CHANGES IN THE SEASONAL ACTIVITY OF BATS OCCURING IN THE KUNENE REGION, NAMIBIA: INFLUENCE OF ENVIRONMENTAL FACTORS

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ABSTRACT

The Kunene region is an arid region with extreme environmental conditions. Understanding how environmental conditions affect bat activity, number and distribution is important for assessing activity and abundance. Monthly bat activity and the effect of environmental factors (temperatures, moon phase) on bat activity were recorded to elucidate factors influencing the distribution of bats. Wildlife Acoustic SM2 detectors were used to detect the bat activity from three sites, altitudinal gradient 238 to 970 m. A total of 6893 bat calls were recorded from five families at the study sites. Two families Vespertilionidae and Molossidae appeared to be present and dominant at all sites. Bat activity was significantly higher in the summer months, community composition was not related to altitude and no endemics were found. The highest activity was recorded at Hoanib (271 m). Temperatures were measured with data loggers at sampling sites and moonlight was compared using lunar phases. Activity was positively correlated with temperature at all sites and rarely occurred when temperatures were ≤ 11°C. Moon lunar phase did not affect activity as there was no significant difference between bright and dark nights ($P>0.005$). Bat activity was greater at the beginning of the night, independent of the presence of the moon at all sites, indicating that foraging just after sunset is adaptive. Bats response to moonlight maybe species-specific. Study results indicate that bat activity was highest at lower altitudes with more vegetation. Such information may be useful in recognizing conservation priorities of bats in the Kunene region. As these lower altitudes are more prone to human impacts which can lead to habitat degradation due to overgrazing and denudation of large trees for firewood. Therefore long-term monitoring of bat activity in the Kunene Region is important where environmental conditions may be extreme and variable.

Keywords

Bats, activity levels, echolocation, acoustic monitoring, bat detectors

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1. INTRODUCTION

1.1. Background of the study

Maintaining biodiversity is a fundamental goal of conservation, but many challenges still remain, particularly a lack of information about most species (Kery, 2002). Approximately 25% of bats globally are threatened, with limited data on African bats, which account for 20% of bat species, it hinders our understanding of their conservation status across this ecologically diverse continent (Cooper-Bohannon *et al.*, 2016). Insufficient knowledge on distribution and natural history are major hurdles for wildlife management and monitoring because they are the basic requirements in order to conserve species (Cooper-Bohannon *et al.,* 2016). We have to know what is present in order to conserve it, but collecting realistic data on organisms especially bats can be challenging to researchers and conservation efforts. Bats are generally a difficult group to survey; most species are relatively small and can be overlooked at roost sites; being nocturnal and able to move large distances through flight can also make it difficult to detect and count them. Field studies of bats maybe hampered by the limited ability to observe them and/or access their habitats (Jacobs, 2016). However, some of these obstacles have been solved, at least in part, by technological advances (e.g., bat detectors and radio telemetry). The high frequency ultrasonic (echolocation) calls of bats can be detected by bat detectors, the development of which has revolutionised bat research over the past few decades (Hayes, 1997; Altringham, 2011). Acoustic monitoring is fundamental for the study of most bat species which were traditionally sampled by visual or capture techniques. Calls are highly important and are used as reliable taxonomic features, especially for insectivorous bats (Arita & Fenton, 1997). Acoustic sampling is an important tool for wildlife management and conservation because it can be used to estimate diversity and relative abundance (Zellweger, Bollmann & Obrist, 2014).

Basic information about bat species distribution is lacking for many African countries including Namibia (Monadjem *et al.,* 2007). Investigating the distribution of bats will give an indication about the risks that bats are facing in terms of prospective climate change (Barclay *et al.,* 2004). Species assemblages have become attributed to species reactions to environmental conditions, including presence of suitable habitat and climate changes which have determined species distribution (Presley *et al.,* 2012). The impact of environmental changes may determine bats future global diversity and functioning of ecosystems (Inkster-Draper, 2017). Factors that are correlated with activity levels differ among studies and may be specific to area and species (Hayes, 1997). One of the most consistent phenomena in ecological communities is the variation in species abundance (Ludwig, 1988). It is assumed that species richness generally decreases with altitude; some research suggests that the highest species richness can be found at intermediate altitudes. Insect feeding bats being small are particularly sensitive to changes in environmental conditions because much their energy is used to maintain a stable body temperature (Jantzen & Fenton, 2013), as well as the functioning of their echolocation system is directly related to climatic factors such as temperature and humidity (Maluleke *et al*., 2017). Conditions such as low temperatures and rain cause additional energetic costs to insectivorous bats by increasing thermoregulatory stress and decreasing activity of their insect prey (Hutson *et al.,* 2001). Therefore the ability to avoid unfavourable conditions by entering periodic torpor is essential for survival for these small insectivorous bats. These are costly for pregnant females, as torpor slows down foetal development which causes delayed parturition (Willis, Brigham & Geiser, 2006). Delayed parturition may result in a significant decrease in the survival rate of females and young due to insufficient preparation for winter. Thus climate plays a role in the distributions of reproductive female bats (Kunz & Parsons, 2009). Several environmental conditions such as temperature, humidity and moonlight have been reported to affect flight activities of insects and is thought to directly or indirectly influence bat activity as well (Meyer, Schwarz & Fahr, 2004). Understanding how weather conditions affect bat activity can provide insight into the limitations on bat distribution, particularly at higher altitudes and in mountainous regions where environmental conditions may be extreme and variable. The most thorough examination of this relationship requires investigation from the short (nightly weather variations) to longer (average monthly conditions). Most studies on activity of insectivorous bats have been conducted in the northern temperate zone. In the case of Africa, studies have been focused on the southern part of the continent but Namibia still remains underrepresented. With limited time and resources, global conservation efforts often focus on areas with high biodiversity, which are frequently determined according to known local species richness hotspots (e.g. Carvalho *et al.*, 2010). While this approach aims to protect the largest number of species, important habitats and/or endemic species (Brooks *et al.,* 2002; Meyer, Schwarz and Fahr, 2004), it can exclude some species such as range-restricted specialists (with restricted niche breadths), threatened or rare species (e.g Orme *et al.*, 2005).

1.2. Statement of the problem

Bats are one of the most successful groups of small mammals, often exhibiting high abundance and diversity even in harsh desert environments (Taylor, 2000). The Kunene Region has a bat fauna of >16 species (Monadjem *et al.,* 2010). At least three of these bat species are listed by IUCN as threatened, the *Hipposideros vittatus, Eidolon helvum* and *Epomophorus angolensis* (Monadjem *et al.,* 2010). Yet there is very little information on the bat biology and species distribution and thus limits conservation initiatives. This lack of information not only makes conservation difficult but also severely limits the kinds of scientific questions that can be addressed. For example understanding the environmental processes that influence how bat communities in certain areas are structured, requires that we know the distributional limits of each species so that we can assess which environmental parameters impact them (Jacobs, 2016). Changes in land use are one of the major causes of global environmental change and have shown to be the driver of biodiversity loss in terrestrial ecosystems. To be able to understand how this affects bats, predator/prey relationships need to be understood and how environmental conditions influence these (Voigt *et al.,* 2016). Distributional limits also give an indication of the climate and habitat tolerances of species, allowing us to predict how habitat degradation as a result of human-induced changes is likely to affect them. Knowing the distributional limits of species allows us to determine the ecological requirements of a species, such as whether it is adapted to arid habitats or prefers mesic climates or whether it is a forest dweller or prefers more open vegetation. Knowing the habitat requirements in terms of both vegetation and availability of food for bats, enables us to determine the influence of human activities on bats, including human-induced climate change (Jacobs, 2016). In order to predict how climate changes will impact a species, either through local extinctions or shifts into new habitats, we need to understand the climatic tolerances of species to begin with. Echolocation calls of free-flying insectivorous bats have proven to be extremely useful for studying the ecology and behaviour of these otherwise elusive animals (Hutson *et al.*, 2001). The importance of the role that the environment, particularly climate, plays in such acoustic signal variation is increasingly being recognized (Luo, Koselj & Goerlitz, 2013). This has resulted in the formulation of the Sensory Drive Hypothesis which proposes that lineage diversification may be driven by environmentally-mediated differences in communication signals (Endler, 2008). This hypothesis thus predicts an adaptive, rather than stochastic, response in acoustic signals to environmental variables. Complex signals with high information content, such as birdsong and the echolocation calls of bats, are particularly sensitive to environmental conditions (Teixeira, Correa & Fischer, 2009). This study has greatly contributed to the baseline ecological data on bats by identifying bat family compositions in the area, which will assist with conservation initiatives. This was done by compiling a call library that is specific to bat families in the Kunene Region and determining which environmental variables influence their distribution.

1.3. Research Questions

a) What effect does season have on bat abundance?

b) What effect does moonlight have on bat activity?

c) What effect does ambient temperature have on aerial-insectivorous bat activity?

1.4. Hypotheses of the study

H_0: There is no significant effect of season on abundance of bats.

H_0: There is no significant effect of moonlight on bat activity.

H_0: Bat activity is not significantly affected by changes in ambient temperature.

1.5. Significance of the study

Estimating numbers of bats that occupy specific bat colonies or those that compose of local, regional and entire species populations is a critical goal for assessing the long-term conservation and survival of bats (Kunz & Parsons, 2009). Accurate and reliable estimates of colonies and population size and indices of abundance of bats are needed to access both short-term and long-term impacts of anthropogenic changes on the earth's natural and managed ecosystems (Kunz & Parsons, 2009). Detailed examination of the responses of different bat families to landscape changes is necessary, as these changes are considered to be the principal cause of population decline in many bat species (Siemers & Kalko, 2001; Hofstede & Fenton, 2005). Bats can also serve as a mammalian indicator species to assess functionality of wetlands as they are closely associated with them (Maslonek, 2010). A mammalian indicator is important because many mammals are believed to benefit from wetland habitats (Maslonek, 2010). Understanding how environmental factors affect activity, number, and spatial distribution of bats in an area, can better assess long-term trends in population size. The echolocation calls of free-flying insectivorous bats have proven to be extremely useful for studying the ecology and behaviour of these animals (Arita & Fenton, 1997).

There is limited information on bat activity in the Kunene Region. This project has produced verified bat echolocation calls with particular reference to the bat families that occurs in the Kunene Region of Namibia, including the echolocation parameters: minimum frequency, maximum frequency, call duration. The project also examined how environmental factors affect monthly patterns of insectivorous bats, making it possible to identify changes in bat activity and family richness. This baseline ecological data on bats will help determine the conservation status of bats in the area and assist with bat conservation initiatives.

1.6. Limitations of the study

Some bat species echolocation calls intensities are very low and cannot be detected on the bat detector. There were only three bat detectors available for this study and thus only three sites were sampled. Habitat accessibility and water availability limited site selections. There was no voucher specimen collection of bats, hence identification was limited. Lack of verified and accurate call library limited bat identification to family level. Clement *et al.* (2014) highlights that acoustic surveys of bats may be prone to an increased number of false positives (i.e. greater Type I statistical error) when not used in combination with other techniques such as voucher specimens or analytical approaches such as occupancy modelling.

2. LITERATURE REVIEW

2.1 Order Chiroptera

Bats are the second largest order of mammals (after the rodents), they're the only mammals naturally capable of true and sustained flight. At present there are 1386 recognised species of bats (Chiroptera) worldwide, about a quarter of all known mammal species (Burgin *et al.*, 2018). Bats occur all over the world except in the extreme polar and harsh desert habitats (Schoeman *et al.*, 2013). The order Chiroptera is divided into two suborders, the Pteropodiformes and Vespertilioniformes (Hutcheon & Kirsch, 2004; Eick *et al.*, 2005). These suborders are made up of 21 families. In southern Africa a total of 121 bat species from 11 families have been recorded according to Monadjem *et al.* (2010)..

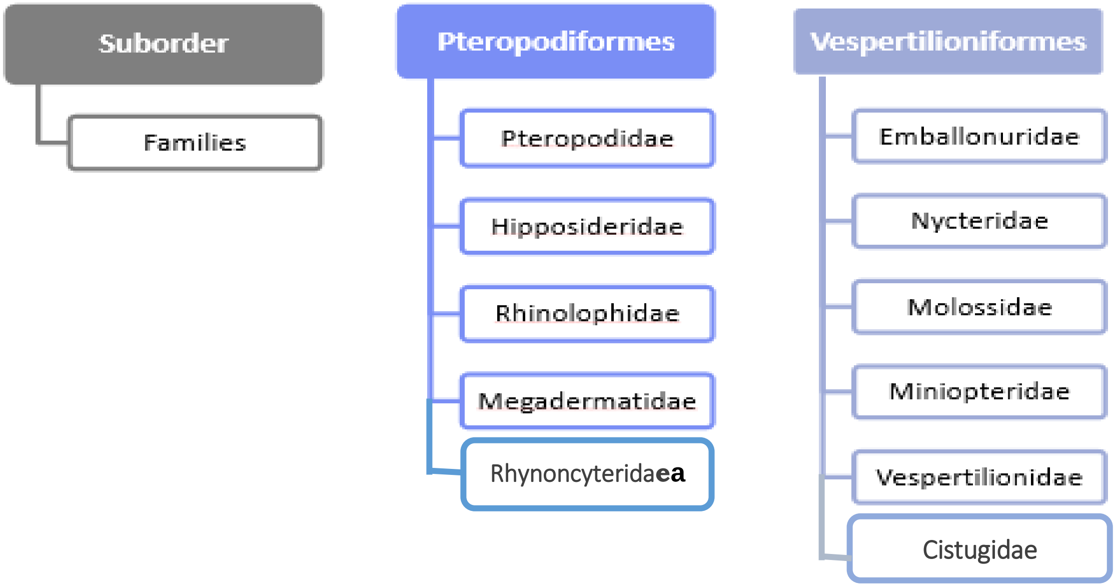

Figure 1. The eleven bat families found in southern Africa (taken from Monadjem *et al.*, 2010).

2.2 General Morphology

2.2.1 Physical characteristics

Bats have become adapted to a wide range of different habitats and diets leading to considerable variation in their form and structure. They range in size from very small with forearms of 22.5 mm, to moderately large with forearms of 115.0 mm. Among the insectivorous bats, some species have nose leaves or other dermal outgrowths above the nostrils or on the lips; a tragus (a lobe of skin inside the pinna of the ear) is usually present; the interfemoral membrane is usually well developed and the tail relatively long; the second digit lacks a claw and the eyes are generally small (Hutson *et al.*, 2001). All insect feeding bats orientate, and most seek and capture food, using a system of echolocation which involves ultrasonic sounds being emitted through the mouth or nose (Jacobs, 2016). About 75% of bats feed on insects, although food sources may also include other invertebrates, fish, amphibians, small mammals (including other bats) and blood. While 25% feed on fruit nectar, leaves and flowers. In the Neotropical family Phyllostomatidae, the majority of species feed on fruit, nectar, and pollen which complement the fruit bats of the Old World (family Pteropodidae). Bats are found all over the world, except for the Arctic and Antarctic and some isolated oceanic islands. The largest families are the Vespertilionidae with a worldwide distribution and the Phyllostomatidae found in the Nearctic and Neotropical regions (Hutson *et al.*, 2001).

Bats and birds are both vertebrates which evolved powered flight independently. Powered flight involves the generation of both lift and forward thrust as opposed to gliding, which is usually a controlled fall (the exception being the use of rising hot air to obtain lift in thermal soaring, by birds and glider pilots). Invertebrate flight, both lift and power is produced by flapping wings. Bats and birds have different ancestors and evolved flight from widely different starting points. Therefore the difference in evolution of wings is not surprising (Jacobs, 2016). Birds have hollow bones strengthened by internal supports (Figure 2), a breast bone with a large flat surface for flight muscle attachment and short, stout humeri. In addition, birds have feathers which are analogous to pterosaur (extinct flying reptiles) wing fibres. The finger bones (phalanges) are reduced and fused to form the tip of the wing skeletal elements. The wing shape is built around this bony skeleton by feathers, thought to have evolved originally for their insulating abilities or to increase the surface area of the forelimbs for one reason or another. Bird wings are rigid because they are made of feathers and few birds are capable of the fluttering, almost moth-like flight of bats (Jacobs, 2016).

The ancestor of bats was probably a small, warm-blooded mammal because mammals use fur and adipose tissue instead of feathers for insulation. Feathers were not available for the evolution of bat wings instead the bats formed wings from bone and skin (Figure 3). This is an example of a biological constraint: feathers had not risen in the lineage that eventually gave rise to bats (Monadjem *et al.,* 2001). In bats, wing evolution was constrained by what had already evolved in mammals. Unlike the wings of birds, bat wings retained all the skeletal components of the vertebrate forelimb and none of the finger bones have been lost, except of the second finger. The bones such as the humerus, forearm and mainly the fingers have become greatly elongated over evolutionary time (Jacobs, 2016).

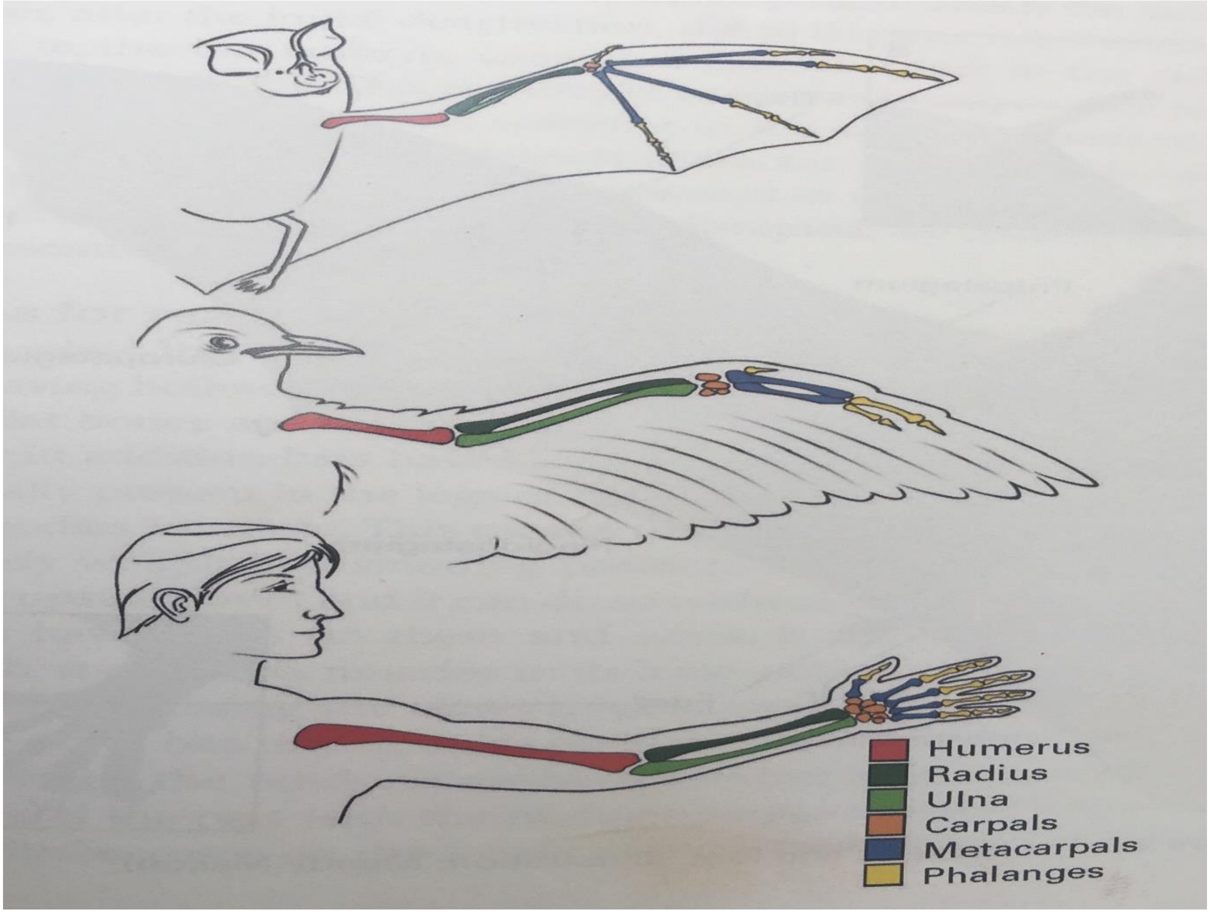

Figure 2. Comparison of skeletal elements of the thoracic extremity in bats, birds and humans. (Illustration: Jacobs, 2016:p.35).

2.2.2 Adaptation for wing surface area

Webbing, which are flaps of skin found in vertebrate limbs such as those of frogs and ducks as well as between the fingers and toes of cats, dogs and humans have not only been retained in the evolution of the bat wing but have become extended to cover the elongated skeletal elements of the forelimb, forming the wings (Kunz & Parsons, 2009). The webbing has also been extended along and between both hind limbs to form the tail membrane, which also provides lift during flight. The tail membrane is supported by two small cartilaginous projections, the calcars, which extend from each heel towards the tail and run along the first part of the trailing edge of the tail membrane (Jacobs, 2016). The tail membrane is also attached to the legs, lower body and tail for support. This is the only new characteristic that evolved in bats for flight. Evolution has simply modified existing parts in the ancestral vertebrate forelimb to form bat wings (Jacobs, 2016).

In the embryo of vertebrates including bats, the growth of the skeletal elements and webbing is influenced by the Sonic Hedgehog Gene (SHH) (Kunz & Parsons, 2009). This gene is activated in the initial stages of development and directs the development of the skeletal elements and webbing. The gene is deactivated at a later stage and the forelimb continues its development. The genes responsible for the development of unique bat wings are not newly developed, they are simply modified (Hockman *et al*., 2008).

2.2.3 Adaptation of wing shape

Wing morphology differs in bats depending on flight performance and flight behaviour (Norberg & Rayner, 1987). With the help of aerodynamics we can understand how different wing shapes are adapted to different flight and hunting modes (Jacobs, 2010). Bats which catch prey while flying in the open air (Aerial hawkers) need to be able to fly fast in order to search a large area quickly and to chase down fast prey (Mutumi, Jacobs & Winker, 2016). Flight speed helps generate lift so the bat does not need wings with large surface areas. Bats hunting in dense vegetation can use aerial hawking, ambush hunting (searching for prey from a perch and intercepting detected prey) and gleaning (taking prey from a substrate such as a branch or the ground). These hunting strategies require slow, manoeuvrable flight, as does trawling (taking prey from the surface or just below the surface of water using their feet and wing membrane) (Monadjem *et al.*, 2010).

Bats hunting at the edge of vegetation need intermediate flight speeds and manoeuvrability. Since flight speed itself increases lift, it is not necessary for the wing area also to increase as a wing with relatively small area can generate enough lift at high speed (Horner & Fleming, 1998).

Since bats flying in open areas are not confined by narrow spaces, sufficient wing area is generated by lengthening the wing. Aerial hawkers can therefore function in open areas with long, narrow wings. Slow flying manoeuvrable bats have short broad wings because drag is not an issue at low flight speeds, wings can be increased by increasing the breath of the wing (Monadjem *et al.,* 2010; Jacobs, 2016).

2.2.4 Adaptation to reduced weight

The bones of bats are lightweight in order to minimize the energy for flight. There has been a reduction the size of large bones and muscle which a normally found in birds and non-flying vertebrates to lighten their bodies for flight (Dumont, 2010). This means that the bats legs no longer support its body weight in a standing position. Instead they evolved the ability to hang upside down without expending any energy. Bat toes have claws which they use when they want to hang onto something, contracting the leg muscles (Kunz & Parsons, 2009). When the muscle contract the tendon moves and the part with the nodules passes into this loop and the nodules lock with recesses on the inside of the loop, locking the tendon in the contracted position and the claws in a locked position, allowing the bat to hang even after it relaxes the muscles (Jacobs, 2016). Bats are able to contact their muscles through a locking and unlocking mechanism when the bat is ready to fly; it contracts the muscles, unlocking the locking mechanism and the claws open. “This mechanism is so efficient that bats can continue hanging from a perch even after they are dead” (Jacobs, 2016).

2.3 Populations and assemblages

The demographics and estimation of bat numbers in specific colonies or those in local, regional and entire species populations is a critical goal for the assessment of long-term conservation and the survival of bats (Kunz & Parsons, 2009). Due to the high sensitivity of bats to disturbances, it is important that researchers are sensitive and take precautions to avoid activities that may affect colony behaviours and ultimately the reliability of estimating colony and population size. Researchers need to pay attention and be alert about the effects of their research and determine whether their research activities can be justified for the importance of gaining additional information at the risk of causing detrimental effects to colonies or bat populations under study (Hayes, 1997; Kunz & Parsons, 2009).

Hibernating bats are especially sensitive to disturbances by people (Tuttle, 1979, 2003). Immediate effects of research activities on hibernating bats may not to be apparent to a one-time visitor but both high metabolic activity and loss of body mass has been documented as resulting from frequent visits to hibernacula by researchers (Kunz & Parsons, 2009). It is suggested that prolonged and repeated visits to hibernating colonies should be avoided. The best way to achieve hibernating bat counts is by counting each individual bat or group of bats as they are encountered or by estimating the mean density of bats in several representative clusters and then extrapolating this density to the total area of the cave wall or ceiling that is covered by bats (Kunz & Parsons, 2009). Census of hibernating bats should be limited to one census period every two years (Thomas, 1995; Johnson, Bracks & Rolley, 1998).

Similarly, maternity colonies of bats are sensitive to disturbance especially excessive activities by researchers in maternity caves can lead to abandonment or mortality of young bats (Thomas, 1995). Young bats are very vulnerable during this time especially when both adults and new-born young are disturbed; immature young bats may be dislodged from the roost substrate when their mothers take flight in their efforts to escape (Kunz & Parsons, 2009). However researchers disturbance to maternity colonies have been seen to vary with species. It is better for visits to be made after adult bats have emerged from their roosts to feed. Young bats can be captured, handled, marked and observed during the time when females are absent with minimal disturbances or induced mortality to flight-less pups. Once young bats have reached the weaning stage, and are capable of sustained flight, captures and observations within the roosts appear to be less disturbing (Kurta *et al.,* 1993).

Traditional methods for conducting a census of bat colonies include visual counts within the roosts and counts during the evening emergence and dispersal flights. While these methods have been the current standards, improved capture and marking methods, and use of visual methods, have increased our ability to more accurately and reliably census and estimate the number of bats present (Carter, Menzel & Saugey, 2003). For most bat species, evening emergence counts provide the most reliable method for estimating colony size. Emergence counts are effective for small colonies and where the emergence routes are known and can be monitored with appropriate number of personnel but may be limited by inadequate lighting and poor visibility (Carter, Menzel & Saugey, 2003).

As long as prolonged disturbance is minimized, counting of small colonies in caves and roosts in open areas such as walls and ceilings may be an acceptable method. To reduce disturbance low-light video cameras, night vision devices or reflectance and thermal infrared cameras should be used and reducing the number of visits to roosts (Kunz & Parsons, 2009). The development of advance detection methods combined with traditional census methods offer better estimation of bats from both small and large colonies. Molecular markers also hold promise for estimating both demographic and effective population sizes, especially rare and invasive species (Gannon, Sherwin & Haymond, 2003).

Mark-recapture methods have generally been unsuccessful for censuring most bat species and populations because recapture rates are low and the assumptions of these methods are rarely met (Kunz & Parsons, 2009). In addition, successful application of the capture mark recapture methods may be compromised because some colonies of certain species frequently separate into smaller groups in fission-fusion societies, with some or all the individuals shifting to alternate and sometimes unknown roost sites (Kunz & Parsons, 2009).

Methods of estimating number of dispersing and foraging bats are more problematic and generally limited to making estimates of activity based on captures, observational, acoustic and radar recordings. Devices suitable for assessing the relative abundance of dispersing and foraging bats include mist nets and harp traps. Photography and videography, using supplemental light sources, and thermal or reflectance infrared cameras can also be used for assessing the relative abundance of bats (Gannon, Sherwin & Haymond, 2003).

Reliable estimation of bat populations for gregarious species will depend on accurate and reliable estimates of colony sizes and assessments of numbers of such colonies present in an area or region of interest (Kunz & Parsons, 2009). Other species especially those rare and elusive taxa, the use of radio telemetry, grid, transects and intensive searches in discrete areas will be needed to adequately assess population sizes (Kunz & Parsons, 2009). Estimation of effective population size for all species requires intensive efforts to collect faeces or tissue from individuals over a range of geographic size for establishing baseline population levels to compare with demographic estimates of population size. Accurate and reliable estimations of bats are important to access both short-term and long-term impacts of anthropogenic changes on the earth’s natural and managed ecosystems (Kunz *et al.*, 2011).

2.4 Echolocation dynamics

Echolocating bats emit sonic signals produced in the larynx and analyse the returning echoes to detect, localize and characterize the reflecting targets (Schnitzler, Moss & Denzinger, 2003). Identification of bats to species levels using their acoustic signals allows for quick survey of the biodiversity of regions (Adams, McGuire & Fenton, 2012), leading to more accurate species counts and occupancy estimates (Parker, 1991). Detection of species that can be easily heard but not easily seen is the true power of acoustic monitoring. For example, high flying bats, such as *Lasiurus cinereus* and *Euderma maculatum*, are rarely included in capture inventories, but are readily detectable in acoustic surveys (O’Farrell & Gannon, 1999). Acoustic methods of species identification represents a powerful approach to study the distribution, ecology and behaviour of animals that broadcast sound for communication (Towsey *et al.,* 2014). Bat detectors allow us to hear and record echolocation calls and to combine these observations with the bats appearance and flight behaviour. Acoustic surveys can provide a more accurate estimate of diversity than capture techniques (Dawson & Efford, 2009) and thus provide the opportunity to learn about organisms from community level to the individual level.

2.4.1 Echolocation: adaptations for detecting objects in complete darkness

"Bats have mastered the night skies largely by using echolocation to perceive their surrounding" (Jones & Teeling, 2006). Flight and echolocation lead to the success, diversity and ability of bats to exploit different habitats. With night vision not good, echolocation made it easy for bats to detect small, fast-moving objects like mosquitoes and moth. Bats evolved a detection system based on sound rather than vision. Sound is reflected off objects in the form of an echo. In bats and other animals this ability is called echolocation. During echolocation bats use sound generated by the larynx and vocal chords, in much the same way humans do (Jacobs, 2016). Bats emit this sound as a call either through their mouth (oral echolocators) or nostrils (nasal echolocators), depending on the species (Jacobs, 2016). Bats have complex folds and flaps of skin around their faces, surrounding the nose and mouth which give some of them a gargoyle appearance, which is most likely associated with echolocation (Jacobs, 2016). Echolocation is the use of sound waves, the call travels in the form of sound waves used to locate where objects are in space. When the sound waves hits an object it produces an echo and this echo bounces off the object and returns to the bats ears as a series of sound pressure waves which the bats ears can detect. The bat's brain then figures out the difference between waves of its call and the returning echo to form an image of its surroundings the same way we use our eyes and light to form images of our surroundings (Jacobs, 2016). The difference is that bats use sound to enable them to identify objects, whereas eyes use vision light (Jacobs, 2016).

The presence of an echo indicates to bats that there is an object nearby, but bats also need to know the size, shape, material, texture and distance of the object. In addition, bats have to be able to differentiate between echoes from a target (such as prey) and echoes from the background substrate or vegetation (called clutter echoes). All this information is encoded in the complex temporal and frequency changes that the bat's call undergoes when it's reflected back as an echo (Jacobs, 2016).

2.4.2 Determining distance, direction and speed

The success of bats has been due to morphological, physiological and behavioural adaptations of sensory and motor systems (Schnitzler, Moss & Denzinger, 2003). Bats emit signals and analyse returning echoes in order to, localise and characterise the reflecting targets. As sound speed is constant with atmospheric conditions at which bats operate, a bat can determine the distance of an object (Jacobs, 2016). Bats are capable of detecting very small time delays, which allows them to differentiate between objects at distances from the bat which differ by as little as 4 mm (Jacobs, 2016). For classification bats will use patterns of echo information to identify targets. They measure the time delay between emitted signal and the returning echo to estimate target distance, and analyse binaural and monaural acoustic cues in order to determine the horizontal and vertical angles of sonar targets. (Schnitzler, Moss & Denzinger, 2003). The bat will lower its call frequency as it approaches a target to determine whether the object is moving towards it or away and at what speed (Jacobs, 2016). These dynamic frequency modulations between calls given out and the echoes are caused by the difference in movement between the bat and the object reflecting the emitted call, this difference is called the Doppler shift (Jacob, 2016).

2.4.3 Determining texture

Bats also distinguish one object from another and from the background by obtaining information about the texture of an object. They do this by using different wavelengths of sound, all in all one call, analogous to how different wavelength of light are used in vision to distinguish, for instance, a blue object from a red background (Kunz & Parsons, 2009; Jacobs, 2016). When two objects are close together, the sound waves in echoes from each of the objects will interfere with one another and produce different patterns of waves from that generated by only one object, which allows the bat to discriminate between that are less than 1 mm apart. Similarly, objects with complex surfaces will reflect waves in different directions, producing different interference patterns to those generated by objects with smoother surfaces, allowing the bat to determine the textures of objects (Jacobs, 2016).

2.4.4 Trade-off between resolution and detection range

As with all natural systems, there is always a trade-off and echolocation is no exception. In order to increase the resolving power of echolocation which is used to detect small objects, determine objects that are close together, to determine the exact distance of an object or texture of an object, bats have to use calls that contain different wavelengths (Jacobs, 2016). However the energy that bats can place in any one call is limited and has to be distributed over all the wavelengths in that call (Jacobs, 2016). Atmospheric attenuation affects bat calls that contain multiple wavelengths by shortening the distance they travel. Bats are forced to reduce the frequency of echolocation calls in order to increase the call intensity and thus resolution decreases, making it difficult to detect small objects (Jacobs, 2016). Thus increasing detection range decreases resolution power and vice versa. Different bat species have evolved different ways of dealing with these trade-offs to optimise the effectiveness of echolocation, which has resulted in many different kinds of calls consisting of different components (Jacobs, 2016).

2.4.5 Species identification

Identification of organisms to species based on their acoustic signals is very important as it allows researchers to quickly survey the biodiversity of regions (Parker, 1991), leading to more accurate species counts and occupancy estimates (Parker, 1991). Birds are the best example of a known group where species identification with acoustic signals provides the most effective sampling approach (Parker, 1991; Riede, 1998). For example, Parker (1991) recorded the vocalizations of 85% of the 287 bird species present in the Bolivian Amazon in seven days, compared with 54 days when using captures. The North American Breeding Bird Survey (BBS) have incorporated standardized acoustic monitoring protocols, such as the BBS, which provide a powerful tool for management and conservation at various geographic scales (Schnitzler, Moss & Denzinger, 2003). Echolocation calls of bats often have species-specific characteristics, and hence are widely used to identify free-flying bats in the field (Neuweiler & Heilmann, 1989). Further, bat echolocation calls are highly variable depending on the echolocation task (Schnitzler, Moss & Denzinger, 2003). For example, bat species that typically feed on flying insects in obstacle-free areas have calls that differ in spectral and temporal characteristics from those that normally feed in more cluttered areas, such as within dense forest vegetation (Neuweiler & Heilmann, 1989). Therefore there is an ever growing need of developing accurate and robust methods of surveying bat populations and monitoring their trends.

2.4.6 Individuals and population structure

Sounds can be used to evaluate fine scale information about communities, including structure of populations and identification of individuals. The vocalizations of bats can vary with group sex, composition, and reproductive status, so recordings could provide valuable information on abundance and population structure, especially when they live in densely forested areas

(Payne *et al.*, 2003). Similarly, blue whale songs can be divided into regional types which can be used to characterize population structure (McDonald *et al.*, 2006). Bird dialects can also play an important role in conservation, from obtaining demographic information (Laiolo *et al.*, 2008) to impacting translocation efforts. Some animals such as wild dogs and sea lions can be identified to the individual-level based on their acoustic signals (Campbell, 2002). Acoustic signals (Hartwig, 2005), which are used for identification in place of physical marks (i.e., tags and bands; Laiolo *et al.*, 2008), provide important information for population monitoring. A limit of data on individual variation currently prevents the identification to the individual level in animals such as insects, frogs, and bats (Obrist, 1995; Chesmore, 2001).

2.4.7 High frequency sounds

"While most sounds recorded during acoustic monitoring are audible to humans, others are not. Toothed whales (Odontoceti; e.g., dolphins) and bats (Chiroptera) are two taxa that use echolocation for communication, foraging, and orientation by emitting pulses of high frequency sound and gathering information based on the returning echoes" (Adams, 2013). The central frequency depends on the intensity of the signal, ranging from 30–60 kHz (low intensity) to ~100 kHz (high intensity). Odontocetes has a much faster information transfer compared to bat echolocation because their signals move through water while echolocation moves through air air (Jacobs, 2016). Bat calls are much more diverse in structure than odontocete signals, varying in duration, from 0.3 to 300 millisecond (ms); in frequency, from 8 to >200 kHz; and in shape, ranging from broadband to constant frequency (Neuweiler & Heilmann, 1989). Detecting both dolphin and bat echolocation calls requires a researcher to rely on technology capable of detecting high frequency sounds. Bats provide additional challenges as they are small, nocturnal animals that cannot be sampled visually and capture success is limited to low flying species. Echolocating bats emit sonic signals produced in the larynx and analyse the returning echoes to detect, localize and characterize the reflecting targets (Schnitzler, Moss & Denzinger, 2003). Echolocation calls of bats often have species-specific characteristics, and hence are widely used to identify free-flying bats in the field (Hofstede & Fenton, 2005). Further, bat echolocation calls are highly variable depending on the echolocation task (Schnitzler, Moss & Denzinger, 2003). For example, bat species that typically feed on flying insects in obstacle-free areas have calls that differ in spectral and temporal characteristics from those that normally feed in more cluttered areas, such as within dense forest vegetation (Neuweiler & Heilmann, 1989).

2.4.8 Components of calls

Frequency-modulated calls

Frequency modulated calls (FM) are calls that have multiple frequencies. They can be narrowband (where the bandwidth is obtained by subtracting the minimum frequency from the maximum frequency in the call, and the difference between the two is small), that has low range of frequencies or broadband (where the bandwidth is large) with a high range of frequencies (Jacobs, 2016).

Narrow band signals are great for target detection but not for target localisation while broad band are great target localisation (Jacobs, 2016). As broad band is affected by atmospheric attenuation and it’s a short detection range , most bats will use a combination of both narrow and broad band calls for localization in order to optimize the detection range switching between the two when needed (Arita & Fenton, 1997; Jacobs, 2016). Echolocation calls are made of a series of harmonics, which are used to resolve small objects and clutter. The first harmonics and a series of higher harmonics called second and third harmonics. Harmonics are used to distinguish between the target object and non-target objects such as echoes the ground, trees and other bat calls (Jacobs, 2016). The clutter echoes make it difficult for the bat to use time delay as the clutter echoes interfere with the bat being able to find its target echo. (Jacobs, 2016). The horizontal width of the echolocation beam is dependent on the sound frequency. The higher harmonics have a narrow beam compared to lower harmonics and therefore generate fewer echoes of lower amplitude from the clutter than from the target. When the target reflects echoes from both the first and higher harmonics that are of higher amplitude than the echoes from clutter, this allows the bat to focus on echoes from the target.

Higher frequency sounds containing higher harmonics attenuates more quickly in air and assists with the isolation of echoes of the target from background clutter (Jacobs, 2016). Echoes from the target have a higher amplitude than echoes from the background, which allows the bat to detect its target object against the back ground clutter (Jacobs, 2016).

Bats are able to increase the bandwidth of their calls by switching from lower to higher frequencies instead of harmonics, but the call durations will be longer than calls with harmonics (Jacobs, 2016). This would increase the potential of temporal overlap of background echoes with all or parts of the call, thus interfering with the processing of the echo time delays by the bat. FM components are used by bats for hunting in dense vegetation, where resolution is of more importance than detection distances. In clustered situations, the distance between bats and objects are relatively small (Jacobs, 2016).

Constant Frequency

Constant frequency (CF) are parts of calls in which there is no change in frequency with time and its represented on time (x-axis)/ frequency (y-axis) graph as a horizontal line. In such parts component energy is concentrated in a single frequency or narrow band of frequencies. Which enables the travel of sound waves through the atmosphere at greater lengthens compared to that of FM components where energy is spread over several frequencies (Jacobs, 2016).

In general CF signals can have longer durations than FM signals if energy is directed along a narrow band of frequencies. The operational range of CF components is much greater than that of FM signals as the higher amplitude can be totaled by the bats auditory system over the entire call as the echoes returning within the narrow frequency bands have a higher amplitude

(Jacobs, 2016*)*. This maintains a constant frequency signal in the auditory system for about 100 milliseconds, where each frequency has an effect that lasts no longer than a few milliseconds (Jacobs, 2016).

Longer call durations increase the probability of parts of the call to be reflected off a distant object. CF components contain single and narrow range wavelengths which are great for the detection of objects but fails in the localisation of objects in time and space (Jacobs, 2016). These signals can be used in open spaces where distances to objects is far and detection range is more important than localisation (Jacobs, 2016). The long narrow signals are used by bats that wait on perches for prey to fly by because it allows perched bats to detect Doppler shifts that are produced by insects moving towards or away from it (Jacobs, 2016). Long-duration CF signals are useful in detecting the amplitude and frequency changes that occur in the echo reflected off the wings of insects when the insect is flapping its wings during flight or while seated on an object. Perched bats use CF components for hunting as their able to detect when the insect flaps its wings (Jacobs, 2016).

When long CF signals hit the wing of an insect the amplitude and frequency of the echo is dependent on the position of the wing and whether the wing moves towards or away from the bat (Jacobs, 2016). Bats are able to see the changes in the amplitude and frequency of echoes as the insect flaps it's wings against the constant echoes of the background clutter (Jacobs, 2016). Collectively these changes are called acoustic glints, which allow bats to detect flapping insect wings against the constant echo from background clutter. Acoustic glints are the same as coloured lights, each has a different brightness, flashing on and off against a background lit by light of constant colour and intensity (Jacobs, 2016).

2.4.9 Duty cycles

Bats use both CF and FM components at some point but are called either CF or FM because some species calls are dominated by CF components and others are dominated by FM components. It is more accurate and biologically informative to talk of low duty cycle (LCD) and high duty cycle (HDC) bats. Bats emit their echolocation as sound or calls (Jacobs, Barclay & Walker, 2007). These calls are separated by silence, during which the bat is not emitting calls. The ratio of the duration of the call to the period of the call is called the duty cycle and is expressed as a percentage. Bats have been split into two groups based on their echolocation cycles: low duty cycles and high duty cycle echolocators (Jacobs, 2016).

2.4.10.1 Low duty cycle (LCD) bats

Bats that use low duty calls emit short duration calls relative to period of the call. The reason for this is for the bats to avoid being deafened by their own calls. Atmospheric attenuation at the high frequency at which this bats operate means that bats have emit calls of high intensities (measured as 110–135 dB at 10 cm in front of the bat) which allows the calls to travel sufficient distances for the bat to detect echoes in time to move in order to avoid an obstacle or catch prey (Jacobs, 2016). However the inner ears of bats have to be sensitive enough to pick up the faintest of echoes. Such a sensitive ear can easily be damaged by sounds greater than 90 dB emitted millimetres from the ear (Jacobs, Barclay & Walker, 2007).

To avoid damage to the inner ear, LCD bats use the same strategy as humans to avoid damage to sonar receivers. Bats achieve this by tiny bones and muscles in the middle ear. The ear has three tiny bones in the middle called auditory ossicles, which are linked in tandem and transmit sound from the ear drum to the cochlea (inner ear). Small muscles are attached to the ossicles (Kunz & Parsons, 2009). These muscles contract and disrupt the linkage between the three ossicles just before the bat emits its echolocation call, thus preventing sound transmission to the cochlea and protecting the sensitive inner ear. The bat will then emit the echolocation call (Jacobs, 2016). The muscles attached to the ossicles will than relax and restore the link between the ossicles after releasing the call and the returning echo can now be transmitted to the cochlea (Jacobs, 2016). The bat can thus separate the emitted call from its returning echo in time and has to wait until the echo from one call returns before releasing the next call to avoid the echo from one call returning while the ear is functionally deaf during the emission of the next call. This is why there is a long period of silence between each call and the duty cycle is low. LDC bats are extremely diverse in their echolocation calls, flight behaviour and habitat. The bat calls have mostly broadband FM components, which are well suited to the habitat in which they hunt and their way of hunting (Arita & Fenton, 1997). These bats hunt in habitats where they forage usually in dense vegetation, edges of vegetation near the ground or water because FM components are useful localisation and to distinguish clutter from target echoes. Some of these bats can be specialists, spending a lot of time in dense vegetation or flexible and spend a lot of time in open habitats (Jacobs, 2016).

LDC bats are able to switch from narrowband calls in an open space to broadband calls when hunting in clutter. Bats whose calls are mostly made up of FM components are generally slow manoeuvrable flyers with a little flexibility and it’s reflected in the shape of their wings (Jacobs, 2016). Bats have different wing shapes depending on the habitats they feed in. Bats in dense habitats have short broad wings while bats in edge habitats have intermediate wings. Long narrow wings are found in bats that hunt in open habitats (Jacobs, 2016).

2.4.10.2 High duty cycle (HDC) bats

High duty cycle bats have long call durations relative to the period of the call. In order to prevent self-deafening these bats have short silent periods with long-duration calls, separating the released call and returning echo frequency (Jacobs, 2016).

The HDC echolocation is found in bats from families Rhinolophidae, Rhynoncyteridae and Hipposideridae, an example is the *Pteronotus parnellii* (family Mormoopidae) (Burgin *et al.,* 2018). Bats that use HDC echolocation are different in that they give off long-duration calls which are dominated by CF components which is followed by a brief FM component (Jacobs, 2016). HDC bats place most of the call energy in the second harmonic rather than the fundamental harmonics as do LCD bats (Jacobs, 2016). Bats that use high duty calls have a region in the auditory system known as the acoustic fovea, it's a region with the over-representation of the neurons sensitive to a unique and narrow range of frequencies called reference frequencies (Jacobs, 2016). In order to prevent self-deafening flying bats will give off a call at a lower frequency so the returning echo is slightly higher; to make sure the returning echo falls within the narrow range of frequencies of the acoustic fovea, protecting the inner sensitive part of the ear (Jacobs, 2016).

The Doppler-shift compensation also means the background echoes are constant in amplitude and frequency (Jacobs, 2016). Bats are able to detect the acoustic glints generated by the flapping wings of insects. This means HDC bats can release calls and receive echoes at the same time while LDC bats give of short duration calls because of the silent periods between calls increasing the duty cycle (Jacobs, 2016). These bats can hunt from a perch while stationary and emit calls which range from 100 Hz to 300 Hz lower than the reference frequency. The frequencies of these calls are known as the resting frequency. The frequency of the bat call echoes of a perched bat will be reflected off an approaching insect and will be shifted up because of the Doppler-effect and will fall within the sensitive range of the bat's acoustic fovea (Jacobs, 2016).

2.4.11 Changes in echolocation during a hunt

Bats are able to adjust their echolocation calls just as humans are able to adjust their vision in order to keep track of a moving or stationary object. This is done by increasing the number of calls they release, duration and frequency of the calls (Jacobs, Barclay & Walker, 2007). A bat's attack sequence is divided into three stages: The search phase, the approach phase and the terminal phase or feeding buzz phase (Jacobs, 2016). During the search phase the bat scans far ahead and as widely as possible to increase the volume of space and maximise the chances of detecting prey. To do so the bat has to use calls that will be less attenuated and can travel further to still produce audible echoes (Jacobs, 2016). So during the search phase bats emit calls at lower frequencies and narrow bandwidth at slower rates because it's probing further and it takes longer for the echo to return. Longer calls increase the probability of at least part of the call being reflected off a distant object as an echo and so search phase calls are usually a longer duration (Jacobs, 2016). Once the object has been detected the bat flies to it, than it has to classify whether the object as prey or something to avoid and to locate the object accurately in time and space (Jacobs, 2016). This requires more resolution than detection distance; the more wavelengths the bat has in its call the greater the resolution of location and type of object (Jacobs, 2016).

In the approach phase the bat will identify the object as either food or to be avoided. If it decides to attack it approaches the prey closer and as the bat gets even closer, it just needs to pinpoint the prey on time and in space to make an accurate capture (Jacobs, 2016). Call rates increase, durations get shorter and the bandwidth decreases. Calls are now rapid and will have one long buzzing sound. This phase is known as the feeding buzz or terminal phase (Jacobs, 2016).

The bat’s combination of flight and echolocation has allowed it to invade almost all terrestrial habitats (with exceptions of frost deserts and snow plains), diversifying their behaviour and diets and leading to more elaboration of the basic mammalian body plan (Jacobs, 2016).

2.5 Technology: Advancement and Limitations

Bat detectors have become a very useful tool for the study of bats because they are easy to use, reduce labour through passive recording options, and the ability to study bats without direct disturbance. The advancement in technology has allowed researchers the ability to collect data that was in the past very difficult to do. Allowing many bat detectors to be placed in the field to record simultaneously and in previous inaccessible habitats, for more accurate biodiversity data (Adams, 2013., Carter *et al.,* 2003; Orme *et al.,* 2005). Studies have shown the importance of old growth or mature forests (Hearn, 2004; Jacobs, Barclay & Walker, 2007) edge and open habitats to bats. Habitat associations have been linked to foraging strategies and morphological characteristics of bat species or guilds (Barclay, Fullard & Jacobs, 1999; Farrell & Bradley, 2015). Acoustic detections of aerial foraging (aerial hawking) species are greater in open and edge habitats where quick flight can be used to capture prey (Barclay, Fullard & Jacobs, 1999). Cluttered habitats are avoided by aerial hawking species, but are regularly used by species that capture insects off the surface of vegetation (Barclay *et al.,* 2004; Farrell & Bradley, 2015).

Bat detector surveys and activity studies are constrained by important assumptions and limitations (Gannon & Sherwin, 2003). Large spatial and temporal variation in bat activity has been noted with bat detectors (Hayes, 1997; Gannon & Sherwin, 2003). Weller & Zabel (2002) found that up to 70% more passes were detected at a single location within a forest depending on orientation of bat detectors toward an opening. This variation can be reduced by controlling the height, angle, and orientation of the detector toward an opening within sampled habitats. Hayes (2000) noted temporal variation in activity throughout the night, summer, and year and recommended simultaneously sampling all habitats of interest to control for variation. In order to compare activity between habitat types, Gannon & Sherwin (2000) suggested that equal detection probabilities between habitat types during each sampling period must also be assumed. Fenton *et al.* (2015) found that detection probabilities between open and cluttered habitat types were not equal because of differing areas of space sampled by detectors.

A variety of ultrasonic detectors are commercially available. There are several different systems of ultrasonic detectors, which have different uses in the field for sampling bats (Georgiakakis *et al.,* 2010). Heterodyne detectors mix an internally generated pure tone with the ultrasonic call to generate a sound at an audible frequency and the frequency can be tuned (Barlow, 1999). These detectors are very sensitive and can be used in the field to determine the approximate frequency of a call. They cannot, however, be used to collect very detailed information about echolocation calls and often are not good enough for positive species identification. Heterodyne detectors also have a limited frequency range and bats producing echolocation calls at frequencies outside the selected frequency will not be detected (Voigt & Kingston, 2016). Species identification is not usually possible with heterodyne detectors. However, they may be helpful for locating roosts or areas of activity, which may be suitable sites to place harp- traps or mist-nets (Towsey *et al.,* 2014). These detectors also have the advantage that they are relatively cheap to buy (Voigt & Kingston, 2016).

Frequency-division detectors reduce the frequency of ultrasound with digital frequency counters (Towsey *et al.,* 2014). Frequency division has the frequency counters. It has the advantage that it is a broadband method and therefore can sample a range of frequencies at one time, but it is less sensitive than heterodyning. Some previous limitations, such as potential damage from water or inclement weather (Barlow, 1999), have been overcome with changes in design. The newest Anabat Express detectors (Titley, Australia) have a waterproof case and microphone. Although some studies have found Anabat detectors to be less sensitive than other types of detectors (Monadjem *et al.,* 2007). The signals can be recorded and analysed, so this method can be used both for monitoring activity and in some cases for species identification (Barlow, 1999). However, sound analysis software is required for species identification, and frequency division detectors are more expensive to buy (Monadjem *et al.,* 2017) than heterodyne detectors. Time-expansion detectors capture and digitise a short sequence of echolocation call. Time-expansion is a broadband method and retains detailed information on echolocation call structure. It is more accurate for species identification than frequency division. Sound analysis software is required for analysis of recorded calls. An example of these bat detectors is Wildlife Acoustic SM4 bat detectors. Time-expansion detectors are the most expensive of all detector types available.

Bat detectors can be used to monitor bat activity in different habitats or different species (Monadjem *et al.,* 2017). Bat activity is usually measured by counting the number of bat passes recorded. A bat pass is the continuous string of echolocation calls heard on a bat detector as a bat flies over within range (Fenton *et al.,* 2015). The number of bat passes in a specified time period are counted to determine bat activity (Barlow, 1999). There are limitations to using bat detectors to sample bats, as there are with capture techniques. Manual identification of species requires expert knowledge and accurate reference library. The greatest drawback is the inability to get an accurate bat count using data from bat detectors as activity is not equal to abundance (Adams, 2013). Bat passes only give a measure of the level of activity (Barlow, 1999; Fenton *et al.,* 2015), which can then be compared among sites. There is no guideline on how to interpret bat activity levels beyond the relative differences in activity of one sample from another (Adams, 2013). Species identification is often very difficult and all species may have to be considered together. Echolocation call intensities differ between species and therefore species have differing detection abilities (Fenton *et al.,* 2015). The advantage of sampling with bat detectors is that a large area can be studied with relative ease (Kunz *et al.,* 2011). The factors that influence which bats are sampled by detectors differ from those that affect which bats are sampled by catching techniques. One study of an insectivorous bat community suggested that temporal activity can be assessed equally well with bat detectors or mist-nets (Monadjem *et al.,* 2007*).* However, a more complete picture of a bat fauna and habitat use may be gained by using both techniques together (Barlow, 1999)**.**

2.6 Movement and habitat use

2.6.1 Movements and migrations

Temperate zone bats may undertake a variety of movements ranging from short distances between roosts and foraging areas (Fenton *et al.*, 2015) to long-range migrations between seasonally occupied sites. The daily feeding range of *Tadarida brasiliensis*, is up to 60 km, which is more than the normal annual movements of many species (Fenton *et al.,* 2015). Bat migration may be to maintain feeding opportunities, or for suitable hibernation sites. In southern Africa, *Eidolon helvum* seasonal appearances and disappearance likely reflect responses to changes in food supplies (Monadjem *et al.,* 2001). In some Southern hemisphere species, it is mainly females that undertake the spring northerly migration to give birth and rear young, e.g., *Tadarida*, *Nyctalus*, and *Lasionycteris*. In *Leptonycteris*, the births are in the south of the range, but the volant young move north with the adult females (Fenton *et al.,* 2015). *Miniopterus natalensis* in Gauteng, Limpopo and the Western Cape (South Africa) migrates between warmer maternity caves where females give birth in summer and colder caves in winter, where mating and hibernation occur. *Myotis tricolor* undertakes similar seasonal migrations, although details are not yet known (Monadjem *et al.*, 2001).

2.6.2 Torpor and Hibernation

Bats are warm-blooded mammals that have fur, give birth to live young and can maintain a constant body temperature (Jacobs, 2016), however some show a remarkable degree of thermolability, which occurs on a daily or seasonal bases. According to Monadjem *et al.* (2001) the body temperature of torpid bats fluctuates in accordance with the ambient temperature and thus colder than that of homeothermic mammals. Daily torpor and hibernation are common in the Vespertilionidae, Miniopteridae, Rhinolophidae and Hipposideridae, and in some Molossidae (Monadjem *et al.,* 2001). Other southern African bats are more conventional thermoregulators and cannot enter torpor, research by Munoz-Garcia *et al.* (2015) in the South African Lowveld has shown that the Angolan free-tailed bat, *Mops condylurus*, routinely selects the hottest roosts under tin roofs, and by allowing its body temperature to rise is able to save energy that would otherwise have been required for cooling (i.e. the reverse of torpor). These same bats readily undergo torpor to conserve energy during daytime roosting in both summer and winter. Like birds some bats migrate to warmer climates during the winter months but many migrate to colder climates for winter (Kunz *et al.,* 2011). These small mammals are able to shut down their metabolism to a basic level in response to the winter cold, thus allowing their body temperature to fall to that of their environment, or to just above freezing in sub-zero temperatures (Kunz *et al.,* 2011). The colder the ambient temperature, the greater the energy saving, through the lowering of their internal body temperature (Monadjem *et al.,* 2001). By switching off their energy-expensive heating system during hibernation, bats can survive cold winters when insects (i.e. fuel reserves) are very scarce (Monadjem *et al.,* 2001). Before hibernation, in late summer, bats will eat large amounts of food to build up their fat reserves, which may comprise up to 26% of their total body weight just before hibernation (Kunz, 1998). These reserves may have to tide them over for up to six months during hibernation. Bats budget their fat reserves very precisely and forced arousal from hibernation consumes huge amounts of energy reserves, and can result in bats starving before the end of winter (Monadjem *et al.,* 2001).

2.6.3 Distribution of bat species along an elevational gradient

Research on mammal diversity in the Neotropics and Neotropical has largely focused on geographical patterns, mainly along latitudinal gradients (Heaney, 2001). Two patterns appeared repeatedly: species richness increased from temperate regions to the Neotropics while Neotropical lowlands hold the highest species diversity. Although very important on global or continental scales, latitudinal patterns of diversity do not provide the information local conservation need. Variation in mammalian diversity along elevational gradients is not well researched, yet it forms a crucial role for conservation action at small geographical scales (Sánchez-Cordero, 2001).

Due to limited research done on species variation along elevational gradients in the past, lowlands tropical forests have generally been thought to hold the highest biological diversity (Patterson *et al*, 1996). Gentry (1988) showed strong evidence of the correlation between precipitation and species richness of large Neotropical plants. Plant species richness declined along the elevational gradient and noted the absence of intermediate increase in species richness. Although Heaney (2001) found that maximum biodiversity was at intermediate elevations in certain communities such as tropical region. This was because the intermediate elevation has increased and seasonal rainfall. There is also evidence that tree species richness is highest at intermediate elevations (Heaney, 2001).

Species distributional patterns in Oaxaca, Mexico have been explained by several hypotheses which include reduction in effective area, change in abiotic parameters and biotic factors correlated with increasing elevation. Distribution patterns of rodents and bats were found to be different along an elevation gradient (Sánchez-Cordero, 2001). Rodent's species richness generally peaked at intermediate elevations whereas bat species richness was highest at low elevations and gradually decreased with elevation (Petterson *et al.,* 1998). There is however still lacking evidence regarding elevational patterns for mammals particularly in regions of high species diversity such as Mexico where conservation is needed

2.6.4 Desert habitat use

Bats have successfully exploited arid areas throughout the world (Happold & Happold, 1988; Murray *et al.*, 1999). Despite this, a search of worldwide literature on bats uncovered only little that addressed the ecology of bats in desert environments (Happold & Happold 1988; Williams *et al.,* 2004). There are several factors that may influence the ability of bats to exploit arid environments. Roost sites and invertebrate prey are essential resources for insectivorous bats to complete life-cycle activities. The availability of free-standing water may also be a resource influencing success in arid environments. Happold & Happold (1988) suggested that bats might be restricted to oases and mesic habitats within desert regions, due to their roosting and foraging requirements. Alternatively, they may migrate to areas containing temporary resources, a strategy illustrated by several species of arid zone birds and mammals (Williams *et al.,* 2004). Deserts receive relatively low and variable rainfall, resulting in little free-standing water for long periods. Arid and semi-arid regions have some of the most unpredictable climates in the world (Murray *et al.,* 1999). Rainfall is both temporally unreliable and patchy in space. Bats occupying arid areas are thought to obtain their necessary water from the insects in their diet and, like rodents, have specialised kidneys that produce concentrated urine (Murray *et al.,* 1999; Fenton *et al.,* 2015).

Neuweiler (2000) recorded insectivorous bats surviving for 72 days without water in the hyper-arid Namib Desert (Namibia). While lack of consistent rainfall hinders drinking, it would also influence food resources. Many insects feed on plants, and vegetation production decreases with reduced rainfall (Williams *et al.,* 2004). In semi-arid New South Wales

(NSW, Australia), bat activity appeared to be concentrated near water sources (Solly, 2002; Velez, 2002). These bats take water directly by drinking or, alternatively, they may be attracted by increased insect activity at water sources. Arid and semi-arid areas cover more than 43% of Africa (James & Landsberg, 1999). Considering this, relatively little research on arid and semi-arid zone bats has been published. As a consequence, the ecology of insectivorous bats in Namibian desert regions is not well known. That said, species occurance data and the predictive niche models based thereon presented in Monadjem *et al.* (2010) have shown that bats do successfully occur in Namibia' arid and semi-arid environments, with general habitat preferences for woodland, riparian vegetation and water sources).

2.7 Economic importance

Ecosystem services are the benefits obtained from the environment that increase human well-being. Economic valuation is conducted by measuring the human welfare gains or losses that result from changes in the provision of ecosystem services (Kunz *et al.*, 2011). . The rich diversity of dietary habits of bats, ranging from species that feed on insects and other arthropods to those that feed on fruit, nectar, and flowers, (Petterson, 2003; Simmons, 2003) provide valuable ecosystem services. Bats provide value to ecosystems as primary, secondary, and tertiary consumers that support and sustain both natural and human dominated ecosystems (Petterson, 2003). Insectivorous species, largely feeding on air borne insects and other arthropods, suppress both naturally occurring and anthropogenically-generated insect populations (such as agricultural pest species and insects that annoy or transmit specific pathogens to humans and other mammals) and contribute to the maintenance of ecosystem stability (Kunz *et al.*, 2011). Various species of prominent agricultural insect pests have been found in the diets of bats based on identification of insect fragments in faecal samples and stomach contents (Kunz *et al.*, 2011). These include insects such as June bee beetles (Scarabaeidae), click beetles (Elateridae), leafhoppers (Cicadelidae), planthoppers

(Delphacidae) the spotted cucumber beetle, (*Diabrotica undecimpunctata*, Chrysomelidae), the Asiatic oak weevil (*Cyrtepistomus castaneus*, Curculionidae), and the green stinkbug (*Acrosternum hilare*, Pentatomidae) (Muscarella, 2007). Whitaker (1995) calculated that a colony of 150 big brown bats (*Eptesicus fuscus*) in the Midwestern United States annually consumes approximately 600000 cucumber beetles, 194000 June beetles, 158000 leafhoppers, and 335000 stinkbugs (Muscarella & Fleming, 2007). Subsequently, assuming that each female cucumber lays 110 eggs, average-sized bat colonies could prevent the production of 33000000 cucumber beetle larvae (corn rootworms), which are severe crop pests. While these calculations include a large number of assumptions and ignore various sources of natural variation, this study took the extra step of translating ecological data into a form more readily appreciated by the public (National Research Council, 2005). With the addition of data on corn rootworm damage to crops in the study area, an economic value for this colony could be estimated. A common challenge in these investigations is the overwhelming lack of basic ecological information regarding foraging behaviour and diet for many species of bats (Kunz *et al.*, 2011).

Studies by Taylor *et al* (2013) examined the economic significance of bats predators of pest insect *Nezara viridula* (stink bug) collect from macadamia orchids in the Levubu Valley, South Africa. Microscopic analysis of faecal pellets revealed 20- 50% of stink bags were found in the bat diets. The studies hint at the immense potential for bats to provide pest suppression services in both natural and agroecosystems; however, more research is needed to adequately document the extent to which bats interact with and limit insect pest populations across the geographical landscape and over time. A detailed resolution of dietary composition across bat species, in which identification of prey items to species rather than only to the family or ordinal level, is needed to track patterns of consumption of agricultural pests spatially, seasonally, and relative to other benign insects (Williams-Guillen *et al.,* 2016).

In addition to insect suppressions, some bat species also play an important role as plant pollinators and seed dispersers in habitats throughout the world. The economic value of their pollination and seed dispersal services, plant-visiting bats provide important ecological services by facilitating there productive success of their food plants, including seed set and the recruitment of new seedlings and saplings. Many of these plants are among the most important species in terms of biomass in their habitats (Troy & Wilson, 2006). Bat-pollinated columnar cacti and agaves are dominant vegetation elements in arid and semiarid habitats in Mexico as are various species of the Bombacoideae sub-family in dry and wet tropical forests throughout the world. Bat-dispersed palms and figs are also common in many tropical forests worldwide. Because they are also eaten by many birds and mammals, figs often act as keystone species (i.e., species whose ecological impact often exceeds their biomass) in tropical forests (Kunz *et al.,* 2011). Figs are important bat-fruits throughout the tropics. Bat dispersed, soft-fruited species of *Cecropia*, *Piper*, *Solanum*, and *Vismia* are critically important early pioneer species that are among the most abundant plants during early primary and secondary succession in the Neotropics. Fruit-eating bats thus play an extremely important role in forest regeneration. This is not necessarily true in the Paleotropics, where most early successional plants are bird dispersed (Muscarella & Fleming, 2007). Pteropodid bats play a more important role in the dispersal of later successional trees than in the dispersal of pioneer species (Muscarella & Fleming, 2007). Some of these plants, such as species of *Pouteria* and *Plaquium* (both Sapotaceae) in Asia and *Milicia* (*Chlorophora*) *excelsa* and *Antiaris africana* (both Moraceae) in Africa, are important timber trees (Jansen & Zuidema, 2001). An exception to this is the dispersal of seeds of pioneer species of *Ficus*. During the recolonization of Krakatau, for example, bird- and bat-dispersed figs were early colonists and attracted frugivorous bats that brought in seeds of other plant taxa (Shilton & Whitaker, 2009). Thus, bat-dispersed figs likely “jump-started” forest regeneration on these islands. One of the most important ecological services that bats provide for their food plants is long distance dispersal of pollen and seeds. This is especially true in arid habitats where *Leptonycteris* species visiting the flowers of columnar cacti have a large foraging area (Horner, Fleminng & Sahley, 1998). Flower-visiting phyllostomatid and pteropodid bats forage in both continuous forest and forest fragments and, thus, help to maintain genetic connections among fragmented plant populations. For example, phyllostomatid bats pollinating *Hymenaea courbaril* trees in tropical dry forest fragments in Puerto Rico often move pollen 600–800 m between individuals (Jenkins & Racey, 2009). In Brazil, *Phyllostomus* species are known to move the pollen of *Hymenaea courbaril* trees 18 km between individuals in riverine forest (Biscaia de Lacerda *et al.*, 2008). Glossophagine bats regularly move pollen between individuals of the canopy tree *Ceiba pentandra* in continuous forest and between forest trees and isolated pasture trees in western Mexico (Quesada *et al.*, 2004). The Australian pteropodid *Syconycteris australis* usually moves pollen <200 m between *Syzygium cormi-florum* trees but also moves pollen up to about 6 km between individuals in different habitat patches (Law & Lean, 1999). Most seed dispersal systems, including those involving vertebrates, produce leptokurtic dispersal distributions. That is, most seeds are dispersed close to parent plants with only a few being dispersed 100s to 1,000s of meters away. Seeds dispersed by frugivorous bats undoubtedly conform to this pattern, but bats can also provide relatively long seed dispersal distances for their food plants. For example, in central Panama the Jamaican fruit bat *Artibeus jamaicensis* carries single fig fruits 100–250 m away from fruiting plants before beginning to feed in a night roost; it often feeds at several trees located a kilometre or more apart in a single night (Morrison, 1978).

Similarly, *Cynopterus sphinx*, the Asian pteropodid ecological analogue of the Neotropical *A. jamaicensis*, is known to forage on more than one island in the Krakatau group in a single night (Shilton & Whitaker, 2009). Although it is generally a short-distance seed dispersers, the phyllostomid *Carollia perspicillata* is known to move 1–2 km between foraging areas and frequently moves seeds between habitats (Morrison, 1978; Muscarella & Fleming, 2007). In contrast to forest-dwelling frugivorous birds, phyllostomatid and pteropodid bats readily fly over open areas and defecate seeds in flight. As a result, phyllostomatid bats eating the small seeds of pioneer plant species provide substantial mobility for their seeds and help them to quickly colonize forest tree fall gaps and disturbed areas such as abandoned pastures and logged forests (Muscarella & Fleming, 2007).

2.8 Disease risks

Emerging infectious diseases in wildlife threaten global biodiversity and public health (Daszak *et al.,* 2000). Bats are able to host a range of zoonotic and potentially zoonotic pathogens. In addition to rabies (RABV) and other lyssaviruses (Kuzmin *et al.,* 2008; Streicker *et al.,* 2010), bats have been identified as the likely reservoir for severe acute respiratory syndrome (SARS) coronavirus (Li *et al.,* 2005; Hayman *et al.,* 2013), Nipah, Marburg viruses (Hayman *et al.,* 2013) and possibly Ebola (Leroy *et al.,* 2005). Most recent, a new distinct lineage of influenza A virus has been discovered in little yellow-shouldered bats (*Sturnira lilium*, family Phyllostomatidae) in the Americas (Hayman *et al.,* 2013; Tong *et al.*, 2012) and a range of paramyxoviruses have been found in bats from four continents (Drexler *et al.,* 2012). Given the potentially harmful effects of these emerging diseases on public health and wildlife conservation (e.g. EBOV and gorillas), it is crucial that we gain more knowledge and understanding of how bat ecology may influence disease dynamics and their susceptibility to serve as reservoirs for emerging pathogens (Arita & Fenton, 1997; Calisher *et al.*, 2006). Ecological drivers of pathogen spill over and emergence in novel hosts, including humans, can be a complex mixture of processes (Lloyd-Smith *et al.,* 2005). Understandably human activities that increase exposure to bats will increase the opportunity for infections to be transmitted between bats and humans or to intermediate hosts such as pets and livestock. However, our knowledge of how and why emerging pathogens spill over from bats is still very limited, and improved understanding of these processes will need cross-disciplinary approaches. Traits of the pathogen and the human-pathogen interactions at the cellular level, such as evolutionary mutation rates and receptor binding affinity, are important in understanding spill over and emergence (Moya *et al.,* 2004; Pulliam, 2008). However, these traits are proximate causes, and the ultimate drivers of spill over and emergence are ecological (Lloyd-Smith *et al.,* 2005). Therefore, it is important to understand host ecology and elements of the human-animal interface as these are essential in the context of pathogen spill over events. For example, host population structure and seasonality may affect the dynamics, viral diversity and virulence of infection in the host population, which may in turn increase the risk of spill over (Boots *et al.,* 2004; Turmelle *et al.,* 2010). Few studies have attempted to understand how host ecology impacts the dynamics of infection in wild animal populations and fewer still for bat populations, and attempts at understanding how infections themselves evolve to persist in wildlife hosts with different ecologies are rarer still. In order to understand the role host ecology plays in disease dynamics, its recommended to combine field and experimental methods iteratively to parameterize mechanistic models, as well as integrative modelling in a comparative context, between species, population cohorts and pathogens (Reynes *et al.,* 2005; Plowright *et al.,* 2011). Only once host and pathogen ecologies are understood, can reliable predictions be made regarding ecological drivers of spatiotemporal infection dynamics and spill over (Keeling & Rohani, 2008). Infection dynamics in bats are most likely influenced by the unique ecology of this diverse group of mammals. Bats differ from other small mammals in that they have potential for rapid and widespread dispersal, high social structures, long lifespans and high survival, with low fecundity (Calisher *et al.,* 2006). The majority of the studies on bat infections to date have focused on bats and zoonotic viral infections, but the ecological generalities may be similar among bacterial (Hayman *et al.,* 2013) and fungal infections of bats (e.g. *Histoplasma capsulatum*, *Pseudogymnoascus destructans*) (Taylor *et al.,* 2005*)*. Although the involved explicit hypothesis testing regarding pathogen associations and the unique ecological characteristics of bats have been recognized as important, still very few studies have been done. Understanding disease dynamics in wildlife populations, especially within bat populations is important to make informed policy and mitigation decisions. "The increase in human and bat contact is inevitable; however, there is potential to manage how these interactions occur" (Hayman *et al.,* 2013).

2.9 Conservation concerns

Bats are vulnerable to any form of development which impacts on their habitats, roosts, food and reproduction. Despite being relatively long-lived most bat species have only about one to two pups a year. According to Jacobs (2016) bat populations are therefore severely affected by disturbance. In most ecosystems bats can be used as bio-indicators of the health of the ecosystem. Bat populations are affected by a wide range of factors such as climate change, deterioration of water quality, agricultural and urban intensification, and loss or fragmentation of habitat, disease, overhunting and fatalities at the sites of wind turbines (Jacobs, 2016). As predators, bats are at the top of the food pyramid and are therefore sensitive to accumulation of pesticides and other toxins. Changes in bat abundance may therefore reflect high levels of pollution or its impact on their prey (Cooper-Bohannon *et al.,* 2016). Apart from being bio-indicators, bats provide several ecosystem services, including pollination and seed dispersal, and reflect the health of the plant populations with which they interact and also productivity of insect communities that are dependent on these plants

(Jacobs, 2016). Heavy metals from pesticides and organic pollutants found in fertilisers find their way in natural and artificial water sources concentrate up the food chain into food eaten by bats. Some metals such as mercury and lead have been found in bats with some species of flying fox showing signs of lead poisoning (Jantzen & Fenton, 2013).

Riverine habitats and water bodies are preferred foraging sites for bats and they use these water bodies for drinking or feeding. According to Jacobs (2001), several studies have shown that the feeding activity of bats upstream of the point at which waste water enters naturally streams or rivers, is higher than sites downstream of the waste water treatment facility. However, this varied between species and may be dependent on the insects associated with the waste water. Unfortunately very little research has been done on the use of polluted urban and agricultural water sources by bats and effects on their health (Linden *et al*., 2014; Jacobs, 2016). Research is therefore urgently needed to determine the extent to which bats are reliant on artificial water sources in both rural and urban environments and whether these water sources are used for both drinking and feeding (Jacobs, 2016).

Urbanisation has increased light pollution, which could destabilize ecosystems by changing biological processes of organisms that depend on light which changes how bats find food, information and refuge (Schoeman, 2016). The effect of light pollution is still a new research field and more needs to be done to understand the consequences on the health of bats. Community compositions may change as some bats are affected by light, some species may benefit from it while others are threatened by it. Schoeman (2016) found that feeding attempts were significantly higher at lit stadiums compared to dark ones, irrespective of season or surrounding human land use. Exhibiting species-specific differences in utilization of stadiums.

Wind turbines have helped in the need to move to renewable sources of energy which is less harmful to the environment. However it may be detrimental to the fauna and flora of a region through mortality or indirect habitat loss (Jacobs, 2016). Studies have shown that bat fatalities have been caused by wind turbines through collision with rotating blades or as a result of barotrauma. Barotrauma is internal injuries to the bat as the result of pressure gradients generated near the tips of the blade, the air in its lungs rapidly expands, causing damage to the lungs and blood vessels, severely wounding the bat or killing it (Kunz *et al.*, 2011; Jacobs, 2016). Although the impact of wind turbines seems to be highest among migratory bats, there is some evidence that the impact on resident species increases during natural changes in their behaviour (Jacobs, 2016). For example the higher rate of bat fatalities around wind turbines in North America coincides with the time when bats engage in mating activity (Jacobs, 2016). Though very little is known about mating behaviour or seasonal activity patterns of most bat species across the world making it difficult to determine which factors lead to bat fatalities at wind turbines.

White-nose syndrome is causing severe declines of bat populations in eastern North America, with many colonies decreasing by 99% within two years of infection (Baerwald & Barclay, 2008). This fungal infection is caused by a cold-adapted fungus called *Pseudogymnoascus destructans*, resulting in increased arousals of bats during hibernation, leading to dehydration and depleted fat reserves (Lloyd-Smith *et al.*, 2005). Since being identified in upper New York State (USA) in 2006, White nose syndrome has spread rapidly, directly by bats as well as by anthropogenic activity (Leroy *et al.*, 2009) through the persistence on equipment, clothing, and shoes. Acoustic monitoring is an effective way to document population declines without the risk of transmission of WNS with traditional capture methods (Parker, 1991; Brooks *et al.*, 2002).

Researchers can hamper the conservation of bats, when hundreds of bats are killed for museum collections or for DNA sequences without any regard to the bat species population size or conservation status (Kunz *et al.*, 2011). Museum collections are important to advance scientific research but it is important that protocols are put in place to ensure that collection is not undertaken indiscriminately and that the collections fulfil the purpose for which their intended. It is also important that there is good communication and collaborations between scientist, museums and regulatory authorities (Jacobs, 2016).

Human activity is having a significant and increasingly negative impact on bats globally (Cooper-Bohannon *et al.*, 2016). It is therefore crucial to accumulate as much knowledge as we can on the biology of bats, so as to determine what the impacts are likely to be on them (Cooper-Bohannon *et al.*, 2016).

3. MATERIALS AND METHODS

3.1 Study Area

The study was conducted in the northern Kunene Region (19.4086° S, 13.9144° E), which is one of the 14 political regions of Namibia. The Kunene Region is about 144255 km^2 in area size and has a current estimated population of 88 300 people. The low population and the large area give a low average population density of 0.77 persons per km^2 (Kunene Regional Council, 2016). Tourism, agriculture, mining, and trade and industry are the major economic sectors in the Kunene Region, with tourism being identified as a key sector development for the Kunene Region (WWF database, 2016). The Kunene Region climate is characterized as a desert climate. The rainy season typically last from January to April, with an annual average rainfall of 200 mm per year. May to December is the dry months, usually with no rainfall at all. The average temperature is 20.7 °C (Hearn, 2004; Kunene Regional Council, 2016).

Fieldwork was carried out from May 2016 – March 2017 covering all the seasons. The main study sites were: Hoanib camp (271 m a. s. l.), located in a broad valley at the convergence of two tributaries of the dry Hoanib River in the northern part of the private Palmwag Concession. Kuidas study site (238 m a. s. l.), is located in the Palmwag Concession, found in the Huab River Valley and Etendeka study site (970 m a. s. l.), is located in the foothills of the Grootberg Massif, in the Etendeka Concession (Hearn, 2004).

Palmwag Concession (19.75506° S, E 13.83314° E) is privately managed, leased by Palmwag Pty (Ltd) from the government and it covers 450 000 hectares of land. The area is managed exclusively for non-consumptive tourism. Within the concession there is an established lodge, two tented camps and about four to five Save the Rhino Trust (SRT) base camps. Palmwag Concession borders with Sesfontein Conservancy to the north, Etendeka Concession to the east, Skeleton Coast National Park to the west and Torra Conservancy to the south. The concession is divided from Torra Conservancy by a veterinary fence, which is aimed at controlling livestock diseases. Palmwag Concession is situated on the Euphorbia basalt foothills, plateaus and gravel plains habitats (Hearn, 2004).

Etendeka Concession is a privately managed land, leased from the government and covers 508 km^2 of land. The area is managed exclusively for non-consumptive tourism within the concession there is an established tented camp. Etendeka Concession borders with Palmwag Concession (Hearn, 2004). Each study site was located 80 to 100 km from each other.

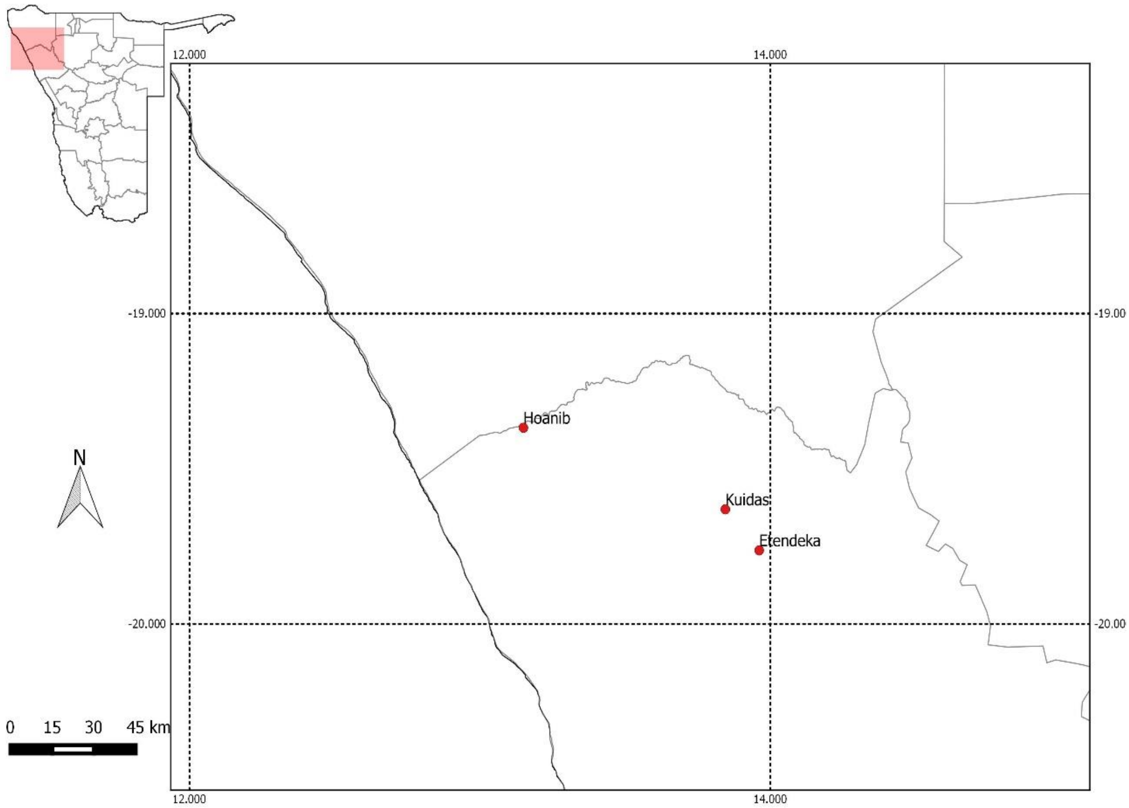

Figure 3. Map of Namibia and Kunene Region showing the study sites. Study sites where bat activity was recorded.

	Etendeka	**Hoanib**	**Kuidas**
Co-ordinates	19.7630° S, 13.9619° E	19.3683 S, 13.150° E	20.6309° S, 13.8453° E
Altitude	970 m	271 m	238 m
Water type	Spring	Borehole	Spring
Vegetation	Mopane trees, *Euclea* and grass	Camel thorn trees	no trees
Landscape	Surrounded by mountains.	Surrounded by mountains.	Surrounded by mountains.

Table 1: Characteristics of study sites

Figure 4. The Etendeka study site.

Figure 5. The Kuidas study site.

Figure 6. The Hoanib study site.

3.2 Research Design

Research collected both qualitative and quantitative data. Qualitative data are data about categorical variables, which may be represented by name, symbol or a number code (Driscoll *et al.,* 2007). In the present study bat families at all study sites were identified from sonograms produced when bat calls were analysed. Quantitative data are measures of values or counts and are expressed as numbers (Driscoll *et al.,* 2007). Bat abundance, family richness, seasonal activity and environmental factors were monitored at the study sites.

3.2.1 Sampling

Two survey methods were used, namely the capturing of bats using mist nets and acoustic sampling with bat detectors. Sampling efforts were standardised across the entire study sites. Three sampling stations were used in this study. Pre-selection of all sampling stations was done in advance, because the research area was sometimes difficult to access, especially at night. The ability to set up the nets and bat detectors was a criterion for choosing a sampling station. Bat detectors used for passive monitoring required batteries changed once a week and this also contributed to sampling sites chosen. Since time was limited, only locations with bat presence were sampled. Once all sampling stations were chosen, mists netting sampling nights were appointed according to new moon phase as bats are able to detect and avoid mist nets on brighter nights.

One mist net (Ecotone 700P) of 9 m length × 2 m height was used per night (Figure 8). Mist nets were placed in an open habitat across a spring or borehole as desert bats are attracted to water sources in dry and hot environments (Kunz & Parsons, 2009). Sampling took place for not more than two consecutive nights at each sampling station, mist nets were deployed for three hours after sunset since capture rate is likely to decrease on subsequent nights (Kunz & Parsons, 2009). Mist nets were set one hour before sunset, so that the expected peak activity right after sunset would not be missed (Barlow, 1999). The mist nets were taken down three hours after sunset. During these three hours the mist nets were constantly monitored, since bats free themselves after a while or damage the nets or themselves (Linden *et al.,* 2014). Species identification was based on the identification matrices in Monadjem *et al*. (2010). Bats were caught and placed in a bag to be weighed, using Pesola spring scales. Bats were then removed and restrained by hand for processing. Bags were reused between individuals and were disinfected after each sampling night and before reuse to prevent any possible disease transfer. During processing, the time of capture, age which was determined by examining of the plates between finger bones, the sex and family of all bats (when possible with visual identification) were determined. Forearm and full head + body measurements were taken with callipers for all bats and they were photographed.

In addition to mist-netting, non-invasive acoustic surveys were conducted using Wildlife acoustic SM2 bat detectors (Figure 9) to monitor the relative abundance and diversity of insectivorous bats at the study sites (Miller, 2001). Each SM2 bat detector is equipped with a water proof acoustic microphone connected to a waterproof unit, which includes four interchangeable flash cards for storing recordings. At each sampling station one Wildlife acoustic bat detector was mounted ~1.5 m above ground on a tree, to prevent false recordings from wind and rain (Monadjem *et al.,* 2010). The microphone placed at a 45° angle pointing at expected fly ways, in an open habitat for eleven months for passive monitoring. Every night was sampled for the 11 months during the sampling period. Recordings of bats were made continuously, starting 30 minutes before sunset to 30 minutes after sunrise as this is the time bats are active (Monadjem *et al.,* 2010). Wildlife Acoustics bat detectors were set at filter switch of 1 kHz, frequency response 10–120 kHz; sampling frequency 307 kHz set to 10× time expansion (Parker & Bernard, 2018). The microphone used was an SMX-US mic 48 dB.

Figure 7. Mist net

Figure 8. The SM2 Wildlife Acoustic bat detector.

3.2.2 Moonlight

To evaluate the effect of moonlight on aerial insectivorous bat activity, astronomical information was obtained from the moon phase calendar; All moon phases were compared at Etendeka from 11 months data while dark nights (new moon) and bright nights (full moon) were compared at all study sites. Bat activity information was obtained from SM2 bat detectors. Fifteen dark nights and fifteen bright nights were included in the final analysis for each study site.

Figure 9. Data loggers.

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Figure 10. Data logger mounted on a tree.

3.2.3 Temperature

Temperature was measured using Maxim iButton DS1923 data loggers manufactured by Fairbridge Technologies which were set to record hourly temperature (Figure 10). One data logger was set at each study site. Data loggers were calibrated and recorded average temperatures and time.

3.3 Data Analysis

Relative activity was measured as the number of Wildlife Acoustic call files per night of sampling (Linden *et al.*, 2014). Activity was calculated as the number of five minutes periods in which species were recorded (Miller, 2001). Wildlife acoustic bat detector recordings were analysed using Wildlife Acoustics Kaleidoscope program (version 4.3.2). To identify calls to families, each individual bat call was compared to bat sonograms for southern African bats (Monadjem *et al.*, 2010). The following parameters: resting frequency (kHz), duration (ms), maximum frequency (kHz), minimum frequency of the frequency modulated tail (kHz), and inter-pulse interval (ms) and time between adjacent calls were measured in Kaleidoscope software. The bandwidth was also calculated by subtracting the minimum frequency from the resting frequency. The mean values of the echolocation parameters were calculated from high quality calls (calls with high signal to noise ratio) for individual bats. All analyses were conducted using XLSTAT (version 2018.1), with a significance level of $\alpha = 0.05$. Multiple One-way Analysis of Variance (ANOVA) with Tukey Post Hoc test was used to compare mean nightly temperatures and bat activity between months, to examine differences in mean nightly temperature among sampling areas. As well as to examine differences in bat activity among sampling sites. The study presents the F statistic and P-value for effects tests. Data was normally distributed, permitting the use of multiple linear regression models. Multiple linear regression models were developed to test the effect of four different independent predictor variables (temperature, moon phase, time and altitude) on bat activity. In order to test the influence of moonlight on bat activity between nights, the number of bat passes per night at each site was recorded. Total bat activity was compared during all the moon lunar phase at Etendeka using ANOVA and between dark and bright nights at all study sites using a Student t-test. Dark nights were those with new moon and bright nights were those with full moon.

Pearson correlation test was used to test the correlation between bat activity and temperature.

4. RESULTS

4.1 Table 2: Summary of bat family calls identified at three sites in the Kunene region, Namibia from May 2016- March 2017.

Families	**Dur (ms)**	**Fmin**	**Fmax**	**Fc (kHz)**	**FK (kHz)**
Molossidae					
Molossidae 1	8-16	12-14	14-16	12-14	12-15
Molossidae 2	3-11	17-24	29-34	20-24	25-26
Molossidae 3	8-11	27-28	43-44	27-30	25-27
Minopteridae					
Miniopteridae 1	2-4	52-55	67-71	45-62	56-57
Vespertilionidae					
Vespertilionidae 1	6-8	30-31	53-60	31-33	37-39
Vespertilionidae 2	5-7	35-39	63-68	39-41	38-46
Vespertilionidae 3	2-4	46-50	63-67	46-51	48-56
Vespertilionidae 4	5-6	35-41	63-67	39-41	46-49
Vespertilionidae 5	4-6	48-54	68-70	54-55	57-59
Vespertilionidae 6	3-5	32-34	63-67	32-35	34-37
Vespertilionidae 7	3-4	28-32	53-60	29-34	34-37
Rhinolophidae					
Rhinolophidae 1	14-15	82-83	85-86	82-87	80-87
Rhinolophidae 2	14-15	80-82	100-110	80-91	80-85
Hipposideridae					
Hipposideridae 1	11-12	55-56	60-62	55-56	56-58
Hipposideridae 2	7-15	79-90	91-145	79-84	80-84
Hipposideridae 3	7-8	129	138	141-144	143-145

Abbreviations: Dur = Duration in ms; Fmin =minimum frequency; Fmax = maximum frequency; Fc= characteristic frequency; fK= frequency at the knee.

4.2 Qualitative approach (sonograms)

Representative Sonograms generated from Kaleidoscope were produced for each family.

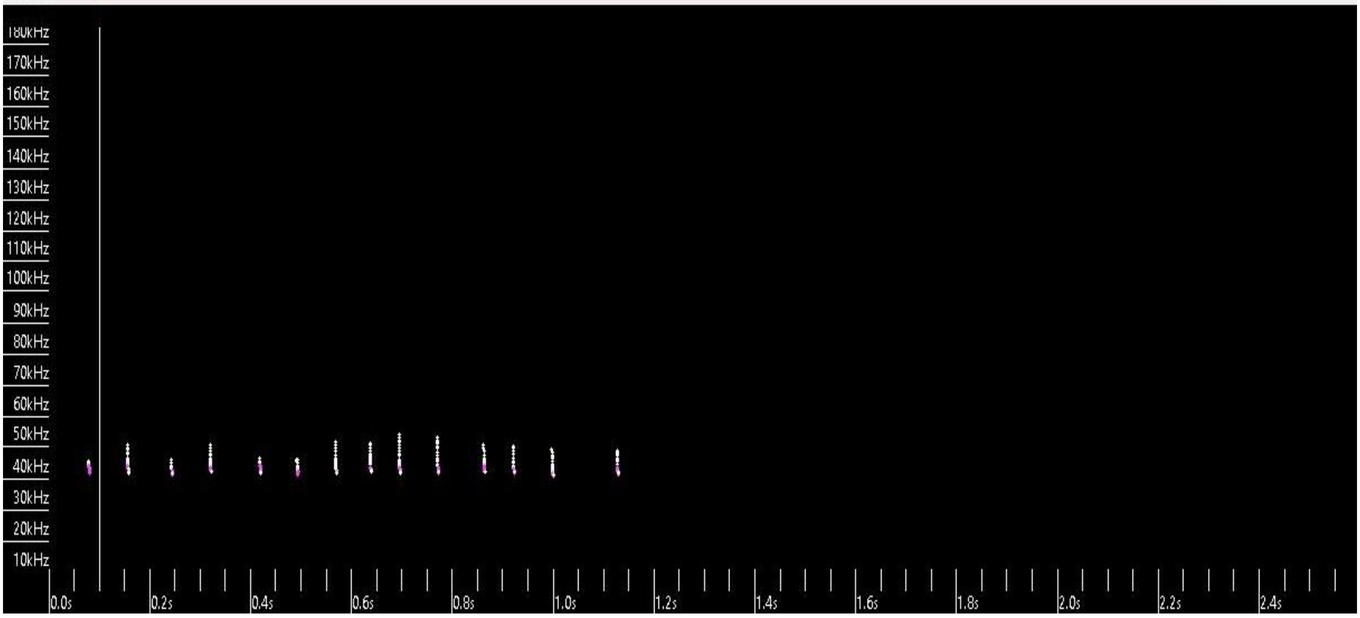


Figure 11 (a) Sonogram of calls belonging to the family Vespertillionidae.

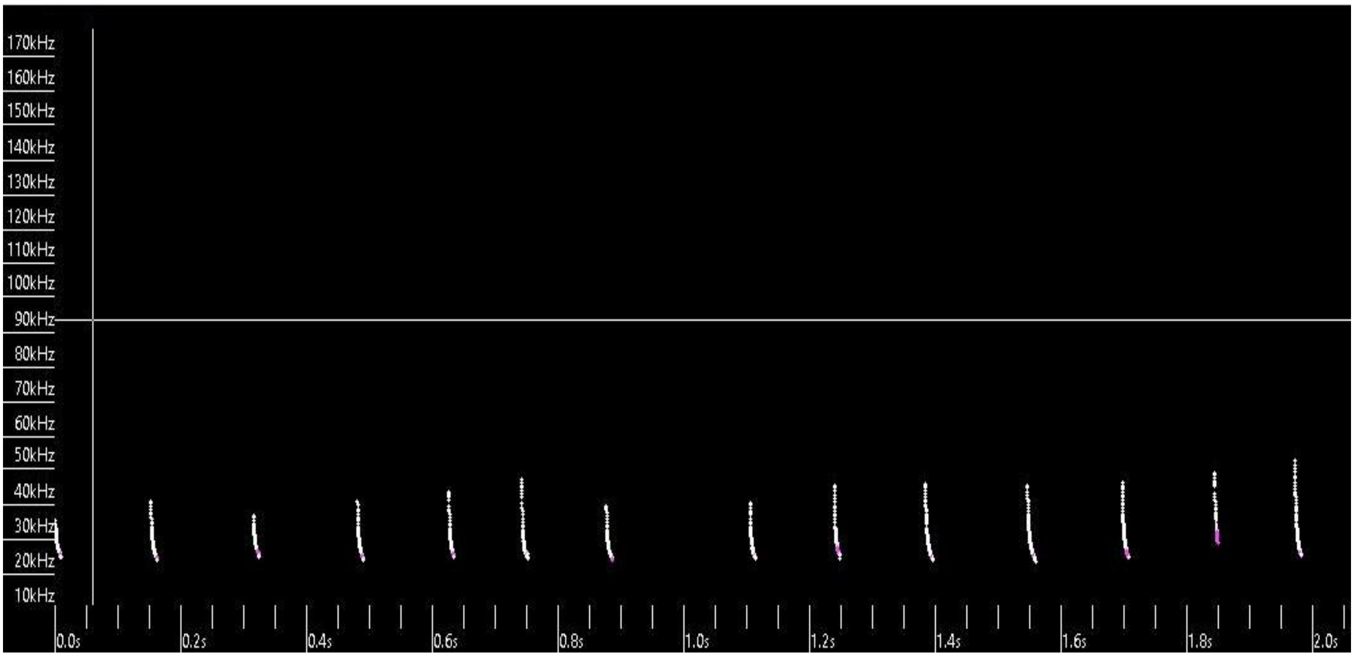


Figure 11 (b) i) Sonogram of calls of a bat belonging to the family Molossidae

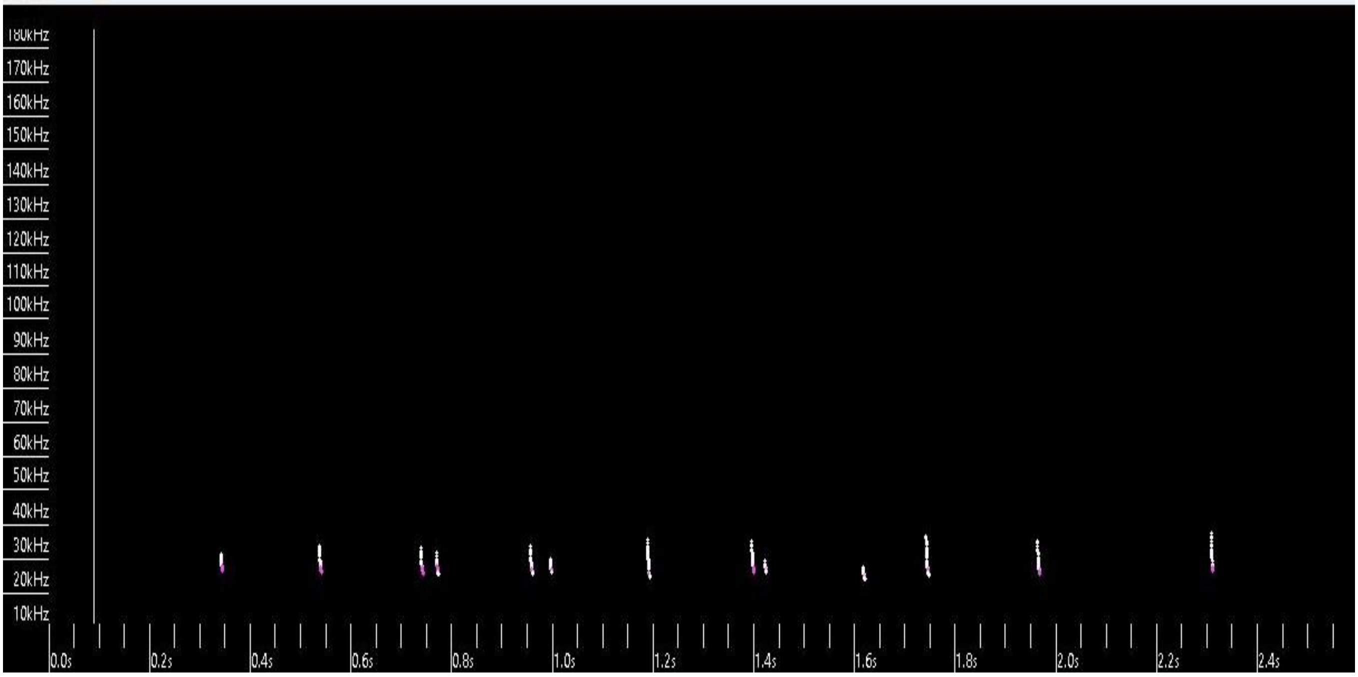


Figure 11 (b) ii) Sonogram of calls of a bat belonging to the family Molossidae.

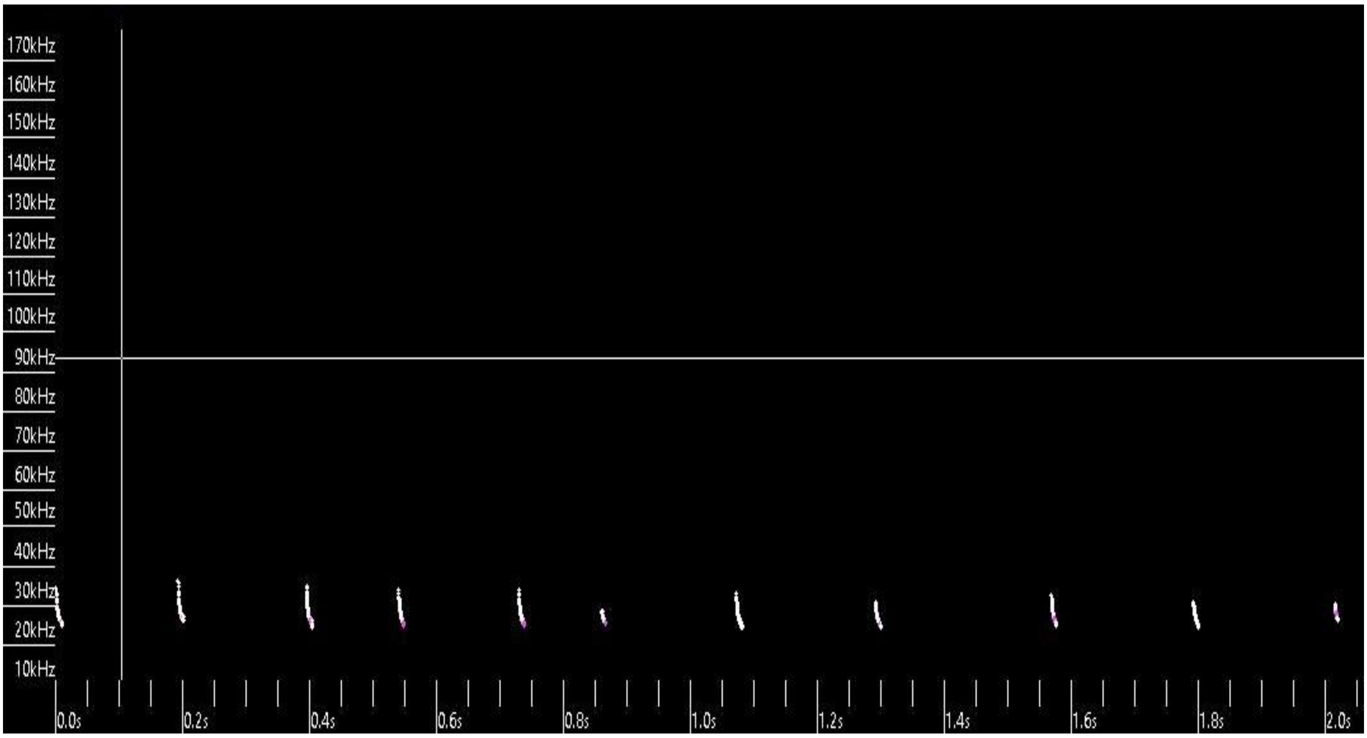
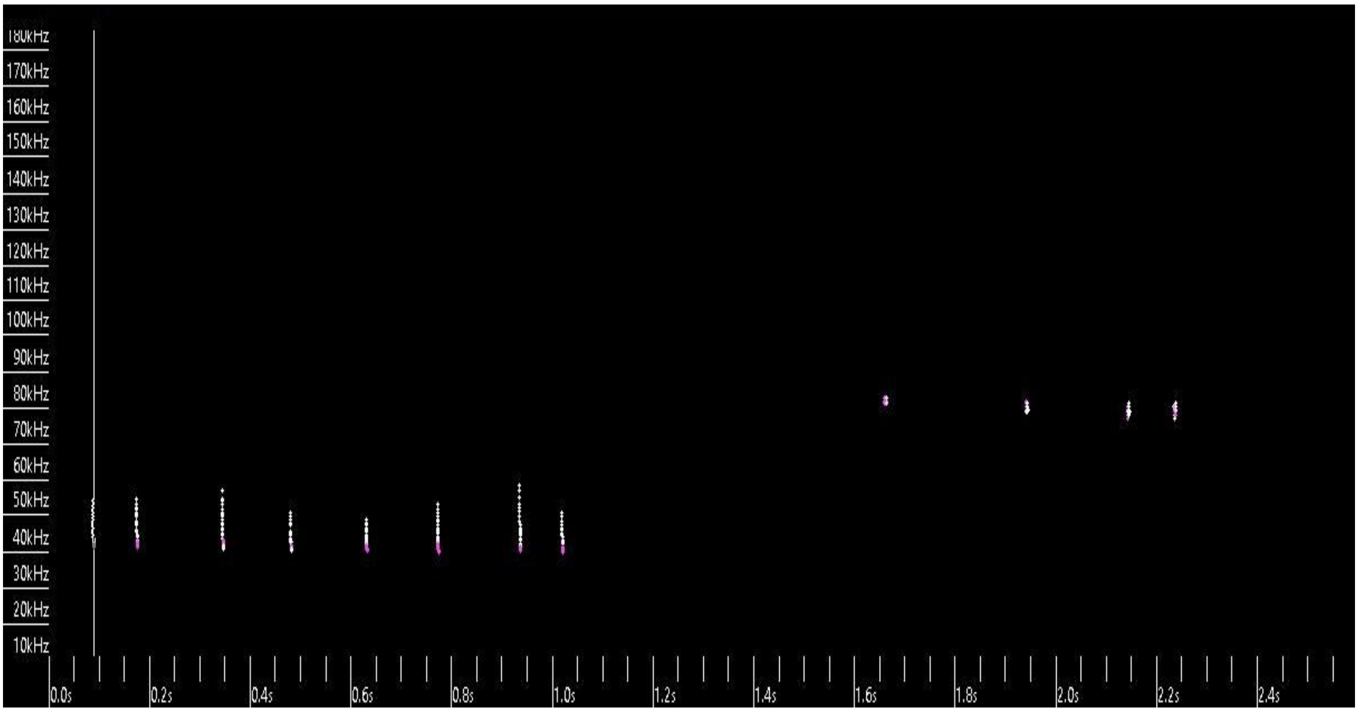


Figure 11 (b) iii) Sonograms of calls of a bat belonging to the family Molossidae.



11(c) Sonogram of calls of a bat belonging to the family Miniopteridae.

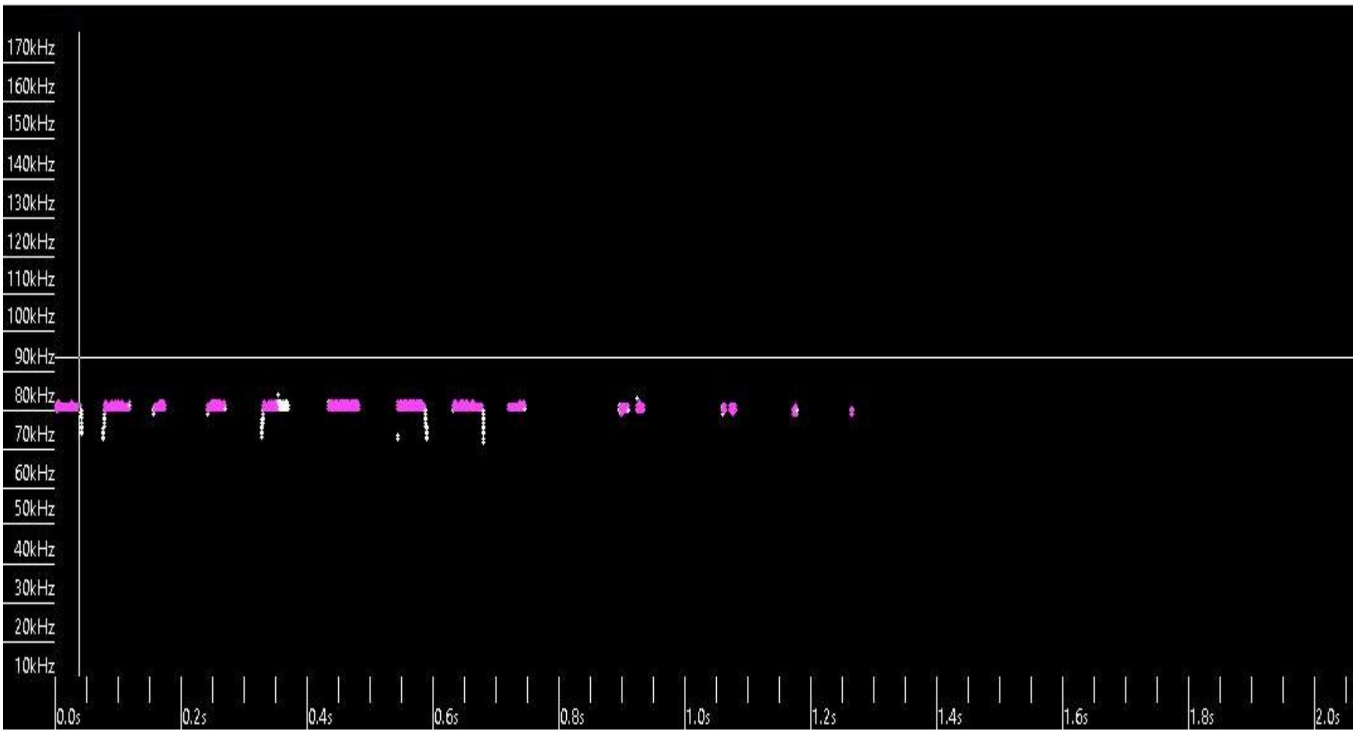


Figure 11 (d) Sonogram of calls of a bat belonging to the family Rhinolophidae.

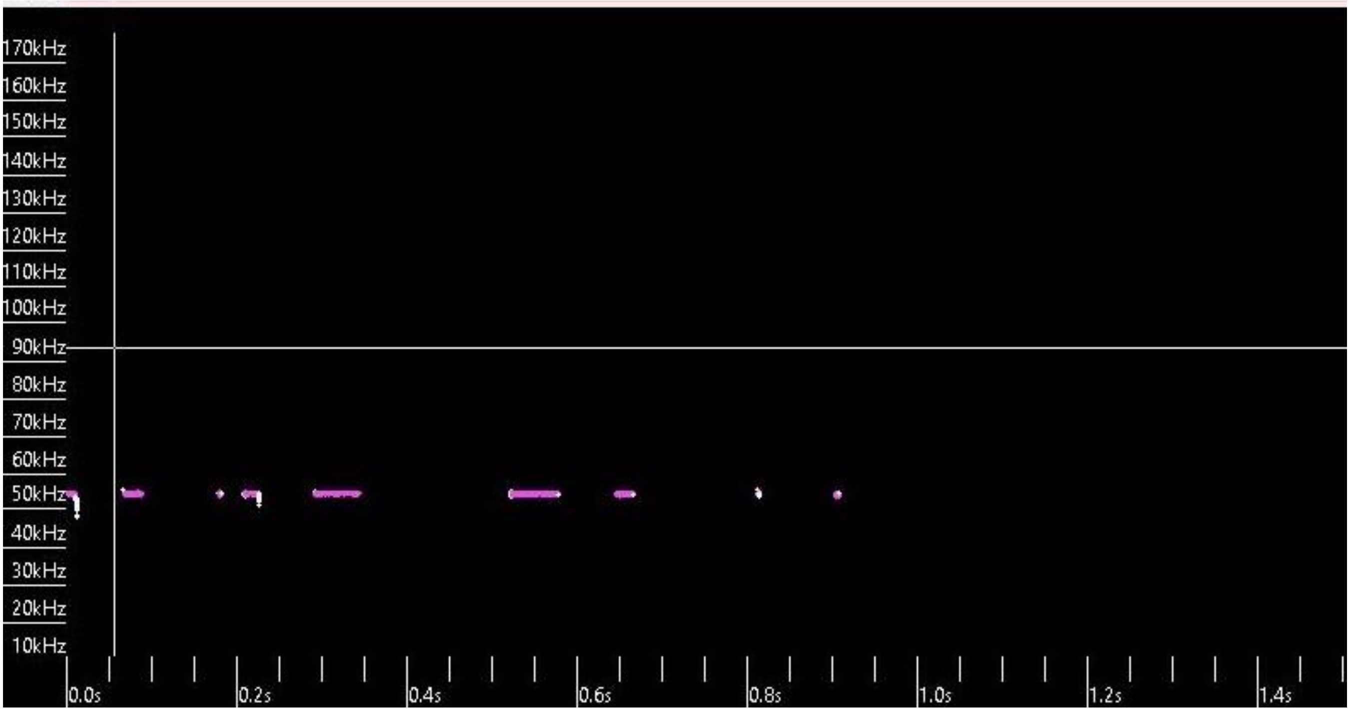


Figure 11(e) Sonogram of calls of a bat belonging to the family Hipposideridae.

4.3. Quantitative approach (seasonal activity, bat abundance, family richness and environmental factors)

During 66 days of mist netting over an 11 months period, 57 bats were captured (Table 3). Most (70 %) were caught at Hoanib (271 m) which consisted of species *Eptesicus hottentotus*, *Cistugo seabrae, Neoromicia zulensis and Sauromys petrophilus*. Overall members of the Vespertillionidae, Molossidae and Cistugidae were the only families captured at all sites (Table 3). *Sauromys petrophilus* was the most dominant specie at all sites (Table 4).

All bats captured belonged to species characterized by QCF or FM-QCF, i.e. species that are commonly assumed to forage in open space or edge and gap habitats. Bats from the family Vespertillionidae were captured less compared to bats from the family Molossidae. At family level, Molossidae did not exhibit any preference with respect to altitude. The slightly higher number of captures of Molossidae may indicate preference for open habitats, however the small sample size did not allow for statistical evaluation.

The table below shows bat family distribution among the three areas surveyed from mist netting sampling. Two families, Molossidae and Vespertilionidae were recorded at all the study sites. It emerged that Molossidae was dominant at Etendeka and Hoanib study sites.

Table 3. Distribution of bat families among surveyed areas from mist netting.

Bat Families	**Study sites**		
	Etendeka	**Hoanib**	**Kuidas**
Vespertilionidae	50 %	7 %	47 %
Molossidae	50 %	83 %	33 %
Cistugidae	0	10 %	20 %
Total	4 %	70 %	26 %

Table 4. Distribution of bat species among surveyed areas from mist netting.

Study sites	**Bat Species**					
	Eptesicus hottentotus	*Cistugo seabrae*	*Neoromica capensis*	*Neoromicia zulensis*	*Chaerephon nigeriae*	*Sauromys petrophilus*
Etendeka	0 (0 %)	0 (0 %)	1 (2 %)	0 (0 %)	1 (2%)	0 (0 %)
Hoanib	2 (3 %)	4 (7 %)	0 (0 %)	1 (2 %)	0 (0%)	33 (58 %)
Kuidas	7 (12 %)	3 (5 %)	0 (0%)	0 (0%)	0 (0 %)	5 (9%)
Total	9 (16 %)	7 (12 %)	1 (2 %)	1 (2 %)	1 (2 %)	38 (67 %)

Acoustic sampling was attempted for eleven months; however equipment failure caused loss of acoustic data for four months at Hoanib and two months at Kuidas study sites, resulting in an overall loss of six months at these two sites. The final results were 11 months of bat activity and moonlight data at Etendeka and five months complete data (bat activity, temperature and moonlight) at all sites.

Monthly bat activity was recorded at Etendeka from the month of May 2016 – March 2017. There was bat activity during all months recorded. Activity varied between the months, with the highest bat activity recorded in May 2016 with 1091 calls. Then bat activity decreased during the winter months of June and July, there was a smaller peak in activity during the month of August 2016 but continued to decrease from September 2016 to March 2017 with the lowest activity in December 2016 with 52 calls (Figure 12).

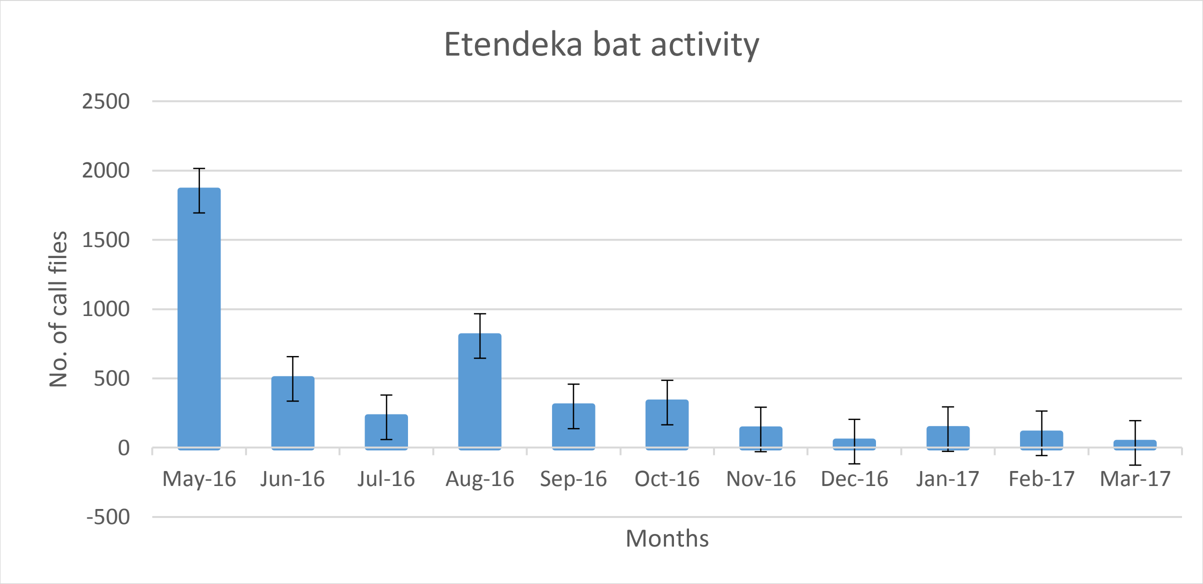


Figure 12. Monthly variation in bat activity (number of call files) from acoustic monitoring for Etendeka.

Over the course of five months bat activity from acoustic monitoring, temperature and moon phase were recorded at the three sites (Table 5). Bats from five families were acoustically recorded at the three main sites, comprising the families Vespertilionidae, Molossidae, Miniopteridae, Rhinolophidae and Hipposideridae, (Table 6). A total of 6893 calls were recorded during the research. Vespertillionidae was found to be the dominant species with 5394 calls or 78.3% of the total calls (Table 6). Molossidae had the second highest count with 1090 calls (15.8%), followed by Rhinolophidae with 318 calls (4.6%) (Table 6). The remaining two families accounted for less than a 100 calls. The number of calls was highest at the Hoanib site. The lowest calls were recorded at Kuidas (Figure 13). No family group was found to be restricted to one study site. All families found on the highest altitude 970m were also found at lower altitudes.

Bat activity was recorded from temperatures above 12 °C, with the highest levels of activity recorded at 23 °C with 300 calls recorded, although hourly samples showed bat activity up to 35 °C.

The effect of moonlight on bat activity was measured using lunar phases. As it is a cofounding variable which may increase or mitigate the effects of elevation on bat activity (Appel *et al.,* 2017). Moonlight intensity did not affect activity level at all sites. Bat activity was greater for all sites at the beginning of the night, independent of the presence of the moon. The regression analyses used the acoustic samples with complete data (bat call files, moon phase and temperature). Mixed regression models were used as it was a much better fit for the data. Moon phase was found to not be a significant predictor of bat activity (P= 0.36734), but all other predictor variables were significant (Table 5). Altitude was not compared as the sites had different vegetation and the difference in altitude between sites was not significant.

One-way ANOVA (Table 8) indicated significant variation in bat activity between the three study areas, with Hoanib having the most activity, followed by Etendeka and then Kuidas. Temperature was also a significant predictor of bat activity (P<0.005) (Table 5).

Table 5. Model parameters from mixed linear regression models showing effect of a) temperature b) moon phase, c) time.

Coefficient	**Estimate**	**SE**
a) temperature:	0.023, P,<0.05	
Intercept	40.991	13.204
Bat activity		0.445
b) moon phase:	0.353, P<0.05	
Intercept	31.462	4.565
Bat activity		4.588
c) time:	0.565, P<0.05	
Intercept	16.117	9.947
Bat activity		0.009

The table below shows bat family distribution among the three areas surveyed from acoustic sampling. The data was also arranged according to proportions of each family at respective points. It emerged that although Vespertilionidae is dominant at all the three areas, Molossidae commands a significant percentage at the Hoanib site (20%).

Table 6. Distribution of bat species among surveyed areas from acoustic sampling.

	Etendeka	**Hoanib**	**Kuidas**
Vespertilionidae	97%	70%	96%
Molossidae	1%	20%	1%
Miniopteridae	1%	2%	0%
Rhinolophidae	0%	6%	2%
Hipposideridae	1%	2%	1%
Total	100%	100%	100%

Because of this significant percentage of Molossidae at the Hoanib station, the following table was also generated to summarize the presence of Molossidae at this station of interest. Molossidae dominated in the months of December, January and February making up 69%.

Table 7. Summary of the data for the Hoanib station.

Months	**Miniopteridae**	**Hipposideridae**	**Molossidae**	**Rhinolophidae**	**Vespertilionidae**
Nov-16	28 (1%)	3 (0%)	700 (16%)	221 (12%)	679 (90%)
Dec-16	19 (2%)	7 (1%)	134 (12%)	188 (17%)	768 (69%)
Jan-17	21 (3%)	9 (1%)	123 (15%)	47 (6%)	610 (74%)
Feb-17	0 (0%)	0 (0%)	802 (69%)	11 (1%)	343 (30%)
Mar-17	4 (3%)	3 (2%)	1 (1%)	2 (1%)	128 (91%)
Total	72 (1%)	22 (0%)	1760 (20%)	469 (5%)	2528 (73%)

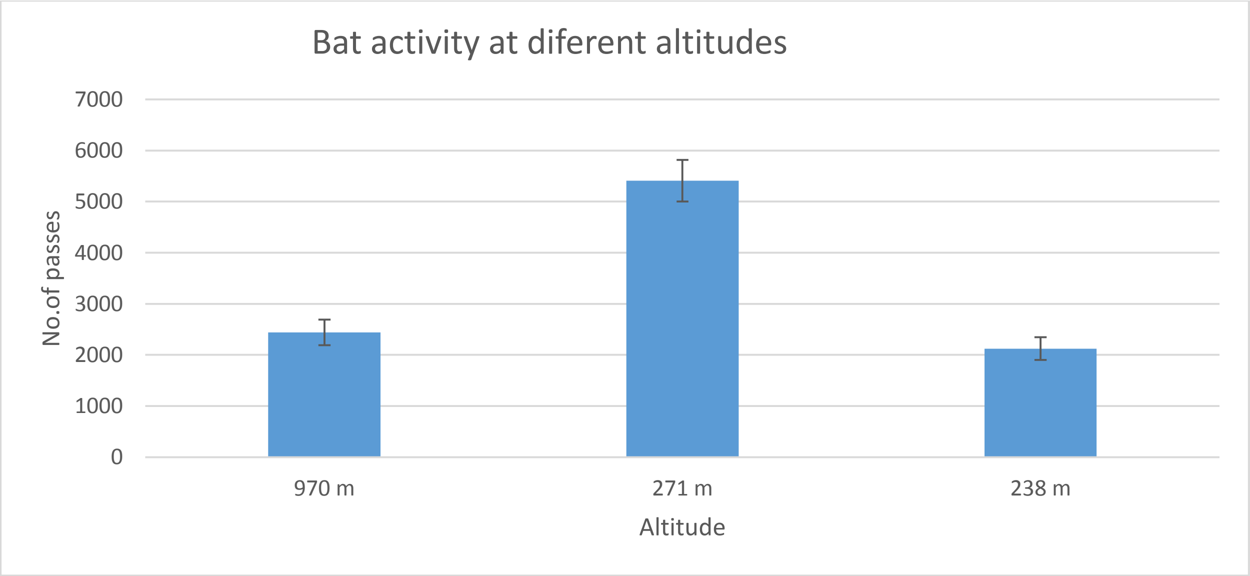


Figure 13. Variation in bat activity (number of call files) from acoustic monitoring between study sites.

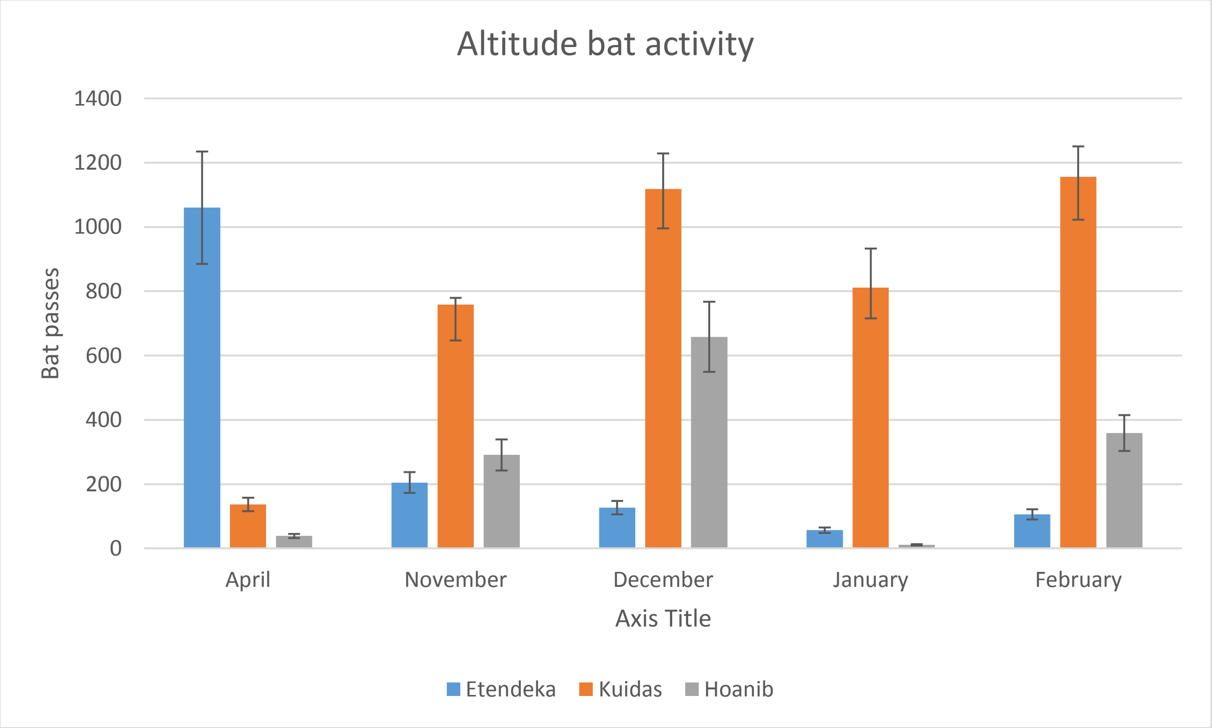


Figure 14. Summer bat activity (number of call files) at three altitudinal gradients.

Table 8. Results of Fischer's test computed in ANOVA with the difference of bat activity between all study sites. Significance value (P≤0.05).

Analysis of variance					
Source	**DF**	**Sum of squares**	**Mean squares**	**F**	**P**
Model	2	57605.292	28802.646	F2=16.901	0.0001
Error	333	567504.125	1704.217		
Corrected Total	335	625109.417			
Computed against model Y=Mean (Y)					

4.4. Effect of moonlight intensity on bat activity

Foraging activity was not related to moonlight intensity, with activity not differing between all moon lunar phases at Etendeka (Table 9) as well as activity levels not differing between bright nights and dark nights at all study sites (Table 5). There was no significant influence of moon phase on bat activity at all sites (Table 10).

Table 9. Results of ANOVA with the difference of bat activity between the four moon phases at Etendeka for 11 months. Significance value (P≤0.05).

Analysis of variance					
	Sum of squares	**df**	**Mean square**	**F**	**P**
Between groups	14687.3	3	4895.78	0.1481	0.9317
Within groups	0.0000132214	40	33053.6		
Total	0.0000133683	43			

Table 10. Results from a Student's t-test with the difference in activity between dark (n= 15) and bright nights (n= 15). Significance values (P≤0.05).

Study sites	**Dark × bright nights**		
	t	d.f	P
Etendeka	0.781	110	0.436
Haonib	0.781	110	0.962
Kuidas	0.781	110	0.171

4.5. Effect of moonlight on bat hourly activity

Bat activity during the night varied between sites and between bright and dark nights. Activity was concentrated at the beginning of the night and end of the night, decreasing their activity between 22h00 and 02h00, regardless of moonlight intensity. Kuidas was the only site having the highest bat activity at 22h00 during the full moon phase.

During dark nights, all sites had only one peak of activity at the beginning of the night. Etendeka and Hoanib had the highest peak of activity at 20h00 (Figures 16 and 18), just after sunset. Kuidas had the highest peak at 03h00, at the end of the night (Figure 20). During bright nights, activity peaks also occurred at the beginning of the night and a second peak at the end of the night for Etendeka and Kuidas (Figure 15 and Figure 19). At Hoanib, activity was fairly constant throughout the night (Figure 17).

Hourly aerial activity of three sites of insectivorous bats on dark nights and bright nights. Dark nights were those considered during new moon phase and bright nights those on full moon phase.

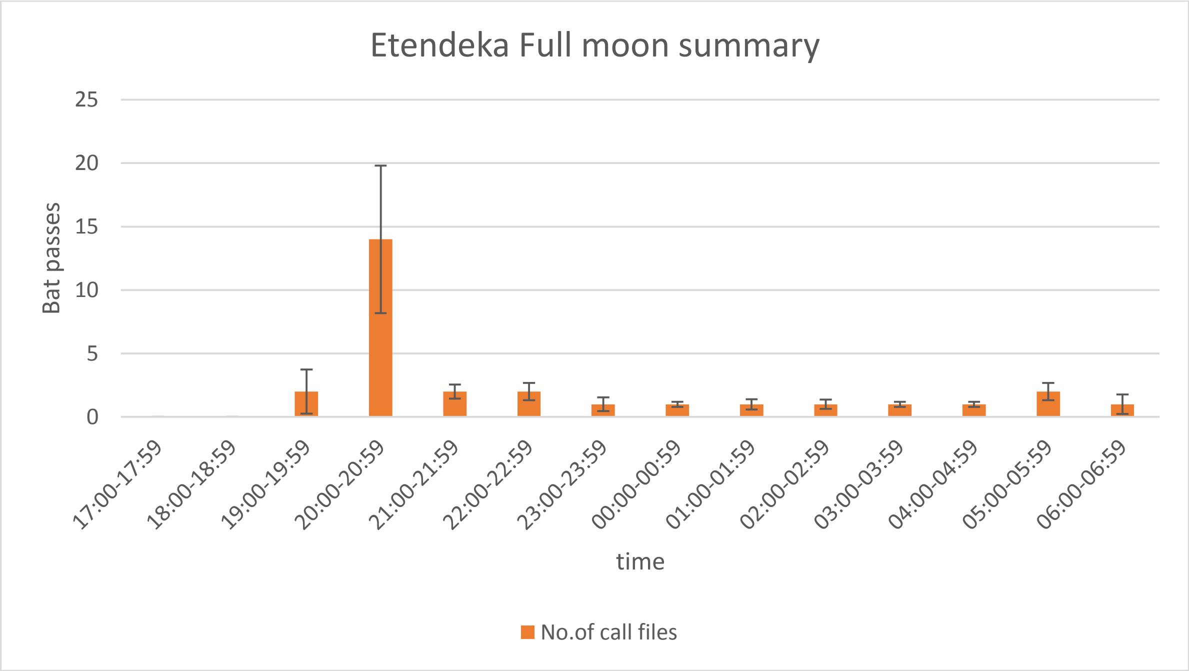


Figure 15. Hourly distribution of activity of Etendeka station during full moon.

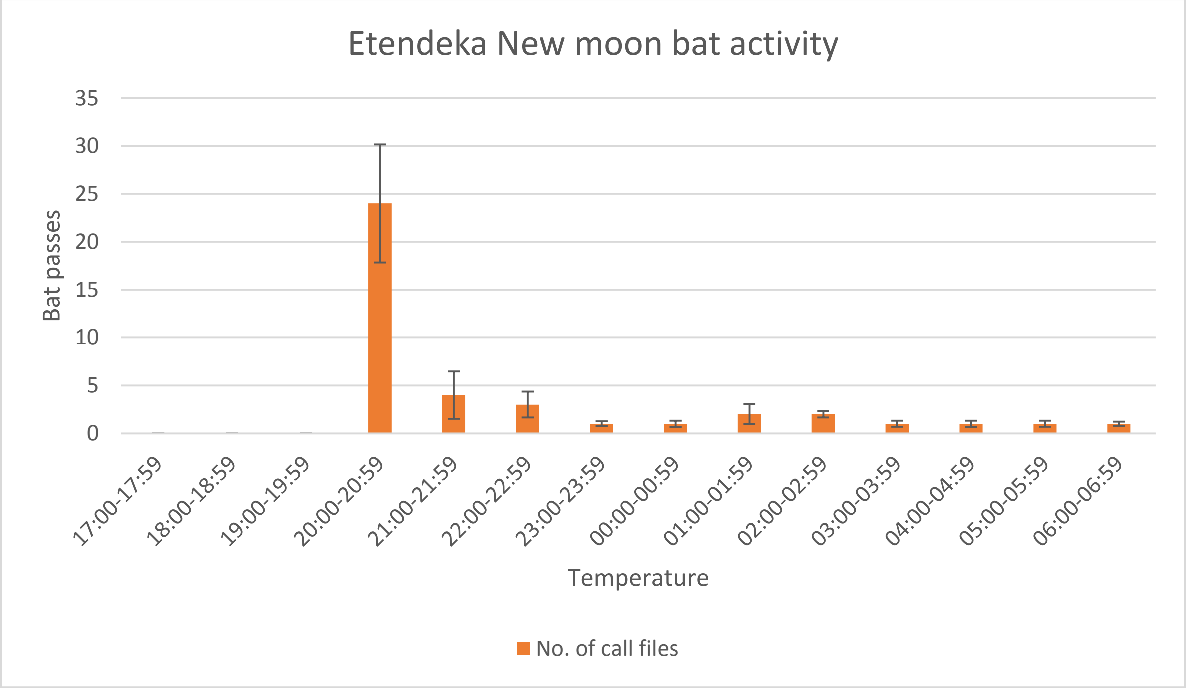


Figure 16. Hourly distribution of activity at Etendeka station during new moon.

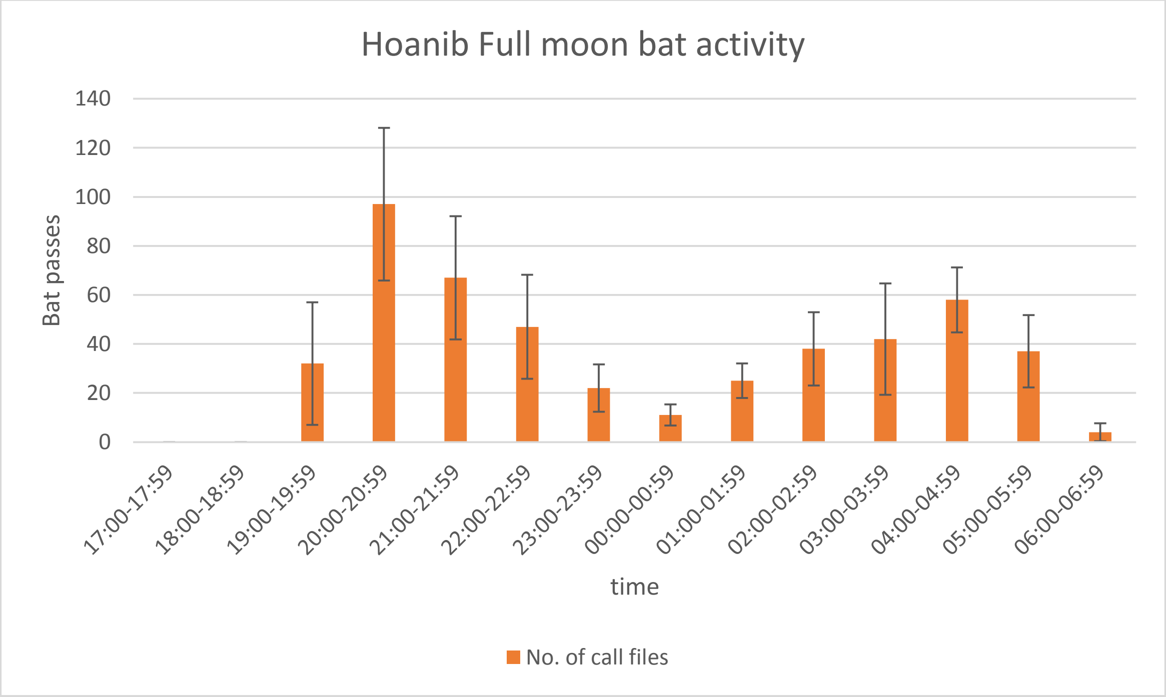


Figure 17. Hourly distribution of activity at Hoanib station during full moon.

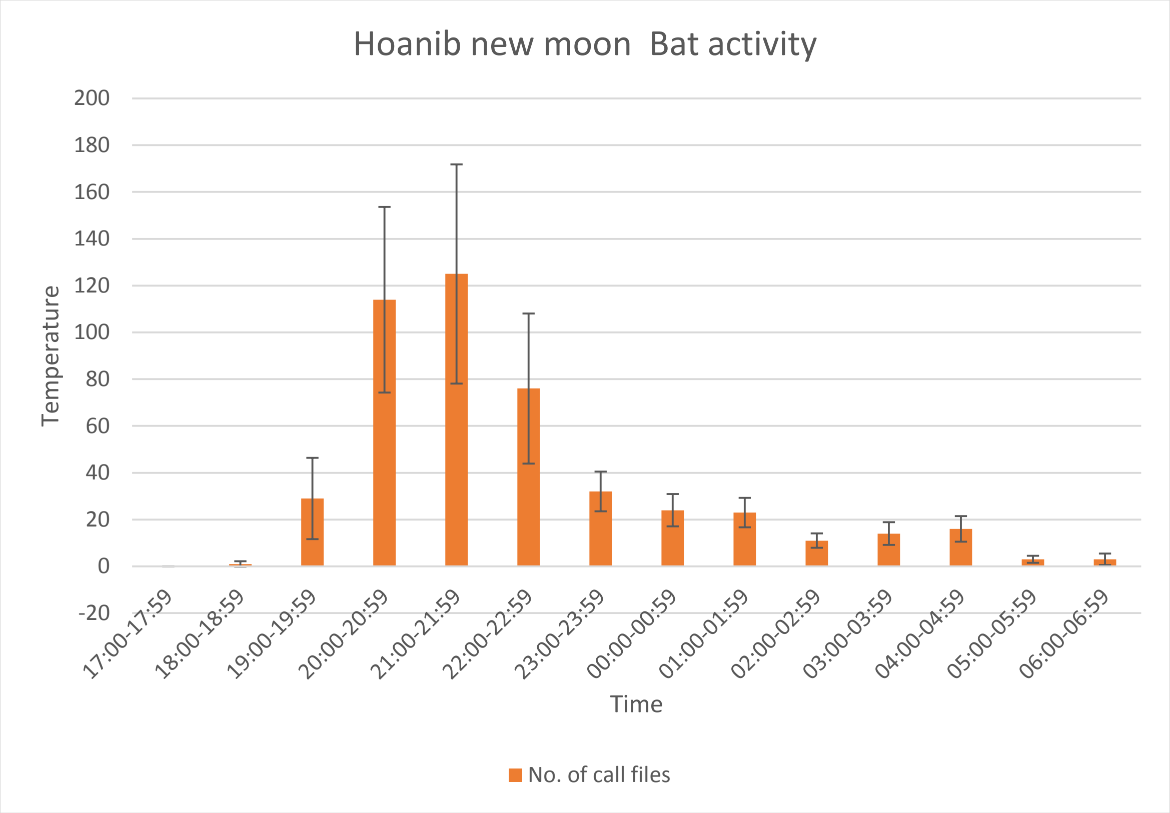


Figure 18. Hourly distribution of activity at Hoanib station during new moon.

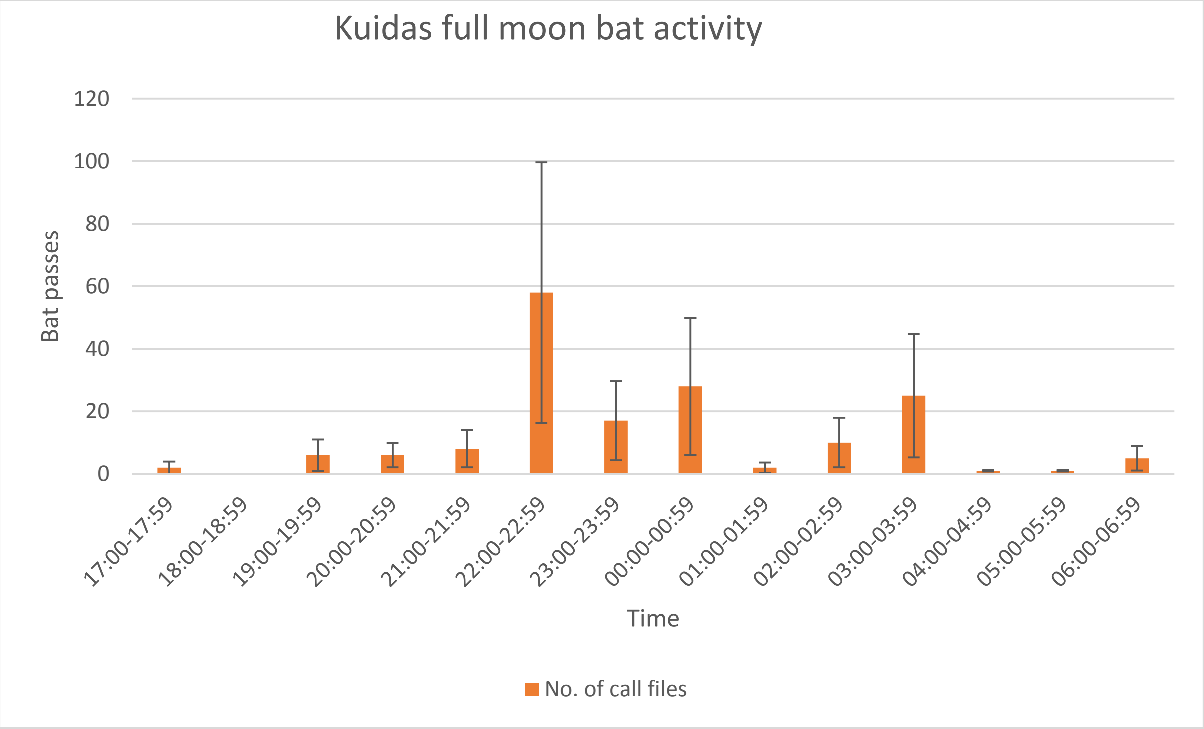


Figure 19. Hourly distribution of activity at Kuidas station during full moon.

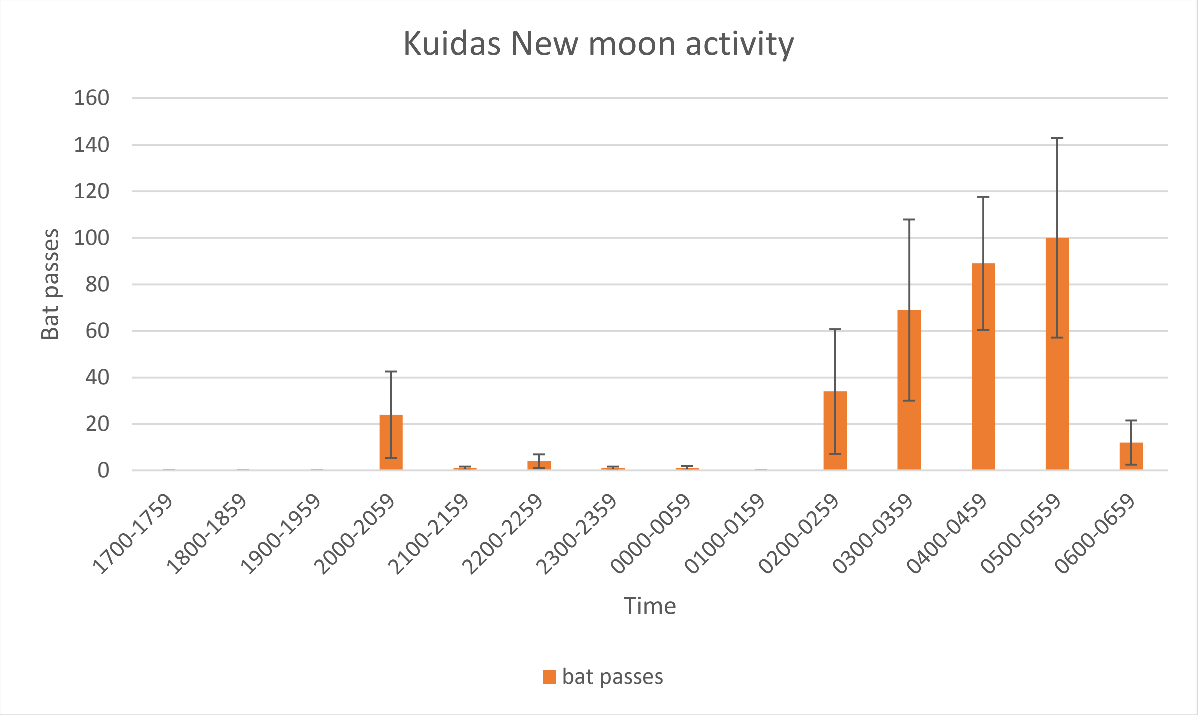


Figure 20. Hourly distribution of activity at Kuidas during new moon.

4.6. Influence of nightly temperature on bat activity

Temperature was recorded during the summer months from November 2016 to February 2017. There was a positive correlation between bat activity and temperature (r= 0.2, df =19, n=39, p=0.001278) (Figure 20). The average temperature range recorded was between 11.5 °C to 43.1 °C. There was a significant difference in temperature between study sites. Etendeka had an average temperature of 24.7 °C, Hoanib 22.3 °C and Kuidas 20.1 °C. Bat activity was observed when the temperature was 12 °C and higher, no bats were observed when temperatures were below 12 °C.

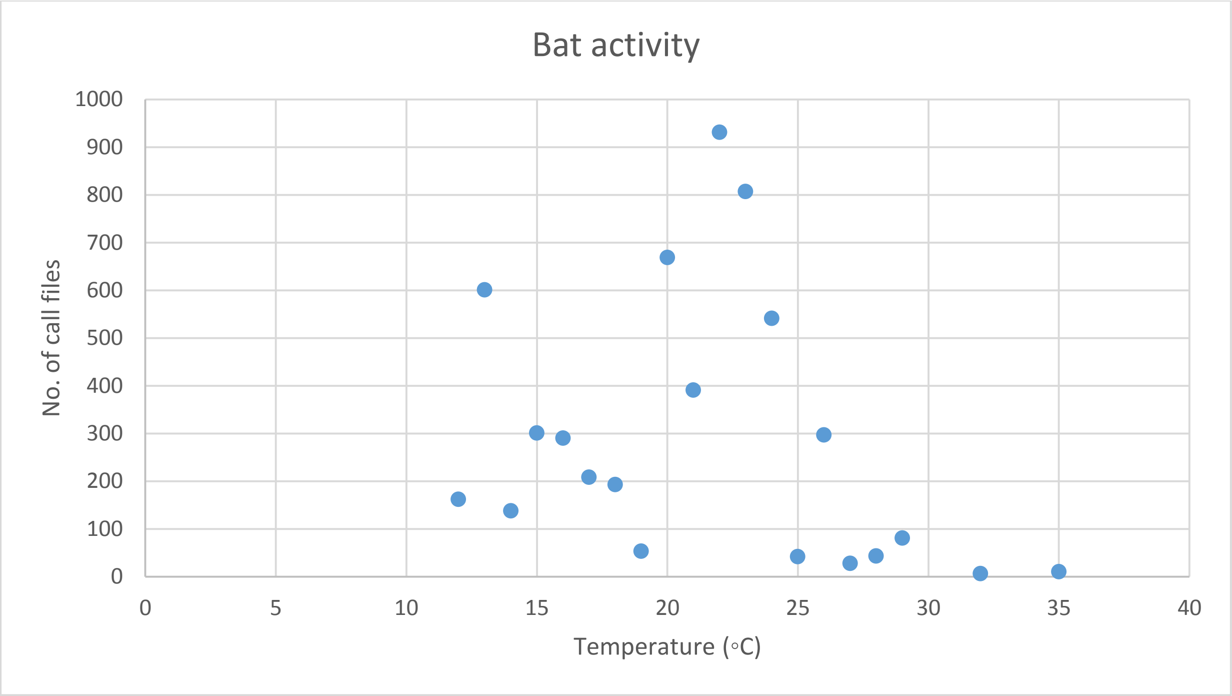


Figure 21: Relationship between bat activity and temperature (°C) at the three study sites.

5. DISCUSSION

The study obtained call parameters from 6893 calls of bats, from six different families (Figure 11). Bats were only identified to family level as no voucher specimens were collected to assist in identifying to species level. Sonograms were used to show typical and variable calls for each family. Based on four call parameters different families of bats could be distinguished, which included bats of the families Vespertilionidae, Molossidae, Rhinolophidae, Hipposideridae and Miniopteridae. There was little or no overlap between the echolocation calls of different bat families. Families of Vespertilionidae, Molossidae, Rhinolophidae, Hipposideridae and Miniopteridae were found at all altitudes surveyed by acoustic sampling.

Calls shown in Figure 11a and b represent low duty cycle bats (Fenton & Bell, 1981; Taylor, 1999): these are species which separate pulse and echo in time, to avoid deafening or jamming themselves by not emitting and receiving at the same time. Search call sequences of low duty cycle bats are characterised by inter-pulse intervals which greatly exceed the duration of individual calls. Compared to high duty cycle bats (Figure 11d) which separate pulse and echo in frequency so that they can emit and receive simultaneously. As a result, these bats can produce echolocation signals almost continuously, with inter-pulse intervals being shorter than call durations. High duty cycle bats typically use the Doppler shift compensation and an acoustic fovea to avoid deafening themselves, and also to enhance their sensitivity to the fluttering of insect wings (Taylor, 1999; Monadjem *et al.,* 2001). Figure 11a represents the family Vespertilionidae. Calls are characteristically steeply frequency-modulated (FM). The shape of FM calls is highly distinctive and useful for identification (O'Farrell, 1997; Taylor, 1999). Their echolocation calls together with their average wingspan and wing area means that most vesper bats are flexible in their foraging behaviour and often switch between open-air and clutter-edge space (Monadjem *et al.,* 2010). The Fc (characteristic frequency) ranged between 29 – 45 kHz at Etendeka, 30-55 kHz at Hoanib and 30- 42 kHz at Kuidas.

Figure 11b (i-iii) shows sonograms of free-tailed bats, family Molossidae. Calls tend to be longer in duration with shallower FM calls at a lower frequency than for the previous bats. They showed the presence of either one or more harmonics. Rydell & Yalden (1997) predicted that based on their low echolocation frequency and the long, narrow wings, the species should be a high-flying moth specialist. A prediction that originates from dietary analysis. Fc (characteristic frequency) ranged between 12-30 kHz at all the study sites.

Figure 11c shows sonogram of Miniopteridae, in the past the Miniopteridae were treated as a subfamily of the Vespertilionidae. This family is represented by a single genus *Miniopterus.* They emit low duty-cycle, frequency modulated calls (LD-FM). In the present study the Fc ranged between 45–62 kHz. They have long, narrow wings with intermediate wing loading and are clutter edge foragers.

Finally, sonograms of the high duty cycle bats belonging to the families Hipposideridae and Rhinolophidae (Superfamily Rhinolophidae) showed that they typically have echolocation calls characterised by high frequencies (Taylor, 1999). The Fc ranged between 74-111 kHz. Family Rhinolophidae tended to have longer duration calls than Hipposideridae (Figure 12d). With some bats having durations of (40 ms), which had CF portion at 86 kHz. Echolocation calls are highly evolved with calls typically high duty cycle, constant frequency (HD-CF) component. The CF component of Hipposideridae bats differs between species and may be used as a guide to their identification (Taylor, 1999). All members of this family have broad wings, allowing them to manoeuvre through cluttered habitats such as dense vegetation (Monadjem *et al.*, 2010). The Fc ranged between 56–145 kHz.

Bat activity, family composition and altitudinal variation

Bat activity at Etendeka varied between the months, with the highest bat activity recorded in May 2016 and decreased during the winter months of June and July 2016, there was a peak in activity during the month of August 2016 but continued to decrease from September 2016 to March 2017 with the lowest activity in December 2016. In arid and semiarid regions, availability of drinking water and temperature can have pronounced effects on abundance, spatial distribution, and activity of mammals in an area. In a study conducted by Christian (1979) it was found that rodents populations of *Gerbillurus paeba* declined during the dry season due to water shortages. Limited water sources in semiarid savannahs of eastern Africa resulted in zebras (*Equus burchellii*), wildebeests (*Connochaetes taurinus*), elephants (*Loxodonta africana*), and cattle (*Bos taurus*) occupying areas around permanent water holes during dry seasons of the year but becoming scattered when temporary pools were available in wet seasons (Linden *et al.,* 2014). Although biologists studying insectivorous bats are not afforded the luxury of counting large-bodied animals in daylight to determine abundance and distribution, Jones & Mucedda (2001) observed a similar pattern of dry-season concentration and wet-season dispersal with insectivorous bats inhabiting mountains in the southwestern United States. Their data showed that bats appear to concentrate around accessible water sources to drink when surface water is scarce in dry seasons but become more dispersed during rainy seasons when surface water is abundant and widespread. Seasonal differences in bat activity in the present study likely does not represent changes in population size but reflect movements associated with changes in availability of drinking water that affect local distributions of individuals. Such a conclusion underscores the importance of understanding the effect of this environmental factor, especially if recordings per unit effort are used as indices of abundance. On the basis of monthly captures of bats in west-central New Mexico, Jones & Mucedda (2001) reported a seasonal relationship between captures and availability of drinking water. Marked differences in abundance of bats from April to October appeared related to timing of heavy rains in July and August and corresponding available drinking water for bats (Jones & Mucedda, 2001). The present study showed patterns of abundance on a monthly basis. High rates of bat activity were recorded during dry season resulting from bats being concentrated around limited water sources, whereas low recordings in wet months of December to March. This may have been due to bats being dispersed across the landscape as there were more water site options. Environmental conditions such as temperature that increase evaporative water loss in animals result in consumption of more water, and consequently, additional time (i.e., more drinking passes) is required at water sources to account for the greater consumption. Temperature also affects bat activity and insect activity. When temperatures are low in the winter months bat activity also decreases as insect abundance decreases. Maternity roosts are often located near permanent water, suggesting that females deliberately select those sites to help compensate for increased water requirements during lactation (Jones & Mucedda, 2001). During droughts, bats also might alter roosting behaviours so that their day roosts are closer to water sources to concomitantly reduce flight time and water loss. Either by choice or chance, having a roost in proximity to an isolated pool likely increases activity around that water source. Changes in prey distribution might have also influenced bat activity in the study sites. Air temperature influences activity of insects, with warm temperatures resulting in increased numbers of flying insects (Williams & Dickman, 2004). Cryan *et al.* (2000) showed that insectivorous bats, primarily reproductive females with high energetic demands imposed by pregnancy and lactation, select lower elevations in mountainous regions where temperatures are warmer and where insects presumably are more abundant. During cool summers in the Bear Trap Canyon, bats (especially reproductively active females) selected lower elevations to roost and forage (Williams & Dickman, 2004). Cooler nights resulted in fewer bat abundance at all study sites site in the present study. Conversely, during warmer nights, there was more bat abundance which may be due to adequate insect populations available. In addition, insects tend to concentrate around isolated pools of water in dry environments and subsequently attract insectivorous predators to those sites (Williams & Dickman, 2004). Such an effect may have contributed to bat activity at the present study sites during the dry months.

While all of the bat families where recorded at Hoanib (271 m) which included Hipposideridae, Rhinolophidae, Molossidae, Vespertilionidae, Cistugidae and Miniopteridae. Molossids and vespertilionids were dominating through-out all altitudes. However, this might be due to the fact that the highest altitude sample >970 m comprised of only open grassland habitat which might exclude some clutter (e.g., Rhinolophidae) and clutter edge (e.g. Miniopteridae) bats. There was bat activity during all the summer months recorded at each site. Etendeka (970 m) was having the highest bat activity in April and Hoanib (270 m) having the highest bat activity in the months of November 2016– February 2017. The study does not indicate any bat family as being 'upland' species which are found exclusively in the habitats of high altitudes. No family was found to show highland endemism, which coincides with the findings of Linden *et al*. (2014). However, bat distributions of species such as as *Myotis welwitschii* (Family Vespertilionidae) have been found to be closely associated with mountain ranges (irrespective of altitude) across Africa (Linden *et al.,* 2014). *Eptesicus hottentotus* (Family Vespertilionidae) has a distribution which is known to be associated with rocky, hilly/mountainous areas (Monadjem *et al.,* 2010). Large Molossidae species such as *Otomops harrisoni*, has an African distribution at high altitudes and exploits caves and crevices as roosting sites (Ralph *et al.,* 2015). Many other Molossidae species have also been found to use crevice roosts in mountainous or rocky areas in southern Africa (Monadjem *et al.,* 2010). Molossids also generally produce low frequency calls compared to other bat families and thus their calls do not attenuate as quickly (Parker & Bernard, 2018). This could explain why the majority of bats caught and recorded were from the Molossidae and Vespertilionidae families at the study sites, which are in mountainous areas or surrounded by mountains. Some rhinolophid species, such as those of the *Rhinolophus hildebrandtii*, found in Zimbabwe and Soutpansberg Mountains have evolutionary histories of being found in elevations higher than 600 m a.s.l. (Taylor *et al.,* 2012). These results indicate the importance of mountain ranges and escarpments as sources of habitat heterogeneity and potential roost availability for bats in the Kunene Region which may drive family richness and abundance of bats. Further study should survey more sites and species to determine the distance (or altitude) at which some species maybe lost.

Moonlight can affect bats differently because of their individual and inherent foraging strategies and different habitat use (Jung & Kalko, 2010). The results from this study indicate that moonlight did not have a significant effect on bat activity, although it has been shown to predict activity in other animals such as insectivorous birds (October & Brigham, 1995). Barker (1962) demonstrated that visually orienting frugivorous bats display lunar phobia and argued that the behaviour likely evolved in response to increased predation pressure during the brightest portion of the lunar cycle. With fewer predators, insectivorous bats in desert climates may not have evolved such responses (October & Brigham, 1995). It is well known that moonlight intensity influences the activity of nocturnal insects (Appel *et al.,* 2017). Changes in flight activity have been reported in previous studies were species such as Dipteria, Lepidoptera, Coleoptera and Hemiptera have been found to fly greater distances during bright nights. This could make them vulnerable to bat species that feed on them. Some species such as *Pteronurus parnellii* have shown to be influenced by prey availability, which might increase substantially on bright nights789 (Yela & Holyoak, 1997). Visual perception of predators increases during periods of higher illumination allowing members of visually-oriented bat species to capture slow-flying insects easily compared to faster flying ones. Bat species characteristics such as flight speed, body size and type of foraging habitat have shown to compromise the ability of species to respond to predator pressure (Appel *et al.,* 2017). Slow-flying bats which are bat species, with shorter and broad wings and low weight avoid sites or periods of the night that have a high light exposure because of the high risk of predation. *Myotis* (Vespertilionidae) have shown to respond negatively to natural and artificial light, reducing their activity in open areas and on bright nights (Negraeff & Brigham, 1995).

Like other studies (Appel *et al.*, 2017) hourly activity tends to be different between dark and bright nights. During dark nights, bats had only one peak of activity, but on bright nights it was observed that there were two peaks of activity. This could be due to the fact that insect activity has two peaks, especially Diptera are known to have activity peaks, one after sunset and the other before sunrise (Appel *et al.*, 2017). This study results showed that within the same night, the activity of bats were higher at the beginning of the night on both bright and dark nights. Their need to feed during the first hours of the night is assumed to be the reason for the first activity peak. With limited foraging time just after sunset allows bats to attain high foraging efficiencies (O’Donnel, 2000). There is lower predation pressures at the beginning of the night and encourages bats to emerge from their roosts and take advantage of the cost-benefit ratio of foraging. There was some bat activity in the middle of the night which could have been large molossids, whose behaviour is known to feed on moths which are more active in the middle of the night. In this study the bats did not respond to the moon phase, bat activity was significantly the same between bright nights and dark nights at all sites sampled. Indicating that other conditions such as rainfall, humidity and temperature may also affect bat activity. Within a single night bat activity was higher in the early evenings regardless of the presence or absence of moonlight. Thus bat activity response to moonlight is not immediate and may be more directly associated to specific bat species.

During the study period, nightly temperatures ranged from 11.5 °C to 43.1 °C (mean 22.4 °C). There was a positive correlation between bat activity and temperatures. As expected, bat activity varied with changes in temperature, and activity was low when temperatures were low. These results are consistent with the common pattern observed for insectivorous bats (Hayes, 1997; O'Donnell, 2000). During periods of low temperature, it is a critical period for the energy balance of insectivorous bats because low temperatures reduce insect abundance and activity (O'Donnell, 2000) and increase heat loss, making foraging less profitable. In the study area, bat activity was positively correlated with temperature, as in other regions (e.g. New Zealand) (O'Donnell, 2000). Kuidas had the lowest average temperature (20.1 °C) which resulted in the lowest bat activity recorded. The low activity levels were a response of bats to low temperatures at the study site.

Ambient temperature and invertebrate abundance have marked effects on levels of activity in bats (Hayes, 1997; Vaughan *et al.,* 1997). Flying invertebrate activity, and hence the amount of food potentially available, generally in the night (O'Donnell, 2000; Baerwald *et al.,* 2008). However, it is not clear if bats responded to temperature or invertebrate activity per se, or to the interaction between increased invertebrate activity and temperature, which would be important to look at in further studies.

6. CONCLUSION AND RECOMMENDATIONS

What the present study confirms is that bats do survive in the Kunene Region desert climate and are active in all the seasons. Bat activity was positively correlated with temperature. Insectivorous bats showed seasonal variation in activity suggesting that bats do not hibernate in the desert, but rather that individuals may go through periods of torpor. This has previously been suggested by William & Dickman (2004). Bat activity patterns are markedly reduced in the winter when temperatures are low and possibly food availability which are reduced (Parker & Bernard, 2018). It is recommended that more bat detectors are set-up to monitor bat activity throughout the Kunene region.

Inherited bat species traits such as flight speed, body size, flexibility in foraging in different habitats, as well as predation pressure and insect availability can influence responses to moonlight. Therefore this study recommends that these factors be considered in future studies, with a call library to be created and specimen vouchers collected to unable bat activity to be looked at species level and include different habitats such as open areas, cluttered areas and fragments to assess how species that use different habitats respond to moonlight intensity. As the study results of bat activity during all moon phases only came from the Etendeka study site, studies on populations and community structure of aerial insectivorous bats should be performed at all the sites as the vegetation is different in order to include periods of high activity for all bat species.

Water appeared to be such a vital resource to bat populations during all seasons in the study area, as the Kunene Region has a desert climate, this study suggest to managers that are concerned with bat conservation maintain a network of water sources bats can utilize throughout the year. During the dry seasons, the environments are water limited, and relative distances to available water sources may further limit use for some species due to the energetic cost of flight. Further, maintaining and increasing water sources available to bats may help mitigate future threats associated with climate change (Intergovernmental Panel on Climate Change 2007). Global climate change will likely reduce the size and availability of natural water sources, which often depend on annual flooding events, or regular amounts of annual precipitation to persist (Razgour & Korine, 2010). Therefore, preserving the health of existing water sources, while increasing the number of available water sources by establishing constructed ponds or ephemeral wetlands (Biebighauser, 2002) will help to address year-round conservation and survival needs of bats. To contribute strategically to the local water network, placement of man-made water bodies can be emphasized in areas that may be especially water-limited (Huie, 2002).

Concerns about the well-being of many bat species has brought focus to worldwide conservation efforts that require knowledge regarding population sizes in designated areas (Cooper-Bohannon *et al.,* 2016). Long-term data sets are needed to detect declining populations before it becomes too late to assist them and to quantify population growth resulting from positive responses to conservation efforts (Cooper-Bohannon *et al.,* 2016). Over the past few decades bat conservation efforts in some areas of the world has greatly improved knowledge of species' trends and ecology, increased public engagement and species protection (Racey, 2013). Africa is home to 20% of bat species, and with growing threats to bats globally there is an urgent need for bat conservation in areas with large knowledge gaps and unknown conservation status of species.

7. RESEARCH ETHICS

The Ethical Clearance for research was provided by the University of Namibia Ethics Committee (FOS/175/2017) and the Ministry of Environment and Tourism of Namibia (Permit No. 2225/2016). Research in the field was performed according to the ethics policy and research ethics guidelines. All accidental bat mortalities from mist-netting were donated to the National Museum of Namibia as museum voucher specimens.

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APPENDIX

Summary tables of bat species identified at three sites in the Kunene region, Namibia from May 2016- March 2017

Etendeka

Field No	Time	SPP	age	sex	Repro	Forearm	head	Weight
1	2045	NECA	adult	M	p/repro	31.9		6
2	2114	CHNI	adult	M	NR	45.4		12.5

Hoanib

	April		SPP	age	sex	Repro	Forearm	head	Weight
Date	Field No	Time	SAPE	Adult	M	NR	40.4	20.1	10
08/04/2016	3	1909	CISE	Adult	F	NR	32.1	16.2	
08/04/2016	4	1916	SAPE	Adult	M	NR	40.6	23.4	14
08/04/2016	5	2023	NEZU	Adult	F	NR	31.1	15.5	3.5
08/05/2016	6	1808	SAPE	Adult	M	NR	39.4	21.9	10
08/05/2016	7	1812	SAPE	Adult	M	NR	41.9	17.8	11
08/05/2016	8	1820	SAPE	Adult	M	NR	39.2	17.2	10
08/05/2016	9	1822	SAPE	Adult	M	NR	41.7	20.8	10.5
08/05/2016	10	1822	SAPE	Adult	M	NR	41.6	14.3	12.5
08/05/2016	11	1822	SAPE	Adult	M	NR	40.2	21.7	11
08/05/2016	12	1822	SAPE	Adult	M	NR	41.2	16.5	10
08/05/2016	13	1834	SAPE	Adult	M	NR	39.3	23.8	12
08/05/2016	14	1835	SAPE	Adult	M	NR	40.1	24.3	12
08/05/2016	15	1845	SAPE	Adult	M	NR	39.6	22.1	11
08/05/2016	16	1845	SAPE	Adult	M	NR	41.9	21.1	12
08/05/2016	17	1850	SAPE	Adult	M	NR	40	20	12
08/05/2016	18	1852	SAPE	Adult	F	NR	42.5	22.3	13
08/05/2016	19	1852	SAPE	Adult	M	NR	40.8	22.5	12.5
08/05/2016	20	1900	SAPE	Adult	F	NR	40.9	21	11.5
08/05/2016	21	1900	CISE	Adult	M	NR	33.6	14.4	4.5
08/05/2016	22	1924	SAPE	Adult	F	NR	41.5	20.8	11
08/05/2016	23	1924	SAPE	Adult	F	NR	40.7	20.7	13.5
08/05/2016	24	1924	SAPE	Adult	M	NR	41.1	23.3	13
08/05/2016	25	2009	SAPE	Adult	F	NR	39.3	22.6	14
08/05/2016	26	2022	SAPE	Adult	M	NR	41.2	22.4	11
08/06/2017	42	1946	CISE	Adult	F	NR	31.3	14.8	3.5
22/07/2017	43	1821	SAPE	Adult	M	NR	39	21.5	8.5
22/07/2017	44	1824	SAPE	Adult	M	NR	40.1	21	10
22/07/2017	45	1836	SAPE	Adult	M	NR	39.5	22.1	9.5
22/07/2017	46	1837	SAPE	Adult	F	NR	41.4	21.2	9.5

22/07/2017	47	1842	SAPE	Adult	F	NR	42	20.8	11
22/07/2017	48	1843	SAPE	Adult	F	NR	39.8	23.3	10.5
22/07/2017	49	1846	SAPE	Adult	F	NR	39.9	21.7	9.5
22/07/2017	50	1848	SAPE	Adult	M	NR	37.8	22.4	9.5
22/07/2017	51	1848	SAPE	Adult	M	NR	40.5	21.8	8.5
22/07/2017	52	1851	SAPE	Adult	F	NR	39.4	22.7	9
22/07/2017	53	1916	EPHO	Adult	F	NR	52.5	29.5	18
22/07/2017	54	1940	SAPE	Adult	F	NR	43.4	23	11
22/07/2017	55	1946	EPHO	Adult	M	NR	49.3	17.3	18
22/07/2017	56	2005	SAPE	Adult	F	NR	39.4	21.9	9
22/07/2017	57	2008	CISE	Adult	F	NR	32.3	18.5	3

Kuidas

Date	Field No	Time	SPP	age	sex	Repro	Forearm	head	Weight
01/06/2017	27	1850	EPHO	A	M	NR	48.9	25.7	17
01/06/2017	28	1911	EPHO	A	M	NR	50.5	21.6	20
01/06/2017	29	1940	CISE	A	F	NR	35.2	16.6	3.5
01/06/2017	30	1946	EPHO	A	F	NR	53	25.6	18
01/06/2017	31	2009	EPHO	A	F	NR	53.2	25.4	18.5
03/07/2017	32	1811	CISE	Adult	M	NR	32	16.8	3.5
03/07/2017	33	1814	CISE	Adult	M	NR	31.7	13.3	4
03/07/2017	34	1917	EPHO	Adult	M	NR	49.3	24.5	17.5
03/07/2017	35	1924	EPHO	Adult	M	NR	46.7	25	15.5
03/07/2017	36	2038	EPHO	Adult	F	NR	51.3	24.8	17
27/08/2017	37	1824	SAPE	Adult	M	NR	39.3	22.5	9
27/08/2017	38	1832	SAPE	Adult	M	NR	40.5	21.6	8.5
27/08/2017	39	1841	SAPE	Adult	M	NR	41.1	21.3	10
27/08/2017	40	1841	SAPE	Adult	F	NR/P	40.7	22.1	9.5
27/08/2017	41	1842	SAPE	Adult	M	NR	40.2	21.8	8