
**ASPECTS OF THE ECOLOGY OF NOACK'S
ROUNDLEAF BAT (*HIPPOSIDEROS* AFF.
RUBER) IN GHANA**



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Declaration

I, Evans Ewald Nkrumah, hereby declare that this thesis, “ASPECTS OF THE ECOLOGY OF NOACK’S ROUNDEAF BAT (*HIPPOSIDEROS AFF. RUBER*) IN GHANA”, consists entirely of my own work produced from research undertaken under supervision and that no part of it has been published or presented for another degree elsewhere, except for the permissible excerpts/references from other sources, which have been duly acknowledged.

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“Our planet is still full of wonders. As we explore them we gain not only understanding, but power. It's not just the future of the whale that today lies in our hands. It's the survival of the natural world in all parts of the living planet. We can now destroy, or we can cherish. The choice is ours”

Sir David Frederick Attenborough (1926 – Present), BBC commentator

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Dedication

This work is dedicated to my parents Mr and Mrs Stephen Nkrumah who supported me in pursuit of a carrier in the Life Sciences and all who share in the vision of Sir David Attenborough.

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Two great scientists once said; “All matter originates and exists only by virtue of a force. We must assume behind this force the existence of a conscious and intelligent Mind. This Mind is the matrix of all matter” (Max Planck, Father of quantum physics and Nobel laureate in Physics 1918 for discovery of quanta energy), and Albert Einstein (originator of General Theory of Relativity and Nobel laureate in Physics 1921 for the law of photoelectric effect) also said “Anyone who becomes seriously involved in the pursuit of Science becomes convinced that there is a Spirit manifest in the laws of the Universe, a Spirit, vastly superior to that of man”. This

‘Mind’ and ‘Spirit’ I called God; so last but not least I thank God for being the matrix behind the success of this work.

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Abstract

The roost of bats in five caves in the central parts of Ghana were investigated. A total of 10,226 bats belonging to nine species were mist-netted within two years. There was a significant difference in species composition of the caves. The Noack's roundleaf bat, *Hipposideros aff. ruber* was found to be the most dominant species roosting inside the cave and some aspects of its ecology were further investigated. The flight activity of *Hipposideros aff. ruber* was limited to certain periods of the night at Kwamang cave one while it was uniform at Kwamang cave two. The estimated mean home range size of this species using radio-tracking was thirty-six hectares with a foraging range of 1.2 km. There was no significant difference in the home range sizes of the males and females. *Hipposideros aff. ruber* used 50% of its home range as the foraging area and 2% as the core area. Pregnant females had smaller home ranges and foraged not more than 0.2 km away from the roost cave. *Hipposideros aff. ruber* used all available habitats around its roost but strongly preferred to forage in fallow lands ahead of other habitats. This bat used tree farms such as cocoa as flight paths to commute between roost caves and foraging areas and exhibited a trimodal activity pattern foraging at dusk, midnight and dawn. *Hipposideros aff. ruber* is a strong flyer commuting over longer distances. A three kilometre radius around its roost should be included in the protection of its home range. In highly impacted agricultural landscapes, fallow lands are recommended as conservation units to support this bat. In such landscapes, provision of canopy trees as flight paths is recommended to allow them to commute between roost and habitats that support higher prey densities.

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List of Abbreviations

ANOSIM	Analysis of Similarities
ANOVA	Analysis of Variance
a.s.l	Above sea level
BBC	British Broadcasting Corporation
BC1	Buoyem Cave One
BC2	Buoyem Cave Two
CF	Constant Frequency
DFG	German Science Foundation
FOC	Forikrom Cave
FM	Frequency Modulated
GS	Grass Savannah
HSD	Honest Significant Differences
HS	Human Settlement
IUCN	International Union for Conservation of Nature
KW	Kruskal-Wallis
KWI	Kwamang Cave One
KW2	Kwamang Cave Two
LoCoH	Local Convex Hulls
MCP	Minimum Convex Polygons

MRPP	Multi Response Permutation Procedure
MW	Mann-Whitney test
NMDS	Non-Metric Multi-Dimensional Scaling
KCCR	Kumasi Centre for Collaborative Research in Tropical Medicine
KNUST	Kwame Nkrumah University of Science and Technology
PAST	Paleontological Statistics Software Package
PERDISP	Permutational Analysis of Multivariate Dispersion
PERMANOVA	Permutational Multivariate Analysis of Variance
PIE	Probability of Interspecific Encounter
R	R Statistical Program
RF	Relative Frequency
RAP	Rapid Assessment Programs
NNCH	Nearest Neighbour Convex Hulls
SD	Standard Deviation
SE	Standard Error
SIMPER	Similarity Percentages-species contributions
SnH	Semi-natural Habitats
TF	Tree Farms
TMF	Traditional Mixed Farms

UTM Universal Transverse Mercator

WSR Wilcoxon signed–rank test

WS Wooded Savannah

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Chapter One

General Introduction

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1. General Introduction

1.1 Background

Bats represent the second most diversified group of mammals in the world after rodents with unique evolutionary adaptations and traits (Saikia, 2007; Koprowski *et al.*, 2005). They are unique among mammals as a result of their true flight capability, echolocation ability, and communal life that could reach several thousands in one assemblage. They also play important role in many ecosystems of the world and regulate complex ecological processes (Thomas, 1993). For instance, some insectivorous bats consume nearly their weight in insect numbers per night forming integral part of food webs (Findley, 1993). Their regulation of insect numbers however affect agricultural activities as some of these consumed insects are important agricultural pest (Peters *et al.*, 2006). It is estimated that the loss of bats in North America could cause agricultural loss amounting to a conservative estimate of more than \$3.7 billion/year (Boyles *et al.*, 2011). Their control of important agricultural pests suggest lesser use of agrochemicals on crop fields. Agrochemicals are known to affect the sexual development of frogs, cause diseases and reproductive failures in fishes, and bats through their pest control services curb some of these challenges (Bruhl *et al.*, 2013; Relyea, 2009; Relyea and Diecks, 2008; Khan and Law, 2005). Some frugivorous bats on the other hand are important seed dispersers. For instance *Eidolon helvum* has been identified as the sole dispersal of the seeds of the threatened *Milicia excelsa* tree (Taylor *et al.*, 1999). Other bats also serve as pollinators in the ecosystem (Hodgkison *et al.*, 2003). Also, majority of ecosystem services are normally provided by the individual abundance of species and larger assemblages of bat communities help in ecosystem balance (Dornelas *et al.*, 2011).

These functions suggest the important role bats play and their absence impoverish ecosystems for which they form part.

Despite the critical role bats play in many ecosystems, in Ghana they remain least studied in comparison to other mammals. Recent studies about bats of Ghana have dwelled on the zoonotic perspective implicating these mammals as host of emerging infectious diseases (Annan *et al.*, 2013; Drexler *et al.*, 2012; Hayman *et al.*, 2012; Biesold *et al.*, 2011; Canuti *et al.*, 2011; Pfefferle *et al.*, 2009; Hayman *et al.*, 2008). Ecologically, little research has been carried out to understand their ecology. This situation may be due to a number of reasons. Their nocturnal behaviour, flight abilities and shifting home ranges of some species become less attractive and disincentive for researchers who wants to study them. Also, financial obligations involved in the acquisition of the required equipment and needed skills for their study pose a challenge. Lastly, there are many cryptic species of bats posing taxonomic challenges which expertise is limiting in Ghana. For instance, two insectivorous bats within the genus *Hipposideros*; *Hipposideros caffer* and *Hipposideros ruber* have been previously considered to be one species (Hayman and Hill, 1971).

Hipposideros caffer and *Hipposideros ruber* are currently not considered conspecific (Simmons, 2005). These two species are widely distributed in sympatry from open forest and savannah that surround the rainforest belt of Africa (Simmons, 2005; Hayman and Hill, 1971). *Hipposideros ruber* however is restricted to the rainforest belt and the forested savannahs of sub-Saharan Africa (Vallo *et al.*, 2008). In the day time, it has been found hanging freely in caves, abandoned buildings, under bridges,

hollow trees and burrows of large mammals (Happold and Happold, 2013). *Hipposideros ruber* emerges around dark and remains active till around 23:00 to 24:00 hours (Fenton and Thomas, 1980). It normally flies slowly with occasional burst of speed (Happold and Happold, 2013). It has been observed to forage in diverse environments such as around buildings feeding close to the ground or at times closer to the tops of trees (Fenton and Thomas, 1980). *Hipposideros ruber* relies on echolocation calls containing both constant frequency (CF) and frequency modulated (FM) components to forage and manoeuvre in very dense and cluttered vegetation (Monadjem *et al.*, 2010a; Wright, 2009; Jones *et al.*, 1993a; Aldridge and Rautenbach, 1987). The frequency of their calls ranged between 130–139 kHz (Vallo *et al.*, 2011). In the islands of the Gulf of Guinea (Central Africa), populations of *Hipposideros ruber* roost with different numbers of congeneric species (Guillen *et al.*, 2000). It has been predicted *Hipposideros ruber* uses slow-hawking and gleaning as foraging strategy like *Hipposideros caffer* (Happold and Happold, 2013). In Liberia, *Hipposideros ruber* feeds actively at dusk with full stomach content after two hours, and foraged again intermittently through the night with peak just before dawn (Happold and Happold, 2013).

In Ghana, ecological studies on bats are limited. Recent interest in the studies of some species such as *Hipposideros ruber* have emerged from their ability to host emerging infectious diseases (Annan *et al.*, 2013; Drexler *et al.*, 2012; Hayman *et al.*, 2012; Biesold *et al.*, 2011; Canuti *et al.*, 2011; Pfefferle *et al.*, 2009; Hayman *et al.*, 2008). Although ecological studies are limited for these group of mammals in Ghana, there exist published records from various parts of Ghana. These few studies more often than not are surveys lasting from few days to weeks (Decher and Fahr, 2007; Weber and Fahr, 2007; Decher *et al.*, 2002; Taylor *et al.*, 1999; Decher, 1997).

The results from these surveys are important in providing first-hand information about species and their assemblages. However, results are limited as they often provide less information on patterns existing within bat communities because of survey longevity and focus. Also, these studies normally account for bats inhabiting forest habitats. Some bats however spend almost all or part of their life living in communal roost especially caves (Monadjem *et al.*, 2009; Glover and Altringham, 2008).

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1.2 Justification of the study

Caves are important resources for large assemblages of bats. Many bats have evolved to spend more than half of their life subject to conditions inside caves (Avila-Flores and Medellin, 2004; Kunz and Lumsden, 2003). Bats may use caves as roost for a number of reasons but mainly due to the provision of stable microclimatic condition and protection from predators (Churchill *et al.*, 1997). Caves are therefore important models for testing ecological, evolutionary and biological predictions (Stewart, 1981). In Ghana, no substantial information exists on the bat communities roosting inside caves and existing ecological patterns within these communities.

In Ghana presently, most pristine forest cover has been lost to agriculture creating more modified habitats (Appiah *et al.*, 2009). This conversion from pristine natural habitats to agriculture makes agriculture habitats increasingly available to many wildlife populations especially foraging bats (Tylianakis *et al.*, 2007). The impacts of this widespread conversion from pristine natural habitats to agriculture remain to be assessed for foraging bats in Ghana. It is not known how bats are utilizing the space and habitats in anthropogenic systems such as agricultural landscapes.

It is imperative, and a conservation priority therefore to investigate the community of bats using human-used caves situated in highly modified habitats such as agriculture to understand their ecology especially in community patterns, spatial requirements and their utilization of space and habitats. To study the spatial requirements and utilization of habitats, the research focuses on *Hipposideros ruber* which is a widely distributed bat in West Africa and Ghana, and also serves as host of emerging virulent infectious diseases. Knowledge on its ecology is crucial in formulating conservation and management strategies that will ensure their long term survival for ecosystem services while providing recommendations that will minimize human interactions with this species.

1.3 Objectives of the study

This work focuses on bats roosting inside human-used caves in Ghana. The aim is to advance knowledge on bats roosting inside Ghanaian caves and make recommendations that will ensure their long term survival. This work therefore identifies four main objectives guiding this thesis:

- ❖ Assessment of bat composition and structure of five human-used caves.
- ❖ Determination of the flight activity of *Hipposideros ruber* at cave entrances.
- ❖ Estimation of the home range size of *Hipposideros ruber*.
- ❖ Determination of the habitat selection and foraging behaviour of *Hipposideros ruber*.

1.4 Study area

The study was conducted in the Ashanti and Brong Ahafo region in Ghana (Fig. 3.1). All selected bat caves were located in agricultural landscapes and used by the humans for various purposes ranging from religious activities, bat hunting, and harvesting of water. Two caves were selected in Kwamang village in the Ashanti Region. The three other caves were selected in Brong Ahafo region; two from Buoyem village and one from Forikrom village. The distance between the caves in the Ashanti and Brong Ahafo regions is approximately one hundred kilometres.

Kwamang village is found in the Sekyere Central District of the Ashanti Region. The village has two caves which is the Mframabuom and Ohene Abutia caves identified in this thesis as KC1 and KC2 respectively. These two caves are separated by a distance of 3.8 km. The geo-morphology of KC1 is led by two entrances into two main caverns with its tunnels also serving as roost for different bats. The size of each cavern is approximately ten meters long and eight meters wide. KC2 has one entrance of length twelve meters. This wide entrance narrows into a tunnel that leads to a thirteen-meter long by ten meters wide cavern. KC1 and KC2 are found at an elevation of 420 meters and 468 meters above sea level (a.s.l) respectively. Water runs from these two caves and are harvested by humans for different purposes.

Forikrom and Buoyem villages are both in the Techiman District (Brong Ahafo region) of Ghana and separated by a distance of nineteen kilometres. In Forikrom, the cave is called Boten cave and is identified in this thesis as FOC. This cave has one large cavern with satellite caverns as bat roosting places. This large cavern in the day time receives sunlight from the large entrance and from its wide opening at the

top of the cave. As a result, it is illuminated during the day time but the satellite caverns are darker and serves as roosting places for the bats. This cave has no running water through it but becomes wet when it rains. The large cavern is eighteen meters long and fifteen meters wide. The elevation of this cave is 365 meters a.s.l.

Buoyem has two caves that are separated by a distance of 0.6 km. These caves are the Mprisi and Dwamerewa caves identified in this thesis as BC1 and BC2 respectively. BC1 has three large caverns with approximate length of thirteen meters long by thirteen meters wide each. There is a small tunnel that joins all three caverns. The third cavern has water running and opening at the top allowing sunlight to penetrate some portions of this cavern. The second cavern is darkest in the day time while the first cavern receives a lot of sunlight due to its openness. Bats at this cave therefore use the second and third cavern for roosting. BC2 has approximate size of thirty meters long by twenty-five meters wide. Some parts of this cave receives sunlight and are illuminated in the day time while other parts are darker due to its geo-morphology. There are several hideouts for bats in this cave. Some parts of this cave have running water with wet conditions while other parts have drier conditions. The elevation of BC1 and BC2 are 438 meters and 449 meters a. s. l. respectively.

1.5 Outline of thesis

This thesis is organised into seven chapters excluding the prefatory sections which ushers in the main chapters and the appendices. The first chapter is dedicated to introducing the work. The second chapter is dedicated to literature review. Chapters three to six provide main research findings. Chapter seven provides a general discussion highlighting the significant findings in chapters three to six.

1.5.1 Chapter one

Chapter one presents a general introduction to this work beginning with the importance of bats and their role in many ecosystems. It presents the reasons for carrying out this research and the objectives guiding this thesis. It also highlights where this research was carried out and ends with a summary of all the various chapters and appendices presented in the thesis.

1.5.2 Chapter two

Chapter two review current understanding in the study of bats. It provides evolutionary history and current challenges in bat systematics especially relating to *Hipposideros caffer* and *Hipposideros ruber* complexes. The chapter further highlights how bats are impacted by habitat modification. The chapter ends by looking at underlining ideas in the movement of animals that is central in this thesis.

1.5.3 Chapter three

Chapter three presents the bat community composition and structure of five human-used caves in Ghana. Approximately 10,000 bats were captured within two years belonging to nine species. *Hipposideros* cf. *ruber* dominated all the five caves studied. Species composition was significantly different among the caves. *Hipposideros jonesi* and *Coleura afra* contributed greatly to community dissimilarity. The caves are important resource for many bats. Despite single species dominance, significant differences in species composition suggest preservation for the conservation of different species of bats.

1.5.4 Chapter four

In chapter four, the flight activity of *Hipposideros aff. ruber* is presented. Flight activity was monitored at KC1 and KC2 and not the other caves. This was due to difficulties in determining whether a captured bat in mist net at BC1, BC2 and FOC was entering or exiting the cave. At KC1 and KC2, the distribution of the nightly flight activity of *Hipposideros aff. ruber* was hypothesised to be concentrated at certain periods of the night. Flight activity was found to be concentrated at certain periods of the night at KC1 and not KC2. Flight activity was generally highest at early hours of the night (around 21:00) and at sunrise (06:00). It is recommended that human activities during peak periods be avoided in order not to disrupt the 'normal' activities of these bats.

1.5.5 Chapter five

In chapter five, the home range of *Hipposideros aff. ruber* was estimated for the first time. The home ranges of thirteen individuals were analysed from radio-tracking studies. The foraging and core areas of this species were also analysed. Data from tracked bats indicated that the mean home range of *Hipposideros aff. ruber* was thirty-six hectares. The foraging and core areas were much smaller, as they formed 50% and 2% of the home range respectively. The foraging range was 1.2 km indicating they are strong flyers despite their lower wing loading and aspect ratios. Protection of its home range should therefore aim at including a minimum of a three-kilometre radius around its roost.

1.5.6 Chapter six

In chapter six, the habitat selection and foraging behaviour of *Hipposideros aff. ruber* is presented. This bat exhibited a trimodal activity pattern at night. Compositional analysis revealed that this bat is adaptable, and foraged in all habitat types around its roost. However, it prefers to forage on fallow lands. Cocoa farms were of less importance for foraging purposes to this bat, but important to it as flight paths to commute between roosts and foraging areas. It is recommended that in highly modified habitats such as agricultural landscapes, a mosaic of canopy trees be provided to allow bats commute between roost and other close by habitats that support higher insect abundance.

1.5.7 Chapter seven

This chapter provides a general overview of the four investigations that were carried out and presented in this thesis. It draws on significant findings from chapters three to six to provide a better understanding of the bat community roosting inside caves and some important aspects of the ecology of *Hipposideros aff. ruber*. It also makes recommendation for specific areas for future research.

1.5.8 Appendices

Annexed to this thesis are Appendices one to four. Appendix one provides results of bat captures from the five caves. Appendix two presents the results of rarefaction from Ecosim. The third appendix present the stress plot from ordination analysis while the fourth present Tukey's multiple comparisons of caves. Also annexed are plates of the nine species captured, plates of field instruments, field activities and the

field team that assisted in data collection. These are categorised as Appendix A and B. Appendix A provide colour plates of nine species of bats. Appendix B is dedicated to field instrumentation and field activities. It also includes the researcher's team that assisted in data collection.

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Chapter Two

Literature Review

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2. Literature Review

2.1 Evolutionary history, phylogeography and phylogenies of bats

Bats form about 26% of the approximate 4600 recognized mammals and their evolution coincide with global rise in temperature in the Eocene (Teeling *et al.*, 2005). Although bats evolved early and share some traits with other mammals such as rodents and carnivores, they have changed relatively little and possess unique characteristics that distinguishes them (Calisher *et al.*, 2006). Bats in general have a poor fossil record and their phylogenetic and phylogeographical relationships have been studied not in great detail (Teeling *et al.*, 2005; Hand, 1984). Nevertheless, the earliest-known bats are represented by an excellent fossil materials comprising whole skeleton from the early and middle Eocene (Novacek, 1985). Their evolutionary history suggests that they appeared as soon as the early Eocene in all continents except for the Antarctica (Tabuce *et al.*, 2009). This approximately dates back to about 50 - 60 million years ago long before modern humans evolved (in about 200,000 years), but the existing bats today looked very much like their ancestors when they appeared (Stewart and Stringer, 2012). It has been suggested that when they appeared, they already had true flight abilities and sophisticated laryngeal echolocation to pursue insects (Eick *et al.*, 2005).

There have been problems and controversies surrounding the evolution of bats which dates back in the time of Charles Darwin who mentioned the vexed issue of how bats evolved from terrestrial ancestors (Darwin, 1859). Significant among them is the unresolved questions on echolocation and powered flight. Why did they have these characteristics? Which one came first: echolocation or powered flight? To achieve

flight capability, aerodynamic requirements are severe. Powered flight in animals such as bats is a difficult and complex adaptation which commands attention as a major feature in adaptive evolution (Kevin, 1985). The sophistication of aerodynamic abilities of animals has captured the attention of many scientists and has generated intense debate in the years gone by (Ostrom, 1974; Bock, 1965; Nopsca, 1907; Marsh, 1880). This led to the development of different theories about the abilities of animals to achieve true flight capabilities.

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2.1.1 Powered flight in bats

Darwin was the first to suggest the arboreal theory for the origin of flight (Darwin, 1859). Later, Marsh (1880) proposed the same theory for birds and the whole theory received considerable reviews in the middle of the 20th century (Ostrom, 1974; Parkes, 1966; Bock, 1965; Heilmann, 1926). The major proposal in this theory reveals that from tree to ground, and tree to tree, quadropedal was born out of the bipedal in this fashion. With control, animals gradually went through a stage of parachuting and gliding stages to achieve a powered flight. The second theory proposed by Nopsca (1907), known as the cursorial theory suggested that animals involved in running flapped their forelimbs to supplement the thrust provided by the hind limbs for a faster terrestrial locomotion. Thus, flapping increases running speed and provides a force for aerial locomotion (Nopsca, 1923, 1907). The central theme of this theory showed that thrust was a prerequisite for powered flight and received support from osteological studies of two dinosaurs that provided a cursorial pathway of flight (Ostrom, 1976a, b). Although there was a common point of interest, Ostrom emphasized power as an impetus for achieving true flight ability or aerial hawking. Detail information of the cursorial pathway can be found in Gerald *et*

al. (1983). This work suggested that forelimbs of bipedal reptile assisted in swatting prey out of air and the enlargement of the flight feathers predicted an adaption for prey capture which gradually developed lift and thrust capability for flight (Ostrom, 1976a, b). These flight theories suggest that, flight capability is highly sophisticated and involve lift, thrust and power, control, while taking into account the aerodynamic principles in physical laws of angular momentum, moment of inertia and gravity (Gerald *et al.*, 1983). Inspired by Ostrom's ideas in evolution of flight, Gerald *et al.* (1983) showed that external lifting devices such as forelimbs could act as stabilizers when in flight and increase the animal's ability to capture insects. Thus, more lift and thrust is does provided by rapid movement and twisting of forelimbs for control and stability. From dinosaurs to bats, Gerald *et al.* (1983) proposed that powered flight in bats followed a similar principle.

2.1.2 Echolocation in bats

Bats are among the few mammals species that have mastered the use of ultrasonic sound in detecting objects (Whitlow and Simmons, 2007; Whitlow and Benoit-Bird, 2003; Whitlow, 1997; Fenton *et al.*, 1995; Speakman and Racey, 1991). Investigations on the use of sonar for ranging and navigation can be traced to Lazzaro Spallanzani and Charles Jurin in 1770s who observed that blind bats became disoriented if they could not hear but could move freely if their eyes were blindfolded in a dark room (Whitlow and Simmons, 2007). Their conclusion was that "*bats require their sense of hearing in order to find their way*". This was prima facie for over a century, but never escaped criticism by scientist such as George Cuvier who argued that bats avoidance of obstacle in the dark could best be explained by their sense of touch in the body or wing membrane (Raghuram and

Marimuthu, 2005). It was until the development of sensitive microphones to detect high frequencies that the understanding of the principles underlining ultra sound was uncovered. Echolocation in bats became well established after the discovery of the first ultrasonic device developed by the physicist William Pierce. Robert Galambos and Donald Griffin in the 1930s then pioneered the understanding of bats echolocation using this device by observing that bats emitted ultrasound and received the echoes (Griffin, 1958). A detailed account on echolocation has been outlined in the work of Raghuram and colleague (Raghuram and Marimuthu, 2005). At least, six Eocene bats were known to be echolocating: *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*, *Hassianycteris*, *Tachypteron* and *Tanzanycteris* (Gunnell *et al.*, 2003; Storch *et al.*, 2002; Habersetzer and Storch, 1992; Novacek, 1987; Novacek, 1985).

2.1.3 Which came first? Echolocation or powered flight.

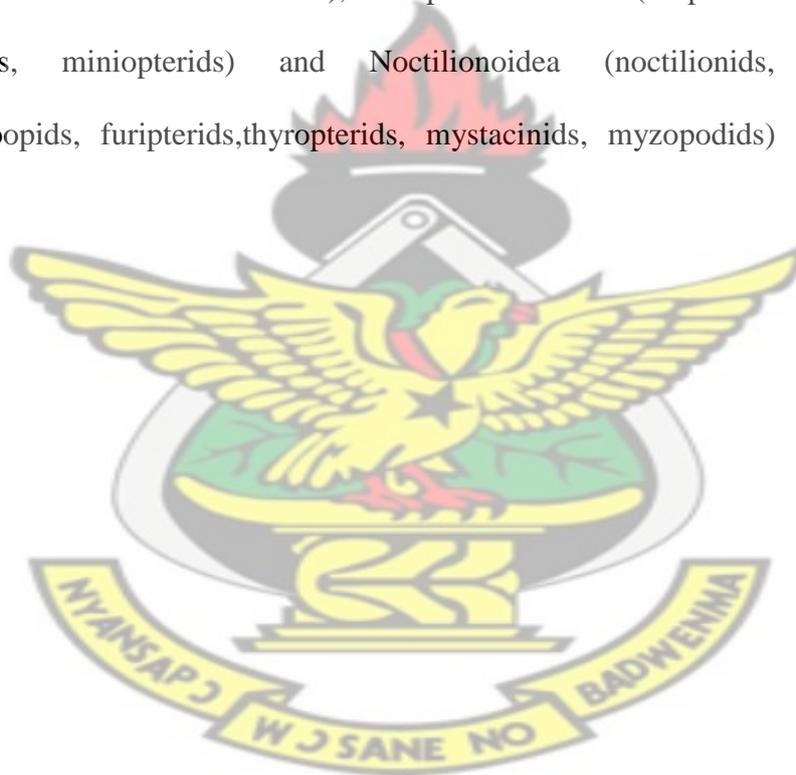
In solving the puzzle as to when echolocation did evolve in bats and its potential use, several scenarios and investigations explored this unusual phenomenon in mammals but popular among bats. The usage of echolocation involves a sophisticated process from the production of acoustic signals in the larynx, sound emission, registration of emitted signals in the brain (for future comparison), reception of echoes through the ears and finally a time comparison pulse of emitted signal and received echoes (Jones and Teeling, 2006). Bats in executing this complex mechanism takes into considerations avoidance of self-deafening and increased detection of prey (Fenton *et al.*, 1995; Fenton, 1974). Several theories have been postulated based on the assumption of monophyletic evolution of bats which begun with ancestors who were nocturnal, arboreal and insectivorous. Notably among these postulations includes

echolocation first, flight first and tandem development hypotheses (Speakman, 2001). Until the discovery of the fossil record of an Early Eocene bat from the Green River of Wyoming USA, echolocation first hypothesis held sway in the argument of echolocation or powered flight first ideas (Jones and Teeling, 2006; Fenton *et al.*, 1995). Popular argument now seems to favour flight first hypothesis based on the massively enlarged cochleae in the ears of echolocators which is comparatively small in recent fossil from the Eocene bat and also arboreal from the examination of the limbs (Simmons *et al.*, 2008; Habersetzer and Storch, 1992). These findings not only form the basis for modern investigations but also indicate how the re-creation of the natural history of bats is incomplete. Recently, a new chapter was open in the evolution books of bats to include molecular analysis of the extant bat families. Molecular data suggest one single origin of flight in bats but possible multiple origin of echolocation (Teeling *et al.*, 2002; Teeling *et al.*, 2000). A thorough review on this debate is outlined in Speakman (2008).

2.1.4 Phylogeography and phylogenies of bats

Three major lineages of bats, belonging to the order chiroptera (meaning; hand-wing) can be traced to Laurasia, possibly in North America in the Paleocene about 50 to 52 million years ago while the fourth lineage is traced to Gondwana land (Teeling *et al.*, 2005). Based on paleontological studies, this order is divided into two suborders; Megachiroptera (megabats) and Microchiroptera (microbats) with megabats relying mostly on vision while microbats on ultrasound (Teeling, 2009). These two lineages is estimated to have branched approximately about 58 million years ago (Teeling, 2009). Recent phylogenetic studies have reclassify this group of mammals. Bats are classified under the order chiroptera, superorder Laurasiatheria

and suborders Yinpterochiroptera (megabats) and Yangochiroptera (microbats) (Teeling *et al.*, 2005; Teeling *et al.*, 2002; Teeling *et al.*, 2000), rejecting Archonta as its superorder, and order Dermoptera as its sister order as previously thought (Adkins and Honycut, 1991). Moreover, the over 1000 species of bats have been grouped into 17-18 families (Fig 2.1) (Teeling, 2009). The most recent review on bat phylogenies is provided in Teeling *et al.* (2012). Four major groups of echolocating microbats have been identified; Rhinolophoidea (rhinolophids, hipposiderids, rhinopomatids, craseonycterids, megadermatids), Emballonuroidea (nycterids and emballonurids), Vespertilionoidea (vespertilionids, molossids, natalids, miniopterids) and Noctilionoidea (noctilionids, phyllostomids, mormoopids, furipterids, thyropterids, mystacinids, myzopodids) (Teeling *et al.*, 2012).



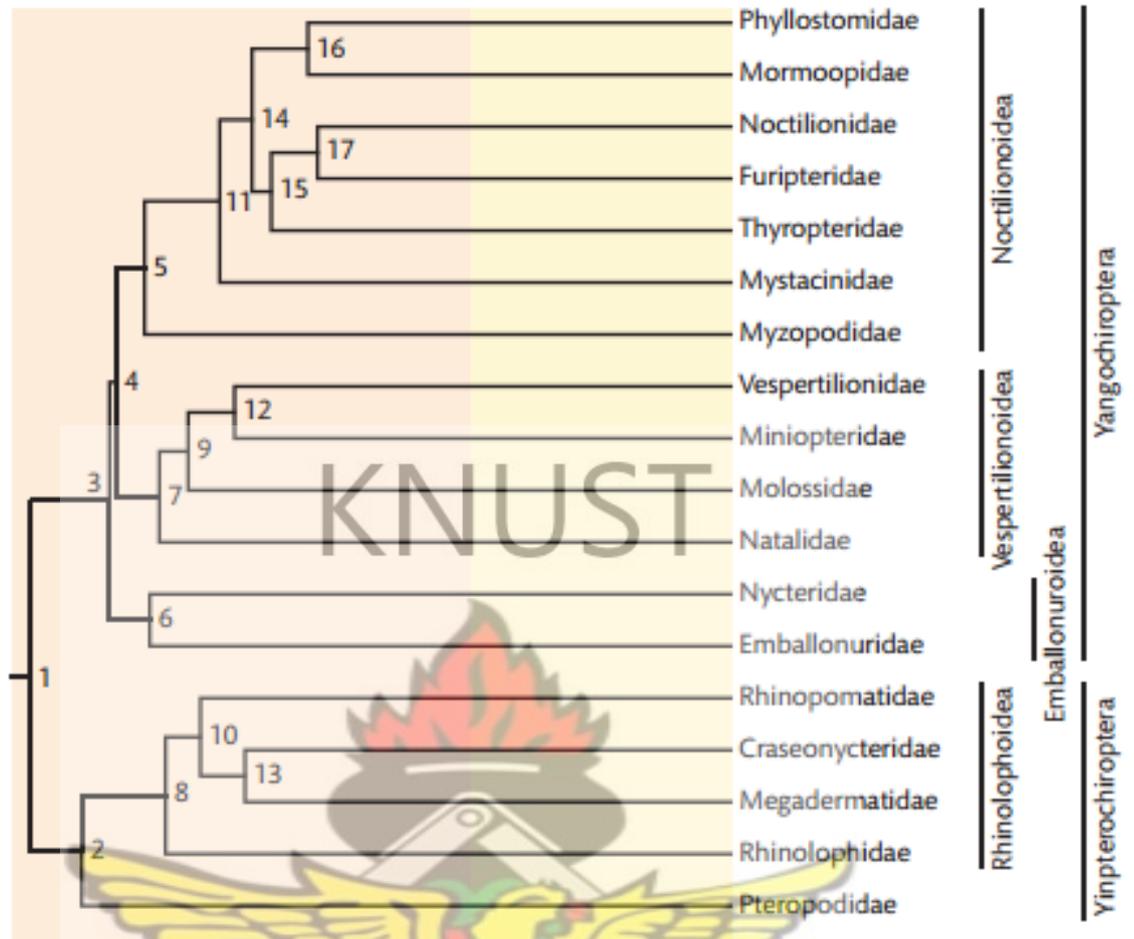


Figure 2.1: Tree of bats (Chiroptera). Adapted from Teeling (2009)

2.1 *Hipposideros caffer* and *Hipposideros ruber* complex

The genus *Hipposideros* belongs to the infraorder Yinochiroptera (Teeling *et al.*, 2012). *Hipposideros* is a Greek name for horse (hippos) and iron (sideros) to refer to the horseshoe-like shape of the nosed-leaf of this genus (Rosevear, 1965). There exist cryptic forms within this genus making morphological identification difficult. *Hipposideros gigas* and *Hipposideros vittatus* for example are cryptic within this genus, so is *Hipposideros caffer* and *Hipposideros ruber*. Taxonomists have considered *Hipposideros caffer* and *Hipposideros ruber* to be two conspecifics within some parts of Africa. There exist great overlap in using the forearm length,

pelage, cranial measurements, nasal swelling compartments in identification (Heller, 1992; Koopman, 1975; Hayman and Hill, 1971; Lawrence, 1964). More morphological data is provided by Wright (2009). Recent genetic studies based on mitochondria DNA suggest at least 4 lineages in Africa (Vallo *et al.*, 2008). The lineages in Ghana is *Hipposideros ruber* lineages (Vallo *et al.*, 2008). In the Ashanti region, lineages B, C, and D have been confirmed (Vallo; *pers. comm.*). However, at KC1 and KC2 in Kwamang, only lineage D is present (Vallo; *pers. comm.*). The lineage D in KC1 and KC2 is hereafter referred in this thesis as *Hipposideros* aff. *ruber*. The lineages in BC1, BC2 and FOC are not known yet, and hereafter referred as *Hipposideros* cf. *ruber*. In Chapter three, *Hipposideros* cf. *ruber* is used in reference to all lineages including the ones in Kwamang.

2.2 Bats and habitat modification

Habitat degradation and conversion of primary forest to agriculture are among the most pervasive anthropogenic activities that threaten the survival and persistence of wildlife populations. These human induced disturbances are increasing at an alarming rate (Daily and Ehrlich, 1995). Habitat modification normally happens in piecemeal fashion that often ends in isolated patches of forest to crop fields (Schulze *et al.*, 2000). These modified habitats are now becoming the only available habitats for some wildlife species such as bats. Bats are mobile animals as a result of their true powered flight and can change between habitats with relative ease (Medellin *et al.*, 2000; Kalko *et al.*, 1999). Due to the wide variation in morphology and foraging ecology of bats, their response to habitat modification vary from species to species (Castro-Luna *et al.*, 2007). Some bats benefits when natural areas are converted to agriculture farms. For example, in the Lama Forest Reserve in Benin the smallest

flying fox in Africa, *Megaloglossus woermanni* was observed to select banana fields around the forest during foraging (Weber *et al.*, 2009). Some bats on the other hand are strongly impacted by changes in their habitats (Fenton *et al.*, 1992). Insectivorous bats are particularly vulnerable to habitat changes due to their use of echolocation for hunting (Schnitzler and Kalko, 2001). Insectivorous bats in their hunting strategy often adapt to the habitats they forage and changes in temperature, humidity and wind currents as a result of habitat modification could affect their hunting success (Schnitzler and Kalko, 2001). Also their insect prey could be severely impacted by such changes within its habitat.

2.3 Animal home ranges

Several factors account for the usage of space by animals and these may be internal and external. Internal factors may be physiological or morphological while external may be environmental or distribution of available resources. The usage of available space by moving animals as home ranges was described thoroughly by Burt (1943). Burt described the home range as '*area traversed by the individual in its normal activities of food gathering, mating and caring for the young*' and summarized it as '*the area, usually around a home site, over which the animal normally travels in search of food*'. Burt however distinguish this from the concept of territoriality which was used interchangeability in the middle of the 21st century as the '*protected part of the home range, be it the entire home range or only the nest*'. These concepts by Burt, however, received criticism among various scientists who think there is lexical ambiguity in his explanation for example, the usage of 'normal' in his definition. In addition, other scientists have equated territorial areas to core use areas, the latter being an affirmative of '*center of activity*' which Hayne

used to describe Scott's 'theater of activity' in 1947 (Mills and Knowlton, 1991; Hayne, 1949). This definition by Burt however implies non randomness of revisit by animals to previously visited places (Gautestad and Ivar Mysterud, 2005), as animals normally return to places that offer important resources such as food and shelter. As a result, areas covered by animals are usually smaller than expected from its general mobility. The home ranges of individual animals are also likely to overlap (Morales *et al.*, 2010)

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Due to the increasing interest in animal movements, variety of methods have been employed in quantifying the home range size of animals. Generally, radio telemetry have proven to be an efficient way in gathering data for home range studies (Alfred *et al.*, 2012; Hart *et al.*, 2012; Kolodzinski *et al.*, 2010; Boyle *et al.*, 2009; Nicholas *et al.*, 2009). Currently in literature, there is no consensus in how best to estimate the home range sizes of animals. The advantages and disadvantages of currently employed methods have been reviewed (Huck *et al.*, 2008; Laver and Kelly, 2008; Getz *et al.*, 2007; Getz and Wilmers, 2004).

The Minimum Convex Polygon (MCP) has been one of the oldest ways of estimating home ranges and the most popular among movement ecologists. Generated home ranges using MCPs are based on the smallest convex polygon that all data points contain. That is, it generates home ranges based on the outmost locations where the animals were recorded. It is useful in providing the minimum area for sustaining animals. It however overestimate areas effectively used by the animal or lacks the ability to generate density distributions (Getz *et al.*, 2007).

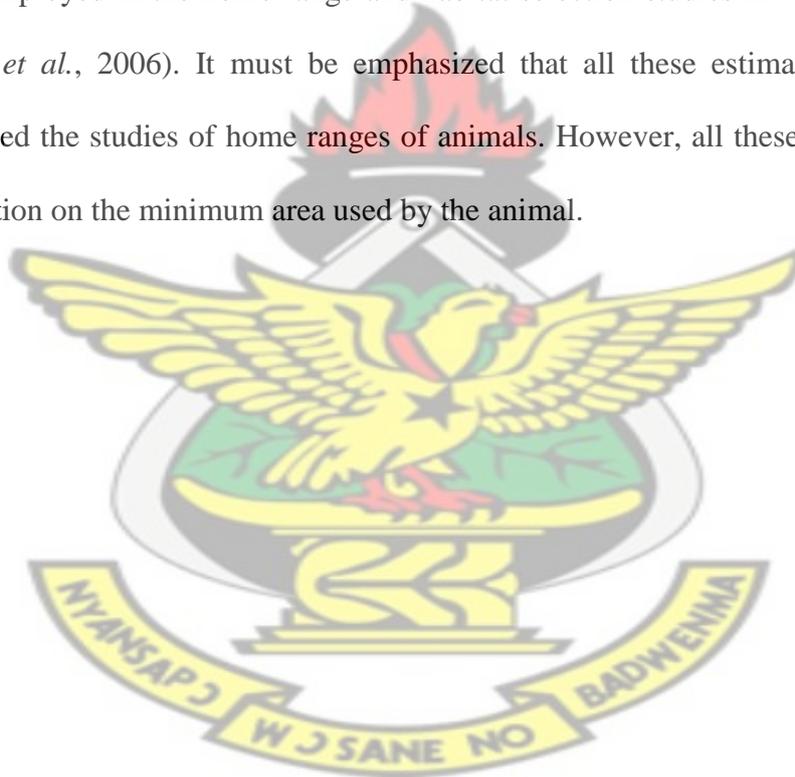
The Alpha-Hull Method suggested by Burgman and Fox (2003) involves creating Delauney triangulations from alpha-hull constructions. The defect with this estimation is that it removes all sizes of the home range longer than the median, leaving points outside the home range. In addition, it is not able to generate density distribution.

One other commonly used method is the Kernel Methods (Laver and Kelly, 2008; Laver, 2005). It produces home ranges by techniques of bivariate normal kernels. It weights the sum of local parametric distributions from each data point in the model. The downside of this technique include the infinite nature of home ranges as it has no boundaries and continues to expand (Getz *et al.*, 2007). Also, it overestimates the area of the distribution (Seaman and Powell, 1996).

The last method, which is more recent in the estimation of home ranges, involves the creation of Localize convex hulls (LoCoH). There are three distinct methods in the family of LoCoH analyzers. The k-LoCoH builds kernels from k-1 nearest neighbors of root points. The fixed r-LoCoH also build kernels from all points within a fixed radius r of each reference point. Lastly, the adaptive a-LoCoH create kernels from all points within a radius 'a' such that the distances of all points within the radius to the reference point sum to a value less than or equal to 'a' (Getz *et al.*, 2007; Getz and Wilmers, 2004). This nonparametric method uses the kernel method in creating polygons from spatially localized subsets of data by adjoining Nearest Neighbor Convex Hulls (NNCH). Hulls merge to form isopleth; with 100% isopleth seen as a lower density containing all fixed points or all animal tracked points with 10%

considered as a high density. Full explanations on the family of LoCoH can be found (Getz *et al.*, 2007; Getz and Wilmers, 2004).

LoCoH seem to be more powerful in estimation of home ranges than previously described methods (Simon *et al.*, 2006). It also provides realistic ideas of the home range and usage within the home range (Getz *et al.*, 2007; Simon *et al.*, 2006; Getz and Wilmers, 2004). Also, LoCoH have superior convergence properties over the other methods as sample size increase (Getz *et al.*, 2007). LoCoH estimations have been employed in the home range and habitat selection studies in African buffaloes (Ryan *et al.*, 2006). It must be emphasized that all these estimates have helped advanced the studies of home ranges of animals. However, all these studies provide estimation on the minimum area used by the animal.



Chapter Three

Community composition and structure of bats in five caves in Ghana, West Africa

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3 Community composition and structure of bats in five caves in Ghana, West Africa

3.1 Abstract

The community composition and structure of bats in five caves were investigated. Bats were captured with mist nets for two years. The caves were assessed for bat composition, richness, dominance and diversity. A total of 10, 226 bats belonging to nine species were sampled. *Hipposideros cf. ruber* contributed 81% to total sample pool and was most dominant species inside all caves. PERMANOVA analysis supported the hypothesis that species composition among the caves was significantly different. SIMPER analysis indicated that *Coleura afra* and *Hipposideros jonesi* contributed greatly to community dissimilarity. The observed species richness in the caves was nearly the predicted richness (Jack 1). The results support the preservation of different caves for the conservation of different species of bats.

3.2 Introduction

Inventories on Ghanaian bats have more often than not been provided by surveys focusing on free ranging bats in the forest (Decher and Fahr, 2007; Weber and Fahr, 2007; Decher, 1997). Survey findings often provide less information on ecological dynamics within populations and communities, probably because of the randomness of the collected data and survey longevity. These inventories also provide less information on the bat communities that have been observed to roost in human-used caves. Identifying caves and netting bats directly provide acceptable data in characterising bat communities especially for insectivorous bats such as Rhinolophids than opportunistic sampling (Flaquer *et al.*, 2007).

Some bats have evolved to spend more than half of their life subject to conditions inside caves (Avila-Flores and Medellin, 2004; Kunz and Lumsden, 2003). Many bats use caves as roost for a number of reasons including provision of stable microclimate, protection from predators and as migratory roost (Churchill *et al.*, 1997). Caves are therefore important models for testing ecological, evolutionary and biological predictions (Stewart, 1981). In Ghana, cave roosting bats have been studied mostly for the viruses they host and little is known about their community composition and structure (Annan *et al.*, 2013; Pfefferle *et al.*, 2009). The measurement of community composition and the determination of diversity and evenness in the caves provide a general description of the local bat assemblage and the hegemony existing within.

In ecological communities, organisms occupy several niches and exhibit differential niches among competing species at the same trophic level (Hubbell, 2005). Ecological communities are thus expected to vary in species composition under different environmental conditions, and in different geographic regions due to the exploitation of different ecological niches by different species (Soriano, 2000). In characterizing an ecological community, a conceptual framework of using abundance data in understanding organismal diversity and their ecological patterns is advocated (Alonso and McKane, 2004). Ecological communities with greater diversity experience lesser dominance by the most abundant species (Hubbell, 2001). Diversity therefore sustains equilibrium in the utilization of all available niches within the ecosystem (Dornelas *et al.*, 2011). Community dominance on the other hand is important in determining community structure which provides insights into

processes underlining community assembly (Dornelas *et al.*, 2011). Dominance of a species in an ecological community is important as majority of ecosystem services are normally provided by the abundances of individual species (Dornelas *et al.*, 2011; Gaston and Fuller, 2008). Consequently, relative shifts in abundances of species can have consequential results that could impoverish the ecosystem functions and services.

Characterising the bat community roosting inside Ghanaian caves will inform where management priorities and interventions are needed to safeguard the survival of many bats for continual support of ecosystem services. The objective of this study was therefore to determine the species of bats roosting inside bat caves in Ghana and ascertain if species composition varies. Also the study investigated the species diversity and evenness among the caves. In this study, it was hypothesised that bat caves differ in species composition due to differences in cave conditions.

3.3 Materials and Methods

3.3.1 Study area

The study was conducted in two regions in Ghana; the Ashanti and Brong Ahafo Regions (Fig. 3.1). Two caves (KC1 and KC2) were selected in Kwamang village in the Ashanti Region. The three other caves were selected in the Brong Ahafo region; two from Buoyem village (two caves; BC1 and BC2) and the other from Forikrom village (one cave; FOC). See chapter one for detail information on the selected caves.

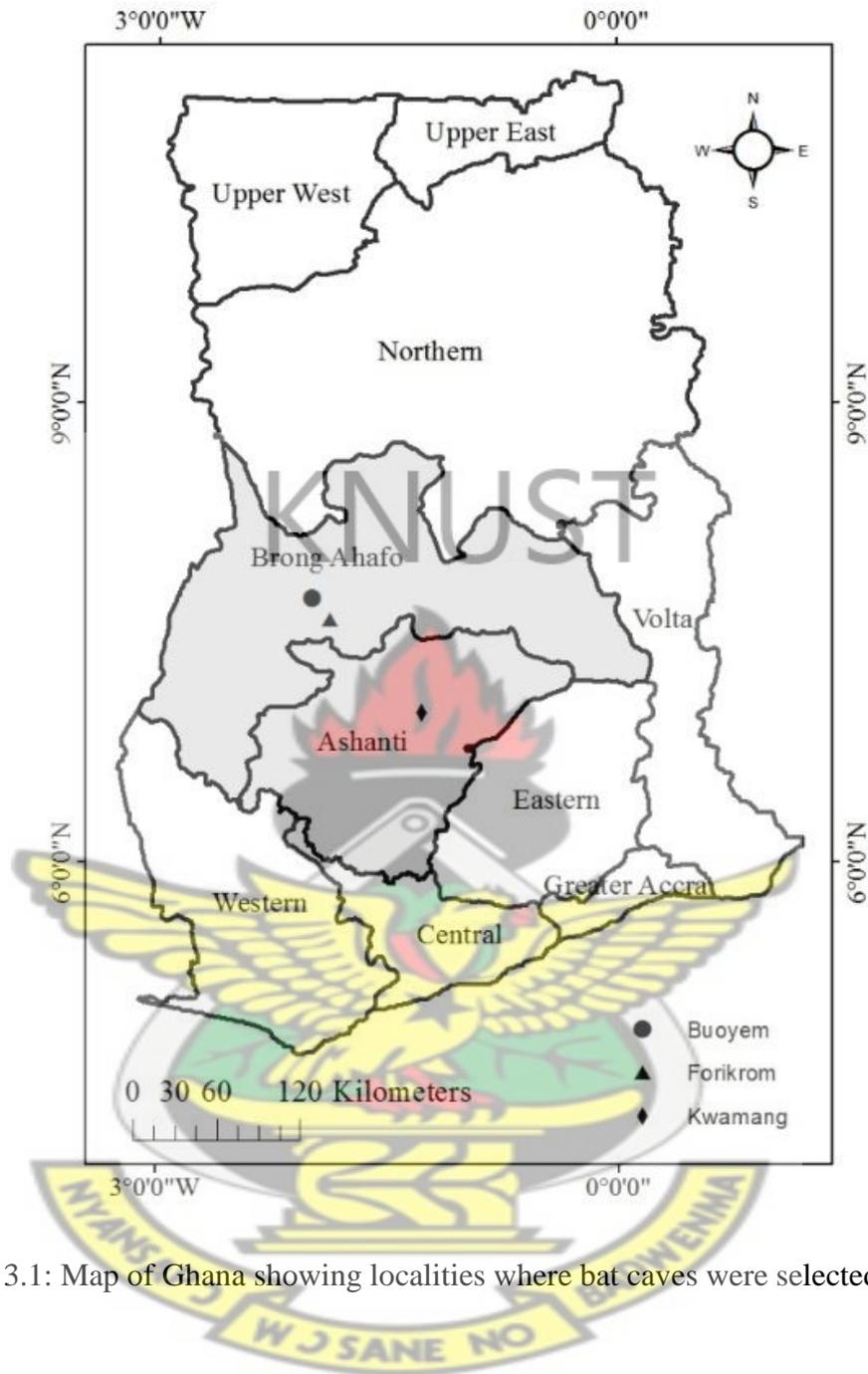


Figure 3.1: Map of Ghana showing localities where bat caves were selected.

3.3.2 Sampling design

Sampling was conducted from October 2010 to July 2012. Sampling was carried out at six weeks intervals at each cave. Two nights were spent at each cave to sample the bat community during each visit. A night was left between the first and second night of sampling. This sampling technique was adopted to ensure minimal disturbance to the bats. Bats were captured with nylon mist nets (Ecotone) mounted in front of the

roost cave (Appendix B, Plate B.2). The number of mist nets mounted varied considerably depending on the entrance shape and practicability of mounting nets. As a result, sampling efforts varied among the caves which was taken into consideration during data analysis. Sampling effort was considered as the product of the length of all nets in meters multiplied by the total hours worked (Aguirre, 2002). The sampling efforts therefore at KC1, KC2, BC1, BC2 and FOC were 138624, 111360, 122176, 352800 and 129792 mist nets length per hour respectively. Mounted nets were generally monitored throughout the night till morning from 19:00 to 06:00 hours. Times nets were not monitored were during rainy moments that prevented mist netting due to difficulties in working with wet nets. During mist netting, captured bats were removed (Appendix B, Plate B.3) and temporarily held in airy bags (Appendix B, Plate B.5) and identified using *The bats of West Africa* (Rosevear, 1965). Fore arm length and body weight of each bat was recorded to aid in species identification (Appendix B, Plate B.4).

3.3.3 Analysis of community composition

Capture rate was used as a standard measure to initially scale abundance data. Capture rate was defined as number of bats caught per mist net hour. Non-Metric Multidimensional Scaling (NMDS) was used to assess the bat community composition of the five caves based on Bray-Curtis coefficient distance matrix (also called Sørensen quantitative index) (Magurran, 2004; Legendre and Legendre, 1998). NMDS ordination method is different from other ordination methods and is commonly regarded in community ecology as most robust unconstrained ordination (Estrada-Villegas *et al.*, 2010). NMDS is an iterative method that minimises distance in original matrix in ordination space to an acceptable value. This has recently been

employed in analysis of bat communities (Threlfall *et al.*, 2012; Estrada-Villegas *et al.*, 2010). NMDS is overly sensitive to rare species so only species with at least five individuals were added in analysis (Naidoo, 2004). To further remove the effects of common species or species dominating the data in the ordination process, abundance data were square root transformed and submitted to Wisconsin double standardization to improve the quality of NMDS.

To test the hypothesis of differences in species composition among the five caves, Permutational Multivariate Analysis of Variance (PERMANOVA) based on Bray–Curtis dissimilarity index and Permutational Analysis of Multivariate Dispersion (PERMDISP) were used. This was implemented by the function ‘adonis’ in ‘vegan’ package of R software. Adonis is a robust technique than the usually used ANOSIM (analysis of similarities) and MRPP (multi response permutation procedure) as it implements multivariate ANOVA using distance matrices and determine F-tests based on sequential sum of squares from permutations of raw data to assess the critical alpha statistical significance (Estrada-Villegas *et al.*, 2010).

PERMDISP is analogous to Multivariate Analysis of Variance (MANOVA) and studies group homogeneities whilst PERMANOVA studies group means. This means a significant result in PERMDISP undermines observed differences in PERMANOVA. Tukey HSD (Honest Significant Differences) multiple comparison of means was used to identify caves that differed significantly at 95% confidence level. Analysis were performed using ‘vegan’ package in R (Joksanen *et al.*, 2013).

SIMPER analysis (Similarity Percentages-species contributions) was used to identify the dominant species responsible for the major differences between the caves (Clarke, 1993). The Bray–Curtis dissimilarity index was used in SIMPER analysis and was implemented in PAST v. 3.0 (Hammer *et al.*, 2001).

3.3.4 Community structure

Analysing diversity is complicated in community ecology and representing it by a single index is often inadequate to characterise the community (Gorelick, 2006). For instance, discordant results could be produced when using Shannon and Simpsons index while new information could be revealed when other indices are considered (Rocchini *et al.*, 2012). Community structure was therefore analysed at three levels; richness, evenness, and diversity. To calculate species richness for each cave and develop sample-based accumulation curves, the data was rarefied first using the ‘Species Diversity’ in EcoSim (Gotelli and Entsminger, 2013) with 1,000 iterations to sample from capture pool data to bring capture data to same abundance level.

During simulation in EcoSim, significance was accepted at 95% confidence interval. Evenness, that is the relative distribution of individuals among species was assessed using Hurlbert’s Probability of Interspecific Encounter (PIE) module in EcoSim (Agrawal and Gopal, 2013). To evaluate the completeness of bat inventory of the five caves, species accumulation of rarefied data from Ecosim was used (Appendix 2). To predict species richness, the first order Jackknife (Jack1) in EstimateS was used (Colwell, 2013). This estimator was selected because it takes into account the movement heterogeneity of mobile animals such as bats making it a good estimator for this study (Brose and D. Martinez, 2004).

The diversity of the five studied caves was compared using Rényi generalised entropy function (Southwood and Henderson, 2000). This analysis was carried out using DivOrd program package (Tothmeresz, 1993). The Rényi diversity, $HR(\alpha)$ is calculated as:

$$HR(\alpha) = \frac{1}{1 - \alpha} \left(\log \sum_{i=1}^s p_i^\alpha \right)$$

Where S denotes the total number of species, p_i is the relative frequency of the i th species, and α is the scale parameter ($\alpha \geq 0$, $\alpha \neq 0$) (Magura *et al.*, 2010). The scale parameter corresponds to four well-known diversity indices (Lövei, 2005; Tothmeresz, 1998), and very robust in scaling abundance data. When $\alpha = 0$ HR corresponds to the logarithm of the species numbers in community, as α increases towards 1 HR corresponds to Shannon diversity, as $\alpha = 2$ HR corresponds to Simpson diversity and lastly as α approaches infinity (∞), HR becomes closely related to Berger-Parker dominance index (Berger and Parker, 1970). This indicates a smaller value of α , HR is influenced by rare species within the community whilst increasing α indicates diversity is being influenced by common species.

It is important to note that, as α value approaches infinity, diversity is affected by only the most common species (Tothmeresz, 1998). When two diversity profiles do not intersect, interpretation is more comprehensible and the profile running on top is more diverse. However, intersecting profiles becomes ambiguous as one community is more diverse for rare species whilst the other is diverse for the common species. This notwithstanding, it is important in ecological studies and may represent vital ecological processes (Tothmeresz, 1998).

3.4 Results

3.4.1 General results

A total of 10,226 bats were captured in the study belonging to nine species (Fig. 3.2, Appendix A). There were variations in the number of individuals caught from the five caves (Table 3.1). KC1 recorded the highest number of individuals captured while the least number of bats were caught from KC2. The relative frequency (RF) of rare species (rare defined as having relative frequency < 0.01) was higher in KC1 and BC1 while the relative frequency of common species (relative frequency > 0.05) was higher in FOC and BC2 caves (Table 3.1). Three species; *Micropteropus pusillus*, *Nanonycteris veldkampi* and *Pipistrellus nanulus* recorded in FOC were considered opportunistic and not included in analysis because of their roosting habits (does not roost in caves) and rarity in capture data (RF = 0.00006).

Table 3.1: Summary of bat capture from the five caves investigated.

Village Cave Identity	Total number of				Relative frequency of	
	Individuals	Species	Non-cave roosting Individuals	Non-cave roosting Species	Rare species ^a	Common species ^b
Buoyem Cave 1 (BC1)	1,619	6	-	-	0.5	0.33
Buoyem Cave 2 (BC2)	2,375	6	-	-	0.33	0.5
Forikrom Cave (FOC)	1,715	10	6	3	0.29 ^c	0.57
Kwamang Cave 1 (KC1)	2,629	6	-	-	0.5	0.17
Kwamang Cave 2 (KC2)	1,888	7	-	-	0.43	0.29

Species were considered rare if relative frequency < 0.01^a. Species were considered common if relative frequency > 0.05^b. ^cEstimation of relative frequency excluded non-cave roosting individuals.

The nine routinely recorded species varied in individual numbers inside the caves (Fig. 3.2, Appendix 1). *Hipposideros cf. ruber* (Appendix A, Plate A.1) contributed 81% of total individuals captured from all caves and was the most abundant. *Hipposideros cf. ruber* and *Hipposideros abae* (Appendix A, Plate A.2) were caught in almost equal proportions within all the caves whilst *Rousettus aegyptiacus* (Appendix A, Plate A.8), *Rhinolophus landeri* (Appendix A, Plate A.7), *Hipposideros jonesi* (Appendix A, Plate A.3), *Hipposideros gigas* (Appendix A, Plate A.4) and *Coleura afra* (Appendix A, Plate A.6) were restricted within some caves (Fig. 3.2). The West African endemic bat *Hipposideros jonesi* was recorded only in Kwamang and was present mainly in KC1. Thirteen individuals of this species were from KC2 while the number doubled in KC1. Individual abundance inside the caves was highest for *Hipposideros cf. ruber* followed by *Hipposideros abae* (Fig. 3.2).

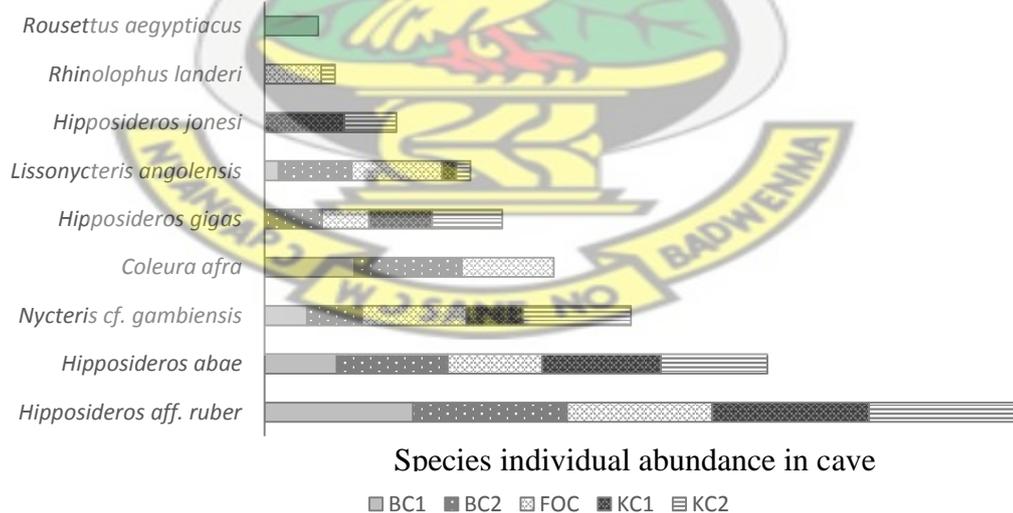


Figure 3.2: Proportion of bat species captured within each cave. Abundance data was log (x+1) transformed. Refer to Appendix 1 for capture results.

3.4.2 Community composition of bat assemblages

A NMDS yielded a 2-dimensional space ordination (for optimal solution). The initial stress (23.9) in the matrix was reduced to 15.2 which is within the recommended range of 10-20 accepted in community ecology (Naidoo, 2004). See Appendix three for stress plot. There were less distortions with a linear fit ($R^2 = 0.84$). NMDS revealed a grouping of caves (Fig. 3.3). The two caves in Kwamang (KC1 and KC2) were closer in ordination space than the two Buoyem caves. Forikrom (FOC) cave was closer to BC2 than any other cave (Fig. 3.3).

The species composition differed significantly among the five caves (PERMANOVA, $DF = 4$, $F = 22.09$, $P = 0.005$; PERMDISP, $DF = 4$, $F = 1.99$, $P = 0.12$). Tukey HSD multiple comparisons of means indicated that only BC1 and KC1 differed significantly from each other in species composition (Appendix 4). SIMPER analysis indicated that *Coleura afra* contributed highest (28%) to overall community dissimilarity between the caves, followed by *Hipposideros jonesi* (20%). These two species together with *Hipposideros gigas* formed the main discriminating species for BC1 and KC1, contributing over 50% to community dissimilarity between these caves (Table 3.2).

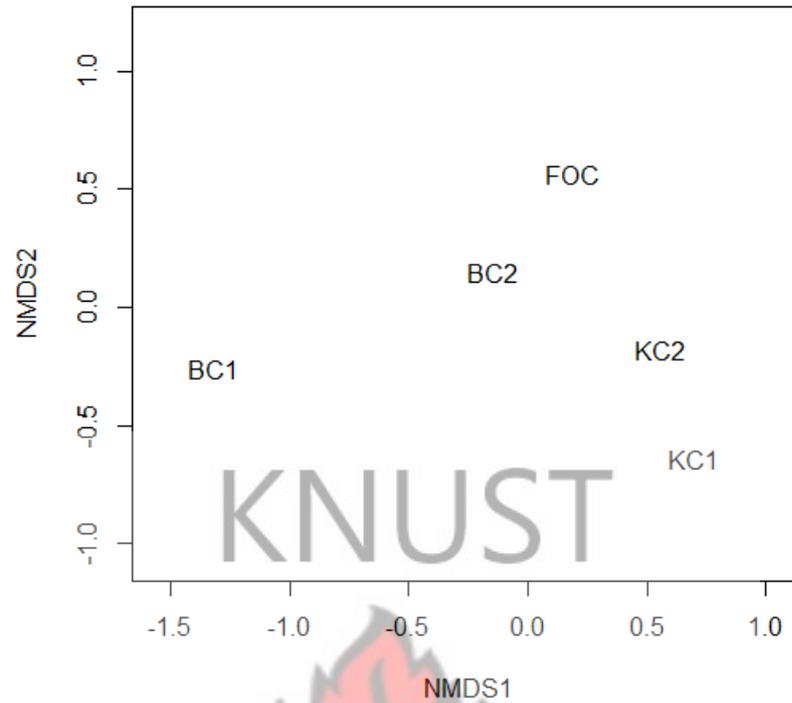


Figure 3.3: Non-metric multidimensional scaling (N-MDS). Ordination based on Bray-Curtis index of dissimilarity for five caves. Ordination axis 1 is NMDS1 and axis-2 is NMDS2. Refer to Table 3.1 for list of abbreviations and Appendix 3 for stress plot. Community composition of the five caves is different as indicated by PERMANOVA.

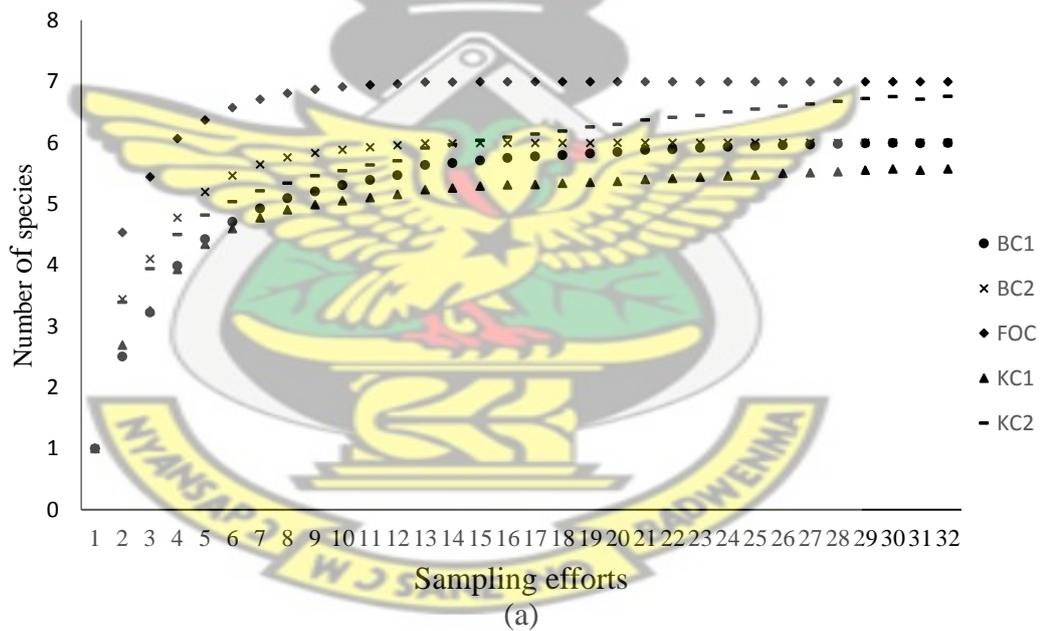
Table 3.2: Results of SIMPER analysis using Bray-Curtis dissimilarity index for species contribution to community dissimilarity.

Compared caves	BCI VS BC2		BC1 VS FOC		BCI VS KC1*		BCI VS KC2		BC2 VS FOC		BC2 VS KC1		BC2 VS KC2		FOC VS KC1		FOC VS KC2		KC1 VS KC2	
	x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y
Species & % contribution	<i>g</i>	22.5	<i>l</i>	23	<i>c</i>	24.8	<i>c</i>	23	<i>n</i>	30	<i>c</i>	41	<i>c</i>	34	<i>c</i>	22	<i>c</i>	30	<i>n</i>	42.4
	<i>l</i>	22.5	<i>n</i>	21	<i>j</i>	21.6	<i>n</i>	19	<i>d</i>	29	<i>j</i>	29	<i>l</i>	19	<i>l</i>	19	<i>l</i>	27	<i>j</i>	21.8
	<i>r</i>	20.8	<i>d</i>	17	<i>g</i>	16.5	<i>g</i>	17	<i>l</i>	11	<i>l</i>	23	<i>n</i>	19	<i>j</i>	19	<i>j</i>	16	<i>d</i>	12.2
	<i>a</i>	18.2	<i>r</i>	16	<i>a</i>	14.8	<i>r</i>	13	<i>a</i>	10	<i>a</i>	4	<i>j</i>	15	<i>n</i>	13	<i>d</i>	12	<i>a</i>	10.8
	<i>c</i>	8.4	<i>g</i>	13	<i>r</i>	13.8	<i>j</i>	12	<i>c</i>	9.5	<i>g</i>	2	<i>d</i>	5.2	<i>d</i>	13	<i>g</i>	8	<i>h</i>	7.2
	<i>n</i>	5.3	<i>a</i>	8	<i>n</i>	3.9	<i>a</i>	10	<i>g</i>	6	<i>h</i>	1	<i>g</i>	4.1	<i>a</i>	6.9	<i>a</i>	4.5	<i>g</i>	5.59
	<i>h</i>	2.44	<i>h</i>	1	<i>h</i>	2.63	<i>d</i>	4	<i>h</i>	5.4	<i>n</i>	1	<i>h</i>	1.9	<i>g</i>	4	<i>n</i>	1.4	<i>r</i>	0
	<i>d</i>	0	<i>c</i>	1	<i>l</i>	1.91	<i>l</i>	2	<i>r</i>	0	<i>r</i>	0	<i>a</i>	1.6	<i>h</i>	3.3	<i>h</i>	1.3	<i>l</i>	0
	<i>j</i>	0	<i>j</i>	0	<i>d</i>	0	<i>h</i>	0	<i>j</i>	0	<i>d</i>	0	<i>r</i>	0	<i>r</i>	0	<i>r</i>	0	<i>c</i>	0

Data was transformed using log (x+1) to base 2 before Bray-Curtis analysis. Column 'x' contains the list of species and column 'y' the species percent contribution to community dissimilarity of the compared caves. The species list in column 'x' is abbreviated: *g_Hipposideros gigas*, *l_Lissonycteris angolensis*, *r_Rousettus aegyptiacus*, *a_Hipposideros abae*, *c_Coleura afra*, *n_Nycteris cf gambiensis*, *h_Hipposideros cf. ruber*, *d_Rhinolophus landeri*, *j_Hipposideros jonesi*. *P < 0.05 (Tukey HSD multiple comparison), p values are not significant for all other comparison.

3.4.3 Bat assemblage structure and diversity profile

The overall predicted species richness for all caves was $S_{jack1} = 9 \pm 0.02$. This value is close to the observed species richness and indicates the near completeness of the bat inventory. Predicted species richness was highest at FOC, KC2, BC2, BC1 and KC1 in order of decreasing species richness. Results of rarefaction comparing the five caves at the same abundance level for species richness is presented in Appendix two. Sample-based accumulation curve from rarefaction did not reach asymptote at KC1 and KC2, but was reached in BC1, BC2 and FOC (Fig 3.4a). Species evenness varied among the caves. Evenness was highest in FOC while BC1 was least even (Fig. 3.4b).



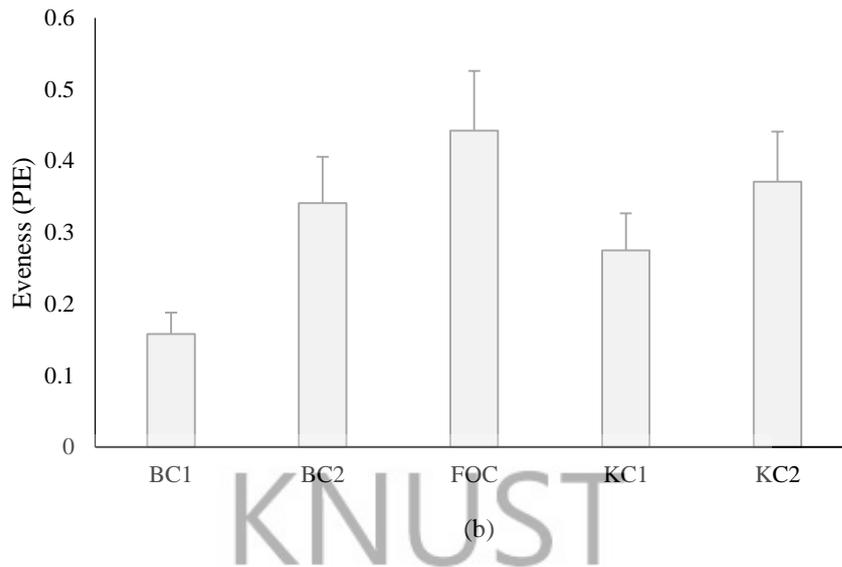
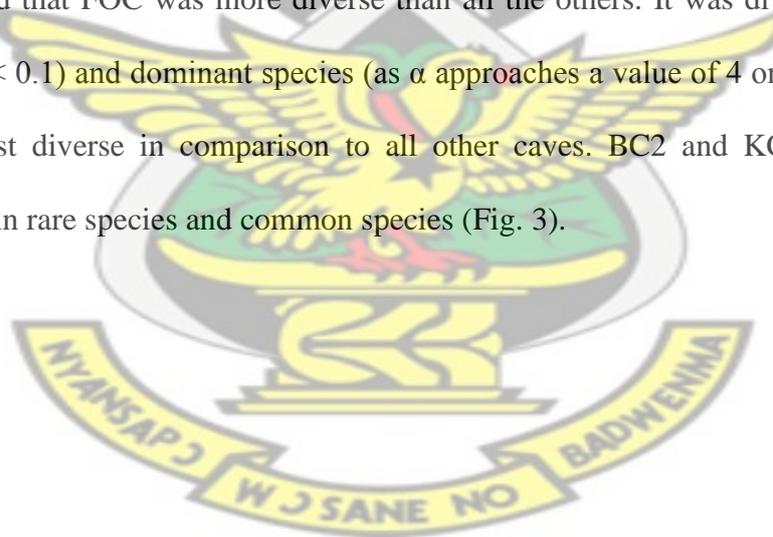


Figure 3.4: (a) Rarefied species richness. (b) Evenness in caves, which is the relative distribution of individuals among species.

The five caves were unequivocally ordered (Fig 3.5). Rényi diversity ordering indicated that FOC was more diverse than all the others. It was diverse in both the rare ($\alpha < 0.1$) and dominant species (as α approaches a value of 4 on the scale). BC1 was least diverse in comparison to all other caves. BC2 and KC2 were equally diverse in rare species and common species (Fig. 3).



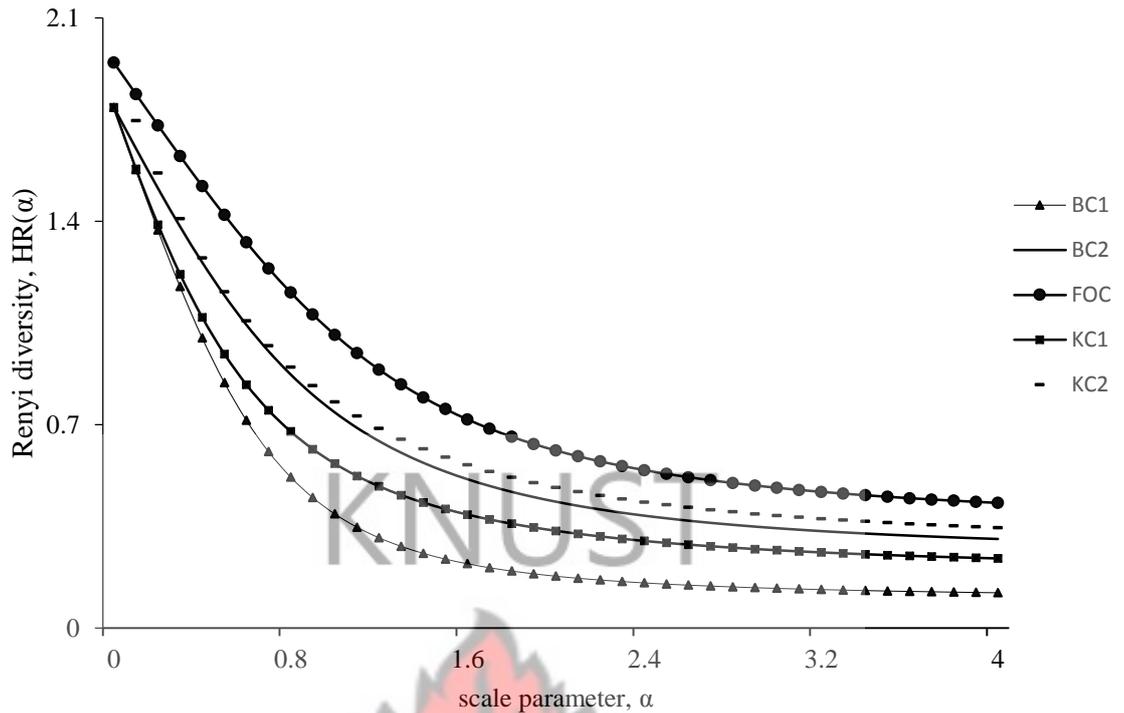


Figure 3.5: The Rényi diversity profiles of five caves.

3.5 Discussion

3.5.1 Community composition

A PERMANOVA analysis confirmed the prediction that the species composition of the five caves were not the same. Caves in the same locality were closer in ordination space with the exception of BC1 (Fig. 3.3). This suggests Kwamang caves are more similar in species composition than the other caves in the Brong Ahafo region. Geographically distant localities are known to exhibit differences in bat species composition (Soriano, 2000). In selecting roost such as caves, bats aim to minimize energy expenditure by selecting roost with suitable microclimatic conditions. They select caves that provide suitable microclimate for their water balance and thermoregulatory needs in humidity and temperature (Churchill *et al.*,

1997; McNab, 1982). The two caves in Kwamang are approximately four kilometres apart and also share similarities in cave conditions such as running water and insulation against direct sunlight that maintains a constant microclimate. Situated in the same locality and sharing similarities in conditions may suggest their ability to host similar species of bats (Anonymous, 2002; Churchill *et al.*, 1997).

FOC and BC2 were closer to each other in ordination space while it was distant from the Kwamang caves. Cave conditions which are possibly altered by daily sunlight into parts of these two caves in the Brong Ahafo region may explain why they shared similarities in species composition and differed from Kwamang caves. BC1 is located in the same area as BC2 and FOC (in relation to Kwamang caves), and also share similarities in receiving direct sunlight into parts of its main cavern. Thus, it was expected to be closer in ordination space to BC2 and FOC but was rather distant from them. This is attributed to the ordination analysis as NMDS is overly sensitive to the presence of rare species (Naidoo, 2004). *Rousettus aegyptiacus* is a pteropodid bat that select dimly lit roost (Happold and Happold, 2013) such as BC1, BC2 and FOC. This species was however captured only in BC1 with relatively smaller individual numbers (Appendix 1) and this might have caused BC1 to be distant from FOC and BC2.

Also, BC1 and KC1 differed significantly (Appendix 4) from each other. Being at the extreme ends on the NMDS1 axis (Fig 3.3), they host very different species of bats. The SIMPER analysis indicated that *Coleura afra* and *Hipposideros jonesi* contributed highest percentages to community dissimilarity. *Hipposideros jonesi* is a West African endemic species closely linked to forested areas but mainly found in

forested areas in Ghana (Fahr, 2013; Fahr and Ebigbo, 2003; Hayman, 1964), while *Coleura afra* in West Africa has isolated populations within the Guinea-Savannah (Happold and Happold, 2013). In Ghana, *Coleura afra* is found in the rainforest-savannah mosaic found in the Brong Ahafo region where FOC, BCI and BC2 are located (Happold and Happold, 2013). These two species therefore do not overlap geographically and exploit different ecological niches causing the observed dissimilarity among these two caves (Happold and Happold, 2013).

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3.5.2 Community structure

Species richness was relatively uniform across all caves. The overall predicted species richness in the studied caves was nine which is close to the observed richness. Convergent evolution in bat morphology predicts similar ecological patterns (Weber *et al.*, 2009). Up to seven species were recorded to use a single root cave consistent with studies in Namibia that investigated ten caves and found seven morphologically similar species to share a single root (Churchill *et al.*, 1997). To assess the species richness of bat communities, mist netting is appropriate in capturing cavity roosting bats and have been found to perform best against other methods (Flaquer *et al.*, 2007). Sample-based rarefaction curves from mist netting data indicated species inventory completeness was asymptotic for the three caves in the Brong Ahafo region; FOC, BC1 and BC2 (Fig. 3.3a). In KC1 and KC2 however, the curves did not flatten indicating the inventory was incomplete at these two caves. This indicates some species were missed in Kwamang caves. Considering the intensity and duration of netting for all caves, it was however not expected. This could indicate important ecological process in Kwamang.

This ecological scenario is therefore envisioned. All the five caves are situated in agricultural landscapes. Alternate roosting such as tree roost have been identified for some bats in Kwamang (Chapter six). Alternate roosting in FOC, BC1 and BC2 could be limiting because the surrounding of these caves are mostly grasses and farmlands with fewer tree numbers in comparison to Kwamang. This may suggest that bats in Forikrom and Buoyem depend very much on the caves whereas in Kwamang, some bats may consider alternate roosting and visit the caves at certain times such as breeding seasons. This could indicate species flexible in their choice of roost that occasionally visit caves may have been missed in Kwamang and long term sampling is needed to sample such species.

Community evenness was highest in FOC suggesting species in this cave were represented by similar abundance of individuals compared to the other caves (Agrawal and Gopal, 2013; Chew and Oheim, 2013). Individual abundance inside all caves showed preponderance hegemony of *Hipposideros cf. ruber* with nearly equal proportions (Fig. 3.2). The relative dominance of a species is expected to reduce with increasing species richness enhancing community evenness (Dornelas *et al.*, 2011; Magurran, 2004). Therefore the observed greater species diversity (Fig. 3.5) at FOC reflects the high species richness and the evenly distribution of individuals among species in comparison to the other caves.

3.5.3 Conservation implications

The investigated caves were dominated by *Hipposideros cf. ruber*. Majority of ecosystem services are usually provided by the abundances of individual species (Dornelas *et al.*, 2011). The caves are important in hosting large assemblages of

species which are needed in ecosystem services. Results from this work supports the preservation of different caves for the conservation of a wider group of species as investigated caves varied in species composition. This will ensure the survival of a variety of species which could potentially be restricted within certain localities such as *Hipposideros jonesi* and *Coleura afra*.

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Chapter Four

Flight activity of *Hipposideros aff. ruber* at two caves in Ghana, West Africa

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4 Flight activity of *Hipposideros aff. ruber* at two caves in Ghana, West Africa

4.1 Abstract

Flight activity of Noack's round-leaf bat, *Hipposideros aff. ruber* was monitored at the entrances of two caves in Kwamang, Ashanti Region, Ghana. To test the hypothesis that flight activity is non-random but concentrated at certain periods, data from 2,712 bats were analysed. Four activity periods were defined from cluster analysis. The hypothesis of concentrated flight activity at night was confirmed in one cave and not the other. Flight activity was highest during early period of the night before 22:00 hours. The caves were used year round and variation in monthly flight activity was not significant. The results also suggest *Hipposideros aff. ruber* might reduce its flight activity when nightly temperature outside the cave drops drastically.

4.2 Introduction

Flight among vertebrates is a demanding metabolic activity (Lancaster *et al.*, 1997). In bats, the energy required could reach fifteen times higher than when they are resting (Voigt and Lewanzik, 2011; Voigt, 2003; Winter and Helversen, 1998). This is particularly challenging for female bats during their reproductive periods because of elevated energy demands. This could reduce flight activity at entrances of female dominated caves or maternity roost. Different bats may show different patterns of flight activity at roost entrances as a result of eco-morphological variations (Jones and Rydell, 1994; Norberg and Rayner, 1987) that influences their foraging behaviour, especially the time of foraging (Rydell *et al.*, 1996). Insectivorous bats increase their flight activity at peak activity periods of their major prey (Rydell *et al.*, 1996) which could also affect the nightly distribution of flight activity. For instance,

aerial hawkers increase their flight activity at early twilight to coincide with peak activity of aerial insects while gleaners forage latter at night (Holland and Fleming, 2002). Predator avoidance is also key in shaping activity of animals, thus influencing flight activity (Brown, 1988).

Flight activity of bats at cave entrances has been monitored in the temperate regions where bats circumvent winter through hibernation (Berkova and Zukal, 2010; Berkova and Zukal, 2006). In tropical environments, non-migratory species may use roost year round and maintain sustained flight activity at roost. Migratory species on the other hand may abandon roost and return to use them latter. Caves are important roosting sites for most bat species (Berkova and Zukal, 2010; Berkova and Zukal, 2006; Churchill *et al.*, 1997; Stewart, 1981). They serve different purposes ranging from resting places, hideouts from predators, transitional roost during migration or permanent roost year round (Berkova and Zukal, 2010; Churchill *et al.*, 1997). They also play important role in the evolution of complex social organisations within populations (Stewart, 1981).

In Ghana, many colonies of bats use caves for roosting (Annan *et al.*, 2013; Pfefferle *et al.*, 2009). The monthly and temporal dynamics of flight activity at the entrances of these caves are not known yet. The objective of this study was to determine the monthly flight activity of Noack's round-leaf bat *Hipposideros aff. ruber* which was the most dominant species at the Kwamang caves. The second objective of the study was to determine the nightly distribution of flight activity at the entrance of the caves. The third objective was to determine the effects temperature have on the flight activity of *Hipposideros aff. ruber*. It was hypothesised that the flight activity of

Hipposideros aff. ruber at roost entrances was concentrated at certain periods of the night.

4.3 Materials and Methods

4.3.1 Study area

This study was undertaken at Kwamang in the Ashanti Region of Ghana beginning in August 2010 to July 2012. The site is characterised by hilly and mountainous formations which constitute natural cavities serving as bat roost. Two bat caves were selected in the landscape of this town. Cave one (UTM: N 687748, W 774491) was separated from cave two (UTM: N 690772, W 772255) by a distance of 3.8 km. Refer to chapter one for description of the caves.

4.3.2 Bat capture and sampling

Monitoring bat flight activity at roost entrances is challenging. The use of automated devices is beneficial in roost with single species dominance as it lacks the ability to distinguish between species (Berkova and Zukal, 2006). Mist netting also pose a challenge as bats avoid nets and physiological stress from capturing and might result in bats leaving the locality entirely. The latter is however, beneficial and provides a satisfactory alternative in situations where multi-taxa group details and sex of the animal is required (Kunz and Brock, 1975). Mist nets were therefore employed. Bats were captured at the entrance of the roost cave with mist nets. At cave one (KC1), two mist nets of length six meters were spread in front of the two entrances that were separated by a distance of ten meters. At cave two (KC2) however, one twelve-meter standard mist net was spread to block the entire entrance of the cave. Flight activity

at the entrance of each cave was monitored for two nights and repeated every six weeks for two years. This adopted sampling technique was to ensure bats were not disturbed more frequently from capture protocols within a relatively short time. In addition, temperature data loggers (Thermochron iButton, Appendix B, Plate B.1) were installed outside and inside of the cave to monitor temperature changes in and around the roost cave. During mist netting, nets were monitored continuously for the entire duration the nets were in place until closure in the morning. Captured bats were carefully removed and placed in airy bags. Once a bat was caught, the time it entered the net and the direction to the cave (entering or exiting the cave) were both written on the bag. Bats that entered the cave were considered arrivals whereas those exiting were classified as departures. Nets were open between 19:00 and 06:00 hours each night of capture.

4.3.3 Data analysis

Flight activity at the entrance of the roost cave was measured using the sum of in-flights (arrivals) and out-flights (departures) per night (Berkova and Zukal, 2006). To assess the nightly distribution of flight activity at the entrance of the cave, the time the bats were captured were grouped using cluster analysis (Fig. 4.2). Based on the cluster analysis, the greatest possible distinctions were grouped as flight activity periods. During clustering, 02:00 hour from KC1 and 20:00, 23:00 and 04:00 hours from KC2 were included in different activity periods than expected. To generate a continuum of activity during analysis, 02:00 hour at KC1 was placed in period C and activity period B was split into two distinct periods as B1 and B2 (Fig. 4.2a). At KC2, four distinct activity periods were identified; from period A to D. Further at

KC2, 20:00 hour was placed in period A, 23:00 hour in period B and 04:00 hour in period D (Fig. 4.2b).

Kruskal-Wallis test (*KW*) was performed to determine the differences in flight activity periods and the months in which bats were captured. Mann-Whitney test (*MW*) was used to find differences in flight activity among sex. Wilcoxon signed-rank test (*WSR*) was used to investigate the arrivals and departures at both caves. During graphical exploration of arrivals and departures (Fig. 4.5 and Fig. 4.6), values representing departures were considered as negatives. The influence of temperature on flight activity was also assessed with Pearson product-moment correlation. This was however assessed at KC1 and not KC2 as temperature data was inconsistently collected at this cave due to failure and misplacement of loggers. Nightly temperature range and its effects on bat flight activity was also assessed. Nightly temperature range ($T_{\text{dif}_{\text{max-min}}}$) was calculated as a function of the difference between the maximum and minimum temperature of the night (Berkova and Zukal, 2010). All statistical tests were performed in Minitab and significance accepted at a probability value of $P < 0.05$.

4.4 Results

Bats were observed to use the caves year round with variations in monthly flight activity (Fig. 4.1). At KC1, male (1,254 individuals) to female (352 individuals) ratio was 4:1. Male (553 individuals) to female (549) ratio at KC2 was 1:1. There was no significant difference between monthly flight activity at both caves (*KW*; KC1, $H = 3.5$, $DF = 5$, $P = 0.62$; KC2 $H = 6.74$, $DF = 5$, $P = 0.24$). There were variations in the monthly flight activity of both males and females and at the two caves (Fig. 4.1).

Monthly flight activity of males at KC1 was significantly higher than females (MW , $W = 543$, $P = 0.0001$), while the observed difference at KC2 was not significant (MW , $W = 261.5$, $P = 0.94$).

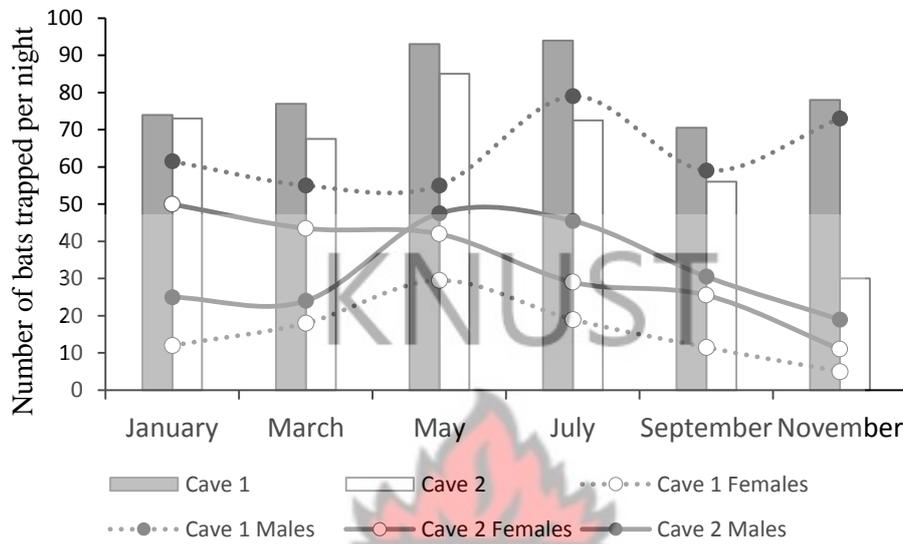
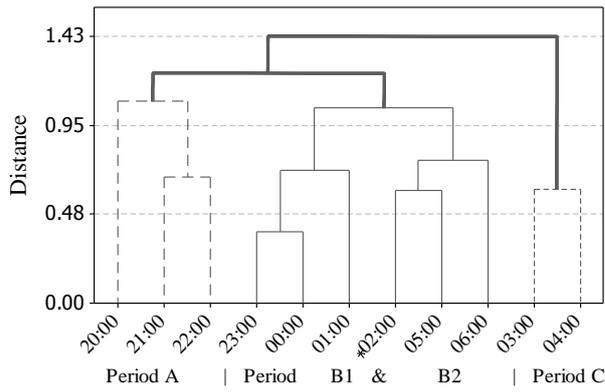


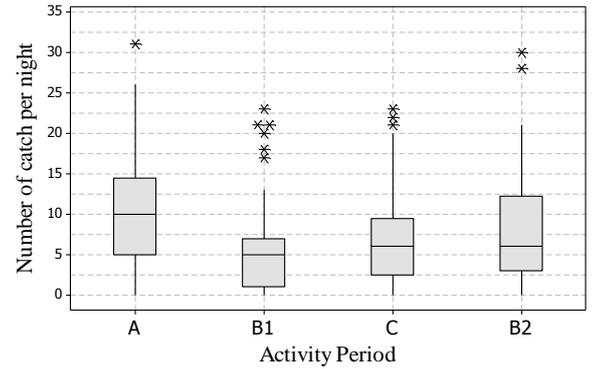
Figure 4.1: Monthly changes in flight activity of bats at the two caves. Bars and lines indicate medians of activity.

4.4.1 Nightly distribution of flight activity

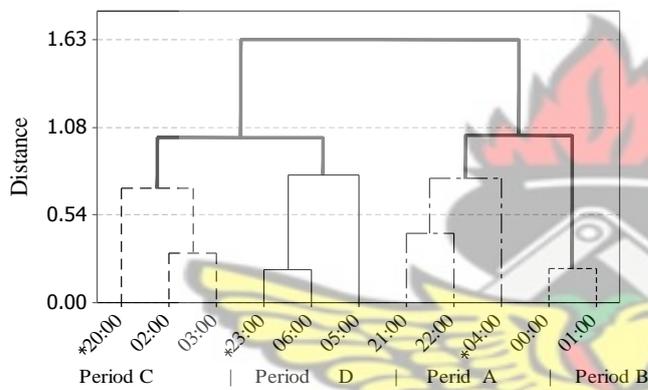
Four activity periods were identified from cluster analysis (Fig. 4.3). The distribution of the nightly flight activity at KC1 was concentrated at certain periods of the night (KW : $H = 14.37$, $DF = 3$, $P = 0.002$, Fig. 4.3a). At KC2, flight activity was not particularly concentrated as observed difference between activity periods were not significant (KW , $H = 6.12$, $DF = 3$, $P = 0.106$, Fig. 4.3b).



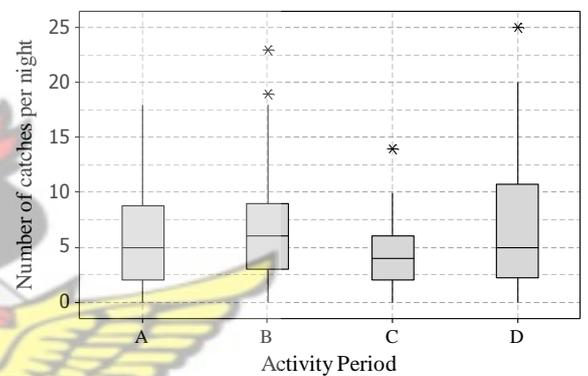
2a) Cluster analysis, cave one



3a) Box and whisker plot for cave one



2b) Cluster analysis, Cave two



3b) Box and whisker plot for cave two

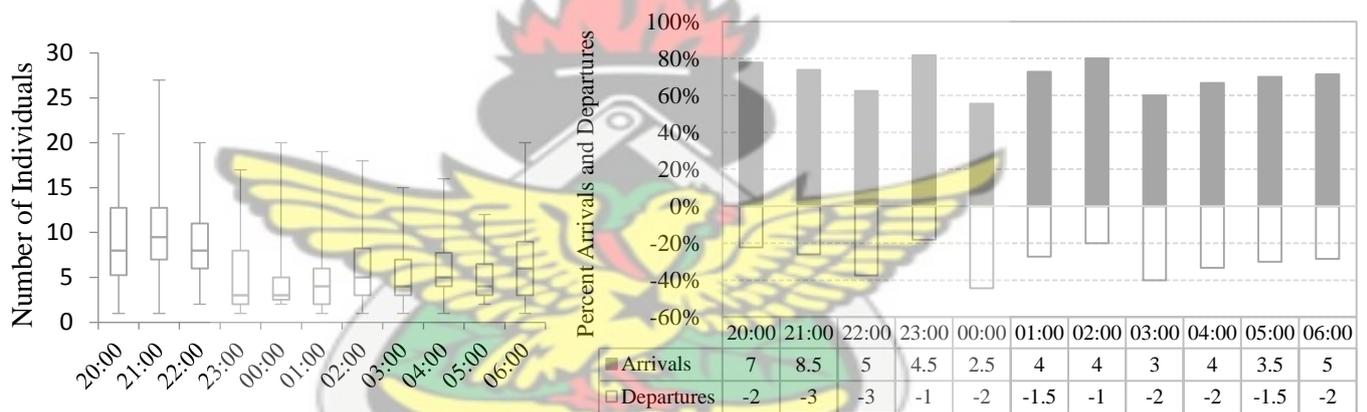
Figure 4.2: Results of cluster analysis (Complete linkage, Euclidean distances). Hours marked with asterisk were shifted to different periods during analysis (Refer to methods).

Figure 4.3: Box and whisker plots for temporal distribution of flight activity occurring in each period at night at the two caves. Asterisks indicate outliers.

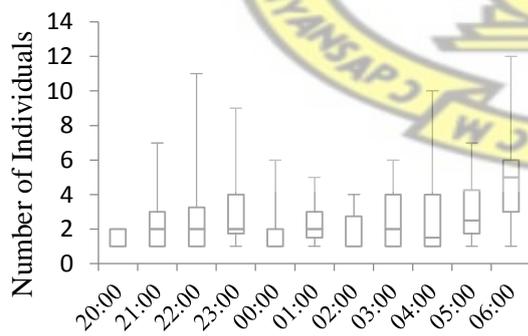
Highest flight activity at KC1 occurred in Period A from fly out until 22:00 hours then it decreased at period B1 (Fig. 4.3a). The decrease in flight activity from period A to B1 was significant (Table 4.1). Period A is also significantly different from B2 (Table 4.1). The nightly flight activity was significantly higher in males than females at KC1 ($MW; W = 187, P = 0.0001$; Fig. 4.4a and b). At KC2, flight activity was not significant among both sexes ($MW; W = 125.5, P = 0.9738$; Fig. 4.4c and d).

Table 4.1: Differences in flight activity periods at KC1. Analysis using Man-Whitney test. Significance level: ***P < 0.0001, *P < 0.01, NS_P > 0.05

Compared	Sample size	w	P
Activity Periods	(n)		
A and B1	57 and 76	4636.5	***
A and B2	57 and 38	2999.5	*
A and C	57 and 38	2945.5	NS
B1 and B2	76 and 38	4092.5	NS
B1 and C	76 and 38	4120.0	NS
B2 and C	38 and 38	1455.0	NS

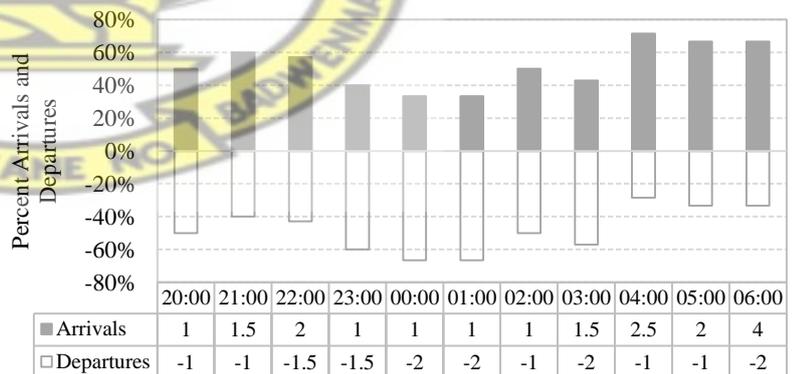


4a). Cave one male bats

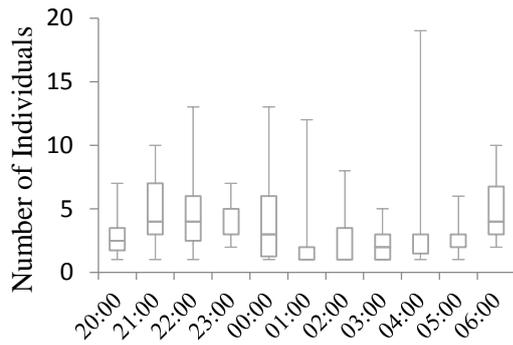


4b) Cave one female bats

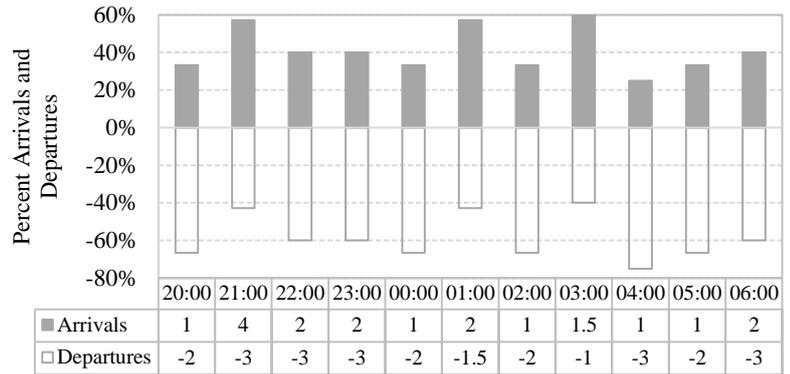
5a).Cave one male bats



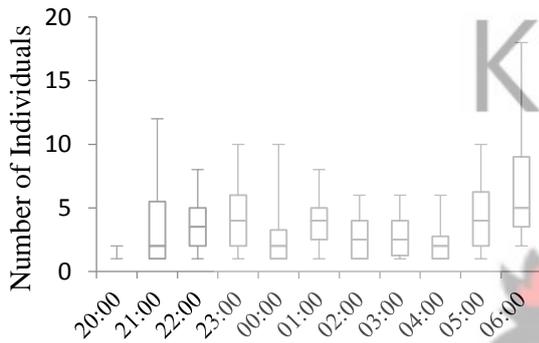
5b). Cave one female bats



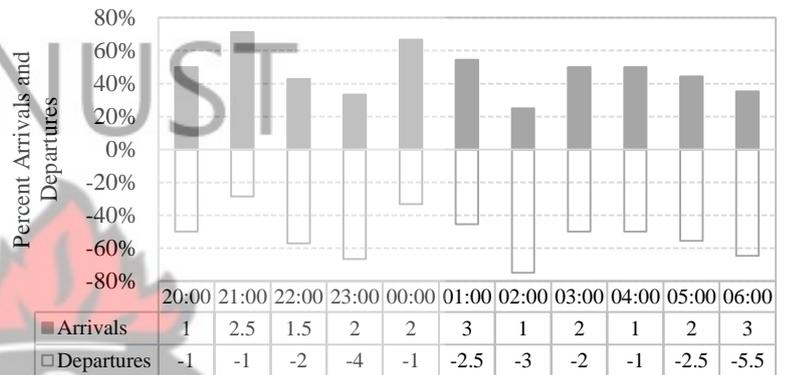
4c) Cave two male bats



5c). Cave two male bats



4d) Cave two female bats



5d). Cave two female bats

Figure 4.4: Box and whisker plots of nightly flight activity of males and females at both caves

Figure 4.5: Arrivals and departures at cave entrances. Median values of each in-flights and out-flights are presented in tables.

4.4.2 Arrivals and departures at the entrance of the caves

The nightly ratio of arrivals to departures were different at both caves (Fig. 4.6a and b). The arrivals at KC1 were significantly higher than departures ($WSR: N = 11, W = 66.0, P = 0.004$). At KC2, the ratio of arrivals to departures were not significantly different ($WSR: N = 11, W = 19.5, P = 0.248$). Peak arrivals at both KC1 and KC2 was 21:00 hours after evening fly-out and 06:00 hours when they return to roost while departures peak at 22:00 hours and 06:00 hours. In contrast to KC1, flight activity at KC2 (both arrivals and departures) remained relatively low until 21:00 hours when flight activity becomes active. Also, flight activity in the morning (06:00

hours) at KC1 is contributed largely by arrivals while the reverse is true for KC2 (Fig. 4.6a and b).

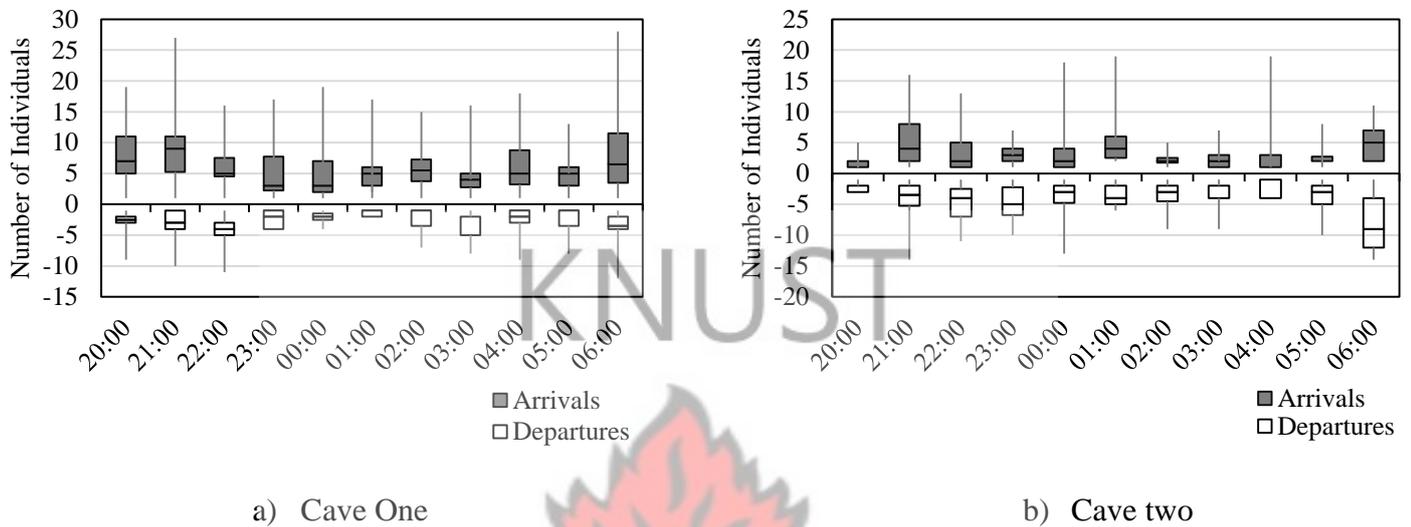


Figure 4.6: Box and whisker plots for arrivals and departures at both cave entrances.

The details of the ratio of arrivals to departures at each cave is presented in Fig. 4.5. KC1 was dominated by the arrival of male bats in comparison to departing males (Fig. 4.5a). The reverse trend was true for KC2, more departing males than arriving males (Fig. 4.5c). The male arrivals at the two caves were highest around 21:00 hours. There was a significant difference between the median number of arrival males to departing males at KC1 ($WSR: N = 11, W = 66.0, P = 0.004$). Similarly, there was a significant difference between the medians of male arrivals to departures at KC2 ($WSR: N = 11, W = 9.5, P = 0.041$). On the contrary, there was no significant difference between arriving and departing females at either cave (KC1, $WSR: N = 11, W = 28.0, P = 0.554$; KC2, $N = 11, W = 11.0, P = 0.363$; Fig. 4.5b and d). Female arrivals were highest in the morning at KC1 (06:00 hours, Fig. 4.5b) whereas at KC2 in the morning, departures were at its peak (Fig. 4.5d).

4.4.3 Effects of temperature on bat flight activity

The effects of temperature on flight activity were investigated at KC1. The mean temperature recorded outside KC1 was 22°C. The minimum and maximum temperatures recorded were 15°C (recorded in January) and 28°C (recorded in March) respectively. The recorded mean temperature within KC1 was 26°C. There was no correlation between bat flight activity and the mean outside ambient temperature (Pearson product-moment correlation: $r = 0.008$, $P = 0.924$). Flight activity was observed to decline with increasing nightly temperature range (Fig. 4.7). Statistical exploration was not carried out as the results would be meaningless considering the wide variation in sample sizes (Fig. 4.7).

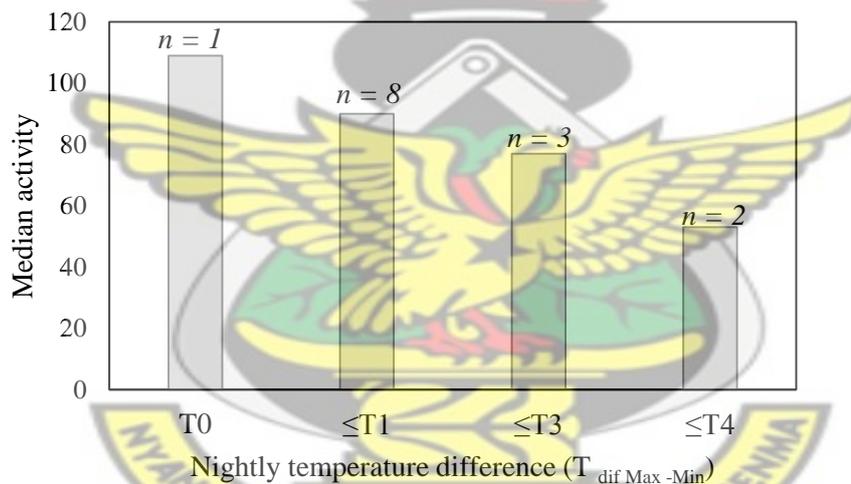


Figure 4.7: Effects of increasing nightly temperature range ($T_{\text{diff Max-Min}}$) on bat flight activity.

4.5 Discussion

4.5.1 Monthly variations in flight activity

Monthly variation in flight activity was observed at the entrance of the two caves but the hypothesis is rejected because there was no significant difference. This is related

to the year-round use of the caves and perhaps stable population numbers of *Hipposideros aff. ruber*. Bat flight activity is influenced by prey abundance (Ciechanowski *et al.*, 2007; Erkert, 1982). Monthly variation in flight activity at cave entrances has been documented mostly for bats in the temperate regions (Berkova and Zukal, 2010; Berkova and Zukal, 2006). In tropical environment where bats are active year round, flight activity is expected to be high in seasons of abundant prey. Insect abundance in Africa peaks a month after peak rainfall (Cumming and Bernard, 1997). Flight activity at both caves was highest in May and July. Peak rainfall in the Ashanti region occurs in June (Opoku-Ankomah and Cordery, 1994). This suggest *Hipposideros aff. ruber* increases their flight activity during these months to perhaps coincide with peak insect abundance during these months. Peak flight activity in May and July may also be contributed by volant young who are active in flight by this time.

Flight activity among males and females was significant at KC1 and not KC2. This is due to the varying degree of sex ratio among the caves. KC1 was male dominated while KC2 had even sex ratio. Variant sex ratios in colonies of *Hipposideros aff. ruber* is not known but has been identified in some insectivorous bats in Africa. In Madagascar, sex ratio is reported to vary among colonies of *Otomops madagascariensis* (Andriafidison *et al.*, 2007). The sex ratio in population of *Hipposideros caffer*, a morphologically similar bat in a Nigerian cave was observed to be even at certain months of the year (Menzies, 1973). The significantly higher flight activity at KC1 indicates the males are more active in flight than the females, consistent with radio-tracking studies (Chapter six). The results indicate that caves

with more male appears to have significantly higher activity at the entrance of the roost.

4.5.2 Temporal distribution of flight activity

The results indicate clearly that the distribution of the nightly flight activity varies with caves. The hypothesis that flight activity is concentrated at certain periods of the night was confirmed at KC1 and not KC2. Major flight activity at KC1 was concentrated in period A, after evening twilight and before 22:00 hours. This is probably linked to availability of prey items at early stages of the night (Jones and Rydell, 1994). The feeding habit of *Hipposideros* aff. *ruber* from these two caves indicate that they eat relatively high proportions of lepidopterans (Badu *et al.*, Unpublished).

In the Neotropical and Afrotropical forests, the flight activity of most lepidopterans (moths) that forage at night is predicted to peak around 18:30 and 21:45 while others peak late night (Brehm *et al.*, 2005; Axmacher *et al.*, 2004). This suggest *Hipposideros* aff. *ruber* increase their flight activity at this time to coincide with increasing activity of moths. This was also expected for KC2 but flight activity was uniformly distributed and not particularly concentrated like KC1. Differences in activity among different colonies of *Hipposideros ruber* have been observed (Russo *et al.*, 2011). In the island of São Tomé (Gulf of Guinea), *Hipposideros ruber* is both diurnal and nocturnal but males are more diurnally inclined while the opposite was true at night (Russo *et al.*, 2011). This suggests different colonies of *Hipposideros* aff. *ruber* might have the tendency to exhibit different ecological patterns in flight. At KC1, flight activity during period A were contributed mostly by arriving male

bats (Fig. 4.5a and b). Aside cave roost, *Hipposideros aff. ruber* also uses other roost such as trees. This could also suggest most of the males at KC1 use other roost aside the cave and make repeated visit to the cave after each foraging bout causing an increase in flight activity at the entrance during this period.

In the morning at KC1 while the bats are returning to roost, the bats at KC2 seem to depart the cave at this time (Fig. 4.6a and b). This perhaps suggest there could be interaction between the two caves. However, this result is preliminary and inconclusive as the caves were not monitored at the same time and this could be attributed to individuals using day roosts in the landscape such as trees.

4.5.3 Influence of temperature on flight activity

There was relatively stable temperature conditions year round inside KC1 which is consistent with reported caves used by morphologically similar bat *Hipposideros caffer* in Namibia (Churchill *et al.*, 1997). There was no correlation between the ambient temperature outside the cave and bat flight activity because of the lack of extreme monthly temperature ranges during observational period. Although there was no correlation, wide variations in nightly temperature range (Fig. 4.7) could reduce their flight activity. Results from captive leaf-nosed bats suggest their extreme sensitivity to temperature (Baudinette *et al.*, 2000). Therefore, a preponderant drop in nightly temperature is likely to impact on the flight activity of *Hipposideros aff. ruber* at the entrance of the cave (Fig 4.7).

Chapter Five

Estimating home range of *Hipposideros aff. ruber*, an insectivorous bat in Ghana, West Africa

KNUST



5 Estimating home range of *Hipposideros* aff. *ruber*, an insectivorous bat in Ghana, West Africa

5.1 Abstract

The home ranges of thirteen individuals of *Hipposideros* aff. *ruber* were studied in Kwamang. Home range estimations were based on 1192 fixes gathered during thirty-eight nights of radio-tracking. The estimated mean home range of the bat was thirty-six hectares (100% isopleths), but home ranges varied from six to ninety-five hectares among individuals. The foraging area (95% isopleths) formed 50% of the entire home range. The core area (50% isopleths) was relatively smaller and formed 2% (mean = 0.8 ha) of the home range. Pregnant females had smaller home ranges (< 10 ha) and foraged mainly ≤ 0.2 km around the roost cave. The mean foraging range for *Hipposideros* aff. *ruber* was 1.2 km. Individual foraging ranges varied between 0.1 to 2.6 km, suggesting the bat is a strong distance flyer considering its low wing loading and aspect ratio. Conservation efforts for the protection of the home range of *Hipposideros* aff. *ruber* should therefore include at least a three-kilometre radius around the roost cave. Results from pregnant females indicate consequences of carrying larger load in flight above 'normal' mass-carrying capability. This study supports adherence to the 5% rule of transmitter to body weight for this species for acceptable home range estimation and relieve of bat from possible increment in energetic cost.

5.2 Introduction:

Understanding the home range of animals is a central question in movement ecology which has crucially contributed to the development of effective management and conservation strategies (Gschweng *et al.*, 2012; Bonaccorso *et al.*, 2005; Mitchell

and Powell, 2003). The home range of an animal shows where it forages, mates and rears its offspring (Burt, 1943). The home range of an animal contains thus areas for gathering and processing of food (foraging area), and the most intensively used area (core area) (Weber *et al.*, 2009). Home range size may be largely determined by the availability of food (Zeale *et al.*, 2012; Elmore *et al.*, 2005; Winkelmann *et al.*, 2003). As metabolic demands, i.e. food requirements are primarily a function of body mass (Meer, 2006) which varies between individuals, they may also affect the individual home range size (Lindstedt *et al.*, 1986; McNab, 1963). Energetic requirements tend to affect in particular the home range size of pregnant and lactating animals (Henry *et al.*, 2002). Some Phyllostomid bats for example, reduce their flight activity considerably during pregnancy (Voigt, 2003), a situation which could affect their home range size. Home range size may vary among sex, age, reproductive class and the season (Henry *et al.*, 2002; Burt, 1943). The home range size might also depend on the colony size as individuals that live in larger colonies and want exclusive areas to themselves have to travel longer distances away from their roost, a concept known as 'refugia' (Jones *et al.*, 1995; Hamilton and Watt, 1970).

Home ranges in the past were inadequately described by mark-recapture data from mist netting studies. Today, techniques in home range studies have been more sophisticated with the evolution of radio telemetry, satellite telemetry and more advanced analysis software. Home range estimations have thus been attempted in instances where these methods have been employed (Alfred *et al.*, 2012; Gschweng *et al.*, 2012; Bonaccorso *et al.*, 2005; Winkelmann *et al.*, 2003; Fenton, 1987). So far only few bats have been radio-tracked in Africa and most of them were from the

southern part of the continent (Noer *et al.*, 2012; Monadjem *et al.*, 2010b; Jacobs and Barclay, 2009; Monadjem *et al.*, 2009; Jacobs *et al.*, 2005; Fenton, 1987). In Sub-Saharan Africa, very limited radio-tracking studies can be found. An example of such studies however, focused on a nectarivorous bat, *Megaloglossus woermanni* (Weber *et al.*, 2009).

This study therefore investigated the home range of *Hipposideros aff. ruber* that was found in chapter three to be the most abundant species roosting inside the caves. This species was also chosen for its wide distribution in Ghana and the rest of Sub-Saharan Africa (Happold and Happold, 2013). The first objective of the study was to estimate the home range of *Hipposideros aff. ruber*, and determine the variation in home range size among both sexes (males and females) and bats belonging to different reproductive classes (that is between pregnant and nullipara females, and between sexually active and inactive males). The second objective was to estimate the foraging and core areas of *Hipposideros aff. ruber*. Lastly, this study investigated the foraging range and speed of *Hipposideros aff. ruber*. It was therefore hypothesized that the home range of *Hipposideros aff. ruber* vary among males and females and also bats belonging to different reproductive classes.

5.3 Materials and Methods

5.3.1 Study area

The study was conducted from February 2011 to August 2012 in Kwamang in the Ashanti region of Ghana. The area has a maximum elevation of 530 m a.s.l. and is characterised by undulating land forms and traditionally forms part of the moist semi-deciduous forest of Ghana (Pappoe *et al.*, 2010). However, recent vegetation

cover is dominated by mosaic of agricultural fields ranging from cocoa, cassava, and fallow lands. In this agricultural landscape is situated natural caves that is used by bats for roosting. In this study, only bats roosting at KC1 (Chapter one) were considered.

5.3.2 Bat capture and mist netting

Bats entering the caves were captured using a 1 x 6 m mist net in the morning from 04:30 to 06:00 hours at the entrance of the roost cave. This approach was adopted as all bats captured and released at night did not return to the roost cave, and could not be located after several attempted efforts. Data were collected on their sex, age, forearm length, weight and reproductive status. Age was categorized based on the degree of closure of the epiphyseal phalanges and included only adult bats in this study (Weber *et al.*, 2009). Female bats were considered pregnant if foetus was palpable and nullipara when foetus was not palpable with hairs surrounding the nipples (Weber *et al.*, 2009). Heavily pregnant female bats were not included in this study. Male bats were considered sexually inactive if their testes were abdominal and almost flat at the base of the penis and considered active when testes were scrotal (Weber *et al.*, 2009).

5.3.3 Radio-tracking

Captured bats were fitted with small miniature position-sensitive transmitters (Holohil Systems Ltd.) weighing 0.65g within the 10% recommendation by Wilkinson and Bradbury (1988). Transmitters (BD-2 Transmitter, Holohil Systems Ltd., Ontario, Canada) were attached to the lower back of twenty-two bats with a

latex adhesive (Osto-Bond, Qc, Canada; Appendix B.6). After transmitter attachment, the bat were then released into the cave at sunrise around 06:00 hours in order to assure that it had time to habituate to the transmitter for twelve hours before flying out again in the evening. Tracking began twelve hours after capture and placement of transmitter on the bat, but data analysis included only data collected after thirty-six hours. This was to ensure that estimated home range was free from inaccuracies due to erratic behaviour immediately after receiving the transmitter. A bat was always tracked in parallel by two observers that regularly took the bearing of the bat from the direction of the strongest signal. Transmitter signals (range of 148-152 MHz) were received with hand held Yaesu receivers (model VR 500, Yaesu Musen Co. Ltd., Japan) with a pre-amplifier that amplified received signals. The pulse rate of the transmitter was twice faster when the bat was in flight than when it was resting. Tracking begun as early as 18:30 hours (± 15 minutes) during the main bat emergence from the cave and ended mostly around 06:00 hours (± 10 minutes) when bats returned in the morning to the roost. Using a compass (Suunto), bearing data were synchronically taken by two trackers and the respective locations were recorded with GPS (Garmin 60CSx, USA, Appendix B.7). Bearings were taken at regular intervals of every two minutes when the bat was in flight, and every five minutes when the bat was resting. Constant communication and synchronicity of bearings between the two trackers was assured via the use of a walkie-talkie (Albrecht CTE 180). To increase accuracy and reduce error, crossing angle of the two bearing directions were aimed at 90° but this was in the field on many occasions not possible.

5.3.4 Triangulation and home range analysis

For determining the crossing point from the two bearings via triangulation, data were exported to LOAS version 4.0.3.8 (Ecological Software Solutions LLC, 1998-2012). Only crossing angles between 15^0 and 165^0 were included in the analysis (Weber *et al.*, 2009). For each resting of a bat for more than two minutes, only a single fix was added to prevent under estimation of the home ranges. Different estimators are available for estimating home ranges, there is however a lack of consensus on the most accurate estimator due to the challenges associated with each estimator used (Kolodzinski *et al.*, 2010; Weinbeer and Kalko, 2004). The two most popular estimators, Minimum Convex Polygon (MCP) (Mohr, 1947) and Kernel Density (Worton, 1989) are generally sensitive to sampling intensity and tend to underestimate home range in low sampling regimes (Kolodzinski *et al.*, 2010). As sample size increases, local convex hulls (LoCoH), a non-parametric method, is increasingly superior over the parametric methods (Getz *et al.*, 2007). Local convex hulls were therefore used to analyse the home range data using the LoCoH web application (<http://locoh.cnr.berkeley.edu>; University of Berkeley) by adjoining nearest neighbour convex hull (NNCH) at a K value of 10 (Getz *et al.*, 2007; Getz and Wilmers, 2004). Home range was defined at 100% isopleths level, including all available fixes. Spatial use within the home range was distinguished as; foraging area and core area (Weber *et al.*, 2009; Henry and Kalko, 2007). Foraging area corresponded to 95% isopleths of the home range, while the core area was included by 50% isopleths. Core area was defined as the most intensively used area within the animal's home range, whereas the foraging area is the general area used for gathering and processing food (Weber *et al.*, 2009). The expected foraging range of each bat was calculated as applied in Jones *et al.* (1995) where foraging range = 0.12

$\times 10^{0.18}$ (aspect ratio). Foraging range was defined as the distance travelled from the roost cave to the farthest point of the bat's foraging area. Polygons of the foraging and core area within the home range were created with ArcGIS version 10. Statistical test for finding differences in home range size among both sexes and different reproductive classes were performed with Minitab using Mann-Whitney test (Minitab, 2010).

5.4 Results

5.4.1 Information on radio-tracked bats

Twenty two bats were fitted with transmitters but only thirteen bats yielded data that could be analysed, data from the remaining nine were not usable for a number of reasons. The first two males disappeared at the first night from the cave vicinity and never returned to the cave. Based on these experiences, the capturing protocol was changed to catching bats prior to sunrise, which provided considerable success. Sometimes bats got disturbed because the cave was used by a group of four to thirty people drumming and dancing inside the cave for religious purposes with some staying for up to two weeks. Lastly some of the transmitters fell off before data could be collected.

The thirteen tracked bats included five females of which three were pregnant and two were non-reproductive (nullipara) and the remaining eight were sexually active and inactive males in equal numbers. Determination of home range, foraging area, and core area for all thirteen bats were based on 1192 valid fixes (mean number of fixes per individual = 92 ± 56 SD). These fixes were gathered over thirty-eight nights with a total contact time of $63 \pm 18\%$ per bat (Males; $60 \pm 19\%$, Females $69 \pm$

15% SD). The total contact time per individual bat ($63 \pm 18\%$) include the time the bat spent in flight, time spent at night roost and time spent at the roost cave. However, determination of the home range and spatial use within the home range was based on contact time of bats in flight, as only one fix was added when a bat rested. This reduced the total contact time per individual bat in flight to $12 \pm 7\%$. There was no significant difference in contact time between females (69 ± 15) and males (60 ± 19), (Mann-Whitney; $W = 57.0$, $P = 0.9417$).

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5.4.2 Home range

Home range sizes of *Hipposideros aff. ruber* ranged from six to ninety-five hectares with a mean of thirty-six hectares (Table 5.1). This estimation is based on all fixes at 100% isopleths, corresponding to Minimum Convex Polygon (MCP). There were no differences in home range sizes of males and females (Mann-Whitney; $W = 18.0$, $P = 0.82$; males $n = 8$ and females $n = 5$). Also, no significant difference was found between home range size of sexually active and inactive males (Mann-Whitney; $W = 8.0$, $P = 0.89$; active males $n = 4$; inactive males $n = 4$). The sample size did not allow a statistic comparison between home range sizes of females, however, nullipara showed larger home range sizes than pregnant females (Table 5.1: nullipara, $n = 2$ and pregnant $n = 3$).

Table 5.1: Home ranges, foraging and core areas of radio-tracked bats. The table also show the foraging range from the roost cave, total contact time and morphological data of the tracked individuals. M1* and M1** indicate data of the same individual before and after switching roost cave, #_Entire home range of M1

Bat Name	Reproductive Status	Tracked Nights	Number of Fixes	Contact Time (%)	Body Mass (g)	Forearm Length (mm)	Number of Core Areas	Foraging range (km)	Home Range	Foraging Area	Core Area
									100% isopleths (ha)	95% isopleths (ha)	50% isopleths (ha)
F1	Pregnant	3	186	79	13.5	50.8	1	0.2	7	1	<1
F2	Pregnant	3	87	46	14.0	48.6	1	0.2	8	1	<1
F3	Pregnant	3	124	65	12.8	48.0	0	0.1	9	1	<1
F4	Nullipara	5	88	85	8.1	48.8	1	2.5	61	15	1
F5	Nullipara	2	33	71	10.1	48.8	1	2.4	91	69	-
Mean ♀									35.2	17.2	<1
M1*	Sexually Inactive	4	119	49	11.5	49.1	2	1.6	95 [#]	32	1
M1**	-	-	-	-	-	-	-	1.2	-	6	3
M2	Sexually Inactive	4	61	91	11.5	48.3	2	0.6	6	3	<1
M3	Sexually Inactive	2	106	44	11.0	49.2	1	0.2	7	2	<1
M4	Sexually Inactive	2	59	58	9.3	48.1	1	2.6	80	48	2
M5	Sexually Active	3	205	84	10.4	47.9	1	1.4	9	1	<1
M6	Sexually Active	2	63	45	10.0	48.2	1	1.0	16	8	1
M7	Sexually Active	3	31	63	9.2	49.6	1	0.8	35	16	2
M8	Sexually Active	2	30	41	10.3	50.0	1	1.0	48	29	-
Mean ♂									43.4	16.1	1

5.4.3 Spatial use within the home range

Sizes of the foraging areas of *Hipposideros* aff. *ruber* ranged from one to sixty-nine hectares (Table 5.1) with a mean of eighteen hectares. The foraging area therefore forms 50% of the home range of the bat. All bats maintained over the observation period a rather stable foraging area, with the exception of M1 and M3 that changed roost because of disturbance by humans (Fig. 5.1). M1 changed its roost to another cave within the same landscape three kilometres away from the original roost (Fig. 5.1). Upon this change it did not return to the previous foraging site but used a new foraging area. Its new roost was a smaller colony of *Hipposideros* aff. *ruber* compared to the first roost. Foraging range varied from 0.1 to 2.6 km. The foraging areas of pregnant females were closer to the roost cave with foraging range of ≤ 0.2 km (Fig. 5.2).

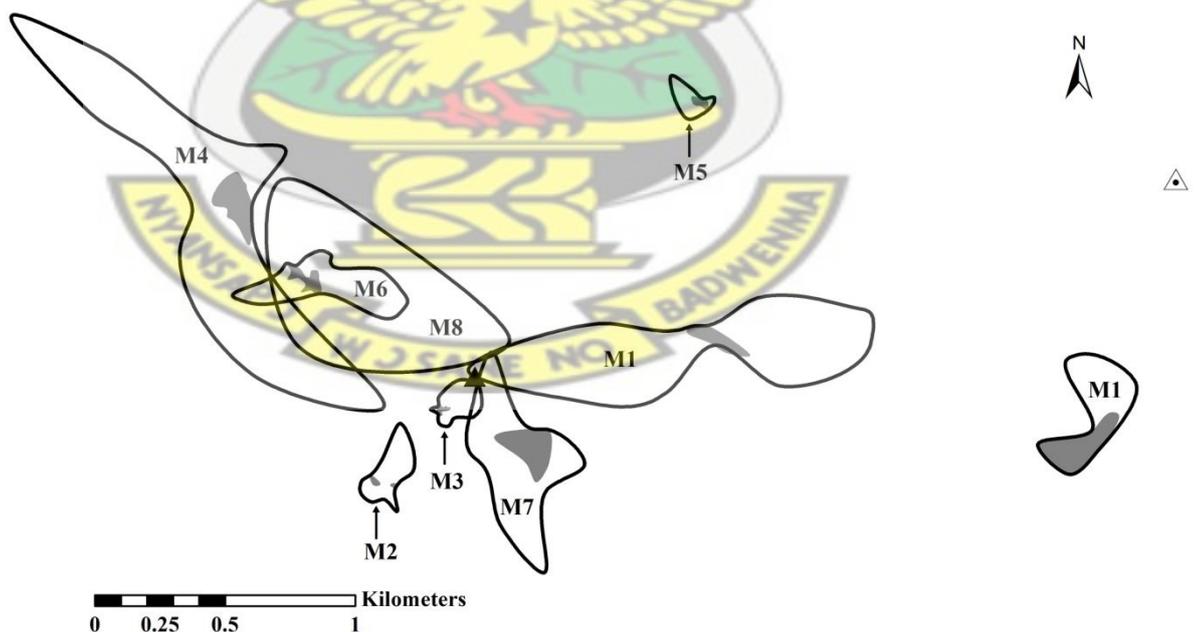


Figure 5.1: Foraging and core areas of male bats. Foraging area (black line), Core area (grey shade), Main roost cave (black triangle), 2nd roost cave of M1 (triangle with black dot at upper right corner).

Most bats had relatively smaller core areas (< 1 ha) with a mean of 0.8 ha. The core area therefore formed about 2% of the home range of the bat and 5% of the foraging area. The largest core area was three hectares and was recorded for M1 in its new foraging site. Interestingly, M1 had a smaller core area (1 ha) at its first foraging site that formed 3% of its foraging area, and three hectares or 50% of its new foraging area after it switched to a new site. Also, core areas of females were not larger than one hectare and generally smaller than those of males.

5.4.4 Overlap of spatial use within home range

About 36% of the total foraging areas of tracked bats were overlapping with the highest overlap of 64% between two sexually active males, M6 and M8 (Fig. 5.1). The highest overlap (M1, M3, M7, F1, F2 and F3) occurred around the roost cave. One male bat, M5 did not share its foraging area with any other tracked bats (Fig. 5.1).

5.4.5 Behavioural patterns of some bats

All bats used in succeeding nights the same place and left the cave towards the same direction to the foraging site. Two post-lactating females, two non-reproductive females and two non-reproductive males were not tracked consistently. Also, signals were received four kilometres away from the roost cave for some bats that were inconsistently tracked so were not included in data analysis.

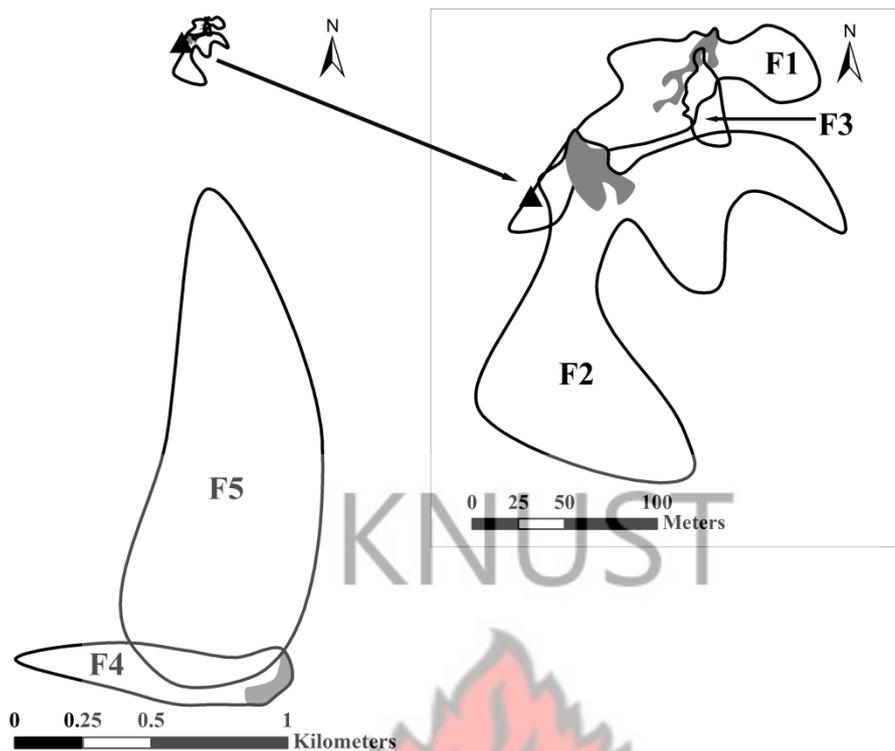


Figure 5.2: Foraging and core areas of female bats. Foraging area (black Line), Core area (grey shade), Main roost cave (black triangle).

5.5 Discussion

5.5.1 Sizes of home ranges, foraging and core areas

Home ranges of insectivorous bats vary widely from smaller than ten hectares (Monadjem *et al.*, 2009; Goiti *et al.*, 2008) to over one thousand hectares (Noer *et al.*, 2012; Zeale *et al.*, 2012; O'Donnell, 2001; Waters *et al.*, 1999). The estimated mean home range of *Hipposideros aff. ruber* was thirty-six hectares, suggesting that they have relatively smaller home ranges. However, home ranges differed significantly among individuals, ranging from less than six hectares to almost one hundred hectares. This is consistent with other studies on insectivorous bats that reported high variability of home ranges within species (Bontadina *et al.*, 2002) which may also differ between habitats (Noer *et al.*, 2012). This emphasizes the need

for including data from more individuals for determining home range sizes in order to make estimates more reliable (Borger *et al.*, 2006). Home range size of species like *Hipposideros aff. ruber*, might also depend strongly on insect availability. Bats tend to have smaller home ranges when there is an abundance of food (Monadjem *et al.*, 2009) and tend to have increased home range size when there is scarcity of food as they have to travel longer distances to find areas of high insect density (Noer *et al.*, 2012; Rydell, 1992).

Home range size in bats is linked to their flight style and morphological characteristics such as wing morphology (Lockwood *et al.*, 1998; Aldridge and Rautenbach, 1987). This may influence the type of vegetation where they can forage as well as the distances covered per night (Noer *et al.*, 2012; Jones *et al.*, 1995) and can potentially influence home range size (Entwistle *et al.*, 2000; Lockwood *et al.*, 1998; Jones *et al.*, 1995). Wing morphology includes wing loading and aspect ratio: the first being the weight of the animal divided by wing area and the latter the wingspan squared divided by wing area (Lockwood *et al.*, 1998). In bats and birds, lower aspect ratio suggests smaller flight ranges (Entwistle *et al.*, 2000; Lockwood *et al.*, 1998; Jones *et al.*, 1995). This finding is consistent with the results of related studies of insectivorous bats in Africa (Table 5.2) and confirms that the aspect ratio of these bats is linked to the sizes of their home ranges.

Table 5.2: Comparison of home ranges of different insectivorous bats in Africa

Species	*Body Mass (g)	#Wing Loading (N.m ⁻²)	#Aspect Ratio	Foraging Range (km)	Home Range 100% MCP or 95% -kernel (ha)
<i>Nycteris thebaica</i> ^a	10	6.3	5.5	1.1	12.9
<i>Hipposideros aff. ruber</i> ^b	10	6.6	6.3	1.2	36
<i>Nycteris grandis</i> ^c	35	11.4	5.2	-	≥50
<i>Chaerephon pumilus</i> ^d	10	11.8	8.6	4.2	1319
<i>Mops condylurus</i> ^e	20	18.0	9.1	4.8	1437

Home range and foraging range: ^a(Monadjem *et al.*, 2009); ^bThis study; ^c(Fenton, 1987) and (Monadjem *et al.*, 2009); ^{d,e}(Noer *et al.*, 2012). Morphometric data: ^{*}(Monadjem *et al.*, 2010a) and [#](Norberg and Rayner, 1987)

Comparable home range studies from Africa are limited. *Hipposideros aff. ruber* however share morphological similarities with *Nycteris thebaica* (Table 5.2). Both species are of the same size and have short rounded wings with low wing loading and similar aspect ratio (Norberg and Rayner, 1987). They are also considered clutter foragers and frequently share roosts (Monadjem *et al.*, 2010a). Bats sharing characteristics in morphology and foraging ecology are expected to be largely similar in spatial use (Weber *et al.*, 2009). This confirms the above assumptions as both species show smaller home ranges, although *Hipposideros aff. ruber* had slightly bigger home range (Table 5.2).

One interesting result from this study was that home range size of females varied depending on the breeding condition. Home range studies on *Rhinolophus hipposideros* indicated that non reproductive females have larger home ranges, twelve times larger than post lactating females (Bontadina *et al.*, 2002). This pattern was true for *Hipposideros aff. ruber*, where non-reproductive females had nine

times bigger home range than pregnant females. Home range of pregnant females ranged from seven to nine hectares with a relatively small foraging area close to the roost cave (Table 5.1). The distinctly smaller home ranges in pregnant females and its nearness to the roost cave is probably caused by the elevated energetic cost of pregnancy which could reduce home range to about 50% as seen for example in *Myotis lucifugus* (Henry *et al.*, 2002). Although heavily pregnant females were avoided in tracking studies, it is probable that the reduction in home range size could be due to the additional weight of the transmitter. Additional weight from carrying radio tags on flying animals affects the animal's energetic cost and their manoeuvrability (Hughes and Rayner, 1993). The average body weight of *Hipposideros aff. ruber* is only ten grams (Table 5.2), implying that the heaviest pregnant bat tracked was already carrying close to 40% of its total weight, consistent with other smaller bats that can carry from 30 to 40% of foetal mass of their weight during pregnancy (Kurta and Kunz, 1987).

There is a wide variation in the ability of flying bats to carry radio tags. Smaller bats (in relation to their body size) are expected to carry larger load than larger bats (Norberg and Rayner, 1987). For instance, the mass-carrying capability of low wing loading bats like the lesser horseshoe bat is expected to be greater (Norberg and Rayner, 1987), and female lesser horseshoe bat has been observed to carry their young of up to 50% of their body mass (Kokurewicz, 1990). *Hipposideros aff. ruber* is a low wing loading bat and thus expected to carry larger mass, but their actual mass-carrying capability is yet to be determined. Therefore the weight of the transmitter in addition to the foetal mass (approximately 46.5% in total) could have exceeded the 'normal' mass-carrying capability of female *Hipposideros aff. ruber*

adding more energetic costs, hence affecting its home range size. These results should be interpreted with caution for a number of reasons. These radio tagged pregnant females chose to forage in cluttered vegetation (Chapter six) indicating the surplus transmitter weight did not affect its manoeuvrability. If the surplus weight did affected its manoeuvrability, then it would be expected to forage in less cluttered vegetation (Aldridge, 1985). Also, carrying a tag could influence foraging stamina which consequently affect food intake, hence reducing the general fitness of the bat (Bontadina *et al.*, 2002). Transmitters were however attached for few days and data collected within a very short time and this effect was probably fairly limited. Lastly, the study did not investigate energetic demands before and after receiving radio tags to make definitive conclusions about possible effects of transmitter increasing energetic costs. It is probable that already elevated energetic demands associated with pregnancy is more likely to explain the smaller home ranges than the effects of the transmitter.

Hipposideros aff. ruber could carry larger mass in flight (e.g radio transmitter) like other low wing loading bats. However, results could be masked by the effects of such a larger transmitter as data from these radio-tracked pregnant females partly supports this claim. It is therefore proposed that the home range size of *Hipposideros aff. ruber* may reduce when extra load have to be carried. It is also proposed that pregnant females of *Hipposideros aff. ruber* should be avoided in tracking studies as collected data is likely to provide equivocal estimate of their home range. The study therefore supports the 5% rule for placement of transmitters (Aldridge and Brigham, 1988) to improve acceptability of estimated home ranges and relieve the animal from

possible increment in energetic cost contrary to arguments favouring the use of larger transmitters.

The results also indicate that *Hipposideros aff. ruber* may use up to 50% of their home range for foraging purposes. Individual foraging area can vary from one to sixty-nine hectares depending on the breeding condition. Some bats changed during the study period their roosting cave and foraging area entirely after being disturbed by humans. While some bats resorted to tree roost (*Ceiba pentandra*), others moved to a new roost cave with a smaller *Hipposideros aff. ruber* colony, about three kilometres away from their previous roost. This indicates that separated colonies within the same landscape interact to ensure the survival of smaller colonies through gene flow. M1 changed its roost and foraging area during the observation period and showed an interesting pattern in spatial use. The core area within its first foraging area formed about 3% of the foraging area, while it formed 50% of its new foraging area. This suggests that the bat first actively explored the new environment (Noer *et al.*, 2012; Rydell, 1992). Once the knowledge on areas with high insect densities is available, exploratory behaviour and core area can decrease again.

5.5.2 Overlapping home ranges and foraging areas

Home ranges and foraging areas did overlapped among most bats tracked. Several studies have reported the overlapping of home and foraging ranges among insectivorous bats (Monadjem *et al.*, 2009; Bontadina *et al.*, 2002; Russo *et al.*, 2002; Fenton, 1987). However, only home and foraging ranges were overlapping while core areas were exclusive to each bat tracked. Highest degree of overlap was observed around the roost cave where bats commuted to foraging areas, similar to

that observed in *Nycteris thebaica* (Noer *et al.*, 2012). It is important to mention that bats were radio-tracked at different times as the study was done over a period of twelve months. The spatial overlap therefore could be as a result of different bats sharing the habitat in temporal dimension. However, the roost cave where radio-tracked bats were caught is a colony of several thousands of bats and it is probable that the observed overlap actually highlights the intra-specific tolerance within home ranges. Therefore, the use of exclusive core areas as observed could be attributed to the relatively small sample size (thirteen individuals) involved in this study in relation to the colony roosting inside the cave. This could change in future studies when more individuals are included.

5.5.3 Foraging range of *Hipposideros aff. ruber*

Based on Jones *et al.* (1995) exponential equation, the expected foraging range of *Hipposideros aff. ruber* is 1.1 km. In this study, the estimated foraging range was 1.2 km which conforms with the estimated travel distance above. This pattern is consistent with other low wing loading bats such as *Nycteris thebaica* and *N. grandis* that may also travel over similar distances (Monadjem *et al.*, 2009; Fenton, 1987). However, there was distinct individual variation in the distances covered. The maximum foraging range observed was 2.6 km. This indicates that although *Hipposideros aff. ruber* is a low wing loading bat, it is a strong flyer and capable of commuting over longer distances (Noer *et al.*, 2012). Similar observations exist from *Rhinolophus euryale*, a temperate insectivorous bat which is similar in size to *Hipposideros aff. ruber*. The aforementioned bat has a foraging range between 1.3 to 4.6 km, depending on sex and reproductive condition (Goiti *et al.*, 2008; Russo *et al.*, 2002). Other similar-sized insectivorous bats can commute over longer distances

of up to twelve kilometres (Lumsden *et al.*, 2002). These apparently longer distances may be linked to roost availability (Lumsden *et al.*, 2002). Moving within the expected distances suggests that roosting opportunities were not limiting for *Hipposideros aff. ruber* in the study area (Monadjem *et al.*, 2009), moreover, findings indicate that they easily switch between roost such as from caves to tree cavities. On the other hand, individuals living in large colonies may have to travel over longer distances from their colony to get exclusive areas to themselves and for foraging (Hamilton and Watt, 1970). Large colony size and heterogeneous distribution of prey might therefore account for the large variation in foraging ranges.

5.6 Conclusion and recommendation

The home range and foraging areas of *Hipposideros aff. ruber* are similar to that of other insectivorous bats of similar size. There was high variation among home range size of individuals. Tracking of more individuals is recommended to improve reliability of home range estimations. Although *Hipposideros aff. ruber* has relatively small body size and aspect ratio, it can fly over remarkably longer distances indicating it to be a strong flyer. Conservation activities targeting the protection of its home range should include a minimum radius of three kilometres from the roost cave. Lastly, the extremely small home ranges of pregnant females of *Hipposideros aff. ruber* might indicate the consequences of having to carry larger load in flight above the 'normal' mass-carrying capability. It is recommended that females of *Hipposideros aff. ruber* should be excluded in tracking studies.

Chapter Six

Habitat selection and roosting behaviour of *Hipposideros aff. ruber* in an agricultural landscape in Ghana, West Africa

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6 Habitat selection and roosting behaviour of *Hipposideros* aff. *ruber* in an agricultural landscape in Ghana, West Africa

6.1 Abstract

Habitat selection and roosting behaviour of *Hipposideros* aff. *ruber* were studied in an agricultural landscape of Kwamang, Ghana. Thirteen individuals were radio-tracked for thirty-eight nights. Compositional analysis revealed a non-random use of habitats around the roost cave (randomisation test; Wilk's lambda = 0.1650, $P < 0.001$). A ranking matrix indicated that *Hipposideros* aff. *ruber* preferred to use semi-natural habitats (fallow lands) for foraging over other habitats. Tree farms (e.g., cocoa farms) were of less importance to foraging bats, but were used as flight paths for commuting between roost cave and foraging areas. Savannah grasslands around the roost cave were least preferred by foraging bats. Analysis of foraging behaviour revealed a trimodal activity pattern at night peaking at dusk, dawn and midnight. Nightly activity pattern did not differ between males and females. Bats used trees and caves as both night and day roost but preferred cave roosts. The results suggest that *Hipposideros* aff. *ruber* readily adapts to anthropogenically modified habitats but uses fallow lands as foraging areas. In highly impacted agricultural landscapes, fallow lands is recommended to be used as conservation units to support foraging bats.

6.2 Introduction

Conversion of tropical forest to agriculture may lead to mosaic of small fields, fallow lands of different succession and remnant patches of mature forest (Schulze *et al.*, 2000). This process severely impacts wildlife (Tylianakis *et al.*, 2007), while highly

modified habitats are increasingly becoming the available habitats for some species (Russell *et al.*, 2003; Turner and Corlett, 1996). Modified habitats present new challenges that animals have to adapt (Tweheyo *et al.*, 2004). Sometimes, it may require distinct behavioural changes. Being highly mobile, bats can change rapidly between different habitat types (Medellin *et al.*, 2000; Kalko *et al.*, 1999). Their ability to fly and cross between habitats provides them the opportunity that allows them to find any potentially available foraging grounds, even within degraded environments. Different species of bats respond in different ways to these modifications, due to the high variation in morphology and foraging ecology (Castro-Luna *et al.*, 2007).

While some bats are strongly impacted by habitat modifications and clearly need pristine forest habitats (Fenton *et al.*, 1992), other bats might benefit from the conversion of natural areas to agricultural fields. For example, *Megaloglossus woermanii*, the smallest pteropodid bat in Africa was observed to frequently access banana plantations near undisturbed natural forest (Weber *et al.*, 2009). In insectivorous bats, exploitation of specific habitats is linked to their motor capability (Aldridge and Rautenbach, 1987) and echolocation behaviour (Schnitzler and Kalko, 2001). For example, bats foraging in cluttered environments require special manoeuvrability aided by the morphology of their wing (Aldridge and Rautenbach, 1987). In addition, they have to vary the frequency structure, duration, and sound pressure level of their echolocation to avoid masking signal to capture prey, navigate landmarks and avoiding collision with objects at the same time (Schnitzler and Kalko, 2001). Insectivorous bats are potentially vulnerable to habitat modifications due to its consequence on insect availability and abundance, and on habitat structure

(Schulze *et al.*, 2000). Bats as part of their hunting strategy often closely adapt to particular habitats therefore their hunting success could be significantly affected by habitat modification. In an intensively used agricultural habitat, *Rhinolophus hipposideros* frequently preferred broadleaf woodlands to other habitats (Bontadina *et al.*, 2002). Lumsden and Bennett (2005) also reported that foraging areas of some insectivorous bats coincided with forested areas and bat abundance declined with the decreasing tree densities.

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The study species, *Hipposideros* aff. *ruber* is a ten-gram common insectivorous bat in Ghana with wide distribution on the African continent (Wright, 2009). *Hipposideros* aff. *ruber* (Vallo *et al.*, 2011) forms a species complex with different lineages in Africa (Vallo *et al.*, 2008). It uses high-duty cycle echolocation calls (Wright, 2009) with CF components varying between 121–153 kHz, depending on the location (Wright, 2009; Jones *et al.*, 1993b). Pye (1972) recorded individuals calling as high as 160 kHz in Nigeria, Kenya and Uganda. The constant frequency (CF) and frequency modulated (FM) components of their calls enable them to forage in very dense and cluttered vegetation (Monadjem *et al.*, 2010a; Wright, 2009; Jones *et al.*, 1993a; Aldridge and Rautenbach, 1987). *Hipposideros* aff. *ruber* is closely tied to the forest (Happold and Happold, 2013; Monadjem *et al.*, 2010a) but also uses wooded savannah (Menzies, 1973). In Ghana they are widely distributed and can be found in savannah, forest and in transition zones (forest-savannah). Roosting habits are very flexible and include hollow trees, caves, rock shelters, rooftops and basement of human dwellings (Wright, 2009). Roosting group size range from few individuals in trees (harem social system) (Bell, 1987) to several thousands in caves and abandoned mines (Menzies, 1973).

Not much is known about the foraging ecology of *Hipposideros aff. ruber* but it is putatively a lepidopteran specialist (Bell and Fenton, 1984), hence *Hipposideros aff. ruber* may be expected to forage within habitats with high densities of lepidopterans. *Hipposideros aff. ruber* is equally successful in using both gleaning and aerial hunting strategies in capturing prey (Bell and Fenton, 1984). In both approaches, it occasionally captures prey in the mouth but frequently scooped prey with wing membrane and transfer to the mouth while in flight (Wright, 2009; Bell and Fenton, 1984). In gleaning approach it scoop prey from surfaces (including cluttered surfaces) and briefly touch down with wrist and feet in some situations (Wright, 2009; Bell and Fenton, 1984).

In Ghana, most pristine areas have either been degraded or lost to agricultural activities. The severity of its impacts on most wildlife populations remain to be assessed. It is not clear how this widespread conversion of pristine forest to agricultural lands is impacting foraging bats. Radio telemetry was therefore used to quantitatively assess for the first time, the foraging behaviour and habitat selection of *Hipposideros aff. ruber* in an agricultural landscape. The objective of this study was to determine the habitat selection and preference of *Hipposideros aff. ruber*. The study also investigated the foraging and roosting behaviour of *Hipposideros aff. ruber*. It was hypothesised that *Hipposideros aff. ruber* uses habitats in proportion to its available around its roost cave.

6.3 Materials and Methods

6.3.1 Study area

Study site was the vicinity of Kwamang in the Ashanti Region of Ghana. The bats' roosting cave (UTM: 30N 687746 774489) is located four kilometres from the town of Kwamang and three kilometres from the next village, Atonsu. The study lasted nineteen months between February 2011 and July 2012. The landscape consists mainly of undulating terrain, ranging from hills to lowlands, between 320 m to 540 m above sea level. The mean annual rainfall is between 1,200 to 1,500 mm with an average temperature of 27°C.

Floristically, the area surrounding the cave formed historically a part of the moist semi-deciduous forests of Ghana (Pappoe *et al.*, 2010) that dominate the lowlands and valleys around the roost cave. The current vegetation at the summit of the hills is, however, dominated by grasslands and a closer look reveals a complex vegetation of agricultural fields, fallow lands with human settlements. This complex vegetation cover was therefore characterised based on actual stand type and canopy cover (Table 6.1).

Table 6.1: Habitat characterization around the roost cave.

Habitat Type	Categories of stand type and definition
Grass Savannah (GS) ^a	Grass-dominated area with very few isolated trees. Dominant grass is <i>Panicum maximum</i> (Guinea grass). This habitat is fire prone and burned in the dry season (generally in January and February) by humans.
Wooded Savannah (WS) ^{a,b}	Mixture of grasses and trees. Dominant stand type is short trees ^a . The trees are more densely packed than GS, providing more canopy cover. Grasses here form an understorey vegetation. This vegetation is also fire prone in the dry season.
Tree Farms (TF) ^b	This category includes tree monocultures. Cultivated trees include mainly cocoa, oil palm and cashew farms. There is complete canopy cover with almost no understorey vegetation. Dominant stand type is the cocoa farms.
Traditional Mixed Farms (TMF) ^b	Includes farm lands with open vegetation, without canopy cover. This category comprises mixed farms cultivating cassava, maize or plantain.
Semi-natural Habitats (SnH) ^b	Include fallow lands with varying degree of succession, vegetation of trees, shrubs and herbaceous plants. There is canopy cover in some areas, while others are open due to early succession or illegal logging activities.
Human Settlement (HS)	Rural dwelling of humans with few ornamental trees.

Tree height approximation: a_(<10 m high), b_ Timber species are present but isolated (*Cola gigantean*, *Ceiba pentandra*)

6.3.2 Bat capture, tagging and radio-tracking

Bats were captured with mist nets in front of the roost cave between 04:30 and 06:00 hours in the early morning. Data recorded from captured bats include forearm length, weight, sex, age and reproductive status (pregnant and nullipara females, sexually active and inactive males), classification followed Weber *et al.* (2009). Only adults were selected for this study. Bats were then fitted with position-sensitive transmitters (BD-2 Transmitter, Holohil Systems Ltd., Ontario, Canada) at the lower back of the bat with latex adhesive (Osto-Bond, Qc, Canada). Weight of transmitters was 0.65g or 6.5% of the body weight, thus corresponding to the 10% recommended by Wilkinson and Bradbury (1988). Bats were released into the roost cave at sunrise after receiving radio transmitters.

Radio-tracking begun the evening after capture. However, data for analysis included only fixes collected at least 36 hours after catching. During radio telemetry, one bat was tracked per night by two trackers equipped with radio receivers (VR 500, Yaesu Musen Co. Ltd., Japan), GPS (Garmin 60CSx), compass (Suunto) and antennas (Wagener Telemetrieanlagen, Köln, Germany). The two trackers communicated by walkie-talkie (Albrecht CTE 180) and recorded the direction of the strongest signal every 2 minutes when the bat was in flight and 5 minutes when resting. The transmitters broadcasted between 148-152 MHz and the pulse rate changed depending on whether the bat was flying or resting. Pulse rate of the transmitters doubled when the bat was flying. This fluctuation in pulse allowed the bats' activity to be monitored. Recorded data include; activity of the bat (resting or flying), bearing data for determining location of the bat and duration of the bat's nightly

activity. The activity included flying and roosting (inside roost cave or the night roost).

6.3.3 Analysis of habitat selection

Bearing data from both observers were used for triangulation in LOAS (v. 4.0. 3.8; Ecological Solutions LLC, 1998-2012). For assuring high data quality, only pairs of bearings with crossing angles larger than 15° and less than 165° (Weber *et al.*, 2009) was included in data analysis. Home ranges of the tracked bats were estimated using the LoCoH web application (<http://locoh.cnr.berkeley.edu>). For the purposes of defining available space to bats around the roost cave, data from all tracked bats were pooled together to generate the home range (100% isopleths) of all bats to correspond to the size or the area of the study area. The foraging area of each bat, i.e. the area used for gathering and processing of food (Weber *et al.*, 2009), was defined as the area limited by the 95% isopleths. Local convex hulls were created by adjoining nearest neighbour convex hull with a smoothing factor of 10 (Getz *et al.*, 2007; Getz and Wilmers, 2004).

For habitat analysis, polygons of the foraging areas were superimposed on the study area map using ArcGIS (v. 10). To assess habitat selection by *Hipposideros aff. ruber*, habitat composition within the foraging area of each bat was compared to habitat availability within the entire study area, defined as the area used by all bats (or 100% isopleths of all bats). This comparison was conducted by a compositional analysis (Aebischer *et al.*, 1993) using the software Compos Analysis v6.3+ (Compositional Analysis Plus Microsoft Excel tool 6.3, Smith Ecology Ltd., Abergavenny, United Kingdom). Randomisation tests (1000 iterations) were

performed to solve the problem of non-normality of the data in multivariate analysis, and 0.01% (less than the smallest non-zero in available or used habitat) was used to replace missing values in use and available habitats (Aebischer *et al.*, 1993). Wilk's λ was calculated as a weighted mean. A ranking matrix was then used to determine the relative importance of different habitats for the foraging bats.

6.3.4 Behavioural analysis

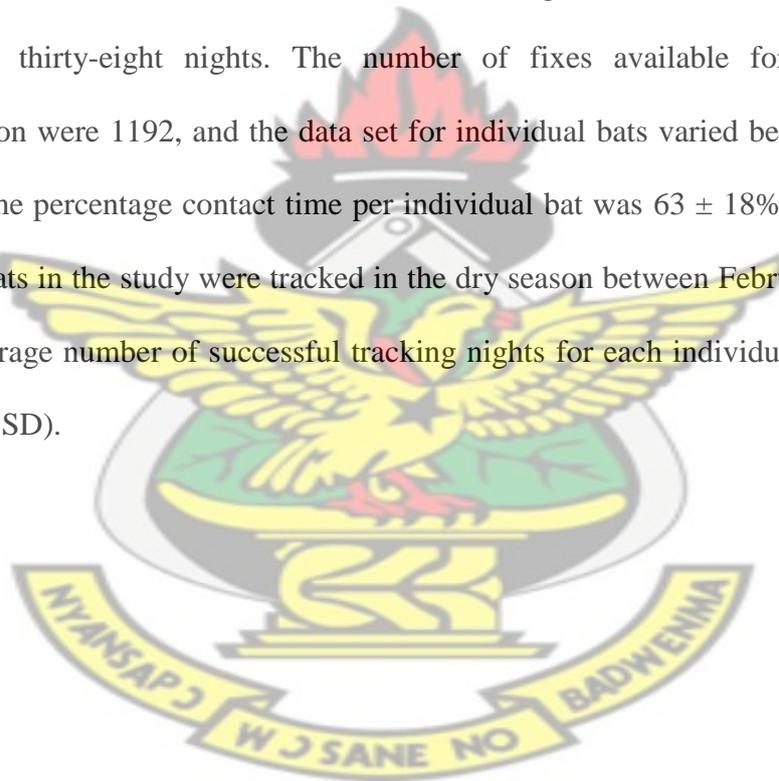
Foraging behaviour of *Hipposideros aff. ruber* was analysed using two factors, the duration of foraging flights, and the number of flights per night, i.e., the number of times the bat flew to foraging after resting. Duration of flight was calculated as the total time spent in flight during all foraging flights per night. All behavioural analyses included only nights with more than 70% contact time with the bat (males, N = 8 bats; n = 19 nights; females, N = 4 bats; n = 12 nights), unless otherwise stated. Maximum contact time possible was 11 hours for each night beginning from 19:00 to 06:00 hours on the next morning.

Roosting behaviour was defined as the duration spent roosting at the day roost cave and at individual night roosts. For all statistical tests, a critical alpha level of $p < 0.05$ was used. Flight speed of *Hipposideros aff. ruber* was also calculated from commuting flights. To calculate the speed, only fixes taken within the first 30 minutes after fly-out from the roost cave were considered (Rhodes and Catterall, 2008). The longest distance between successively tracked radio fixes within the first 30 minutes before signal was lost was selected. Speed was then calculated from the distance covered over change in time between the two fixes ($\Delta t = 2$ minutes). All statistical analyses were performed using Minitab v. 16 (Minitab, 2010).

6.4 Results

6.4.1 Tracking success

The total number of bats that were initially tagged was twenty-two. Thirteen of these animals yielded reliable results. Data were not available for the remaining bats for a number of reasons such as premature drop-off of transmitters or disappearance of the bat beyond reach. The signal range of the transmitter varied greatly, depending on the topography and vegetation type, but generally was around three hundred meters. Analysis included data from five females and eight males that were tracked for a total of thirty-eight nights. The number of fixes available for foraging area estimation were 1192, and the data set for individual bats varied between 30 to 205 fixes. The percentage contact time per individual bat was $63 \pm 18\%$ ($\bar{x} \pm SD$). Most of the bats in the study were tracked in the dry season between February and March. The average number of successful tracking nights for each individual bat was 2.9 ± 0.9 ($\bar{x} \pm SD$).



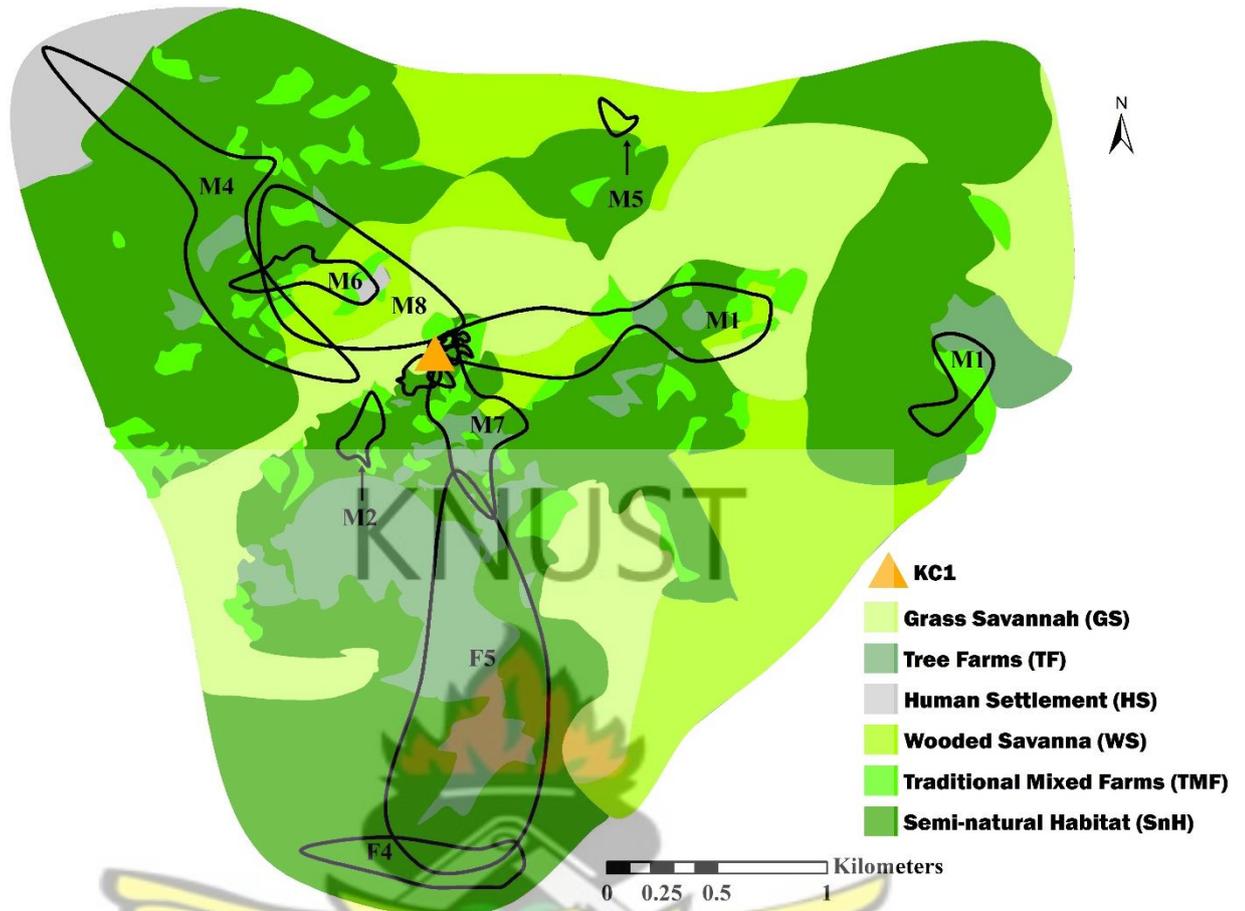


Figure 6.1: Habitat selection in the foraging area (95% isopleths) of thirteen bats in the study area (100% isopleths of all tracked bats). M = males, F = females.

6.4.2 Habitat selection

The thirteen individuals selected a variety of habitats during foraging (Fig. 6.1). The comparison of the proportional habitat use within the foraging area of tracked individuals to the available habitats within the entire study areas (Fig. 6.2) indicates a non-random habitat use by the foraging bats (Weighted mean Wilk's $\lambda = 0.1650$, Chi Square test = 23.4234, $P = 0.0003$ or $P < 0.001$ by randomisation, $DF = 5$). This analysis allowed ordering of habitats according to their relative importance to the bat and to access significant differences between them.

Table 6.2: Ranking matrix for *Hipposideros* aff. *ruber* (n = 13) based on comparison of percentage habitat use within foraging area (95% isopleths) to available habitat within the study area (home range of all tracked bats at 100% isopleths)

	Semi-natural Habitats	Tree Farms	Wooded savannah	Grass savannah	Traditional Mixed Farms	Human settlement	Rank
Semi-natural Habitats		+++	+(+++)	+++	+	+++	5
Tree Farms	---		-	+	-(---)	-	1
Wooded savannah	-(---)	+		+	-	+	3
Grass savannah	---	-	-		---	-	0
Traditional Mixed Farms	-	+(+++)	+	+++		+	4
Human settlement	---	+	-	+	-		2

The table shows the log-ratio differences from each of the thirteen individuals weighted by the square root of the corresponding number of observations. The habitat in every row is compared to the corresponding habitat in the column. The symbol ‘+’ indicate habitat in row category were more used by the bat than expected, compared to the habitat in the corresponding column while ‘-’ indicate a lesser use. In either case where ‘+’ or ‘-’ symbol appears, there was no observed significant difference between the two compared habitats ($P > 0.05$). Whereas the triple symbols ‘+++’ or ‘---’ indicates ‘preference’ and ‘least preferred’ respectively at a significance of $P < 0.05$. These significances are chosen from the randomisation results but instances where significance was observed from standard t-test from the data, they are shown in parenthesis. The rank for each habitat was calculated from the number of ‘+’ or ‘+++’ in the rows. The number indicate the relative importance of the habitat to the bat from zero (least important) to five (most important).

The bats used the available habitats in the following order, from most to least used: semi-natural habitats > traditional mixed farms > wooded savannah > human settlement > tree farms > grass savannah with no significant difference observed between adjacent habitats (Table 6.2). Semi-natural habitats were significantly preferred (+++) over all other habitats with the exception of the traditional mixed farms (+). The ranking matrix also indicates that tracked bats preferred traditional mixed farms (++) over tree farms. Lastly, the grass savannah was the least important habitat for foraging bats although more of it was available in comparison to traditional mixed farms, tree farms and human settlement (Fig. 6.2).

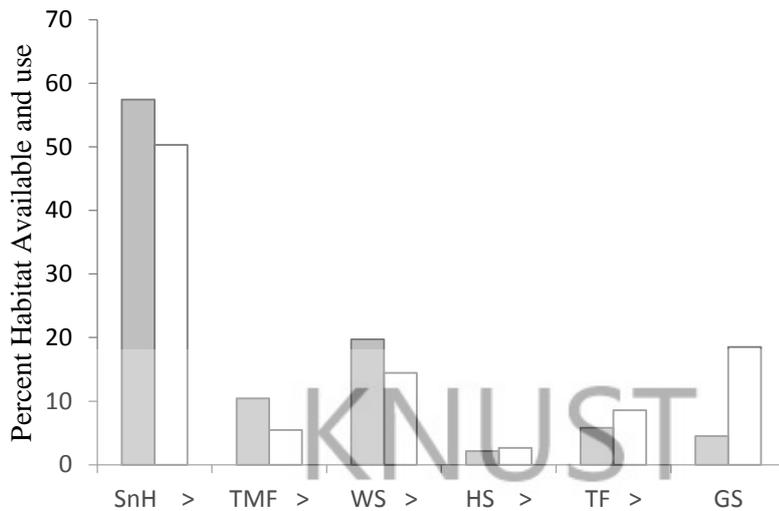


Figure 6.2: Comparison of use (grey shade) and available (white shade) habitat around roost cave and their relative importance to *Hipposideros* aff. *ruber* (n = 13). Habitat on the left were selected over those on the right but no observed significant difference between adjacent habitats (i.e., where there is '>'). Abbreviations listed in Table 6.1.

6.4.3 Foraging behaviour

Foraging activity showed a trimodal pattern (Fig. 6.3). Flight activity peaked immediately after emergence in the evening, around midnight and again in the morning. Emerging time of the bats was around 18:25 hours, characterized by flying multiple times in and out of the cave before finally leaving to forage. The calculated mean commuting speed to the foraging area from the roost cave after evening emergence was 8.3 m/s (N = 7 bats, n = 17 flights), with a maximum of 10.4 m/s and a minimum speed of 5.1m/s. Males tended to be more active throughout the night than their female counterparts (Fig. 6.3). No significant difference was observed in the activity patterns of the males and females (Mann-Whitney; W = 173, P = 0.192). The foraging activities of bats appeared to be higher in the first half of the night than in the second; but there was no significant difference (Mann-Whitney: W= 179, P =

0.093). The estimated mean foraging duration per individual bat was 109 minutes (SD: ± 62 minutes) per night. There was a significant difference between the flight duration of males and females (Mann-Whitney; $W = 68.0$, $P = 0.048$) with the males spending more time. The flight duration was however not significant between the reproductively active and inactive males (Mann-Whitney, $W = 13$ $P = 0.194$). The female reproductive class was not compared as a result of the sample size as interpretation from analysis could be misleading.

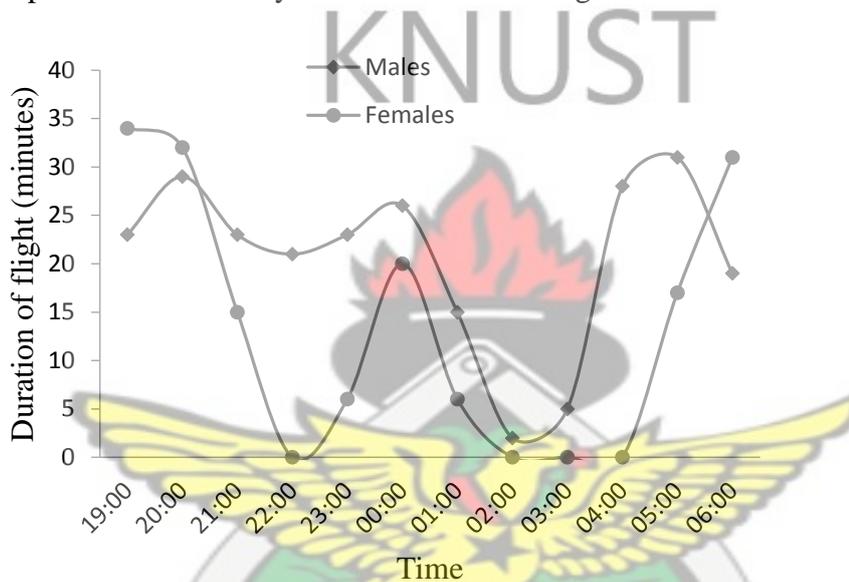


Figure 6.3: Nightly activity pattern of male ($n = 8$) and female ($n = 4$) *Hipposideros aff. ruber*

6.4.4 Roosting behaviour

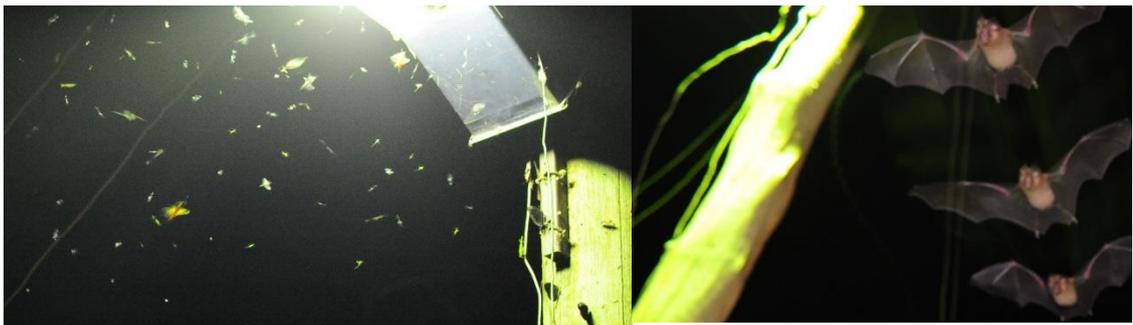
Bats made repeated visits to the day roost cave as the night progressed. The mean number of visits per bat to the roost cave per night was three times ($SE \pm 0.6$). There was a significant difference between the visitation by both sexes (Mann-Whitney; $W = 11$, $P = 0.0128$), with males (4.3 ± 0.7 visits; $\bar{x} \pm SE$) visiting the cave more often than females (1.4 ± 0.2 visits; $\bar{x} \pm SE$). There was a significant difference in duration of the use of the roost cave during the night and the usage of additional temporal

night roosts (Mann-Whitney: $W = 187$, $P = 0.0337$) with longer use of the cave. Female bats spent at night more time roosting inside the cave (386.3 ± 65.1 minutes; $\bar{x} \pm SE$) than males (150 ± 52 minutes; $\bar{x} \pm SE$), but there was no significant difference (Mann-Whitney; $W = 40$, $P = 0.0504$). There was also no significant difference in duration spent inside the day roost cave at night between sexually active and inactive males (Mann-Whitney: $W = 20$, $P = 0.665$).

6.4.5 Field observation and recorded photographic images of *Hipposideros aff. ruber*

During radio-tracking, *Hipposideros aff. ruber* while resting at the foraging area usually embarked on short duration flight. The duration of this flight was about 4 seconds and could be repeated about 7 times per night varying among the bats. This activity was however difficult to quantify for analysis due to the relatively shorter span of this activity.

Images of *Hipposideros aff. ruber* were captured while feeding around street light in the Kwamang town (Plate 6.1). It must be clarified that, these photographic images are not bats that were involved in radio-tracking but opportunistically recorded within the study area.



a). Street light teaming with insects

b). *Hipposideros* aff. *ruber* in flight around street light



c). *Hipposideros* aff. *ruber* in flight around street light

d). *Hipposideros* aff. *ruber* with prey in mouth

Plate 6.1: Activity of *Hipposideros* aff. *ruber* around one street light in Kwamang town

6.5 Discussion

6.5.1 Habitat selection

How animals cope with anthropogenically modified habitats is of prime importance to conservation and wildlife management. The initial hypothesis that *Hipposideros* aff. *ruber* uses habitats in proportion to its availability was rejected based on the compositional analysis. The bat preferred to forage in semi-natural habitats, followed by the traditional mixed farm areas. Savannah grasslands were least utilised by foraging bats, followed by tree farms. Preference for a single habitat type during foraging is uncommon among insectivorous bats and the results are consistent with other studies reporting the use of multiple habitat types (Zeale *et al.*, 2012; Zukal and Zdeněk, 2006). Foraging in all habitat types around the roost cave indicates considerable flexibility in habitat use. Little is known about the habitat preference of

Hipposideros aff. *ruber*, but convergent evolution in diet and morphology to similar bats might indicate similarities in foraging preferences (Weber *et al.*, 2009). Its close lineage, *Hipposideros* *caffer* is closely associated with the savannah woodlands (Wright, 2009; Menzies, 1973) whereas *Hipposideros* *ruber* is associated with the forest (Monadjem *et al.*, 2010a).

Bats in the genus *Hipposideros* have been tied to the group of foragers called the highly cluttered space aerial insectivores species based on the nature and structure of their echolocation, that is the use of long-duration, medium to high CF and CF-FM signals (Schnitzler and Kalko, 2001). The semi-natural habitats around the roost cave are made of fallow lands with trees, shrubs and herbaceous plants forming a well-developed undergrowth thicket. This cluttered environment might perhaps explain why *Hipposideros* aff. *ruber* preferred this habitat over the others. Additionally, prey availability and distribution also affect where a bat concentrates its foraging activities (Zukal and Zdeněk, 2006; Warren *et al.*, 2000). Insectivorous bats are known to respond opportunistically to areas with high prey densities (Rydell, 1992), so their presence within a particular habitat type is strongly linked to prey availability (Kusch *et al.*, 2004). The semi-natural habitats present a higher structural complexity than the other modified habitats, which might enhance insect diversity and abundance (Lassau and Hochuli, 2005). *Hipposideros* aff. *ruber* is highly specialised in hunting lepidopterans (Dunning and Krüger, 1996; Bell and Fenton, 1983) and thus can be expected to select habitats rich in lepidopteran densities over other habitats. Prey availability in the various habitats around the roost cave was not investigated, but data on dietary requirements from the study area (Badu *et al.*, Unpublished) suggest *Hipposideros* aff. *ruber* is a lepidopteran

specialist. Their preference for the semi-natural habitats indicate higher densities of lepidopterans within this habitat type. Future studies should therefore include also an assessment of lepidopteran availability within the study area.

Although *Hipposideros aff. ruber* preferred semi-natural habitats for foraging over other habitats, there was no significant difference in the use of this habitat over traditional mixed farms (Table 6.2), indicating that these might also support a high abundance of insect prey for the bats. This finding also suggests that a foraging bat might place the highest priority on availability of prey, instead of which habitat type to select for foraging. A decision favouring prey availability might imply risking foraging in open areas such as traditional mixed farms and around street lights (Plate 6.1), irrespective of a potentially increased exposure to predation. Provided there is availability of sufficient prey, open habitats could be selected over more cluttered areas, in spite of less protection from predators than in other more sheltered habitat types such as savannah woodland or tree farms. However, at similar prey availability, habitats providing more cover from predators like the semi-natural habitats should be preferred over more open areas (e.g., traditional mixed farms) as indicated in Table 6.2.

This finding, however, contrasts other reports stating that the primary decision a foraging bat makes is the type of habitat, with prey availability being the second (Johnson *et al.*, 2007; Whitaker Jr., 1994). This contrary findings however, need clarifications through future studies that also consider local prey availability in the different habitats. Actually, telemetry data reflect not only the habitat choice of a bat individual, but also to some extent prey availability. A bat will not choose to stay too

long in a habitat that provides no prey. On the other hand, prey availability for a particular bat species depends also on the plant species composition of a given habitat, how insects are distributed in the habitat structure and how this structure matches the species-specific echolocation behaviour. In consequence, habitat and prey availability are probably rather closely linked to each other.

The least used habitats during foraging were the savannah grasslands. This might be a consequence of the season in which bats were tracked at which time most places were burnt and could support little to no prey items. Contrary to expectation, tree farms, mainly cocoa farms, were the next under-utilized habitat by foraging bats after grass savannah. Even human settlements were more frequently used for foraging than the tree farms. Insectivorous bats respond to areas with high insect abundance and the street lights (Plate 6.1) within human settlement are potentially attractive places for many insect species (Rydell, 1992). For example, *T. teniotis* and *T. brasiliensis* have been observed to forage opportunistically in illuminated cities and rural settlements (Avila-Flores and Fenton, 2005; Carmel and Safriel, 1998). At the study area (Kwamang town) *Hipposideros* aff. *ruber* was recorded on many occasions catching prey around streetlight (Plate 6.1).

The results also indicate that the cocoa farms were of less importance to foraging bats. The severe use of agrochemicals on these farms by farmers might have decreased insect availability for *Hipposideros* aff. *ruber* (Desneux *et al.*, 2007). Also, the lack of understory vegetation in these farms probably reduced insect diversity and abundance (Lassau and Hochuli, 2005). Bats therefore use these farms predominantly as flight paths for commuting between roost cave and foraging areas,

as the canopy closure provided good coverage from predators such as owls that were ubiquitous in the study area. From a conservation point of view, this underlines the importance of availability of areas with canopy closure that provides cover from predators in anthropogenically modified habitats (Russo *et al.*, 2007; Jones and Rydell, 1994).

6.5.2 Foraging behaviour

Hipposideros aff. ruber emerged from the roost cave at a darker twilight phase. Emergence before full darkness might increase the predation risk from raptorial birds (Jones and Rydell, 1994), such as crows and black kites. It was expected that the emergence of *Hipposideros aff. ruber* from the day roost cave coincide with the flight activity of moth as is considered a moth specialist. The flight activity of most moth species in both the Neotropic and Afrotropical forests is predicted to peak around 18:30 and 21:45 (Brehm *et al.*, 2005; Axmacher *et al.*, 2004). However some geometrid moths, one of the largest families of moth with over 21,000 species (Scoble, 1999) is predicted to peak at late night (Brehm *et al.*, 2005).

Foraging activity of *Hipposideros aff. ruber* followed a distinct trimodal pattern (Fig. 6.3) with major peaks in early night and morning. A trimodal activity pattern is not new to insectivorous bats (Kronwitter, 1988). Prior to midnight, activity increases but declines sharply after midnight. *Hipposideros aff. ruber* emerges immediately after the darker twilight to perhaps coincide with the first peak activity period of moths. In addition, it could be that their early emergence immediately after the twilight is to take advantage of the peak abundance of other insects as its diet can include up to 15 different prey items (Wright, 2009), although it forms a lesser

percentage of its food. Also, it is very likely that *Hipposideros aff. ruber* increases its foraging activities around midnight probably to coincide with some moth species such as those in the family geometridae that have a very late activity peak (Brehm *et al.*, 2005).

Foraging activity patterns in the study did not differ significantly between males and females. Females' activities, however, stopped completely around 22:00 hours and between 02:00 to 04:00 hours, whereas the males kept up at least some minimal activity during this time. This might explain why there was a significant difference between the duration each sex spent flying. It was noticed in the field that the bats made short flies that lasted for about 4 seconds while resting at the foraging area. It is suspected that these short flight events represent brief feeding flight towards an insect detected through echolocation by a perch hunting bat. Although this is highly speculative, perch hunting has been recorded in other Hipposiderid bats such as *Hipposideros commersoni* (Terry, 1977) and *Hipposideros diadema* (Brown and Berry, 1983) and confirmation of this strategy in *Hipposideros aff. ruber* could be very informative.

6.5.3 Roosting behaviour

There was a significant difference between visits made to the roost cave by both sexes at night with many visit by male bats. Males of *Hipposideros ruber* have been reported to defend harems in tree roost (Wright, 2009; Bell, 1987), but defence of harems in larger colonies such as caves may pose a greater challenge (Kunz *et al.*, 1983; Morrison and Morrison, 1981). Some male bats used individual tree roost (*Ceiba pentandra*) in the day and made repeated visits to the communal roost cave at

night. Making several trips to the roost cave at night by male bats might predict behavioural display of attempting to either look for mating partners or perhaps maintain harems if it exist in large colonies such as those in caves. This therefore might explain why repeated visits to the roost cave were preponderance of male bats. All tracked bats however used both individual roosts in their foraging area and the communal roost cave at night but the latter was preferred ($P < 0.05$). The usage of communal roost cave underlines the central role as a spatial platform for evolution of complex social organisation within populations of *Hipposideros* aff. *ruber* as reported in other Hipposiderid bats (Bell, 1987) and in other bats such as *Tadarida australis* (Rhodes and Catterall, 2008). The usage of communal roost cave and individual tree roost indicate their adaptability in roosting behaviour. Their reliance on tree as both day and night roost make them vulnerable to tree clearance and activities that removes dead trees (Waters *et al.*, 1999). Selected night roost of each bat was within their foraging area whereas day roost was farther away. It is conceivable that minimizing distance travelled at night to foraging area or communal roost cave predicted the location of night roost.

6.5.4 Conclusion and conservation implications

Increasing modified habitats as a result of loss of pristine forest are prominent factors affecting bat populations (Stebbing, 1995). The finding from this study suggests *Hipposideros* aff. *ruber* is adapted to foraging in many habitat types and requires a matrix of habitats to survive, but benefit greatly from fallow lands as hunting ground. In addition, some agricultural activities might prove threatening to their survival especially in instances where severe use of agrochemicals is evident. In such severely impacted agricultural landscapes, the only chance for bats is the

provision of tree canopies to allow bats commute to other regions within the landscape that support higher prey densities. It is recommended that fallow lands in agricultural landscapes be used as conservation units to support foraging bats. Lastly, the reliance of *Hipposideros aff. ruber* on trees as both day and night roost increases their vulnerability to anthropogenic activities, thus tree clearance from the landscape could threaten their survival.

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Chapter Seven

General Discussion

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General Discussion

7.1 Introduction

Bats form integral components of many ecosystems and provide important services such as pollination (Hodgkison *et al.*, 2003), dispersing of seeds of plants (Taylor *et al.*, 1999), control of insect numbers of which most are important agricultural pest (Boyles *et al.*, 2011), and their guano as important habitats for numerous species of animals (Fenolio *et al.*, 2006). Bat communities in the tropics are usually the most species-rich group of mammals. They are regarded as suitable indicator group for assessing habitat conditions as a result of their high diversity, endemism and species-specific habitat requirements (Weber and Fahr, 2007). In Ghana, these diverse group of mammals have been studied relatively little in comparison to other mammals. Aside the few records (Grubb *et al.*, 1999), and limited surveys from forest habitats (Decher and Fahr, 2007; Weber and Fahr, 2007; Decher and Bahian, 1999), bats roosting in caves have not been intensively studied.

Bats exploit different roost types such as caves, abandoned mines, rock crevices, hollow trees and branches of trees. Other bats are synanthropic and exploit human habitation. Caves are key resource for many bat species for protection from predators and provision of stable microclimatic (Churchill *et al.*, 1997). Some bat species have evolved to spend nearly their entire life roosting inside caves (Avila-Flores and Medellin, 2004; Kunz and Lumsden, 2003). Species like *Hipposideros jonesi* is a cave dependent insectivorous bat (Mickleburgh *et al.*, 2013).

Caves serve as platforms for community assembly and aggregation of several species of bats. In Ghana, the bat composition in caves, their community patterns and changes is not completely known. Also, the natural history of some of these bats is poorly understood. Moreover, most of Ghana's forest ecosystem has changed to agricultural ecosystems that severely impact wildlife. Their effects on foraging bats are yet to be assessed. There is therefore the need to provide information about the community of bats that roost in caves and assess the spatial and habitat requirement of some of these species in highly impacted agricultural landscape.

The main objective of this study was therefore to investigate the bat communities inside caves and ascertain the spatial and habitat requirements of *Hipposideros aff. ruber* which is the most abundant bat species roosting inside the investigated caves. To achieve this objective, five bat caves were studied for two years and thirteen individuals of *Hipposideros aff. ruber* were radio-tracked to understand some aspects of its ecology.

This chapter summarises significant findings from this study which is already provided in great detail from chapters three to six to gain a better understanding of communities of bats roosting inside Ghanaian caves. It provides a synopsis of the spatial requirements, foraging and roosting behaviour of *Hipposideros aff. ruber* presented in chapters four to six. Lastly it provides recommendations for future research.

7.2 Bat composition within caves in Ghana

About eighty-six species of bats are known to occur in Ghana (Weber and Fahr, 2007). Out of these species, nine were recorded from the five bat caves studied. Up to seven species were recorded to share a single roost. This is consistent with similar studies in Namibia that investigated ten different bat caves and found up to seven species sharing a single roost (Churchill *et al.*, 1997). Although one single cave can host several thousands of bats, they were populations of few species indicating that only few species are adapted to using cave roost. Due to the high variation in bat morphology, roosting behaviour, cave conditions and availability of other roost, it is not surprising that only few bats exploit cave roosting.

Bats select roost suitable to their thermoregulatory and water balance needs (Churchill *et al.*, 1997). Temperature and humidity are among the most influential factors in roost selection of bats (Rodríguez-Duran, 1995; McNab, 1982). The choice of roost may therefore vary from species to species. However, convergent evolution in morphology and diet also extends to ecological similarities in behaviour and patterns (Weber *et al.*, 2009). With the exception of *Rousettus aegyptiacus* and *Lissonycteris angolensis*, all recorded species were insectivorous bats. The study included only five bat caves, the total number of bat caves in the country is not known. As more caves are studied, it is possible to identify other species that also share cave roost with species identified in this work (Table 7.1). In this study, the predicted species richness (Jack 1) was almost the observed richness (Chapter three).

One interesting results in this work is that there was a significant difference in species composition among caves. Composition was significantly different among

the five caves (chapter three). Findings from this work suggest other bat caves in Ghana could host entirely different species. There was no significant difference between caves found in the same locality. Bat caves found in the same locality are thus expected to host similar species. It must be emphasized that this study investigated only five caves and results should be interpreted with caution. Nevertheless, significant difference in species composition suggest the preservation of different caves for the conservation of different species of bats.

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Approximately 10, 000 individual bats were sampled and *Hipposideros* cf. *ruber* (*Hipposideros* aff. *ruber* for lineages in Kwamang) was most abundant. Individual abundance was large for most of the species (Chapter three). Individual abundance of species is necessary in performing ecosystem services (Dornelas *et al.*, 2011). The conservation status of the nine species as indicated by the International Union for Conservation of Nature (IUCN) is provided in Table 7.1. Only the West African endemic bat *Hipposideros jonesi* is categorized as Near Threatened and almost vulnerable (Mickleburgh *et al.*, 2013). It depends on caves and other similar roost, usually roosting in few dozens and not recorded in any protected area (Mickleburgh *et al.*, 2013). The species roosts in few dozens and the largest population (300 individuals) was known from Ghana when it was described (Fahr, 2013). This species was only recorded in Kwamang suggesting the importance of Kwamang caves and its ecosystem for the survival of this species. Based on IUCN's assessment and results from this study, Kwamang caves may be key to the survival of this species and their protection constitutes a conservation priority.

Table 7.1: IUCN categorization of species

Species List	IUCN Red List #
<i>Hipposideros gigas</i>	Least concern
<i>Rousettus aegyptiacus</i>	Least concern
<i>Hipposideros abae</i>	Least concern
<i>Coleura afra</i>	Least concern
<i>Lissonycteris angolensis</i>	Least concern
<i>Rhinolophus landeri</i>	Least concern
<i>Hipposideros jonesi</i>	Near threatened
<i>Nycteris cf. gambiensis</i>	*
<i>Hipposideros cf. ruber</i>	*

#Date accessed, 23rd October 2013 (www.iucnredlist.org). *Taxonomy is incomplete so their conservation status was not checked.

7.3 Flight activity, foraging and roosting behaviour of *Hipposideros aff. ruber*

Findings in chapter four indicate that the sex of bats is important in determining flight activity level at the entrance of bat caves. The sum of in-flights and out-flights (arrivals and departures respectively) of individual bats per night were used as a measure of flight activity (Berkova and Zukal, 2006). Sex ratio for the two studied caves, KC1 and KC2 was not the same. This finding is consistent with studies reporting variation in sex ratios of bat populations (Andriafidison *et al.*, 2007). Variation in sex ratio in colonies of bats have been reported in populations of *Otomops madagascariensis* in Madagascar (Andriafidison *et al.*, 2007). Also, sex ratio in populations of *Hipposideros caffer* in Nigeria vary seasonally (Menzies, 1973). Sex ratio at KC1 was four males to one female and flight activity was

considerably higher at the entrance of this roost than KC2 where sex ratio was almost even. Male bats from KC1 contributed greatly to the increased flight activity at this cave. In addition, the activity of bats is closely linked to availability and occurrence of food within their home range (Erkert, 1982). Flight activity at the entrance of the roost caves is expected to increase considerably when food becomes abundant during some seasons.

The effects of temperature on flight activity was not included in the statistical analysis because of sample size (Fig. 4.7). Graphical exploration however indicated that when there is wide variation in nightly temperature range (i.e. difference between nightly maximum and minimum), flight activity tends to reduce with increasing temperature range. Temperature has been found to significantly affect the flight activity of temperate bats (Berkova and Zukal, 2010). Confirmation of this in future studies is recommended. Moreover, the distribution of flight activity was not similar for both caves. Flight activity was concentrated at certain parts of the night in KC1 and this was statistically significant. From chapter four, flight activity at the entrance of KC1 is busiest before 22:00 hours. Flight activity of most species of moths (major prey of *Hipposideros aff. ruber*) is expected to peak before 22: 00 hours in the tropics which could be a contributing factor (Brehm *et al.*, 2005; Axmacher *et al.*, 2004).

From radio-tracking studies (chapter six) although the activities of females reduces as it approaches this time 22:00 hours, males keep a sustained activity and makes repeated visits to the cave than females (chapter six). Males of *Hipposideros aff. ruber* defend harems in tree roosts (Bell 1987, Wright 2009). The bias sex ratio at

KC1 is caused by male repeated visits to the cave in order to perhaps secure mating partners or defend harems if it occurs in caves. At KC2 however, flight activity was not concentrated, it was uniform throughout. From chapter six, *Hipposideros aff. ruber* uses other roost such as hollow *Ceiba pentandra* trees within the agricultural landscape. At KC2, flight activity becomes active from 21:00 hours (chapter four) which is contributed mostly from arrivals (Fig. 4.6b) indicating most use day roost and visit after the first foraging bout. This is more evident during the morning when the number of those departing the cave exceeds those who are entering (Fig 4.6b). From chapter six (Fig. 6.3), *Hipposideros aff. ruber* has a trimodal foraging activity. It forages very actively in the first half of the night than the second night. Other insectivorous bats also exhibit a trimodal activity pattern (Kronwitter, 1988).

7.4 Spatial requirement of *Hipposideros aff. ruber*

In chapter five, the home range and spatial use within the home range of *Hipposideros aff. ruber* was investigated. Results from the thirteen radio-tracked individuals indicate that this bat uses a minimum of thirty-six hectares of land around its roost as the home range. There was however wide variation in the home range of the thirteen bats that were studied similar to observations in other insectivorous bats (Noer *et al.*, 2012; Zeale *et al.*, 2012; Goiti *et al.*, 2008). The home range of individuals could reach up to nearly one hundred hectares (Table 5.1), suggesting future studies should consider including many individuals to improve on the estimated home range. Within the home range of *Hipposideros aff. ruber*, findings in this thesis suggest up to 50% of this is used as the foraging area. The core use area of this bat was relatively small and forms about 2% of its home range. Insectivorous bats respond to areas of high insect abundance (Noer *et al.*, 2012;

Rydell, 1992). The core use area of a foraging bat in a new foraging area could form up to 50% but once knowledge of high insect densities are discovered, it reduces. Home ranges of this species were overlapping as reported for other species of bats (Monadjem *et al.*, 2009; Bontadina *et al.*, 2002; Russo *et al.*, 2002; Fenton, 1987). High intra-specific tolerance in home range is reported in some insectivorous bats (Rodrigues and Palmeirim, 2008; Lumsden, 2004) while others do not (Kerth *et al.*, 2001).

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The radio-tracked pregnant bats had smaller home ranges. The home range of some female insectivorous bat could be distinctly small in post lactating periods than when they are non-reproductive (Bontadina *et al.*, 2002). Non reproductive females of *Hipposideros aff. ruber* were found to have home ranges nine times larger than pregnant females. It is suspected that smaller home ranges in pregnant females are due to elevated energetic cost during pregnancy. In addition, the use of radio tags on flying animals affects their energetic cost and manoeuvrability (Hughes and Rayner, 1993). It is also possible that the use of the radio tags affected their home range size. It is proposed that pregnant females of *Hipposideros aff. ruber* should be avoided in future tagging studies till their mass carrying capacity established. The study therefore supports the 5% rule for placement of transmitters (Aldridge and Brigham, 1988) to that of studies that seemingly propose the use of larger transmitters for smaller bats.

Lastly, the estimated foraging range of *Hipposideros aff. ruber* was 1.2 km, close to predicted foraging range based on Jones *et al.* (1995) exponential equation. Other low wing loading insectivorous bats like *Nycteris thebaica* and *N. grandis* also travel

similar distances (Monadjem *et al.*, 2009; Fenton, 1987). *Hipposideros aff. ruber* is a low wing loading bat however a strong flyer capable of covering longer distances above 2.6 km as observed in this study. At least, a radius of three kilometres around its roost should be included in the protection of its home range.

7.5 Habitat preference for *Hipposideros aff. ruber*

Wildlife populations are severely impacted by habitat modification resulting from loss of pristine areas to habitats such as agriculture (Tylianakis *et al.*, 2007). The impact of these modified habitats which are mostly human induced are yet to be accessed for most species especially in Ghana. In chapter six, *Hipposideros aff. ruber* was monitored in a highly impacted agricultural landscape. The data suggest *Hipposideros aff. ruber* is adaptable and forages in many habitat types like other insectivorous bats (Zeale *et al.*, 2012; Zukal and Zdeněk, 2006). It however exhibits preference for some particular habitats that provide enough prey and canopy cover from predator during foraging. *Hipposideros aff. ruber* is a lepidoteran specialist (Dunning and Krüger, 1996; Bell and Fenton, 1983) and has been confirmed at Kwamang during dietary studies that it is a moth specialist (Badu *et al.*, Unpublished) and thus expected to select habitats rich in moth densities over other habitats. Among the six habitats available around its roost, it preferred to forage in semi-natural habitats which were mainly fallow lands within the landscape. Habitats like cocoa farms although had good canopy cover for protection from predators, were less important for foraging. This was primarily so because they lack understorey vegetation that could support enough prey insects, and secondly the few available insects could be impacted severely from the use of agrochemicals by farmers to improve crop yield.

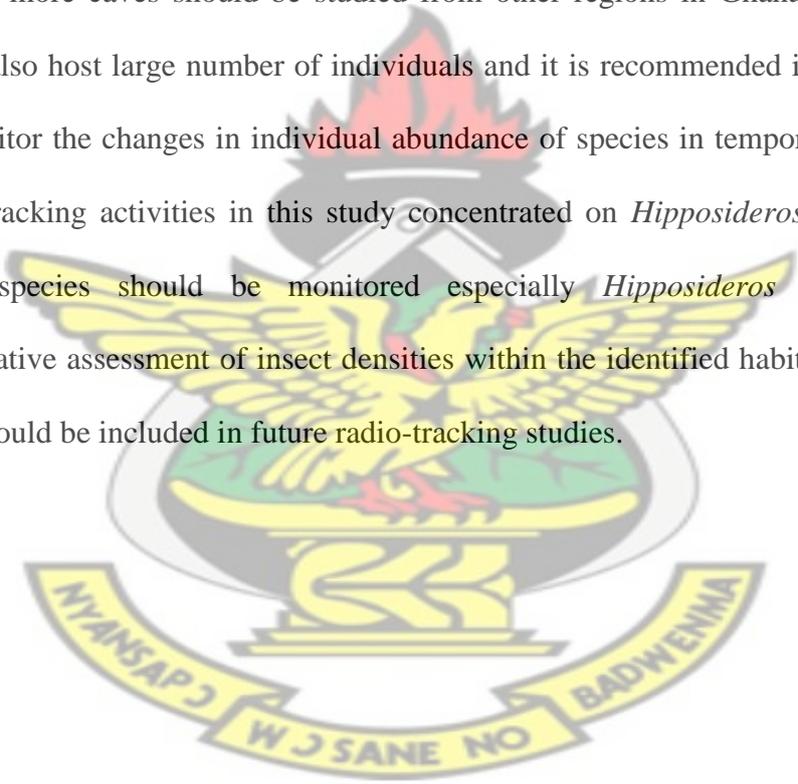
Severe use of agrochemicals significantly impacts insects (Desneux *et al.*, 2007). This could prove threatening to many foraging insectivorous bats. However, cocoa farms were predominantly used as flight paths to commute between roost cave and foraging areas as a result of good canopy cover protecting them from predators like owls that are ubiquitous in the landscape. This underlines the importance of canopy trees for foraging bats in highly impacted agricultural ecosystem. It is proposed that in highly impacted ecosystems, a mosaic of canopy trees should be provided to allow bats commute from roost to nearby habitats that provide enough prey.

7.6 Conclusion and recommendation

Ghanaian caves are important roosting sites for many bats and may be a haven for some threatened species such as *Hipposideros jonesi*. The investigated caves in this study are dominated by *Hipposideros cf. ruber*. The study found differences in species composition of five caves. Despite dominance by *Hipposideros cf. ruber*, results support preservation of different caves for the conservation of different species of bats. The spatial requirement of one of the most common bat species in Ghana, *Hipposideros aff. ruber* is provided for the first time. It uses a minimum of about thirty-six hectares around its roost as the home range. Despite its low wing loading ability, it is capable of flying over remarkably longer distances. Conservation activities seeking for the protection of their home range should consider including a minimum of three-kilometre radius around its roost. Also for *Hipposideros aff. ruber* dominated caves, it is expected that flight activity is busiest from flight out till about 22: 00 hours and human activities at the cave during this

period should be avoided. In addition, *Hipposideros* aff. *ruber* selected fallow lands during foraging in a highly impacted agricultural ecosystem whilst using cocoa farms as flight paths. It is recommended that in highly modified habitats such as agricultural landscapes, canopy trees should be provided to allow bats to commute to nearby habitats that provide enough prey to ensure their survival.

Four recommendations are made for future research based on the findings in this thesis. First, in order to get a holistic view of the species of bats using caves in Ghana, more caves should be studied from other regions in Ghana. Secondly, the caves also host large number of individuals and it is recommended in future studies to monitor the changes in individual abundance of species in temporal scales. Also, radio-tracking activities in this study concentrated on *Hipposideros* aff. *ruber* and other species should be monitored especially *Hipposideros jonesi*. Lastly, quantitative assessment of insect densities within the identified habitats in the study area should be included in future radio-tracking studies.



References

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Appendices

KNUST



Appendix 1

Proportions of species sampled from each cave.

Species	BC1	BC2	FOC	KC1	KC2	Grand Total
<i>Coleura afra</i>	82	193	92	0	0	367
<i>Hipposideros abae</i>	35	227	103	343	184	892
<i>Hipposideros gigas</i>	0	17	10	22	31	80
<i>Hipposideros jonesi</i>	0	0	0	50	13	63
<i>Hipposideros aff. ruber</i>	1478	1887	1242	2197	1457	8261
<i>Lissonycteris angolensis</i>	2	36	85	1	1	125
<i>Rousettus aegyptiacus</i>	14	0	0	0	0	14
<i>Rhinolophus landeri</i>	0	0	16	0	2	18
<i>Nycteris cf. gambiensis</i>	8	15	167	16	200	406



Appendix 2

Results from rarefaction performed in Ecosim. Rarefaction compares the five caves for their species richness and inventory completeness at the same abundance level. Results were used to plot species accumulation curves for inventory completeness.

Sampling Efforts	BC1	BC2	FOC	KC1	KC2
1	1	1	1	1	1
2	2.5065	3.444	4.5367	2.6914	3.393
3	3.223	4.1009	5.4443	3.2541	3.9379
4	3.9898	4.773	6.0687	3.9295	4.4972
5	4.4258	5.2004	6.3721	4.3438	4.8182
6	4.7084	5.4639	6.5769	4.5993	5.0385
7	4.9275	5.6492	6.713	4.7779	5.2134
8	5.0926	5.7625	6.8102	4.9081	5.3411
9	5.2011	5.8368	6.8711	4.9903	5.4585
10	5.3092	5.8861	6.9132	5.0539	5.5443
11	5.3924	5.9302	6.9459	5.1027	5.6356
12	5.4697	5.9578	6.9617	5.1587	5.7049
13	5.634	5.9895	6.9909	5.2331	5.9111
14	5.6664	5.9917	6.9947	5.2596	5.9691
15	5.7097	5.9961	6.9975	5.2901	6.0366
16	5.7538	5.9967	6.9987	5.3121	6.0895
17	5.7775	5.9981	6.9991	5.32	6.1442
18	5.7989	5.9991	6.9992	5.3401	6.192
19	5.8259	5.999	6.9998	5.3544	6.2559
20	5.8511	5.9996	6.9998	5.372	6.2999
21	5.8801	5.9998	6.9999	5.4035	6.37
22	5.8922	6	6.9999	5.4147	6.413
23	5.9165	5.9998	7	5.4383	6.4471
24	5.9338	6	7	5.4613	6.5014
25	5.9482	6	7	5.4732	6.5499
26	5.9624	6	7	5.5005	6.597
27	5.9724	6	7	5.5136	6.6353
28	5.9809	6	7	5.5277	6.6768
29	5.9904	6	7	5.5531	6.7214
30	5.9942	6	7	5.574	6.7552
31	5.9897	6	7	5.5526	6.7106
32	5.9947	6	7	5.5762	6.7565

Appendix 3

Call:

```
metaMDS(comm = comm, distance = "bray", k = 2, trymax = 20, noshare = 0.1,  
expand = T, trace = 1, plot = F)
```

```
Data: wisconsin(sqrt(comm))
```

```
Distance: bray shortest
```

```
Dimensions: 2
```

```
Stress:
```

```
Data Stress:
```

```
initial value 23.890523
```

```
iter 5 value 17.105345
```

```
iter 10 value 15.605901
```

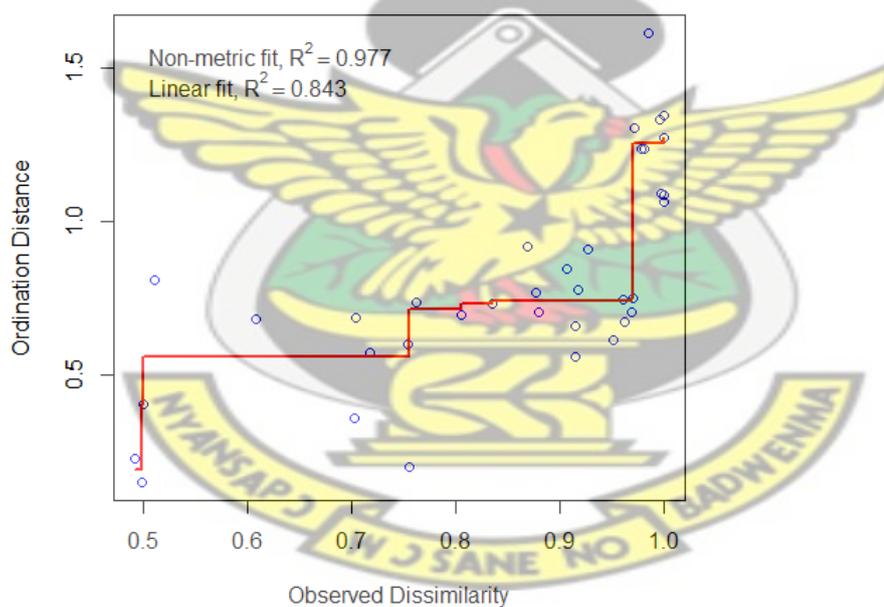
```
final value 15.248499
```

```
converged
```

```
Scaling: centring, PC rotation, halfchange scaling
```

```
Species: expanded scores based on 'wisconsin(sqrt(comm))'
```

Stress plot of data



Appendix 4

TukeyHSD(mod)

Tukey multiple comparisons of means

95% family-wise confidence level

Fit: aov(formula = distances ~ group, data = df)

\$group

Compared Caves	Difference	Lower	Upper	P-Adjusted
BC2-BC1	-0.10760378	-0.24935994	0.034152	0.2081116
FOC-BC1	-0.09687188	-0.24290306	0.049159	0.3293784
KC1-BC1	-0.13200562	-0.27376179	0.009751	0.047731
KC2-BC1	-0.09223363	-0.23398979	0.049523	0.3481986
FOC-BC2	0.0107319	-0.12511514	0.146579	0.9993641
KC1-BC2	-0.02440184	-0.15564255	0.106839	0.9827241
KC2-BC2	0.01537015	-0.11587056	0.146611	0.9970267
KC1-FOC	-0.03513374	-0.17098078	0.100713	0.9434879
KC2-FOC	0.00463825	-0.13120879	0.140485	0.9999773
KC2-KC1	0.039772	-0.09146871	0.171013	0.9037324



Appendix A



Plate A.1: *Hipposideros* cf. *ruber*

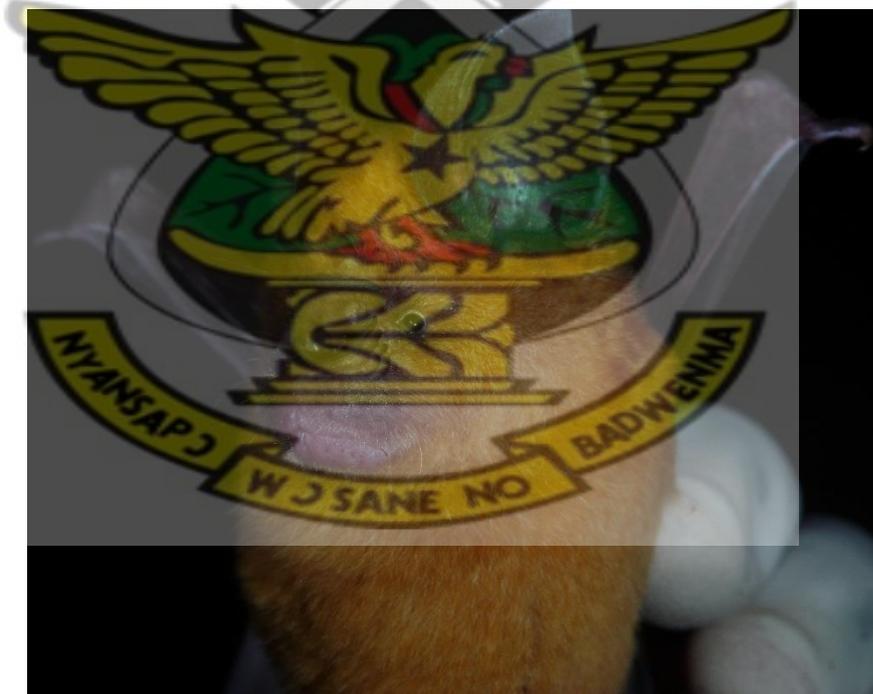


Plate A.2: *Hipposideros* *abae*



Plate A.3: *Hipposideros jonesi*

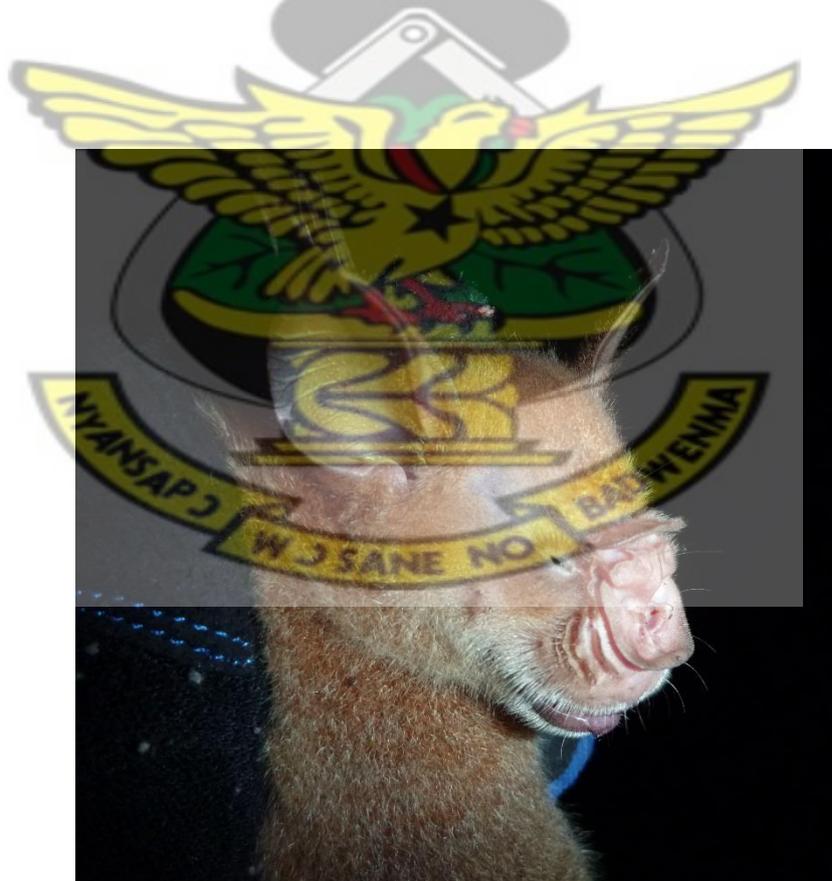


Plate A.4: *Hipposideros gigas*



Plate A.5: *Nycteris* cf. *gambiensis*

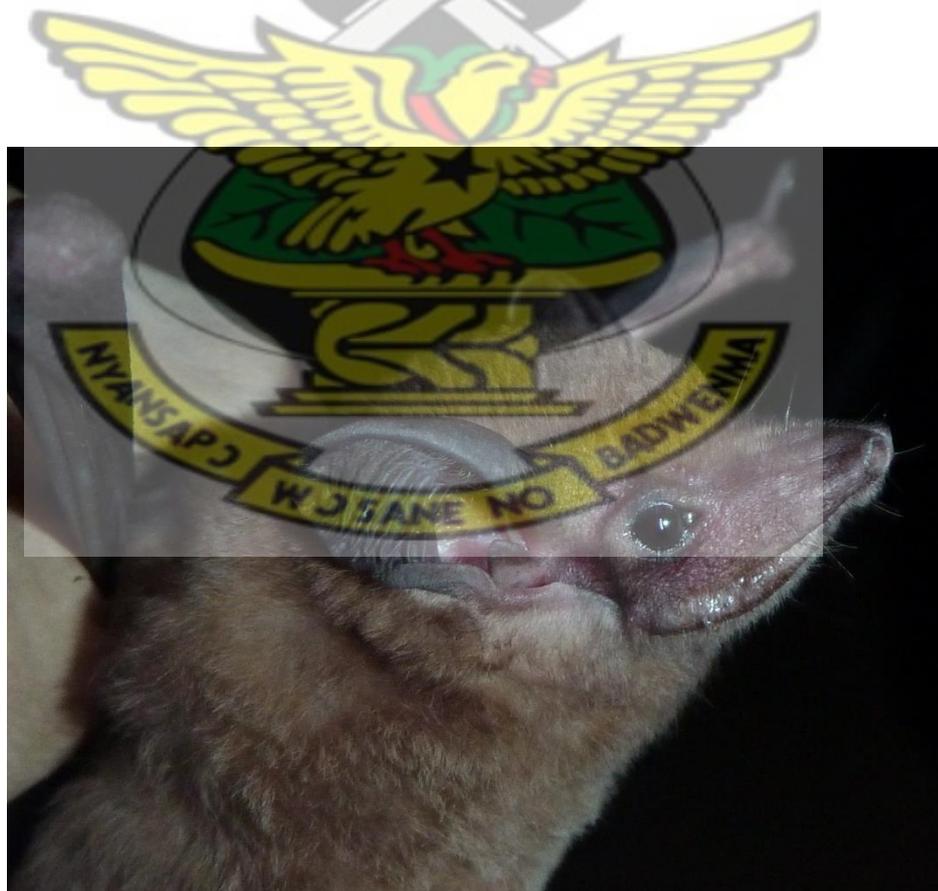


Plate A.6: *Coleura afra*



Plate A.7: *Rhinolophus landeri*

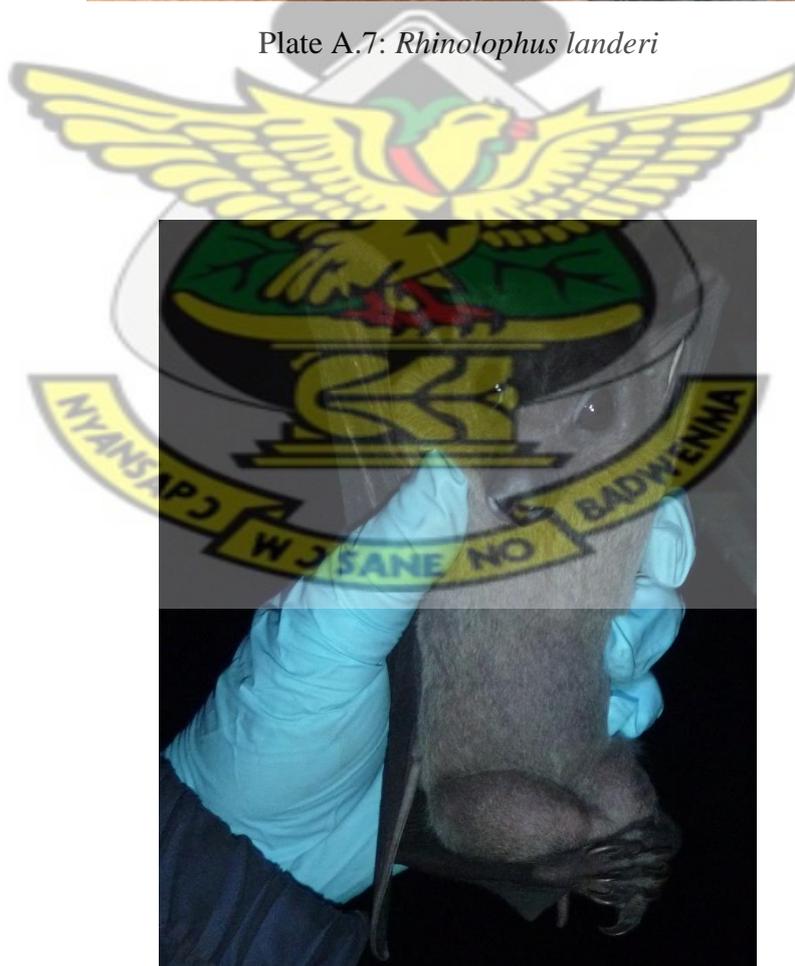


Plate A.8: *Rousettus aegyptiacus*



Plate A.9: *Lissonycteris angolensis*



Appendix B



Plate B.1: iButton temperature and humidity data logger

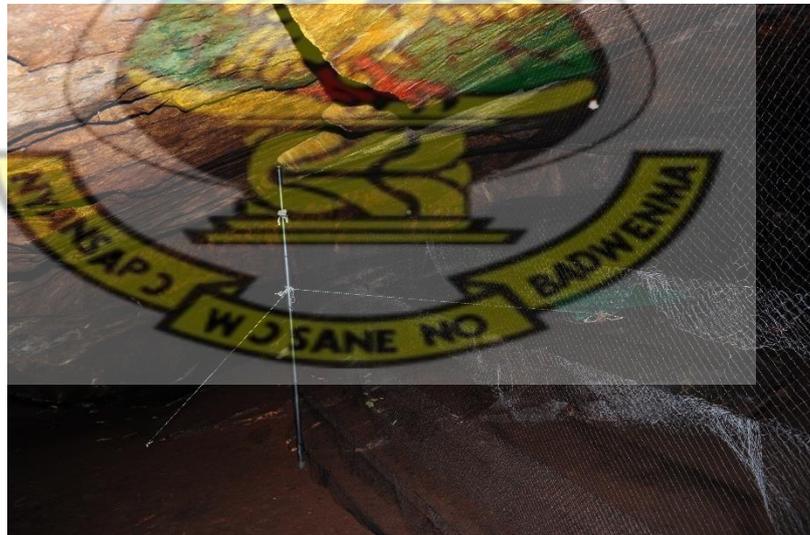


Plate B.2: Mist net in front of root cave



Plate B.3: Researcher removing a netted bat

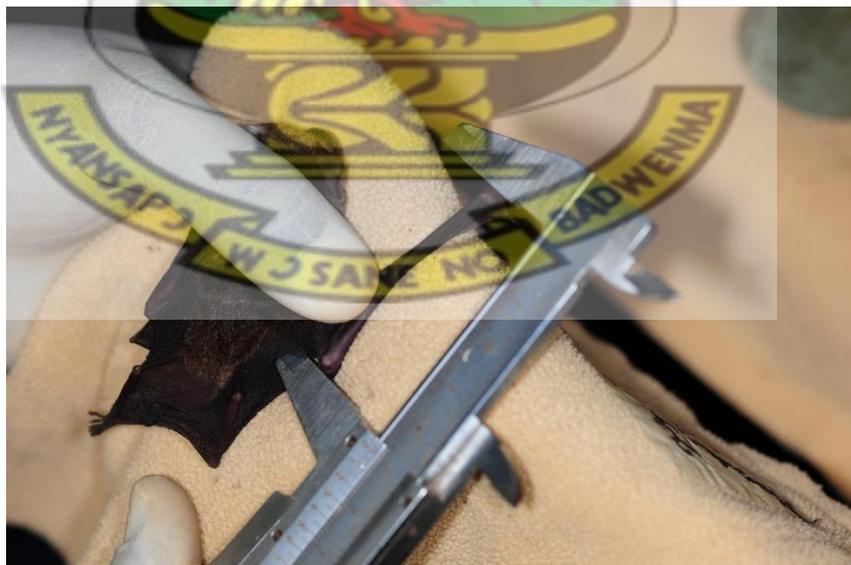


Plate B.4: Measuring of forearm length of bat



Plate B.5: Researcher recording details of bats. Top right: hanged bats (inside airy bags)

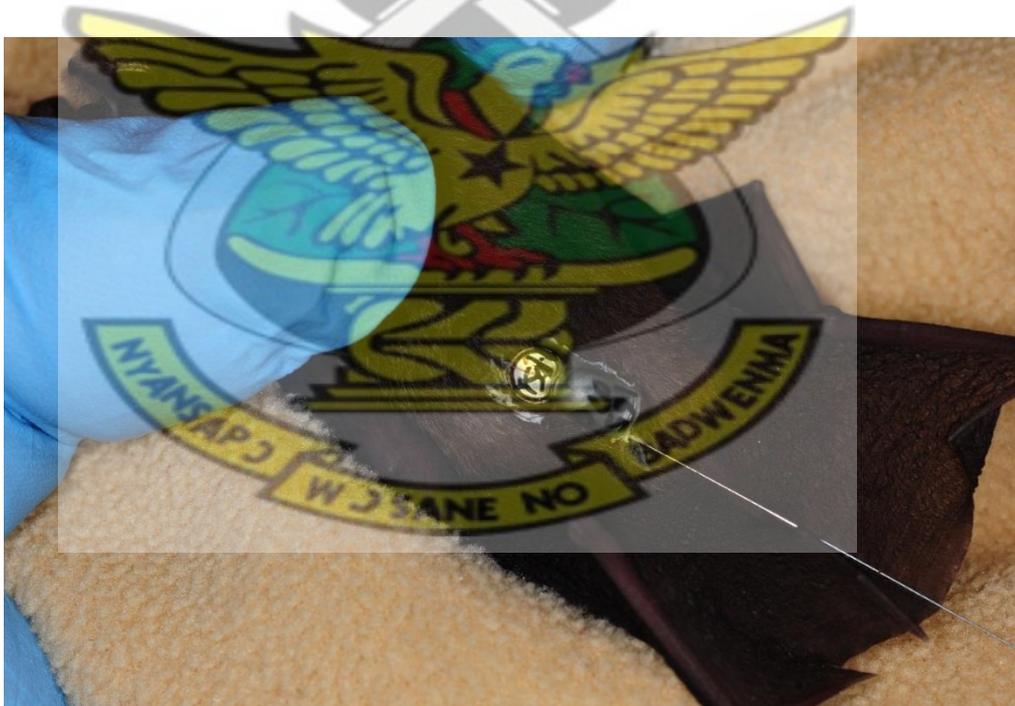


Plate B.6: A recaptured bat with position sensitive transmitter after radio-tracking



Plate B.7: Researcher looking for radio signal



Plate B.8: Research team that assisted in data collection