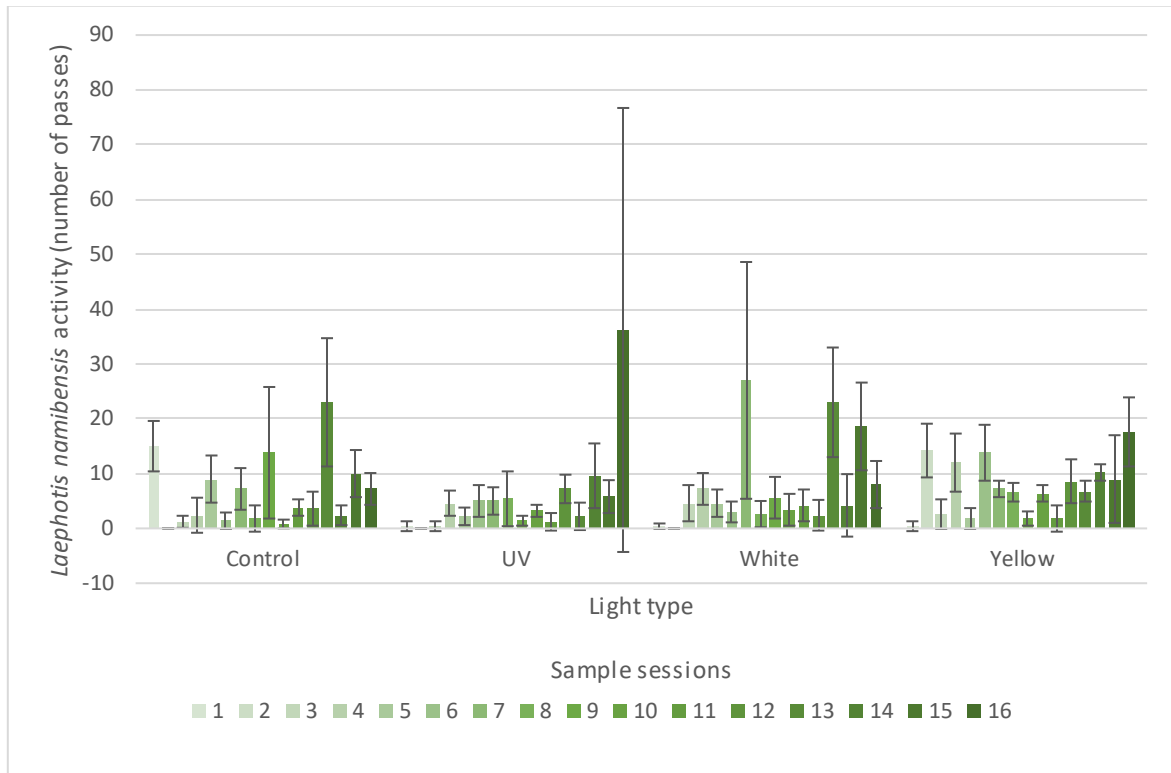
Figure 3.15: Mean *Laephotis namibensis* activity at each light type for each of 16 sample sessions which were recorded between September 2017 and February 2018 in the Kuiseb River, Central Namib Desert, Namibia. There seemed to be no discernible pattern to changes in activity throughout the study. In addition changes in activity were not consistent at all light types during the same sample sessions.

3.3.7 *Rhinolophus damarensis* (Damara horseshoe bat)

From the 16 sample sessions a combined total number of 165 echolocation passes were recorded for *Rhinolophus damarensis* during the experiment. Of these 51 were recorded in darkness at the control, 39 were recorded at the UV light, a change in activity of -24% relative to the control, 28 were recorded at the white light, a change in activity of -45% relative to the control and 47 were recorded at the yellow light, a of -8% change in activity relative to the control (Figure 3.16). The means per sample session were: 3.2 ± 3.7 passes at the control, 2.4 ± 2.2 passes at the UV light, 1.8 ± 1.8 passes at the white light and 2.9 ± 3.2 passes at the yellow light.

A Kruskal-Wallis test found that *Rhinolophus damarensis* activity was not significantly affected by artificial lighting, H (3) = 1.2597, p = 0.7387. As an indication of effect size using a focused, multi-comparison post-hoc Kruskal test at a significance level of p = 0.05, the critical difference was 15.76 while the difference at the UV light was 1.00, the difference at the white light was 5.47 and the difference at the yellow light was 0.09. A general post hoc Kruskal test comparing light types to each other found no significant difference between light types. Values are summarised in Appendix 4.
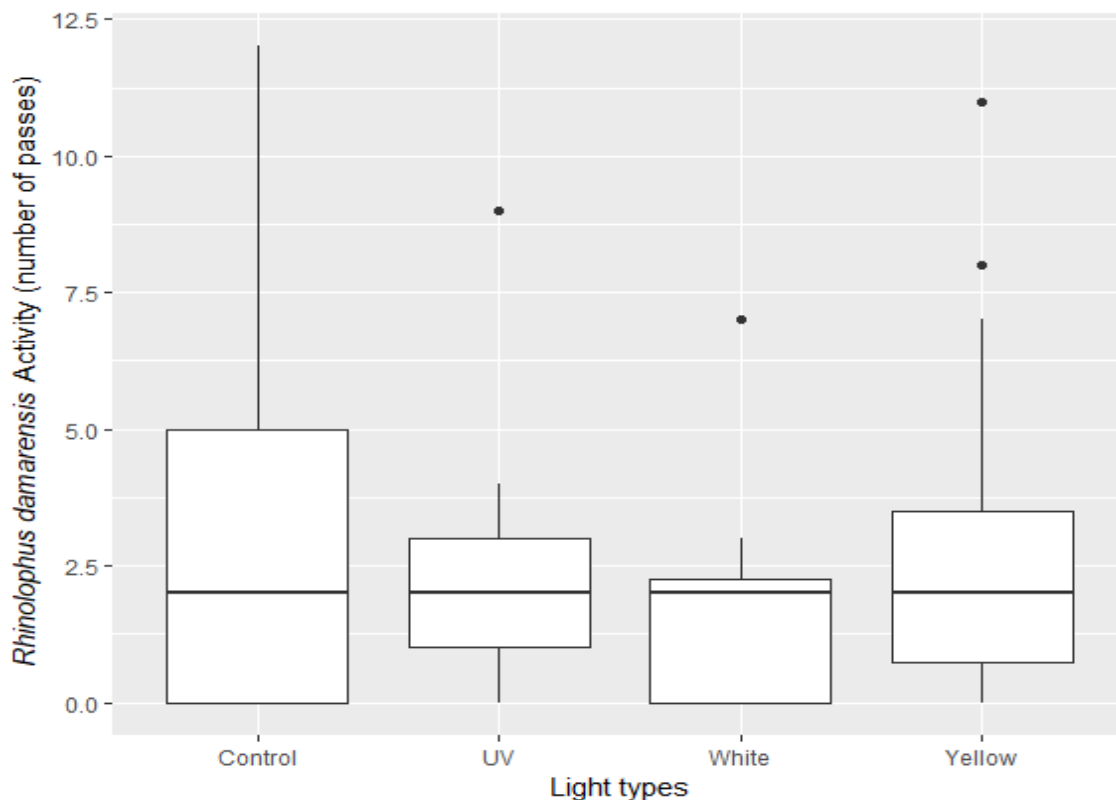

Figure 3.16: *Rhinolophus damarensis* activity for each light type in the Namib Desert. There were no significant differences between the UV light, the white light or the yellow light and the control. The slight reduction in activity depicted in the graph suggest that further study with a larger sample size may reveal the same light avoidance trend seem in species of this genus elsewhere (Stone, Jones and Harris, 2009). The sample size was 16 and values for the median number of passes at each light type are: the control, 2.0 passes, the UV light, 2.0 passes, the white light, 2.0 passes and the yellow light, 2.0 passes.

Mean *Rhinolophus damarensis* activity for each of 16 five-night sample sessions at each light type has been plotted in Figure 3.17 to show temporal changes in activity

over the course of the experiment. No obvious pattern was observed and neither were similarities to other species already discussed
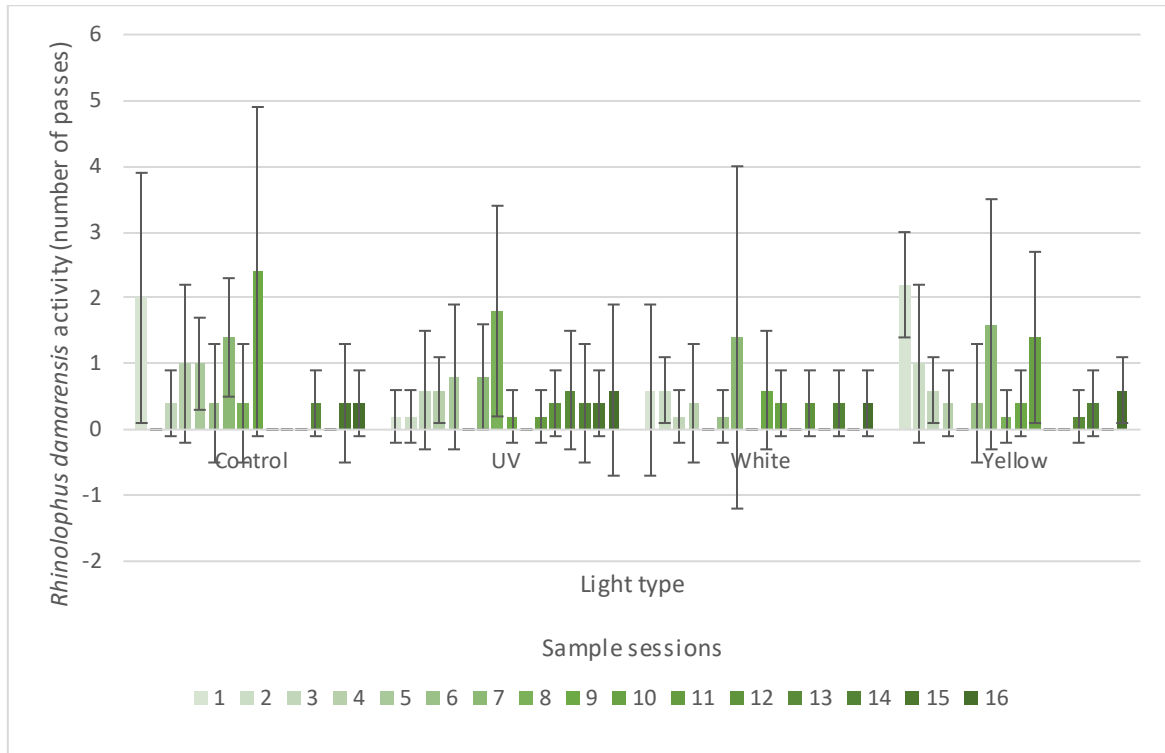
Figure 3.17: Mean *Rhinolophus damarensis* activity at each light type for each of 16 sample sessions showing the temporal variation over the course of the experiment which ran from September 2017 to February 2018 in the Kuiseb River, Central Namib Desert, Namibia. There was no apparent pattern observed for changes in activity and no similarity to any previously discussed species

3.3.8 *Nycteris thebaica* (Egyptian slit-faced bat)

A total of four echolocation passes were recorded for *Nycteris thebaica* during the artificially illuminated experimental period. The illuminated conditions consisted of 80 nights divided into 16 sample sessions of five nights each between the 11th September 2017 and the 24th January 2018. Of these, three passes were recorded at the UV light and one pass was recorded at the yellow light. There were no passes recorded in darkness at the control or at the white light. Due to the low number of passes no statistical analysis was performed for this species.

3.3.9 Possible causes for the large standard deviations and outliers

The results for all species had very large standard deviations due to the presence of many outliers. Much of the variability in activity both within sample sessions, and between sample sessions, can be explained by changes in temperature. Bat activity is known to increase with increasing temperature (Grüebler, Morand and Naef-Daenzer, 2008; Pellegrino *et al.*, 2013; Halat *et al.*, 2018). This may be in response to an increase in insect activity at increasing temperatures or due to the fact that many bat species are heterothermic and the energetic cost of raising body temperature to optimum operating temperature is less at higher ambient temperatures than at lower ambient temperatures (Ciechanowski *et al.*, 2007).

Figure 3.18 plots the effect of the temperature at 20H00, around the time of emergence for most bat species in summer, on mean overall bat activity recorded at the dark control site during the study. Activity rises steadily until the temperature reaches 26 ˚C, after which it increases rapidly and peaks at around 30 ˚C. As the temperature increases above 30 ˚C activity declines steeply.
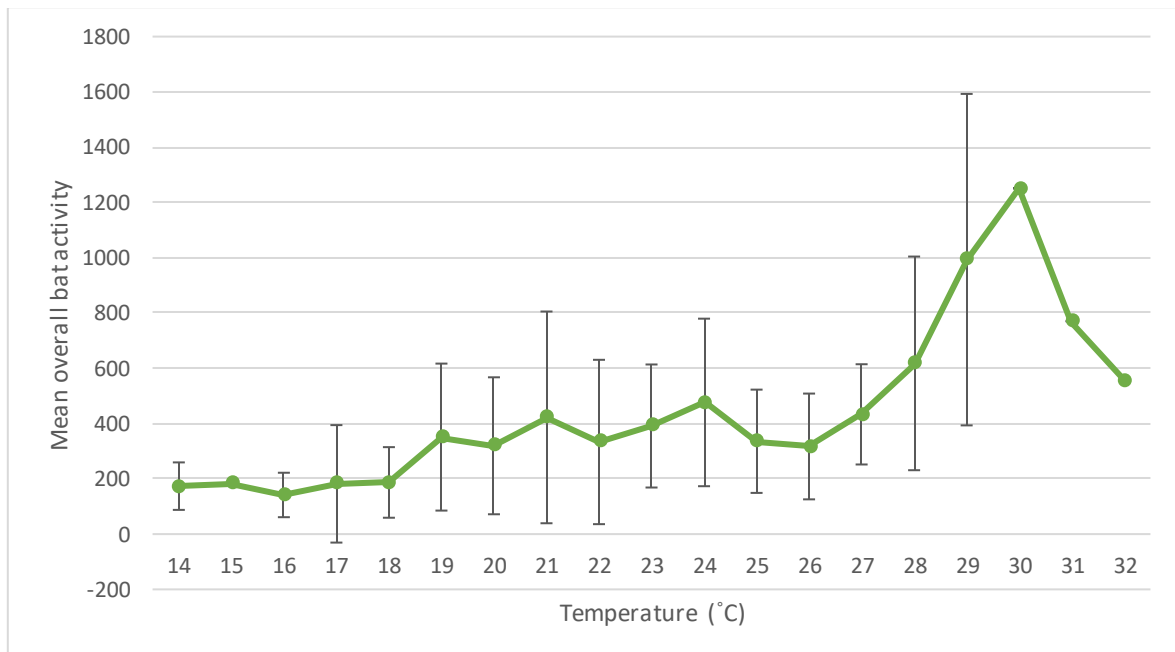
Figure 3.18: Mean Overall bat activity in relation to the temperature at 20H00 showing increasing activity with increasing temperature until the temperature reached 30 ˚C after which activity declined sharply as the temperature continued to rise.

When overall bat activity from the dark control site recorded for the duration of the experiment is plotted on the same graph as the temperature at 20h00 over the same time period the increases in bat activity almost mirror increases in temperature over the same period (Figure 3.19)
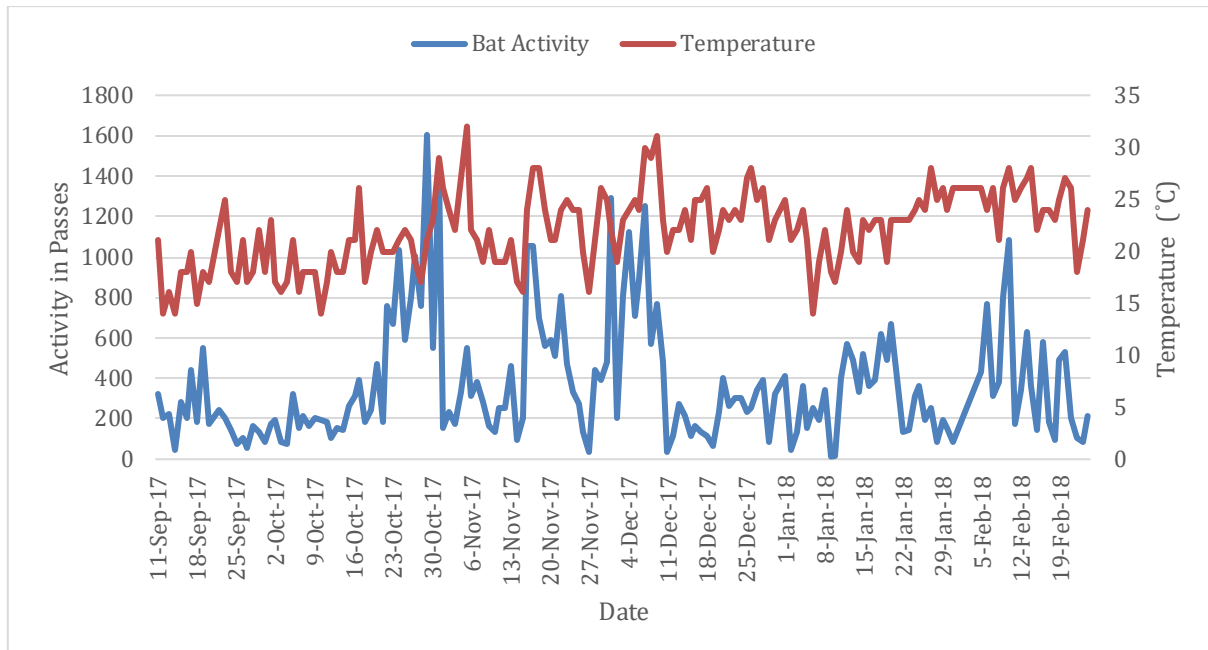
Figure 3.19: Overall bat activity at the dark control site in relation to temperature at 20H00 (close to time of emergence for most species during the summer months) for the duration of the study.

Another variable which could have contributed to the high number of outliers and resultant large standard deviations between sample sessions is the fact that the lights rotated between sites and some sites recorded higher activity than others. The lights were rotated between sites to rule out the effect of a single site causing changes in activity rather than the effect of the different light types. All sites were used four times by each light type and all sites were selected to be as homogenous as possible. When mean overall bat activity recorded simultaneously at each site during the dark period of each sample session was compared between sites mean activity at Site 3 appeared highest and mean activity at Site 2 the lowest. Standard deviations were also high, possibly affected by changes in temperature as discussed above and firm conclusions cannot be drawn (Figure 3.20).
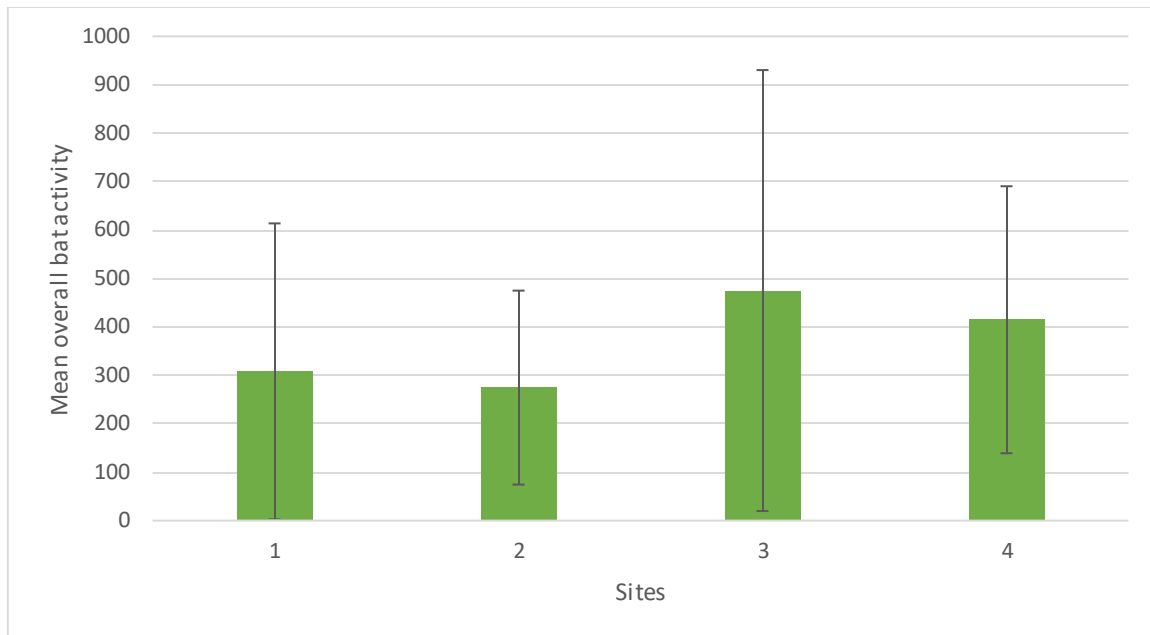
Figure 3.20: Mean overall bat activity at each of the sites measured simultaneously during the dark periods of each sample session. Mean activity at Site 1 was 308.1 ± 305.6 passes, at Site 2 was 274.6 ± 200.2 passes, at Site 3 was 475.0 ± 455.3 and at Site 4 was 414.7 ± 275.7.

Another factor which could have contributed to the outliers and resultant large standard deviations seen in the data is the sudden and unpredictable emergence of different species of insects. Increased abundance of insects at the lights on some nights would be expected to increase bat activity on these nights. Unfortunately insect abundance was not measured during the experiment.

3.4 Results from generalised mixed effects models

The two "global models" with the fixed factors: "Temperature + Light type" (AIC = 108609) and "Temperature (20:00) + Light type" (AIC = 116303) with "sample|month" as random factors were the lowest scoring AIC models. The most simple model that produced the third best fitted model was light type only as the fixed factor (AIC = 139594).

The estimates plotted for the various light types and temperature indicate (Figure 3.21) where temperature had positive influence on bat activity, with the UV light a positive effect above that of the "control" (intercept estimate) of 4.2 (Table 3.1). White light presented the strongest estimate effect, with yellow light second

strongest effect. These results correspond to the Kruskal-Wallis test findings presented earlier.
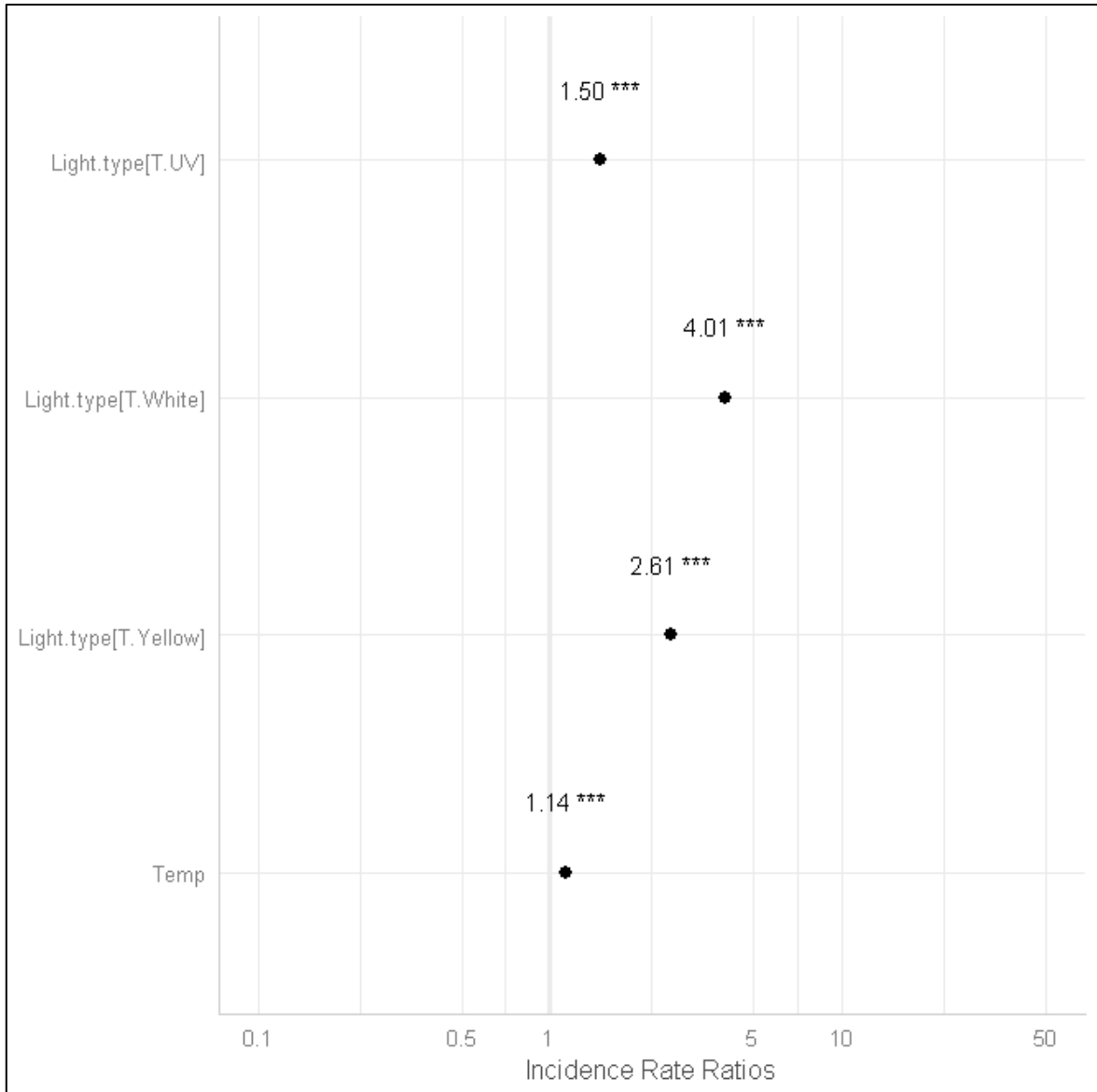
Figure 3.21: Incidence Rate Ratios presented for the effect of the different light treatments (UV, Yellow and White Light) and average Temperature per night for experiment measuring the activity of bats in Gobabeb Namib Research Institute.

Table 3.1: Fixed effect components with Control (intercept) and Temperature (average), Light colour Ultraviolet (UV), White globe and Yellow globe. * = P<0.05; ** = P<0.02; *** = P<0.001.

Fixed effects:

	Estimate	Std. Error	z	value	Pr(>|z|)
Intercept	4.200732	1.799123	2.335	0.0195	*
Temperature	0.128962	0.000737	174.987	<2e-16	***
Light type [UV]	0.402902	0.007384	54.561	<2e-16	***
Light type [White]	1.388196	0.006391	217.224	<2e-16	***
Light type [Yellow]	0.961128	0.006722	142.983	<2e-16	***

3.5 Species richness at each light type

Eight species were identified during the experiment. These were *Tadarida aegyptiaca* (Egyptian free-tailed bat), *Sauromys petrophilus* (Robert's flat-headed bat), *Neoromicia zuluensis* (Zulu serotine), *Eptesicus hottentotus* (long-tailed serotine*), Laephotis namibensis* (Namibian long-eared bat), *Neoromicia capensis* (Cape serotine), *Rhinolophus damarensis* (Damara horseshoe bat) and *Nycteris thebaica* (Egyptian slit-faced bat). With the exception of *Nycteris thebaica* (Egyptian slit-faced bat) for which only four passes were recorded, all species identified were found at each light type and in darkness at the control. Species richness was unchanged between light and dark conditions.

3.6 Discussion

3.6.1 Activity of bats around lights

Overall bat activity increased significantly at the white light and was dominated by three species, *Neoromicia zuluensis* (Zulu serotine), *Tadarida aegyptiaca* (Egyptian free-tailed bat) and *Sauromys petrophilus* (Robert's flat-headed bat). These three species, individually, showed significant increases in activity at the white light as did *Eptesicus hottentotus* (long-tailed serotine). *Neoromicia capensis* (Cape serotine) showed the same trend at the white light although this was not significant. *Neoromicia zuluensis* (Zulu serotine) also showed significantly higher activity at the yellow light although not as high as at the white light. This trend was also observed in the other four species, *Tadarida aegyptiaca* (Egyptian free-tailed bat), *Sauromys*

petrophilus (Robert's flat-headed bat), *Eptesicus hottentotus* (long-tailed serotine) and *Neoromicia capensis* (Cape serotine). Two of these species, *Tadarida aegyptiaca* (Egyptian free-tailed bat) and *Sauromys petrophilus* (Robert's flat-headed bat) belong to the aerial hawking foraging guild while the other three, *Neoromicia zuluensis* (Zulu serotine), *Neoromicia capensis* (Cape serotine) and *Eptesicus hottentotus* (long-tailed serotine)*,* belong to the clutter-edge foraging guild. These results mirror those found in other studies where broadband white light has caused an increase in bat activity in bats in these foraging guilds (Gaisler *et al.*, 1998; Avila-Flores and Fenton, 2005; Rydell, 2006; Mathews *et al.*, 2015; Minnaar *et al.*, 2015; Stone, Harris and Jones, 2015; Spoelstra *et al.*, 2017).

Streetlights have traditionally been broadband white mercury vapour (MV) lights, broadband yellow high pressure sodium (HPS) lights and narrowband orange/yellow low pressure sodium (LPS) lights (Rydell, 2006). White light is composed of a greater range of wavelengths, which allows for good colour discrimination in humans although wavelength composition varies between brands and technology (Gaston *et al.*, 2013). Phototaxic insects are most strongly attracted to short wavelength light particularly at the ultraviolet end of the spectrum (Eisenbeiss and Hanel, 2009; Wakefield *et al.*, 2016, 2018). MV streetlights emit a larger proportion of short wavelength light than the HPS and LPS streetlights attracting more insects. Bat activity of bats in the aerial hawking and clutter-edge foraging guilds has been found to be highest around these lights (Rydell, 2006).

Like the MV streetlights the white compact fluorescent lights used in this experiment were also the most broadband of the three light types used. Figure 2.6 in Chapter 2 showed the emission spectra from the three experimental light types. Dominant wavelengths emitted by the experimental lights were: two peaks at 405 nm (violet) and 436 nm (violet) emitted by the UV light, five peaks at 611 nm (orange), 546 nm (green), 542 nm (green), 487 nm (blue) and 436 nm (violet) emitted by the white light and two peaks at 611 nm (orange) and 546 nm (green) emitted by the yellow light.

Like the MV lights in Europe, the white experimental lights recorded the highest increase in bat activity. The five species, *Tadarida aegyptiaca* (Egyptian free-tailed bat), *Sauromys petrophilus* (Robert's flat-headed bat), *Neoromicia zuluensis* (Zulu

serotine), *Eptesicus hottentotus* (long-tailed serotine) and *Neoromicia capensis* (Cape serotine) showing the greatest increases in activity are also in the aerial hawking and clutter-edge foraging guilds (Monadjem *et al.*, 2010).

Yellow HPS streetlights are not as broadband as MV streetlights but do still emit some short wavelength light. In Europe an increase in bat activity was recorded at HPS streetlights although not to the same extent as at the MV lights (Rydell, 2006). Like HPS streetlights, the yellow compact fluorescent experimental lights also emit some shorter wavelengths of light but are not as broadband as the white experimental lights. Similarly, an increase in activity in the same species found at the white light, was recorded at the experimental yellow lights although of a lower magnitude.

Yellow/orange LPS streetlights emit a narrowband almost monochromatic medium to long wavelength of light with no short wavelength light emissions. In Europe very little increases in activity were found at these lights (Rydell, 2006). There was no comparable light source used in the experiment.

The short wavelength light emitted by the experimental white and yellow lights used in the present research, will have been more attractive to insects (Eisenbeis, 2006; Justice and Justice, 2016; Wakefield *et al.*, 2016, 2018) and therefore bats (Rydell, 1992a, 2006) with the shorter purple and blue component of the white light being the most attractive.

In line with this interpretation are findings by Lewanzik and Voigt (2017) in Germany that bat activity at white light from light emitting diode (LED) lamps emitting a small component of short wavelength light is lower than bat activity at traditional white MV lamps emitting a larger range of short wavelength light.

An unexpected result from the experiment was the relatively small increase or even decrease in activity at the short wavelength UV light for the species most active at the white and yellow lights, *Tadarida aegyptiaca* (Egyptian free-tailed bat), *Sauromys petrophilus* (Robert's flat-headed bat), *Neoromicia zuluensis* (Zulu serotine), *Neoromicia capensis* (Cape serotine) and *Eptesicus hottentotus* (long-tailed serotine).

The greatest increases in activity were expected for this light as it would have attracted the most insects. No comparable light source was used in any of the European streetlight studies as UV light has no application for streetlighting as humans cannot see pure UV light and have trouble discriminating colour in near UV violet light (Gaston *et al.*, 2013). Increases in bat activity have been reported at UV light alone in the USA and Australia but without comparison to white light (Bell, 1980; Adams, Law and French, 2005)

Similar results to the current study were found by Spoelstra *et al.* (2017) in the Netherlands. Bats in the clutter-edge foraging genus, *Pipestrellus,* showed significantly greater increases in activity at a white light than at a short to medium wavelength green light. Insect activity was the same at both the green and the white lights. Bats in the genus *Pipestrellus* are among the most common species found foraging around street lights in Europe (Ancillotto *et al.*, 2016).

In this study only 165 passes were detected for the clutter feeding species, *Rhinolophus damarensis* (Damara horseshoe bat). Population densities of most bat species in Namibia are unknown and the low number of passes may be due to there being too few individuals in the area. This would be exacerbated by the fact that this bat uses a high frequency echolocation call with a peak frequency around 85 kHz (ACR, 2018). Higher frequencies of sound attenuate more quickly in the atmosphere and do not travel as far as lower frequencies. Bats using high frequency echolocation calls are more difficult to detect than bats using lower frequency echolocation calls as they need to be closer to the microphone to be detected (Monadjem *et al.*, 2017). *Rhinolophus damarensis* (Damara horseshoe bat) in this study showed the same light avoidance trend seen in species the same genus in the United Kingdom (Stone, Jones and Harris, 2009, 2012; Stone *et al.*, 2015; Stone, Harris and Jones, 2015) although it is difficult to draw conclusions with the small sample size.

Laephotis namibensis (Namibian long-eared bat) showed little reaction to any light type. This species is described as a clutter-edge forager (Monadjem *et al.*, 2010) but has very large ears and may employ a different foraging technique, which is unaffected by insects at light. Bats with large ears often rely on prey-generated sounds to detect prey (Altringham and Fenton, 2003).

Only four passes were recorded for *Nycteris thebaica* (Egyptian slit-faced bat) during experimental conditions. This is probably due to the fact that this gleaning species has a very low intensity echolocation call and has to be very close to the microphone to be detected (Monadjem *et al.*, 2010). This species is quite commonly seen around the study site. It is an interesting observation that all of the recorded passes were close to artificial lights, three at the UV light and one at the yellow light and not at the control, which would not be expected for a gleaning bat. *Nycteris thebaica* (Egyptian slit-faced bat) is known have a varied diet which includes scorpions (ACR, 2018). Scorpions fluoresce under UV light (Leeming, 2013) and it may be an advantage for this species to see in the UV range to visually detect scorpions. This warrants further investigation.

3.6.2 Species richness

With the exception of *Nycteris thebaica* (Egyptian slit-faced bat) with too few passes recorded, all species were recorded at all lights and the control during both dark and light phases. Species richness as measured by presence or absence was unchanged. This may be due to the fact that the study site on the edge of the treeline was in close proximity to habitat utilized by all three foraging guilds and those averse to light could quickly take cover. This could also be due to the short duration of the experiment with light periods interspersed with dark periods to limit any impact on the environment.

Chapter 4 Conclusion

4.1 Introduction

The results of this study showed clear evidence that activity levels of bats in the Namib Desert are affected by artificial lighting on a small scale and for a short duration. This suggests that the large-scale, long-term introduction of artificial lighting that goes with development has the potential to disrupt nocturnal desert ecosystems. Effects on bat activity levels were species specific and related to the foraging guilds to which the species belong and to the wavelengths of light emitted by the different colours of light used in the experiment.

4.2 Light sources and foraging guilds

Bat species within the same foraging guilds showed similar changes in activity at the different light sources. Open air foragers and clutter-edge foragers showed increased activity at the white light followed by the yellow light and very little increase in activity at the ultraviolet light. While the sample size was too small to draw firm conclusions, activity for the clutter feeding bat appeared to decrease most at white light, followed by ultraviolet light, with the least reduction at the yellow light.

4.4.1 Open air and clutter-edge foraging guilds

The small increase in activity at the ultraviolet light for bats in the open air and clutter-edge foraging guilds in comparison to the increases in activity at the white light found in this experiment was unexpected. Spoelstra *et al.* (2017) obtained a similar result in the Netherlands for a clutter-edge foraging genus *Pipestrellus* when comparing activity at a broadband white light to activity at a short to medium wavelength green light. They reported significantly higher activity at the white light compared to sites with shorter wavelength, green light. Insect activity was the same at both the green and the white lights. Bats in the genus *Pipestrellus* are the most common species found foraging around street lights in Europe.

Results from the present study, suggest that it is the combination of medium or long wavelength light together with the short wavelength light that is found in broadband

light sources, such as the experimental compact fluorescent white light, that result in the largest increases in bat activity, rather than short wavelength light alone.

Why the broadband white lighting would cause a greater increase in activity by these bats is unknown. A possible explanation is that some species of light tolerant bats are integrating information obtained through echolocation with information obtained through vision at broadband light sources especially when foraging in low intensity light on the periphery of the light cone.

All insectivorous bats have functional eyes although reliance on vision is probably species specific (Bell, 1985; Bell and Fenton, 1986; Altringham and Fenton, 2003; Appel *et al.*, 2017). The retinas of insectivorous bat eyes consist largely of rods for vision in dim light but some species do have a small number of cones, which enable colour vision in bright light in diurnal animals (Eklöf, 2003). An insectivorous bat, *Myotis velifer* (cave myotis), along with two fruit bats have functional S opsin and L/M opsin genes used for vision in short wavelength and medium to long wavelength light unusual in a nocturnal mammal (Wang *et al.*, 2003). This may be widespread among other bat species. Many bat species have shown increased obstacle avoidance ability in dim light when compared to either bright light or darkness indicating that vision may be important (Chase, 1981; Bell and Fenton, 1986; Eklöf, 2003; Orbach and Fenton, 2010; Boonman *et al.*, 2013). Voigt *et al.* (2017) found that migratory *Pipistrellus nathusii* (Nathusius's pipistrelle) responded to green light with positive phototaxis at distances greater than the echolocation detection range for insects during the migratory period suggesting that they are visually detecting the light source and using it for navigation.

Echolocation is superior to vision in locating small nearby targets but vision outperforms echolocation for larger targets further away especially in dim light (Boonman *et al.*, 2013). Larger sizes of moths are attracted to artificial lights, which may be more easily detected with a combination of vision and echolocation (van Langevelde *et al.*, 2011). Species foraging in open air unobstructed by vegetation may be more likely to integrate vision and echolocation, relying vision to detect larger prey items over longer distances while relying on echolocation at closer distances.

The only natural light sources bats evolved with, were moonlight and firelight. Moonlight is reflected sunlight and contains the same wavelengths as sunlight but in different proportions. Moonlight is red shifted, containing a greater proportion of long wavelength light due to the reflective properties of the surface of the moon and the fact that short wavelength light falls away travelling over longer distances (Ciocca and Wang, 2013). Many birds forage around natural fires, which are a natural source of long wavelength orange light, taking advantage of fleeing insects (Komarek, 1969). It is unknown if bats do the same. This suggests that vision in long and medium wavelengths of light may have an adaptive advantage.

Comparison of the emission spectra for narrowband low pressure sodium and broadband high pressure sodium, metal halide and light emitting diode streetlights with wavelengths of peak, visual-pigment, light absorbance of 213 species of arthropod, bird, mammal and reptile found that broadband light from HPS, MH and LED lighting was most likely to contain wavelengths falling within the range of peak absorbance for many taxa (Davies *et al.*, 2013). Mammals and birds benefitted more than arthropods and reptiles from the long wavelength narrowband LPS light.

Visual acuity and reliance on vision is highly species specific (Bell and Fenton, 1986; Appel *et al.*, 2017). Some species increase activity on moonlit nights while others become less active. The slower flying, clutter feeding and gleaning bats tend to avoid light, possibly to avoid predation or disorientation when temporarily blinded by bright light (Stone, Jones and Harris, 2009; McGuire and Fenton, 2010). Clutter feeding bats may be more reliant on echolocation due to the crowded nature of their optimal foraging habitat and the superiority of echolocation in detecting small objects as close range (Boonman *et al.*, 2013).

In this study the exception was *Laephotis namibensis* (Namibian long-eared bat)*.* This bat is also classified as a clutter-edge foraging bat (Monadjem *et al.*, 2010) but showed very little change in activity at any light source. While *Laephotis namibensis* (Namibian long-eared bat) is classified as a clutter-edge forager, it has very large ears and a short, low intensity echolocation call similar to some gleaning bats (Monadjem *et al.*, 2010) suggesting that it may be more reliant on hearing faint echoes and prey generated sounds than other bats in this guild. If the increase in activity at the broadband light sources for bats in the open air and clutter-edge

foraging guilds is due to greater integration of vision and echolocation rather than the presence of the prey aggregation alone and *Laephotis namibensis* (Namibian long-eared bat) is more reliant on auditory cues for foraging, then similar increases in activity at the lights would not be expected for this species.

4.2.2 Clutter feeding and gleaning bats

There were two bats in this guild. Sample sizes for both species were very small. Results for *Rhinolophus damarensis* (Damara horseshoe bat) at all light types were insignificant but hinted at the same trend of reduced activity at artificial lighting. For *Nycteris thebaica* there was insufficient data to include in the analysis.

4.3 Implications of increased bat activity at artificial lights

As development and artificial lighting spread into previously dark areas various changes can be expected in the long term. Bats that benefit from prey aggregations at light sources are likely to increase in numbers due to access to an abundant food source (Ancillotto *et al.*, 2016; Zhigalin and Moskvitina, 2017).

Schoeman (2016) classifies bats into three different guilds depending on how well they adapt to living in an urban environment. These guilds are: urban exploiters, urban adaptors and urban avoiders. Urban exploiters thrive in human environments, roosting in buildings and foraging around lights. Urban adaptors adapt their behaviour to survive in an urban environment. Urban avoiders reduce in numbers. Urban exploiters and urban adaptors are most often bats in the open air or clutter feeding guilds while urban avoiders tend to be clutter feeding or gleaning bats.

Of the bat species in the study which showed increased activity at artificial lighting, *Tadarida aegyptiaca* (Egyptian free-tailed bat) and *Neoromicia capensis* (Cape serotine) are already well known to exploit urban environments as they use human structures in buildings and houses as roost sites and forage around lights (Monadjem *et al.*, 2010; Minnaar *et al.*, 2015; Schoeman, 2016). In the natural environment *Sauromys petrophilus* (Robert's flat-headed bat) roosts in narrow rock crevices, *Neoromicia zuluensis* (Zulu serotine) is thought to roost in vegetation as the species is closely associated with riparian woodland and *Eptesicus hottentotus* (long-tailed serotine) is associated with hollows in rocky outcrops and buildings (Monadjem *et al.*, 2010; ACR, 2018). Human buildings have concrete and wooden

structures which could provide similar crevices and hollows to the natural roost sites of these species.

Increasing abundance of these species in direct association with human habitation due to an artificially created ecosystem centred on an abundance of prey around artificial lighting could have implications for human health. In South Africa Duvenhage's disease, Marburg disease, Lagos Bat Fever and a MERS-like corona virus are thought to have bats as primary hosts (Liebenberg *et al.*, 2006; Swanepoel *et al.*, 2007; Hayman *et al.*, 2010; Corman *et al.*, 2014). Research is needed in urban areas in Namibia to determine the most common species to be urban exploiters and adapters so this information can be utilized by virologists to direct research into areas where the greatest threat of emerging diseases could be expected.

Aside from the immediate threat to human health the artificially increased abundance of these species is likely to have detrimental effects on nocturnal desert ecosystems. The bulk of phototaxic insects around lights are Lepidopterans. These insects are extremely important nocturnal pollinators (Frank, 2006; MacGregor *et al.*, 2015; Macgregor *et al.*, 2017; van Langevelde *et al.*, 2018). Bats opportunistically feed on these insects as they aggregate around artificial lights. As a result a greater proportion of lepidopterans have been found in the diet of *Neoromicia capensis* (Cape serotine) when foraging around lights than when foraging in darkness (Minnaar *et al.*, 2015). Removal of these insects from the environment in large numbers due to increased predation by bats is likely to affect plant pollination (Macgregor *et al.*, 2015, 2017; Knop *et al.*, 2017).

4.4 Mitigating measures

White light caused the largest changes in activity, both negative and positive, for all foraging guilds overall. Unfortunately white light is being used more frequently in streetlights because its broadband composition improves human colour perception at night (Gaston *et al.*, 2013).

There are some general mitigating measures which can be taken to decrease the impact of artificial lighting on the environment which are relevant worldwide (Stone, Harris and Jones, 2015; The International Dark-Sky Association, 2018).

1. Use lighting only when necessary.

2. Commercial lighting that emits more longwave light, and the minimum amount of shortwave light necessary for its intended purpose, can be used in place of broadband white light.

3. Lighting can be directed to the area that needs to be lit.

4. Lights can dimmed to a level where illumination is sufficient but not excessive or switched off entirely during non-peak times or triggered to come on when movement is detected.

5. Lights can be shielded on top to reduce the amount of light leaking upwards.

6. Dark corridors and dark areas can be created in areas with populations of light aversive bats to enable them to commute to their foraging grounds and forage undisturbed.

In addition for the Namib Desert in particular, care should be taken to minimise artificial lighting in areas bordering the ephemeral rivers and associated riparian woodland, which provide valuable habitat for many organisms (Jacobson, Jacobson and Seely, 1995) and where bat activity is highest. Care should also be taken with development in the vicinity of potential bat roosting sites especially caves. *Rhinolophus damarensis* (Damara horseshoe bat), which may be light avoidant, roosts in caves and rock hollows. Other clutter feeding and gleaning bats reported from the Namib Desert, *Rhinolophus denti* (Dent's horseshoe bat), *Hipposideros caffer* (Sundevall's leaf-nosed bat), *Nycteris thebaica* (Egyptian slit-faced bat) and *Macronycteris vittatus* (striped leaf-nosed bat) all roost in caves or rock hollows and may also be light avoidant. In Europe species in the *Rhinolophus* genus have abandoned roost sites and suffered retarded growth rates when roost sites were aesthetically illuminated (Onkelinx, 2017). Where development is essential in these areas, lights can be directed away from the sensitive areas and limited to narrowband long wavelength light sources providing illumination but causing the least environmental disturbance.

4.5 Use of artificial light as a bat repellent

While it is illegal in Europe to cause harm or disturbance to any bat roost (UK Government, 2014) this is not the case globally. In Namibia over 100 poisoned bats have been found outside the Zambian High Commission on two separate occasions

in what was suspected to be targeted extermination of a bat roost with pesticide (Hartman, 2014). Ultraviolet light has been used on wind turbines to repel *Lasiurus cinereus semotus* (Hawaiian hoary bat) (Gorresen *et al.*, 2015).

During the course of this study the researcher was frequently asked for methods to humanely relocate bats from houses and deter roosting in certain structures due to hygiene and disease concerns. This study has shown that artificial white light in a potential roosting area may repel *Rhinolophus damarensis* (Damara horseshoe bat) and possibly other rhinolophid and clutter feeding species (Rowse *et al.*, 2016; Onkelinx, 2017). The activity of *Tadarida aegyptiaca* (Egyptian free-tailed bat), *Sauromys petrophilus* (Robert's flat-headed bat), *Neoromicia zuluensis* (Zulu serotine), *Neoromicia capensis* (Cape serotine) and *Eptesicus hottentotus* (long-tailed serotine) increased at white light during foraging hours, however most bat species choose dark roosts (Monadjem *et al.*, 2010). A future avenue for research would be to investigate the effect of artificial light within roosts during the day. While disturbing roosts should be avoided if possible, especially during maternity periods, the use of artificial lighting to deter bats from roosting or to relocate bats from roost sites is preferable to extermination at a later date.

4.6 Strengths and shortcomings of this experiment and areas for future research

A strength of this experiment was that it took place in a minimally developed rural setting in a National Park 100 km from the nearest town. This limited the confounding effects on bat activity due to additional anthropogenic changes to the environment other than the introduction of artificial lighting that may have been present in an urban environment.

Another strength of this experiment was that it compared bat activity at an almost monochromatic source of short wavelength near-ultraviolet lighting with activity at more traditional broadband white and yellow sources. This enabled a more precise understanding on the effects on bat activity of short wavelengths of light alone without the confounding effects of additional longer wavelengths found in more broadband light sources.

A shortcoming of this experiment was that it was localised to one place in the Central Namib Desert. It should be repeated at other locations for future research. In particular it should be repeated in an area with a higher population density of bats from the families Rhinolophidae, Hipposideridae and Nycteridae. Currently there is very little known globally about how artificial lighting affects the activity of hipposiderids and nycterids. Bats in these families are predominantly clutter feeding and gleaning bats so it would be predicted that they would avoid artificial lighting, however, the fact that four of the five passes recorded for *Nycteris thebaica* during the experiment were at lights suggests that this species may increase in activity at artificial lighting.

Further research should quantify and identify insects at the different light sources in different localities. The unexpected lack of increase in bat activity at the ultraviolet light made this a shortcoming of the current experiment even though there is a large volume of literature describing the effects of different light sources on the attraction of phototaxic insects (Barghini and De Medeiros, 2012; Justice and Justice, 2016). Anecdotally, however, the researcher has conducted numerous night walks for school groups in the area using an ultraviolet flashlight to detect scorpions. Insects attracted to the ultraviolet flashlight frequently become so numerous that ultraviolet flashlight is only used intermittently in favour of a white flashlight. The diet of various bat species could be compared under both lit and dark conditions to the insect species attracted to the lights.

Another area for future research would be to examine which bat species have benefited from the artificial ecosystem created by urbanisation and are most commonly found living in close association with humans. This information could be valuable to both conservationists and virologists and possibly to farmers wanting to increase bat abundance on farms to make use of bat ecosystem services.

4.7 Conclusion

The study showed clear changes in bat activity levels in response to the introduction of artificial lighting. Responses were species specific related to foraging guild and dependent on the wavelength composition of the light emitted from the different light sources. The results imply that the introduction of large scale artificial lighting with development has the potential to cause large changes to the environment with

ramifications for human health but there are steps that can be taken to minimise the impact. In addition artificial lighting could also be used to repel bats in some circumstances. The study has generated many questions and highlighted some new avenues for future research.

References

Acharya, L. and Fenton, M. B. (1999) 'Bat attacks and moth defensive behaviour around street lights', *Canadian Journal of Zoology*. NRC Research Press Ottawa, Canada , 77(1), pp. 27–33. doi: 10.1139/z98-202.

ACR (2018) *African Chiroptera Report 2018*. Pretoria. Available at: http://www.africanbats.org.

Adams, M. D., Law, B. S. and French, K. O. (2005) 'Effect of lights on activity levels of forest bats: Increasing the efficiency of surveys and species identification', *Wildlife Research*. doi: 10.1071/WR04060.

Agranat, I. (2013) 'Bat species identification from zero crossing and full spectrum echolocation calls using Hidden Markov Models, Fisher scores, unsupervised clustering and balanced winnow pairwise classifiers', 010016, pp. 010016–010016. doi: 10.1121/1.4799403.

Aldridge, H. D. J. N. and Rautenbach, I. L. (1987) 'Morphology, Echolocation and Resource Partitioning in Insectivorous Bats', *The Journal of Animal Ecology*. British Ecological Society, 56(3), p. 763. doi: 10.2307/4947.

Altringham, J. D. and Fenton, M. B. (2003) 'Sensory Ecology and Communication in the Chiroptera', in Kunz, T. H. and Fenton, M. B. (eds) *Bat Ecology*. 1st edn. Chicago: The University of Chicago Press, pp. 90–117.

Ancillotto, L. *et al.* (2016) 'Extraordinary range expansion in a common bat: The potential roles of climate change and urbanisation', *Science of Nature*, 103(3–4). doi: 10.1007/s00114-016-1334-7.

Appel, G. *et al.* (2017) 'Aerial insectivorous bat activity in relation to moonlight intensity', *Mammalian Biology - Zeitschrift für Säugetierkunde*, 85, pp. 37–46. doi: 10.1016/j.mambio.2016.11.005.

Ast Reisen (no date) *Ast Reisen Namib Naukluft map - Google Search*. Available at: https://www.google.com.na/search?q=Ast+Reisen+Namib+Naukluft+map&rlz=1C1 CHMO_en-

GBNA586NA586&tbm=isch&source=iu&ictx=1&fir=s_Mxq6wiM6cc3M%253A%252Ct_IEA5HvoLTDoM%252C_&usg=AFrqEzeB35Y8kIvwM5MNIRxs9x4EE5qgfg&sa=X&ved=2ahUKEwj99PCosOLcAhVDAsAKHQP6Bz0Q9QEwAX (Accessed: 10 August 2018).

Avila-Flores, R. and Fenton, M. B. (2005) 'Use of Spatial Features By Foraging Insectivorous Bats in a Large Urban Landscape', *Journal of Mammalogy*. Oxford University Press, 86(6), pp. 1193–1204. doi: 10.1644/04-MAMM-A-085R1.1.

Azam, C. *et al.* (2015) 'Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats?', *Global Change Biology*. doi: 10.1111/gcb.13036.

Azam, C. *et al.* (2016) 'Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program', *Landscape Ecology*, 31(10), pp. 2471–2483. doi: 10.1007/s10980-016-0417-3.

Azam, C. *et al.* (2018) 'Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity', *Landscape and Urban Planning*, 175(December 2016), pp. 123–135. doi: 10.1016/j.landurbplan.2018.02.011.

Barghini, A. and De Medeiros, B. A. S. (2012) 'UV Radiation as an Attractor for Insects', *The Journal of the Illuminating Engineering Society*, 9(1), pp. 47–56. Available at: https://www.tandfonline.com/doi/abs/10.1582/LEUKOS.2012.09.01.003 (Accessed: 20 August 2018).

Bates, D. *et al.* (2019) 'Package "lme4"'. Available at: https://github.com/lme4/lme4/.

Beier, P. (2006) 'Effects of Artificial Night Lighting on Terrestrial Mammals', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 19–43.

Bell, G. P. (1980) 'Habitat use and response to patches of prey by desert insectivorous bats', *Canadian Journal of Zoology*. doi: 10.1139/z80-256.

Bell, G. P. (1985) 'The sensory basis of prey location by the California leaf-nosed bat Macrotus californicus (Chiroptera: Phyllostomidae)', *Behavioral Ecology and Sociobiology*. Springer-Verlag, 16(4), pp. 343–347. doi: 10.1007/BF00295547.

Bell, G. P. and Fenton, M. B. (1986) 'Visual acuity, sensitivity and binocularity in a

gleaning insectivorous bat, Macrotus californicus (Chiroptera: Phyllostomidae)', *Animal Behaviour*. Academic Press, 34(2), pp. 409–414. doi: 10.1016/S0003-3472(86)80110-5.

Bennie, J. *et al.* (2016) 'Ecological effects of artificial light at night on wild plants', *Journal of Ecology*, 104(3). doi: 10.1111/1365-2745.12551.

Blake, D. *et al.* (1994) 'Use of lamplit roads by foraging bats in southern England', *Journal of Zoology*, 234(3), pp. 453–462. doi: 10.1111/j.1469-7998.1994.tb04859.x.

Boonman, A. *et al.* (2013) 'It's not black or white—on the range of vision and echolocation in echolocating bats', *Frontiers in Physiology*. Frontiers, 4, p. 248. doi: 10.3389/fphys.2013.00248.

Brüning, A. *et al.* (2015) 'Spotlight on fish: Light pollution affects circadian rhythms of European perch but does not cause stress', *Science of The Total Environment*. Elsevier, 511, pp. 516–522. doi: 10.1016/J.SCITOTENV.2014.12.094.

Brüning, A. *et al.* (2016) 'Impact of different colours of artificial light at night on melatonin rhythm and gene expression of gonadotropins in European perch', *Science of The Total Environment*. Elsevier, 543, pp. 214–222. doi: 10.1016/J.SCITOTENV.2015.11.023.

Chase, J. (1981) 'Visually guided escape responses of microchiropteran bats', *Animal Behaviour*. Academic Press, 29(3), pp. 708–713. doi: 10.1016/S0003-3472(81)80005-X.

Ciechanowski, M. *et al.* (2007) 'Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter', *Canadian Journal of Zoology*, 86(3), pp. 236–236. doi: 10.1139/Z08-025.

Ciocca, M. and Wang, J. (2013) 'By the light of the silvery Moon: fact and fiction', *Physics Education*. IOP Publishing, 48(3), pp. 360–367. doi: 10.1088/0031-9120/48/3/360.

Cleveland, C. J. *et al.* (2006) 'Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas', *Frontiers in Ecology and the Environment*. Wiley-Blackwell, 4(5), pp. 238–243. doi: 10.1890/1540-9295(2006)004[0238:EVOTPC]2.0.CO;2.

Coetzee, B. (2019) *Light pollution: the dark side of keeping the lights on*, *The Conversation*. Available at: http://theconversation.com/light-pollution-the-dark-side-of-keeping-the-lights-on-113489 (Accessed: 11 August 2019).

Corman, V. M. *et al.* (2014) 'Rooting the Phylogenetic Tree of Middle East Respiratory Syndrome Coronavirus by Characterization of a Conspecific Virus from an African Bat', *Journal of Virology*, 88(19), pp. 11297–11303. doi: 10.1128/JVI.01498-14.

Cunningham, P. (2002) 'Colubridae: Lamprophis fuliginosus, brown house-snake. Foraging.', *African Herp News*, (34), pp. 28–29.

Davies, T. W. *et al.* (2013) 'Artificial light pollution: Are shifting spectral signatures changing the balance of species interactions?', *Global Change Biology*, 19(5), pp. 1417–1423. doi: 10.1111/gcb.12166.

Degen, T. *et al.* (2016) 'Street lighting: sex-independent impacts on moth movement', *The Journal of animal ecology*, 85(5). doi: 10.1111/1365-2656.12540.

Dominoni, D. M., Borniger, J. C. and Nelson, R. J. (2016) 'Light at night, clocks and health: from humans to wild organisms', *Biology Letters*, 12(2). doi: 10.1098/rsbl.2016.0015.

Dominoni, D. M., Partecke, J. and Partecke, J. (2015) 'Does light pollution alter daylength? A test using light loggers on free-ranging european blackbirds (turdus merula)', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667). doi: 10.1098/rstb.2014.0118.

Dusquene Light (2013) *Commercial Energy Library*, *Apgee Interactive Inc.* Available at: https://c03.apogee.net/contentplayer/?coursetype=ces&utilityid=duquesnelight&id=19163 (Accessed: 17 July 2019).

Dwyer, R. G. *et al.* (2013) 'Shedding light on light: Benefits of anthropogenic illumination to a nocturnally foraging shorebird', *Journal of Animal Ecology*, 82(2), pp. 478–485. doi: 10.1111/1365-2656.12012.

Eckardt, F. D. *et al.* (2013) 'The nature of moisture at Gobabeb, in the central Namib Desert', *Journal of Arid Environments*. Academic Press, 93, pp. 7–19. doi: 10.1016/J.JARIDENV.2012.01.011.

Eisenbeis, G. (2006) 'Artficial Night Lighting and Insects: Attraction of Insects to Streetlamps in a Rural Setting in Germany', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 281–304.

Eisenbeiss, G. and Hanel, A. (2009) 'Light pollution and the impact of artificial night lighting on insects', in McDonnell, M. J., Hahs, A. H., and Breuste, J. H. (eds) *Ecology of Cities and Towns*. 1st edn. Cambridge: Cambridge University Press, pp. 243–263. Available at: http://wikinight.free.fr/wp-content/uploads/anpcen/Spectre lampes vs Environnement nocturne v2/Impact biodiversite/Chapter 15 Eisenbeis and Hanel with pictures_final2.pdf (Accessed: 3 September 2018).

Eklöf, J. (2003) *Vision in Echolocating Bats*. Göteborg University.

Falchi, F. *et al.* (2016) 'The new world atlas of artificial night sky brightness', *Science Advances*, 2(6). doi: 10.1126/sciadv.1600377.

Federico, P. *et al.* (2008) 'Brazilian free-tailed bats as insect pest regulators in transgenic and conventional cotton crops', *Ecological Applications*. Wiley-Blackwell, 18(4), pp. 826–837. doi: 10.1890/07-0556.1.

Field, A., Miles, J. and Field, Z. (2012) *Discovering statistics using R*. 1st edn. London: Sage Publications.

Frank, K. (2006) 'Effects of Artificial Night Lighting on Moths', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 305–344.

Froidevaux, J. S. P. *et al.* (2017) 'Factors driving population recovery of the greater horseshoe bat (Rhinolophus ferrumequinum) in the UK: implications for conservation', *Biodiversity and Conservation*, 26(7), pp. 1601–1621. doi: 10.1007/s10531-017-1320-1.

Gaisler, J. *et al.* (1998) 'Habitat preference and flight activity of bats in a city', *Journal of Zoology*. Wiley/Blackwell (10.1111), 244(3), pp. 439–445. doi: 10.1111/j.1469-7998.1998.tb00048.x.

Gaston, K. J. *et al.* (2013) 'The ecological impacts of nighttime light pollution: a mechanistic appraisal', *Biological Reviews*. Wiley/Blackwell (10.1111), 88(4), pp. 912–927. doi: 10.1111/brv.12036.

Gaston, K. J. *et al.* (2017) 'Impacts of Artificial Light at Night on Biological Timings', *Annual Review of Ecology, Evolution, and Systematics*. Annual Reviews , 48(1), pp. 49–68. doi: 10.1146/annurev-ecolsys-110316-022745.

Gaston, K. J. and Bennie, J. (2014) 'Demographic effects of artificial nighttime lighting on animal populations', *Environmental Reviews*, 22(4), pp. 323–330. doi: 10.1139/er-2014-0005.

Gaston, K. J., Visser, M. E. and Hölker, F. (2015) 'The biological impacts of artificial light at night: the research challenge.', *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*. The Royal Society, 370(1667), p. 20140133. doi: 10.1098/rstb.2014.0133.

Gauthreaux, S. and Belser, C. (2006) 'Effects of Artificial Night Lighting on Migrating Birds', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 67–93.

Giraudox, P. (2018) 'pgirmess: Spatial Analysis and Data Mining for Field Ecologists'. Available at: https://cran.r-project.org/package=pgirmess.

Gorresen, P. M. *et al.* (2015) 'Dim ultraviolet light as a means of deterring activity by the Hawaiian hoary bat Lasiurus cinereus semotus', *Endangered species research*, 28, pp. 249–247. doi: 10.3354/esr00694.

Grüebler, M. U., Morand, M. and Naef-Daenzer, B. (2008) 'A predictive model of the density of airborne insects in agricultural environments', *Agriculture, Ecosystems and Environment*, 123(1–3), pp. 75–80. doi: 10.1016/j.agee.2007.05.001.

Halat, Z. *et al.* (2018) 'Sociality and insect abundance affect duration of nocturnal activity of male parti-colored bats', *Journal of Mammalogy*, 99(6). doi: 10.11821/dlxb201802008.

Hale, J. D. *et al.* (2015) 'The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats', *Global Change Biology*, 21(7). doi: 10.1111/gcb.12884.

Hartman, J. (2014) 'More control needed over pesticides', *The Namibian*, 22 May. Available at: https://www.namibian.com.na/print.php?id=123562&type=2.

Hayman, D. T. S. *et al.* (2010) 'Long-Term Survival of an Urban Fruit Bat Seropositive for Ebola and Lagos Bat Viruses', *PLoS ONE*, 5(8), pp. 2008–2010.

doi: 10.1371/journal.pone.0011978.

Hölker, F., Wolter, C., *et al.* (2010) 'Light pollution as a biodiversity threat.', *Trends in ecology & evolution*. Elsevier, 25(12), pp. 681–2. doi: 10.1016/j.tree.2010.09.007.

Hölker, F., Moss, T., *et al.* (2010) 'The dark side of light: A transdisciplinary research agenda for light pollution policy', *Ecology and Society*, 15(4). doi: 10.5751/ES-03685-150413.

Jackle, J. A. (2001) *City Lights: Illuminating the American night.* Baltimore: John Hopkins University Press.

Jacobson, P. J., Jacobson, K. M. and Seely, M. K. (1995) *Ephemeral Rivers and their catchments: Sustaining People and Development in Western Namibia.* Windhoek: Desert Research Foundation of Namibia.

Jones, G. *et al.* (2009) 'Carpe noctem: the importance of bats as bioindicators', *Endangered Species Research*, 8(1–2), pp. 93–115. doi: 10.3354/esr00182.

Jones, G. and Rydell, J. (2003) 'Attack and Defense: Interactions between echolocating bats and their insect prey', in Kunz, T. H. and Fenton, M. B. (eds) *Bat Ecology.* 1st edn. Chicago: The University of Chicago Press, pp. 301–345.

Justice, M. J. and Justice, T. C. (2016) 'Attraction of Insects to Incandescent, Compact Fluorescent, Halogen, and Led Lamps in a Light Trap: Implications for Light Pollution and Urban Ecologies', *Entomological News*. American Entomological Society , 125(5), pp. 315–326. doi: 10.3157/021.125.0502.

Kalka, M. B., Smith, A. R. and Kalko, E. K. V (2008) 'Bats limit arthropods and herbivory in a tropical forest.', *Science (New York, N.Y.).* American Association for the Advancement of Science, 320(5872), p. 71. doi: 10.1126/science.1153352.

Knop, E. *et al.* (2017) 'Artificial light at night as a new threat to pollination', *Nature*, 548(7666). doi: 10.1038/nature23288.

Komarek, E. V (1969) *Fire and Animal Behavior.* Available at: http://talltimbers.org/wp-content/uploads/2014/03/Komarek1969_op.pdf (Accessed: 27 September 2018).

Korine, C. *et al.* (2015) 'Effect of water quality on species richness and activity of desert-dwelling bats', *Mammalian Biology*, 80(3). doi:

10.1016/j.mambio.2015.03.009.

Krauel, J. J. and LeBuhn, G. (2016) 'Patterns of Bat Distribution and Foraging Activity in a Highly Urbanized Temperate Environment', *PLOS ONE*. Edited by L.-F. Bersier. Public Library of Science, 11(12), p. e0168927. doi: 10.1371/journal.pone.0168927.

Kuijper, D. P. J. *et al.* (2008) 'Experimental evidence of light disturbance along the commuting routes of pond bats (Myotis dasycneme)', *Lutra*, 51(1), pp. 37–49. Available at: http://www.vzz.nl (Accessed: 3 September 2018).

Kunz, T. H. *et al.* (2011) 'Ecosystem services provided by bats', *Annals of the New York Academy of Sciences*, 1223(1), pp. 1–38. doi: 10.1111/j.1749-6632.2011.06004.x.

Kyba, C. C. M. *et al.* (2011) 'Cloud Coverage Acts as an Amplifier for Ecological Light Pollution in Urban Ecosystems', *PLoS ONE*. Edited by J. Añel. Public Library of Science, 6(3), p. e17307. doi: 10.1371/journal.pone.0017307.

Kyba, C. C. M. *et al.* (2017) 'Artificially lit surface of Earth at night increasing in radiance and extent', *Science Advances*. American Association for the Advancement of Science, 3(11), p. e1701528. doi: 10.1126/sciadv.1701528.

Lacoeuilhe, A. *et al.* (2014) 'The influence of low intensities of light pollution on bat communities in a semi-natural context', *PLoS ONE*. doi: 10.1371/journal.pone.0103042.

Lancaster, J., Lancaster, N. and Seely, M. (1984) 'Climate of the central Namib Desert', *Madoqua*. Sabinet, 14(1), pp. 5–61. Available at: https://www.ingentaconnect.com/content/sabinet/madoqua/1984/00000014/00000 001/art00002 (Accessed: 24 July 2018).

van Langevelde, F. *et al.* (2011) 'Effect of spectral composition of artificial light on the attraction of moths', *Biological Conservation*. Elsevier Ltd, 144(9), pp. 2274–2281. doi: 10.1016/j.biocon.2011.06.004.

van Langevelde, F. *et al.* (2018) 'Declines in moth populations stress the need for conserving dark nights', *Global Change Biology*, 24(3). doi: 10.1111/gcb.14008.

Lebbin, D. J. *et al.* (2007) 'Nocturnal Migrants Foraging at Night by Artificial Light', *The Wilson Journal of Ornithology*, 119(3), pp. 506–508. doi: 10.1676/06-139.1.

Leeming, J. (2013) *Scorpions of Southern Africa*. 1st edn. Cape Town: Random House Struik (Pty) Ltd.

Lewanzik, D. and Voigt, C. C. (2017) 'Transition from conventional to light-emitting diode street lighting changes activity of urban bats', *Journal of Applied Ecology*, 54(1). doi: 10.1111/1365-2664.12758.

Liebenberg, C. *et al.* (2006) 'Fatal Human Infection with rabies related Duvenhage virus, South Africa', *Emerging infectious diseases*, 12(12), pp. 12–14. doi: https://dx.doi.org/10.3201%2Feid1212.060764.

Limpens, H. (2004) 'Field Identification: Using bat detectors to identify species', in Brigham, R. et al. (eds) *Bat Echolocation Research: Tools, Techniques and Analysis*. 1st edn. Austin: Bat Conservation International, pp. 46–57. Available at: https://www.researchgate.net/publication/281210205 (Accessed: 6 August 2018).

Luedecke, D. and Schwemmer, C. (2019) 'Package "sjPlot"'. Available at: https://github.com/strengejacke/sjPlot.

Macgregor, C. J. *et al.* (2015) 'Pollination by nocturnal Lepidoptera, and the effects of light pollution: A review', *Ecological Entomology*, 40(3), pp. 187–198. doi: 10.1111/een.12174.

Macgregor, C. J. *et al.* (2017) 'The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport', *Global Change Biology*, 23(2). doi: 10.1111/gcb.13371.

MacGregor, C. J. *et al.* (2015) 'Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review.', *Ecological entomology*, 40(3), pp. 187–198. doi: 10.1111/een.12174.

Manfrin, A. *et al.* (2017) 'Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem', *Frontiers in Environmental Science*, 5(OCT). doi: 10.3389/fenvs.2017.00061.

Mathews, F. *et al.* (2015) 'Barriers and benefits: Implications of artificial night-lighting for the distribution of common bats in britain and ireland', *Philosophical Transactions of the Royal Society B: Biological Sciences*. Royal Society of London, 370(1667). doi: 10.1098/rstb.2014.0124.

McGuire, L. P. and Fenton, M. B. (2010) 'Hitting the Wall: Light Affects the Obstacle

Avoidance Ability of Free-Flying Little Brown Bats (*Myotis lucifugus*)', *Acta Chiropterologica*. Museum and Institute of Zoology at the Polish Academy of Science , 12(1), pp. 247–250. doi: 10.3161/150811010X504734.

Minnaar, C. *et al.* (2015) 'Stacking the odds: Light pollution may shift the balance in an ancient predator-prey arms race', *Journal of Applied Ecology*, 52(2). doi: 10.1111/1365-2664.12381.

Monadjem, A. *et al.* (2010) *Bats of Southern and Central Africa*. 1st edn. Edited by M. Mossmer. Johannesburg: Wits University Press.

Monadjem, A. *et al.* (2017) 'Acoustic Call Library and Detection Distances for Bats of Swaziland', *Acta Chiropterologica*, 19(1), pp. 175–187. doi: 10.3161/15081109ACC2017.19.1.014.

Montevecchi, W. (2006) 'Influences of Artificial Light on Marine Birds', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 94–113.

Namiba Statistics Agency (2011) *Namibia Population and Housing Census Data - Namibia Data Portal*, *Namibia Statistics Agency*. Available at: http://namibia.opendataforafrica.org/NDPNPHCV2017/namibia-population-and-housing-census-data (Accessed: 26 July 2018).

Namibia Statistics Agency (2011) *Population census - GRN Portal*, *Namibian Government*. Available at: http://www.gov.na/population#main-content (Accessed: 26 July 2018).

Namibian Government (2016) *Target Sectors - Invest in Namibia Conference 2016*. Available at: http://www.investnamibia.com.na/about/target-sectors (Accessed: 25 July 2018).

Neuweiler, G. (1981) 'Sinnesadaptation am Beispiel echoortender Fledermause', *Nova Acta Leopoldina*, (54), pp. 487–503.

New Era (2014) *Gondwana's innovative hotel in Swakopmund | New Era Newspaper Namibia*, *New Era*. Available at: https://www.newera.com.na/2014/09/11/gondwanas-innovative-hotel-in-swakopmund/ (Accessed: 26 July 2018).

New Era (2016) *Mass houses' allocation resumes at the coast*, *New Era*. Available

at: https://www.newera.com.na/2016/05/30/mass-houses-allocation-resumes-coast/ (Accessed: 26 July 2018).

New Era (2017) 'Desert Rose Project go ahead', *New Era*, 28 June. Available at: https://www.newera.com.na/2017/06/28/desert-rose-project-to-go-ahead/.

Nordhaus, W. (1996) 'Do Real-Output and Real-Wage Measures Capture Reality? A History of Lighting suggests not', in Breshnahan, T. and Gordon, R. (eds) *The Economics of New Goods*. 1st edn. Chicago: University of Chicago Press, pp. 27–70. Available at: http://www.nber.org/chapters/c6064.pdf (Accessed: 19 July 2018).

Onkelinx, T. (2017) 'Comment on "age of enlightenment: Long-term effects of outdoor aesthetic lights on bats in churches"', *Royal Society Open Science*, 4(11). doi: 10.1098/rsos.171312.

Orbach, D. N. and Fenton, B. (2010) 'Vision Impairs the Abilities of Bats to Avoid Colliding with Stationary Obstacles', *PLoS ONE*. Edited by R. Arlettaz. Public Library of Science, 5(11), p. e13912. doi: 10.1371/journal.pone.0013912.

Ottolenghi, R. and Watson, B. (2010) *Toward a National Urbanization Strategy for Namibia: Issue analysis and key recommendations*. Windhoek. Available at: http://ilmi.nust.na/sites/default/files/towards-a-national-urbanization-strategy-Namibia.pdf (Accessed: 6 September 2019).

Ouyang, J. Q. *et al.* (2015) 'Stressful colours: corticosterone concentrations in a free-living songbird vary with the spectral composition of experimental illumination.', *Biology letters*. The Royal Society, 11(8), p. 20150517. doi: 10.1098/rsbl.2015.0517.

Ouyang, J. Q., Davies, S. and Dominoni, D. (2018) 'Hormonally mediated effects of artificial light at night on behavior and fitness: linking endocrine mechanisms with function', *The Journal of Experimental Biology*, 221(6). doi: 10.1242/jeb.156893.

Park, K. J. (2015) 'Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators', *Mammalian Biology - Zeitschrift für Säugetierkunde*. Urban & Fischer, 80(3), pp. 191–204. doi: 10.1016/J.MAMBIO.2014.10.004.

Parsons, S. and Szewczak, J. (2009) 'Detecting, Recording, and Analysing the Vocalizations of Bats', in Kunz, T. and Parsons, S. (eds) *Ecological and Behavioral Methods for the Study of Bats*. 2nd edn. Baltimore: The John Hopkins University

Press, pp. 91–111.

Pattinson, C. L. *et al.* (2016) 'Environmental Light Exposure Is Associated with Increased Body Mass in Children', *PLOS ONE*. Edited by M. Vinciguerra. Public Library of Science, 11(1), p. e0143578. doi: 10.1371/journal.pone.0143578.

Pellegrino, A. C. *et al.* (2013) 'Weather Forecasting by Insects: Modified Sexual Behaviour in Response to Atmospheric Pressure Changes', *PLoS ONE*, 8(10), pp. 1–5. doi: 10.1371/journal.pone.0075004.

Perry, G. and Fisher, R. (2006) 'Night Lights and Reptiles: Observed and Potential Effects', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 169–191.

Plainis, S., Murray, I. J. and Pallikaris, I. G. (2006) 'Road traffic casualties: understanding the night-time death toll.', *Injury prevention : journal of the International Society for Child and Adolescent Injury Prevention*. BMJ Publishing Group, 12(2), pp. 125–8. doi: 10.1136/ip.2005.011056.

Plecher, H. (2019) • *Namibia - urbanization 2007-2017*, *Statista*. Available at: https://www.statista.com/statistics/455894/urbanization-in-namibia/ (Accessed: 6 September 2019).

Polak, T. *et al.* (2011) 'Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert', *Journal of Zoology*. doi: 10.1111/j.1469-7998.2011.00808.x.

R Core Team (2018) 'R: A language and environment for statistical computing.' Vienna: R Foundation for Statistical Computing. Available at: http://www.r-project.org.

Raap, T., Pinxten, R. and Eens, M. (2015) 'Light pollution disrupts sleep in free-living animals', *Scientific Reports*. Nature Publishing Group, 5(1), p. 13557. doi: 10.1038/srep13557.

Razorlux Lighting (2019) *How tall is a street light?*, *Razorlux Lighting*. Available at: https://www.razorlux.com/how-tall-is-a-street-light.html (Accessed: 8 September 2019).

Rich, C. and Longcore, T. (2006) 'Introduction', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island

Press, pp. 1–15.

Robinson, H. S. and Robinson, P. J. M. (1950) 'Some notes on the observed behaviour of lepidoptera in the vicinity of light sources together with a description of a light-trap designed to take entomological samples', *Entomologist's Gazette*, (11), pp. 121–132.

Rodríguez, A. *et al.* (2017) 'Seabird mortality induced by land-based artificial lights', *Conservation Biology*. Wiley/Blackwell (10.1111), 31(5), pp. 986–1001. doi: 10.1111/cobi.12900.

Roer, H. (1971) 'Zur Lebensweise einiger Microchiropteren der Namibwueste (Mammalia: Chiroptera)', *Zoologische Abhandlung: Staatliches Museum fur Tierkunde in Dresden*, 32(4), pp. 43–55. Available at: http://www.the-eis.com/data/literature/Zur Lebensweise einiger Microchiropteren der Namibwueste.pdf (Accessed: 6 September 2019).

Rowse, E. G. *et al.* (2016) 'Dark Matters: The Effects of Artificial Lighting on Bats', in *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Cham: Springer International Publishing, pp. 187–213. doi: 10.1007/978-3-319-25220-9_7.

Rowse, E. G., Harris, S. and Jones, G. (2016) 'The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights', *PLoS ONE*, 11(3). doi: 10.1371/journal.pone.0150884.

Rowse, E. G., Harris, S. and Jones, G. (2018) 'Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats', *Royal Society Open Science*, 5(6). doi: 10.1098/rsos.180205.

Russo, D. *et al.* (2017) 'Adverse effects of artificial illumination on bat drinking activity', *Animal Conservation*, 20(6), pp. 492–501. doi: 10.1111/acv.12340.

Russo, D. and Ancillotto, L. (2015) 'Sensitivity of bats to urbanization: a review', *Mammalian Biology - Zeitschrift für Säugetierkunde*, 80(3), pp. 205–212. doi: 10.1016/j.mambio.2014.10.003.

Rydell, J. (1992a) 'Exploitation of Insects around Streetlamps by Bats in Sweden', *Functional Ecology*, 6(6), p. 744. doi: 10.2307/2389972.

Rydell, J. (1992b) 'Exploitation of Insects around Streetlamps by Bats in Sweden', *Functional Ecology*. British Ecological Society, 6(6), p. 744. doi: 10.2307/2389972.

Rydell, J. (2006) 'Bats and Their Insect Prey at Streetlights', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 43–62.

Rydell, J., Eklof, J. and Sanchez-Navarro, S. (2017) 'Age of enlightenment: Long-term effects of outdoor aesthetic lights on bats in churches', *Royal Society Open Science*, 4(11), pp. 1–8. doi: 10.1098/rsos.171312.

Sack, R. L. *et al.* (1992) 'Circadian rhythm abnormalities in totally blind people: incidence and clinical significance.', *The Journal of Clinical Endocrinology & Metabolism*. Oxford University Press, 75(1), pp. 127–134. doi: 10.1210/jcem.75.1.1619000.

Saghir, J. and Santora, J. (2018) *Urbanization in Sub-Saharan Africa*, *Center for Strategic and International Studies*. Available at: https://www.csis.org/analysis/urbanization-sub-saharan-africa (Accessed: 13 August 2019).

Salmon, M. (2006) 'Protecting Sea Turtles from Artificial Night Lighting at Florida's Oceanic Beaches', in Rich, C. and Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. 1st edn. Washington: Island Press, pp. 141–168.

Schoeman, M. C. (2016) 'Light pollution at stadiums favors urban exploiter bats', *Animal Conservation*. Wiley/Blackwell (10.1111), 19(2), pp. 120–130. doi: 10.1111/acv.12220.

Seely, M. and Pallet, J. (2012) *Namib: Secrets of a desert uncovered*. 1st edn. Windhoek: Venture Publications.

Shanyengana, E. . *et al.* (2002) 'Exploring fog as a supplementary water source in Namibia', *Atmospheric Research*. Elsevier, 64(1–4), pp. 251–259. doi: 10.1016/S0169-8095(02)00096-0.

Simmons, N. (2005) 'Order Chiroptera', in Wilson, D. and Reeder, D. (eds) *Mammal species of the World: A taxonomic and geographic reference*. 3rd edn. Baltimore: John Hopkins University Press, pp. 312–529.

Spoelstra, K. *et al.* (2017) 'Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light', *Proceedings of the Royal Society B: Biological Sciences*, 284(1855), p. 20170075. doi:

10.1098/rspb.2017.0075.

Stevens, R. G. (2006) 'Artificial Lighting in the Industrialized World: Circadian Disruption and Breast Cancer', *Cancer Causes & Control*. Kluwer Academic Publishers, 17(4), pp. 501–507. doi: 10.1007/s10552-005-9001-x.

Stone, E. L. *et al.* (2015) 'The impacts of new street light technologies: experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide.', *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*. The Royal Society, 370(1667), p. 20140127. doi: 10.1098/rstb.2014.0127.

Stone, E. L., Harris, S. and Jones, G. (2015) 'Impacts of artificial lighting on bats: A review of challenges and solutions', *Mammalian Biology*. doi: 10.1016/j.mambio.2015.02.004.

Stone, E. L., Jones, G. and Harris, S. (2009) 'Street Lighting Disturbs Commuting Bats', *Current Biology*. Cell Press, 19(13), pp. 1123–1127. doi: 10.1016/J.CUB.2009.05.058.

Stone, E. L., Jones, G. and Harris, S. (2012) 'Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats', *Global Change Biology*. Wiley/Blackwell (10.1111), 18(8), pp. 2458–2465. doi: 10.1111/j.1365-2486.2012.02705.x.

Swanepoel, R. *et al.* (2007) 'Studies of Reservoir Hosts for Marburg Virus', *Emerging infectious diseases*, 13(12), pp. 1847–1851. doi: https://dx.doi.org/10.3201%2Feid1312.071115.

Taylor, P. J. (2000) *Bats of Southern Africa*. 1st edn. Scottsville: University of Natal Press.

Taylor, P. J. *et al.* (2013) *Bats eat pest green vegetable stink bugs (Nezara viridula): Diet analyses of seven insectivorous species of bats roosting and foraging in macadamia orchards*, *African Growers Association Yearbook*. Available at: https://www.researchgate.net/profile/Peter_Taylor6/publication/263938045_Bats_ eat_pest_green_vegetable_stink_bugs_Nezara_viridula_Diet_analyses_of_seven _insectivorous_species_of_bats_roosting_and_foraging_in_macadamia_orchards/ links/0046353c6421bb64d60000 (Accessed: 27 July 2018).

Taylor, P. J. *et al.* (2017) 'Diet Determined by Next Generation Sequencing Reveals Pest Consumption and Opportunistic Foraging by Bats in Macadamia Orchards in South Africa', *Acta Chiropterologica*. Museum and Institute of Zoology at the Polish Academy of Science , 19(2), pp. 239–254. doi: 10.3161/15081109ACC2017.19.2.003.

Taylor, P. J. *et al.* (2018) 'Economic value of bat predation services – A review and new estimates from macadamia orchards', *Ecosystem Services*. Elsevier, 30, pp. 372–381. doi: 10.1016/J.ECOSER.2017.11.015.

The International Dark-Sky Association (2018) *The Intenational Dark-Sky Association*. Available at: www.darksky.org (Accessed: 31 August 2018).

The Namibian (2016) *Uranium production to triple in 2017*, *The Namibian.* Available at: https://www.namibian.com.na/148890/archive-read/Uranium-production-to-triple-in-2017 (Accessed: 26 July 2018).

Threlfall, C. G., Law, B. and Banks, P. B. (2013) 'The urban matrix and artificial light restricts the nightly ranging behaviour of Gould's long-eared bat (Nyctophilus gouldi)', *Austral Ecology*, 38(8), pp. 921–930. doi: 10.1111/aec.12034.

UK Government (2014) *Bats: Protection and Licences*, *Natural England*. Available at: https://www.gov.uk/guidance/bats-protection-surveys-and-licences (Accessed: 8 January 2019).

UNESCO (2013) *Namib Sand Sea - UNESCO World Heritage Centre*. Available at: https://whc.unesco.org/en/list/1430 (Accessed: 15 January 2019).

Voigt, C. C. *et al.* (2017) 'Migratory bats respond to artificial green light with positive phototaxis', *PLoS ONE*, 12(5), pp. 1–12. doi: 10.1371/journal.pone.0177748.

Wakefield, A. *et al.* (2015a) 'Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls', *Royal Society Open Science*, 2(8), pp. 1–6. doi: 10.1016/j.dsr.2010.12.007.

Wakefield, A. *et al.* (2015b) 'Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls', *Royal Society Open Science*, 2(8). doi: 10.1098/rsos.150291.

Wakefield, A. *et al.* (2016) 'Experimentally comparing the attractiveness of domestic lights to insects: Do LEDs attract fewer insects than conventional light types?',

Ecology and Evolution, 6(22). doi: 10.1002/ece3.2527.

Wakefield, A. *et al.* (2018) 'Quantifying the attractiveness of broad-spectrum street lights to aerial nocturnal insects', *Journal of Applied Ecology*, 55(2), pp. 714–722. doi: 10.1111/1365-2664.13004.

Walvis Bay Corridor Group (2018) *Walvis Bay Corridor Group: Newsletters*. Available at: http://www.wbcg.com.na/news-info/newsletters.html (Accessed: 25 July 2018).

Wang, D. *et al.* (2003) 'Molecular Evolution of Bat Color Vision Genes', *Molecular Biology and Evolution*. Oxford University Press, 21(2), pp. 295–302. doi: 10.1093/molbev/msh015.

Warren-Rhodes, K. A. *et al.* (2013) 'Physical ecology of hypolithic communities in the central Namib Desert: The role of fog, rain, rock habitat, and light', *Journal of Geophysical Research: Biogeosciences*. Wiley-Blackwell, 118(4), pp. 1451–1460. doi: 10.1002/jgrg.20117.

Wickam, H. (2016) 'ggplot2: Elegant Graphics for Data Analysis'. New York: Springer Verlaag. Available at: http://ggplot2.org.

Williams-Guillén, K., Perfecto, I. and Vandermeer, J. (2008) 'Bats limit insects in a neotropical agroforestry system.', *Science (New York, N.Y.)*. American Association for the Advancement of Science, 320(5872), p. 70. doi: 10.1126/science.1152944.

Willmott, N. J. *et al.* (2019) 'Guiding lights: Foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night', *Ethology*, 125(5), pp. 289–297. doi: 10.1111/eth.12852.

Witherington, B. E. and Bjorndal, K. A. (1991) *Influences of Artificial Lighting on the Seaward Orientation of Hatchling Loggerhead Turtles Caretta caretta*, *Biological Conservation*. Available at: https://s3.amazonaws.com/academia.edu.documents/46140617/0006-3207_2891_2990053-c20160601-5344-1s2539f.pdf?AWSAccessKeyId=AKIAIWOWYYGZ2Y53UL3A&Expires=1547748722&Signature=YvOybuXWF%2BHAkBnjDZRab6fDLyQ%3D&response-content-disposition=inline%3B filename%3DInfluences_of_artificial_lighting_on_the.pdf (Accessed: 17 January 2019).

Zhigalin, A. V. and Moskvitina, N. S. (2017) 'Fecundity of the parti-coloured bat Vespertilio murinus L., 1758 (Chiroptera, Vespertilionidae) in urban and suburban environments', *International Journal of Environmental Studies*. Routledge, 74(5), pp. 884–890. doi: 10.1080/00207233.2017.1284385.

Appendix 1: Copy of UNISA Ethics Approval and Renewal of Ethics Approval

UNISA | university of south africa

UNISA CAES ANIMAL RESEARCH ETHICS REVIEW COMMITTEE

Date: 08/09/2017

Dear Ms Curtis

NHREC Registration # : REC-170616-051

ERC Reference # : 2017/CAES/121

Name : Ms AL Curtis

Student #: 7318820

Decision: Ethics Approval from 07/09/2017 to 30/09/2018

Researcher(s): Ms AL Curtis
7318820@mylife.unisa.ac.za

Supervisor (s): Dr M Keith
Mark.keith@up.ac.za; (012) 420-2569

Mr E Seamark
Earnest.seamark@africanbats.org; 082-335-6879

Mr WM Strauss
strauwm@unisa.ac.za; (011) 471-2163

Working title of research:

The effects of artificial lighting on Namib desert bats (Mammalia: Chiroptera)

Qualification: MSc Nature Conservation

Thank you for the application for research ethics clearance by the Unisa CAES Animal Research Ethics Review Committee for the above mentioned research. Ethics approval is granted for a one-year period. After one year the researcher is required to submit a progress report, upon which the ethics clearance may be renewed for another year.

Due date for progress report: 30 September 2018

Please note the point below for further action:

University of South Africa
Preller Street, Muckleneuk Ridge. City of Tshwane
PO Box 392 UNISA 0003 South Africa
Telephone: +27 12 429 3111 Facsimile: +27 12 429 4150
www.unisa.ac.za

92

1. Please clarify the researcher's movements during the research: will she set up the equipment and leave, or will she remain on site for the duration of the time the lights are active? If she will be on site, will she be alone or accompanied by someone? As the electricity cables will be removed after the lights were switched off, this implies that the researcher will move around the site during the dark. What measures will be put in place to ensure the researcher's safety?

---

*The **low risk application** was **reviewed** by the CAES Animal Research Ethics Review Committee on 07 September 2017 in compliance with the Unisa Policy on Research Ethics and the Standard Operating Procedure on Research Ethics Risk Assessment.*

The proposed research may now commence with the provisions that:
1. The researcher(s) will ensure that the research project adheres to the values and principles expressed in the UNISA Policy on Research Ethics.
2. Any adverse circumstance arising in the undertaking of the research project that is relevant to the ethicality of the study should be communicated in writing to the Committee.
3. The researcher(s) will conduct the study according to the methods and procedures set out in the approved application.
4. The researcher will ensure that the research project adheres to any applicable national legislation, professional codes of conduct, institutional guidelines and scientific standards relevant to the specific field of study. Adherence to the following South African legislation is important, if applicable: Protection of Personal Information Act, no 4 of 2013; Children's act no 38 of 2005 and the National Health Act, no 61 of 2003.
5. Only de-identified research data may be used for secondary research purposes in future on condition that the research objectives are similar to those of the original research. Secondary use of identifiable human research data require additional ethics clearance.
6. No field work activities may continue after the expiry date. Submission of a completed research ethics progress report will constitute an application for renewal of Ethics Research Committee approval.

Note:
*The reference number **2017/CAES/121** should be clearly indicated on all forms of communication with the intended research participants, as well as with the Committee.*

URERC 25.04.17 - Decision template (V2) - Approve

Yours sincerely,

Prof MA Antwi
Acting Chair of CAES Animal Research ERC
E-mail: antwima@unisa.ac.za
Tel: (011) 670-9391

Prof MJ Linington
Executive Dean : CAES
E-mail: lininmj@unisa.ac.za
Tel: (011) 471-3806

URERC 25.04.17 - Decision template (V2) - Approve

UNISA | university of south africa

CAES ANIMAL RESEARCH ETHICS COMMITTEE

Date: 29/10/2018

Dear Ms Curtis

NHREC Registration # : REC-170616-051
REC Reference # : 2017/CAES/121
Name : Ms AL Curtis
Student #: 7318820

Decision: Ethics Approval
Renewal after First Review from
01/10/2018 to 30/09/2019

Researcher(s): Ms AL Curtis
7318820@mylife.unisa.ac.za

Supervisor (s): Dr M Keith
Mark.keith@up.ac.za; (012) 420-2569

Mr E Seamark
Earnest.seamark@africanbats.org; 082-335-6879

Mr WM Strauss
strauwm@unisa.ac.za; (011) 471-2163

Working title of research:
The effects of artificial lighting on Namib desert bats (Mammalia: Chiroptera)

Qualification: MSc Nature Conservation

Thank you for the submission of your progress report to the CAES Animal Research Ethics Committee for the above mentioned research. Ethics approval is renewed for a one-year period. After one year the researcher is required to submit a progress report, upon which the ethics clearance may be renewed for another year.

Due date for progress report: 30 September 2019

*The **low risk application** was **reviewed** by the CAES Animal Research Ethics Review Committee on 07 September 2017 in compliance with the Unisa Policy on Research Ethics and the Standard Operating Procedure on Research Ethics Risk Assessment.*

The proposed research may now commence with the provisions that:

1. The researcher(s) will ensure that the research project adheres to the values and principles expressed in the UNISA Policy on Research Ethics.

2. Any adverse circumstance arising in the undertaking of the research project that is relevant to the ethicality of the study should be communicated in writing to the Committee.

3. The researcher(s) will conduct the study according to the methods and procedures set out in the approved application.

4. The researcher will ensure that the research project adheres to any applicable national legislation, professional codes of conduct, institutional guidelines and scientific standards relevant to the specific field of study. Adherence to the following South African legislation is important, if applicable: Protection of Personal Information Act, no 4 of 2013; Children's act no 38 of 2005 and the National Health Act, no 61 of 2003.

5. Only de-identified research data may be used for secondary research purposes in future on condition that the research objectives are similar to those of the original research. Secondary use of identifiable human research data require additional ethics clearance.

6. No field work activities may continue after the expiry date. Submission of a completed research ethics progress report will constitute an application for renewal of Ethics Research Committee approval.

Note:

*The reference number **2017/CAES/121** should be clearly indicated on all forms of communication with the intended research participants, as well as with the Committee.*

Yours sincerely,

Prof EL Kempen
Chair of CAES AREC
E-mail: kempeel@unisa.ac.za
Tel: (011) 471-2241

Prof MJ Linington
Executive Dean : CAES
E-mail: lninmj@unisa.ac.za
Tel: (011) 471-3806

Appendix 2: Permit

MINISTRY OF ENVIRONMENT AND TOURISM

RESEARCH/COLLECTING PERMIT

Permit Number 2284/2017
Valid from 1 May 2017 to 30 April 2018

Permission is hereby granted in terms of the Nature Conservation Ordinance 1975 (Ord. 4 of 1975) to:

Name: **Ms. A. Curtis**
Address: **P.O. Box 11255**
Windhoek
Namibia
Coworkers: **E. Marais, S. Eiseb, A.T. Iiyambula, S. Combrink, E. Seamark and T. Kearney**

How the introduction of artificial lighting affects the behaviour of bat species in the Namib Desert at Namib Naukluft Park, Erongo, Hardap, Kunene, Karas, Khomas, Otjozondjupa and Oshikoto Regions, subject to attached conditions.

IMPORTANT: This permit is not valid if altered in any way.

2 2 MAR 2017

Private Bag 13306, Windhoek
Tel: 2842111 • Fax: 258861

....
Authorising Officer

IMPORTANT
This permit is subject to the provisions of the Nature Conservation Ordinance, 1975 (Ordinance 4 of 1975) and the regulations promulgated thereunder, and the holder is subject to all such conditions and regulations.

Enquiries: Conservation Scientist, email iita.matheus@met.gov.na
Private Bag 13306, Windhoek, Namibia

RESEARCH/COLLECTING PERMIT CONDITIONS
****

1. You must report to the Park Chief warden and / or Regional Office of the Ministry of Environment and Tourism prior to arrival in fieldwork area, and must present your permit.
2. This permit does NOT entitle the holder to free entry to the protected areas or state land outside protected areas.
3. The permission of the land owner is required to work/collect on private lands.
4. The permission of the concession holder is required to work/collect in concession areas.
5. The permission of the communal authority is required to work/collect in communal areas.
6. No commercial filming will be permitted without prior approval by the Ministry of Environment and Tourism.
7. Duplicates of publications and / or final report should be made available to MET.
8. Voucher specimens should be lodged with National Museum of Namibia.
9. No palaeontological and or archaeological samples may be taken without a permit from the National Heritage Council.
10. The specimens and their derivatives may be used for the purposes of this study only and may not be patented, commercialised, donated or sold to a third party without the written consent of the Ministry of Environment and Tourism.
11. All results (raw materials) or technology derived directly or indirectly from this research must be made available free of charge without reservations to the Ministry of Environment and Tourism.
12. Please submit a report on the work conducted under this permit to this office not later than one month after the expiry of this permit as well as to regional office in whose area research was conducted.
13. Applications for renewal of this permit must reach this office at least three months prior to the expiry of this permit.
14. Habitat destructive collecting methods must not to be used.
15. Veterinary restriction may apply in the case of movement of samples.
16. All field teams must be in possession of the permit and permit copy must accompany the transport of specimens.
17. You are subject to all conditions listed on the entry permit to any of the protected areas, unless specifically exempted.
18. Failure to adhere to the conditions will lead to cancellation of the research permit.
19. It is your responsibility to make the necessary contacts and arrangements as specified above.

Appendix 3: Summary statistics for each sample session

Summary statistics for each of the five night sample session for each species at each light type. The total number of passes, mean number of passes and the standard deviation for each species by light types.

		Light types			
Sample Session Dates	Species	Control Total Mean ± SD	UV Total Mean ± SD	White Total Mean ± SD	Yellow Total Mean ± SD
Sample session 1	Overall	1550 310.0 ± 174.7	842 168.4 ± 96.5	5218 1043.6 ± 582.4	2606 521.2 ± 254.8
	Tadarida aegyptiaca	677 135.4 ± 83.5	251 50.2 ± 36.1	2410 482.0 ± 166.1	2151 430.2 ± 198.6
	Sauromys petrophilus	160 32.0 ± 24.0	57 11.4 ± 17.4	931 186.2 ± 340.0	211 42.2 ± 31.7
16 Sep 17 to 20 Sep 17	*Neoromicia zuluensis*	624 124.8 ± 94.6	526 105.2 ± 62.3	1808 361.6 ± 293.3	225 45.0 ± 29.4
	Eptesicus hottentotus	2 0.4 ± 0.9	1 0.2 ± 0.4	61 12.2 ± 27.3	3 0.6 ± 1.3
	Neoromicia capensis	2 0.4 ± 0.5	4 0.8 ± 0.8	3 0.6 ± 0.5	3 0.6 ± 0.9
	Laephotis namibensis	75 15.0 ± 4.6	2 0.4 ± 0.9	2 0.4 ± 0.5	2 0.4 ± 0.9
	Rhinolophus damarensis	10 2.0 ± 1.9	1 0.2 ± 0.4	3 0.6 ± 1.3	11 2.2 ± 0.8
Sample Session 2	Overall	616 123.2 ± 52.3	982 196.4 ± 63.8	1206 241.2 ± 127.1	2083 416.6 ± 162.3
	Tadarida aegyptiaca	107 21.4 ± 10.1	525 105.0 ± 83.6	751 150.2 ± 134.4	795 159.0 ± 114.1
	Sauromys petrophilus	73 14.6 ± 20.7	99 19.8 ± 18.7	190 38.0 ± 44.2	257 51.4 ± 42.2
27 Sep 17 To 1 Oct 17	*Neoromicia zuluensis*	433 86.6 ± 35.0	353 70.6 ± 24.5	256 51.2 ± 63.7	948 189.6 ± 118.8
	Eptesicus hottentotus	1 0.2 ± 0.4	1 0.2 ± 0.4	1 0.2 ± 0.4	6 1.2 ± 2.2
	Neoromicia capensis	2 0.4 ± 0.9	3 0.6 ± 0.5	5 1.0 ± 2.2	1 0.2 ± 0.4
	Laephotis namibensis	0 0.0 ± 0.0	0 0.0 ± 0.0	0 0.0 ± 0.0	71 14.2 ± 4.9
	Rhinolophus damarensis	0 0.0 ± 0.0	1 0.2 ± 0.4	3 0.6 ± 0.5	5 1.0 ± 1.2
Sample	Overall	956 191.2 ± 18.4	1129 225.8 ± 87.4	5631 1126.2 ± 700.5	1432 286.4 ± 186.0

Sample Session Dates	Species	Light types			
		Control Total Mean ± SD	UV Total Mean ± SD	White Total Mean ± SD	Yellow Total Mean ± SD
Session 3 7 Oct 17 to 11 Oct 17	*Tadarida aegyptiaca*	453 90.6 ± 41.9	761 152.2 ± 87.4	4044 808.8 ± 524.6	336 67.2 ± 70.5
	Sauromys petrophilus	125 25.0 ± 32.1	114 22.8 ± 24.0	627 125.4 ± 78.8	101 20.2 ± 19.6
	Neoromicia zuluensis	342 68.4 ± 23.9	244 48.8 ± 42.3	932 186.4 ± 195.2	970 194.0 ± 155.1
	Eptesicus hottentotus	26 5.2 ± 11.1	3 0.6 ± 1.3	1 0.2 ± 0.4	7 1.4 ± 2.2
	Neoromicia capensis	2 0.4 ± 0.5	2 0.4 ± 0.5	3 0.6 ± 0.9	2 0.4 ± 0.5
	Laephotis namibensis	6 1.2 ± 1.1	2 0.4 ± 0.9	23 4.6 ± 3.3	13 2.6 ± 2.7
	Rhinolophus damarensis	2 0.4 ± 0.5	3 0.6 ± 0.9	1 0.2 ± 0.4	3 0.6 ± 0.5
Sample Session 4 17 Oct 17 to 21 Oct 17	Overall	1471 294.2 ± 129.7	3391 678.2 ± 251.0	10774 2154.8 ± 799.6	5372 1074.4 ± 643.6
	Tadarida aegyptiaca	876 175.2 ± 89.1	963 192.6 ± 128.4	5771 1154.2 ± 636.8	4200 840.0 ± 593.3
	Sauromys petrophilus	143 28.6 ± 39.1	195 39.0 ± 39.6	744 148.8 ± 109.7	328 65.6 ± 79.6
	Neoromicia zuluensis	421 84.2 ± 70.9	2190 438.0 ± 288.4	4194 838.8 ± 280.2	759 151.8 ± 129.5
	Eptesicus hottentotus	10 2.0 ± 4.5	12 2.4 ± 3.6	22 4.4 ± 9.3	23 4.6 ± 10.3
	Neoromicia capensis	4 0.8 ± 1.3	5 1.0 ± 1.0	5 1.0 ± 0.7	0 0.0 ± 0.0
	Laephotis namibensis	12 2.4 ± 3.2	23 4.6 ± 2.3	36 7.2 ± 2.9	60 12.0 ± 5.3
	Rhinolophus damarensis	5 1.0 ± 1.2	3 0.6 ± 0.5	2 0. 4 ± 0.9	2 0.4 ± 0.5
Sample Session 5 27 Oct 17 to 31 Oct 17	Overall	5333 1066.6 ± 441.8	1085 217.0 ± 70.6	2107 421.4 ± 201.5	3113 622.6 ± 398.5
	Tadarida aegyptiaca	463 92.6 ± 53.5	416 83.2 ± 54.8	1093 218.6 ± 201.8	814 162.8 ± 116.2
	Sauromys petrophilus	179 35.8 ± 22.2	81 16.2 ± 14.3	124 24.8 ± 22.2	130 26.0 ± 20.5
	Neoromicia zuluensis	4604 920.8 ± 463.1	565 113.0 ± 31.0	859 171.8 ± 52.0	2118 423.6 ± 377.6
	Eptesicus hottentotus	6 1.2 ± 1.3	0 0.0 ± 0.0	0 0.0 ± 0.0	4 0.8 ± 0.8
	Neoromicia capensis	31 6.2 ± 5.4	8 1.6 ± 1.5	8 1.6 ± 2.1	38 7.6 ± 5.8
	Laephotis namibensis	45 9.0 ± 4.3	11 2.2 ± 1.6	23 4.6 ± 2.5	9 1.8 ± 1.9
	Rhinolophus damarensis	5 1.0 ± 0.7	4 0.8 ± 1.1	0 0.0 ± 0.0	0 0.0 ± 0.0

Sample Session Dates	Species	Light types			
		Control Total Mean ± SD	UV Total Mean ± SD	White Total Mean ± SD	Yellow Total Mean ± SD
Sample Session 6	Overall	1285 257.0 ± 103.8	3003 600.6 ± 231.8	9541 1908.2 ± 731.5	10061 2012.2 ± 637.7
	Tadarida aegyptiaca	242 48.4 ± 14.8	1623 324.6 ± 174.6	5326 1065.2 ± 537.0	2864 572.8 ± 424.2
6 Nov 17 to 10 Nov 17	*Sauromys petrophilus*	39 7.8 ± 4.2	342 68.4 ± 29.1	1806 361.2 ± 133.4	567 113.4 ± 71.5
	Neoromicia zuluensis	986 197.2 ± 104.3	991 198.2 ± 91.1	2303 460.6 ± 279.7	6526 1305.2 ± 346.6
	Eptesicus hottentotus	0 0.0 ± 0.0	3 0.6 ± 0.5	89 17.8 ± 22.6	11 2.2 ± 2.6
	Neoromicia capensis	9 1.8 ± 0.8	19 3.8 ± 2.2	1 0.2 ± 0.4	22 4.4 ± 3.2
	Laephotis namibensis	7 1.4 ± 1.5	25 5.0 ± 2.9	15 3.0 ± 1.9	69 13.8 ± 5.1
	Rhinolophus damarensis	2 0.4 ± 0.9	0 0.0 ± 0.0	1 0.2 ± 0.4	2 0.4 ± 0.9
Sample Session 7	Overall	3963 792.6 ± 248.2	9312 1862.4 ± 583.1	26580 5316.0 ± 472.6	16688 3337.6 ± 653.1
	Tadarida aegyptiaca	1831 366.2 ± 157.5	3325 665.0 ± 319.1	10598 2119.6 ± 495.8	5236 1047.2 ± 552.4
16 Nov 17 to 20 Nov 17	*Sauromys petrophilus*	727 145.4 ± 121.9	1285 257.0 ± 161.8	6455 1291.0 ± 763.4	2343 468.6 ± 364.6
	Neoromicia zuluensis	791 158.2 ± 112.4	4315 863.0 ± 574.8	7228 1445.6 ± 53.9	7286 1457.2 ± 408.7
	Eptesicus hottentotus	259 51.8 ± 64.1	293 58.6 ± 81.1	2032 406.4 ± 380.7	755 151.0 ± 202.6
	Neoromicia capensis	312 62.4 ± 82.3	65 13.0 ± 19.3	125 25.0 ± 24.7	1024 204.8 ± 94.0
	Laephotis namibensis	36 7.2 ± 3.8	25 5.0 ± 2.5	135 27.0 ± 21.6	36 7.2 ± 1.5
	Rhinolophus damarensis	7 1.4 ± 0.9	4 0.8 ± 0.8	7 1.4 ± 2.6	8 1.6 ± 1.9
Sample Session 8	Overall	1485 297.0 ± 200.4	4292 858.4 ± 409.0	4773 954.6 ± 459.1	1716 343.2 ± 160.4
	Tadarida aegyptiaca	626 125.2 ± 72.5	877 175.4 ± 181.8	2768 553.6 ± 396.9	966 193.2 ± 108.3
26 Nov 17 to 30 Nov 17	*Sauromys petrophilus*	203 40.6 ± 50.3	205 41.0 ± 35.5	232 46.4 ± 64.5	260 52.0 ± 49.6
	Neoromicia zuluensis	626 125.2 ± 105.1	3120 624.0 ± 265.4	1586 317.2 ± 98.4	350 70.0 ± 14.8
	Eptesicus hottentotus	8 1.6 ± 2.6	3 0.6 ± 0.9	19 3.8 ± 6.9	12 2.4 ± 3.9
	Neoromicia capensis	11 2.2 ± 2.9	51 10.2 ± 16.9	155 31.0 ± 8.0	94 18.8 ± 6.2
	Laephotis namibensis	9 1.8 ± 2.4	27 5.4 ± 5.0	13 2.6 ± 2.4	33 6.6 ± 1.7

Sample Session Dates	Species	Light types			
		Control Total Mean ± SD	UV Total Mean ± SD	White Total Mean ± SD	Yellow Total Mean ± SD
	Rhinolophus damarensis	2 0.4 ± 0.9	9 1.8 ± 1.6	0 0.0 ± 0.0	1 0.2 ± 0.4
Sample Session 9	Overall	3957 791.4 ± 303.3	2270 454.0 ± 285.8	10344 2068.8 ± 109.2	7776 1555.2 ± 723.2
	Tadarida aegyptiaca	1457 291.4 ± 217.4	1032 206.4 ± 180.9	2834 566.8 ± 265.8	1724 344.8 ± 110.5
	Sauromys petrophilus	653 130.6 ± 79.6	310 62.0 ± 45.1	3034 606.8 ± 453.9	1100 220.0 ± 100.7
6 Dec 17 to 10 Dec 17	*Neoromicia zuluensis*	1720 344.0 ± 89.8	851 170.2 ± 87.8	2779 555.8 ± 326.0	4861 972.2 ± 701.0
	Eptesicus hottentotus	31 6.2 ± 7.4	19 3.8 ± 5.2	723 144.6 ± 172.2	41 8.2 ± 9.2
	Neoromicia capensis	15 3.0 ± 1.0	50 10.0 ± 8.0	943 188.6 ± 210.3	39 7.8 ± 6.3
	Laephotis namibensis	69 13.8 ± 12.0	7 1.4 ± 0.9	28 5.6 ± 3.8	9 1.8 ± 1.3
	Rhinolophus damarensis	12 2.4 ± 2.5	1 0.2 ± 0.4	3 0.6 ± 0.9	2 0.4 ± 0.5
Sample Session 10	Overall	715 143.0 ± 63.7	2476 495.2 ± 257.0	8863 1772.6 ± 370.9	8735 1747.0 ± 956.2
	Tadarida aegyptiaca	147 29.4 ± 35.7	1279 255.8 ± 204.1	2811 562.2 ± 492.1	1472 294.4 ±227.8
	Sauromys petrophilus	84 16.8 ± 12.6	367 73.4 ± 29.1	661 132.2 ± 72.9	340 68.0 ± 42.6
16 Dec 17 to 20 Dec 17	*Neoromicia zuluensis*	479 95.8 ± 30.5	794 158.8 ±73.1	5320 1064.0 ± 841.2	6851 1370.2 ± 731.1
	Eptesicus hottentotus	0 0.0 ± 0.0	10 2.0 ± 2.8	42 8.4 ± 10.4	20 4.0 ± 5.3
	Neoromicia capensis	1 0.2 ± 0.4	10 2.0 ± 2.3	10 2.0 ± 2.9	13 2.6 ± 1.7
	Laephotis namibensis	4 0.8 ± 0.8	16 3.2 ± 1.1	17 3.4 ± 2.9	32 6.4 ± 1.5
	Rhinolophus damarensis	0 0.0 ± 0.0	0 0.0 ± 0.0	2 0.4 ± 0.5	7 1.4 ± 1.3
Sample Session 11	Overall	818 279.2 ± 117.3	2265 291.4 ± 241.0	3061 938.4 ± 427.6	1476 340.8 ± 209.8
	Tadarida aegyptiaca	335 67.0 ± 68.9	556 111.2 ± 121.0	309 61.8 ± 57.7	79 15.8 ± 14.8
	Sauromys petrophilus	192 38.4 ± 32.1	197 39.4 ± 38.9	309 61.8 ± 64.7	91 18.2 ± 16.5
26 Dec 17 to 30 Dec 17	*Neoromicia zuluensis*	691 138.2 ± 77.5	672 134.4 ± 88.1	4003 800.6 ± 387.5	1467 293.4 ± 202.2
	Eptesicus hottentotus	4 0.8 ± 0.8	2 0.4 ± 0.5	21 4.2 ± 6.4	6 1.2 ± 1.3
	Neoromicia capensis	155 31.0 ± 13.1	23 4.6 ± 3.4	29 5.8 ± 4.3	52 10.4 ± 6.8

Sample Session Dates	Species	Light types			
		Control Total Mean ± SD	UV Total Mean ± SD	White Total Mean ± SD	Yellow Total Mean ± SD
	Laephotis namibensis	19 3.8 ± 1.5	6 1.2 ± 1.6	21 4.2 ± 2.9	9 1.8 ± 2.4
	Rhinolophus damarensis	0 0.0 ± 0.0	1 0.2 ± 0.4	0 0.0 ± 0.0	0 0.0 ± 0.0
Sample Session 12 6 Jan 18 to 10 Jan 18	Overall	818 163.6 ± 144.6	2265 453.0 ± 324.0	3061 612.2 ± 512.4	1476 295.2 ± 257.9
	Tadarida aegyptiaca	480 96.0 ± 81.7	231 46.2 ± 44.6	172 34.4 ± 32.5	537 107.4 ± 98.8
	Sauromys petrophilus	198 39.6 ± 54.3	202 40.4 ± 37.9	314 62.8 ± 109.0	322 64.4 ± 80.5
	Neoromicia zuluensis	107 21.4 ± 24.0	1746 349.2 ± 245.9	2218 443.6 ± 408.5	397 79.4 ± 58.4
	Eptesicus hottentotus	9 1.8 ± 2.0	25 5.0 ± 6.7	15 3.0 ± 3.4	20 4.0 ± 4.7
	Neoromicia capensis	6 1.2 ± 1.3	21 4.2 ± 6.4	328 65.6 ± 58.9	157 31.4 ± 48.6
	Laephotis namibensis	18 3.6 ± 3.1	36 7.2 ± 2.6	12 2.4 ± 2.8	43 8.6 ± 4.0
	Rhinolophus damarensis	0 0.0 ± 0.0	2 0.4 ± 0.5	2 0.4 ± 0.5	0 0.0 ± 0.0
Sample Session 13 16 Jan 18 to 20 Jan 18	Overall	2539 507.8 ± 133.8	2236 447.2 ± 379.4	8336 1667.2 ± 167.9	4340 868.0 ± 546.9
	Tadarida aegyptiaca	340 68.0 ± 46.5	186 37.2 ± 25.6	1329 265.8 ± 148.7	857 171.4 ± 107.5
	Sauromys petrophilus	267 53.4 ± 26.3	118 23.6 ± 21.9	924 184.8 ± 214.0	408 81.6 ± 72.3
	Neoromicia zuluensis	1778 355.6 ± 109.2	1762 352.4 ± 323.6	3820 764.0 ± 546.1	2996 599.2 ± 413.3
	Eptesicus hottentotus	28 5.6 ± 7.6	16 3.2 ± 2.9	43 8.6 ± 14.8	15 3.0 ± 3.5
	Neoromicia capensis	9 1.8 ± 1.8	139 27.8 ± 13.6	2105 421.0 ± 333.8	29 5.8 ± 4.3
	Laephotis namibensis	115 23.0 ± 11.7	11 2.2 ± 2.5	115 23.0 ± 10.0	34 6.8 ± 1.9
	Rhinolophus damarensis	2 0.4 ± 0.5	3 0.6 ± 0.9	0 0.0 ± 0.0	1 0.2 ± 0.4
Sample Session 14 27 Jan 18 To	Overall	775 155.0 ± 73.1	2376 475.2 ± 261.5	2253 450.6 ± 353.4	2494 498.8 ± 323.4
	Tadarida aegyptiaca	287 57.4 ± 31.4	1670 334.0 ± 275.6	843 168.6 ± 53.7	843 168.6 ± 45.5
	Sauromys petrophilus	90 18.0 ± 13.8	193 38.6 ± 19.2	194 38.8 ± 22.9	482 96.4 ± 23.1
	Neoromicia zuluensis	364 72.8 ± 41.6	357 71.4 ± 70.4	1146 229.2 ± 268.8	1095 219.0 ± 293.2
	Eptesicus hottentotus	0 0.0 ± 0.0	6 1.2 ± 0.8	8 1.6 ± 2.1	17 3.4 ± 4.4

		Light types			
Sample Session Dates	Species	Control Total Mean ± SD	UV Total Mean ± SD	White Total Mean ± SD	Yellow Total Mean ± SD
31 Jan 18	*Neoromicia capensis*	22 4.4 ± 3.8	100 20.0 ± 30.5	39 7.8 ± 14.7	4 0.8 ± 1.8
	Laephotis namibensis	12 2.4 ± 1.8	48 9.6 ± 5.9	21 4.2 ± 5.7	51 10.2 ± 1.5
	Rhinolophus damarensis	0 0.0 ± 0.0	2 0.4 ± 0.9	2 0.4 ± 0.5	2 0.4 ± 0.5
Sample Session 15 10 Feb 18 to 14 Feb 18	Overall	2595 519.0 ± 355.3	4677 935.4 ± 658.3	15348 3069.6 ± 095.4	7795 1559.0 ± 693.6
	Tadarida aegyptiaca	1703 340.6 ± 300.2	2036 407.2 ± 340.3	1627 325.4 ± 343.5	332 66.4 ± 54.1
	Sauromys petrophilus	471 94.2 ± 57.2	805 161.0 ± 89.3	1734 346.8 ± 307.7	452 90.4 ± 94.7
	Neoromicia zuluensis	310 62.0 ± 12.8	1759 351.8 ± 264.7	11805 2361.0 ± 820.0	4320 864.0 ± 428.4
	Eptesicus hottentotus	10 2.0 ± 2.3	37 7.4 ± 7.0	47 9.4 ± 14.9	48 9.6 ± 5.2
	Neoromicia capensis	49 9.8 ± 5.9	9 1.8 ± 1.3	42 8.4 ± 5.3	2597 519.4 ± 377.2
	Laephotis namibensis	50 10.0 ± 4.3	29 5.8 ± 3.0	93 18.6 ± 8.0	45 9.0 ± 8.0
	Rhinolophus damarensis	2 0.4 ± 0.9	2 0.4 ± 0.5	0 0.0 ± 0.0	0 0.0 ± 0.0
Sample Session 16 20 Feb 18 to 24 Feb 18	Overall	1141 228.2 ± 178.1	3982 796.4 ± 829.8	3886 777.2 ± 597.4	2604 520.8 ± 432.4
	Tadarida aegyptiaca	693 138.6 ± 84.9	546 109.2 ± 76.7	340 68.0 ± 40.3	744 148.8 ± 66.2
	Sauromys petrophilus	218 43.6 ± 51.0	280 56.0 ± 44.8	317 63.4 ±101.9	314 62.8 ± 55.9
	Neoromicia zuluensis	188 37.6 ± 48.4	2957 591.4 ± 799.7	2531 506.2 ± 361.8	828 165.6 ±209.5
	Eptesicus hottentotus	2 0.4 ± 0.5	6 1.2 ± 1.8	20 4.0 ± 5.1	4 0.8 ± 1.1
	Neoromicia capensis	2 0.4 ± 0.9	9 1.8 ± 1.8	636 127.2 ± 165.4	623 124.6 ± 136.1
	Laephotis namibensis	2 0.4 ± 0.9	9 1.8 ± 1.8	636 127.2 ± 165.4	623 124.6 ±136.1
	Rhinolophus damarensis	2 0.4 ± 0.5	3 0.6 ± 1.3	2 0.4 ± 0.5	3 0.6 ± 0.5

Appendix 4: Results of the post hoc Kruskal test comparing all light types to each other

Results of the general post hoc Kruskal test for each species				
Species	Comparison	Observed difference	Critical difference	TRUE or FALSE
Tadarida aegyptiaca	Control –UV	8.16	17.37	FALSE
	Control – White	20.66	17.37	TRUE
	Control – Yellow	13.06	17.37	FALSE
	UV – White	12.50	17.37	FALSE
	UV - Yellow	4.91	17.37	FALSE
	White - Yellow	7.59	17.37	FALSE
Sauromys Petrophilus	Control –UV	4.06	17.37	FALSE
	Control – White	21.97	17.37	TRUE
	Control – Yellow	14.47	17.37	FALSE
	UV – White	17.91	17.37	TRUE
	UV - Yellow	10.41	1737	FALSE
	White - Yellow	7.50	17.37	FALSE
Neoromicia zuluensis	Control –UV	9.88	17.37	FALSE
	Control – White	24.13	17.37	TRUE
	Control – Yellow	17.00	17.37	FALSE
	UV – White	14.25	17.37	FALSE
	UV - Yellow	7.13	17.37	FALSE
	White - Yellow	7.13	17.37	FALSE
Eptesicus hottentotus	Control –UV	1.06	17.37	FALSE
	Control – White	15.88	17.37	FALSE
	Control – Yellow	10.19	17.37	FALSE
	UV – White	14.81	17.37	FALSE
	UV - Yellow	9.13	17.37	FALSE
	White - Yellow	5.69	17.37	FALSE
Neoromicia capensis	Control –UV	5.59	17.37	FALSE
	Control – White	10.81	17.37	FALSE
	Control – Yellow	9.34	17.37	FALSE
	UV – White	5.22	17.37	FALSE
	UV - Yellow	3.75	17.37	FALSE
	White - Yellow	1.47	17.37	FALSE
Laephotis namibensis	Control –UV	4.81	17.37	FALSE
	Control – White	1.91	17.37	FALSE
	Control – Yellow	6.66	17.37	FALSE
	UV – White	6.72	17.37	FALSE
	UV - Yellow	11.47	17.37	FALSE
	White - Yellow	4.75	17.37	FALSE
Rhinolphus damarensis	Control –UV	1.00	17.37	FALSE
	Control – White	5.47	17.37	FALSE
	Control – Yellow	0.09	17.37	FALSE
	UV – White	6.47	17.37	FALSE
	UV - Yellow	0.91	17.37	FALSE
	White - Yellow	5.56	17.37	FALSE