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ECOLOGY OF FRUIT BATS IN GHANA, WITH SPECIAL FOCUS ON  
*EPOMOPHORUS GAMBIANUS*, AND THE ROLE OF FRUIT BATS IN ZOOLOGICAL  
DISEASE TRANSMISSION

BY

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## DECLARATION

I hereby declare that this thesis and the work presented in it are my own and have been generated by me as the result of research work undertaken under supervision.

I certify that to the best of my knowledge, this thesis has neither been presented wholly nor partially to any other University for a degree. I confirm that this work contains no material previously published or written by another person, except where reference to other people's work has been clearly stated and any help received duly acknowledged.

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## ABSTRACT

Bats are a unique order of mammals that are known to play vital roles in ecosystems and are also an important source of emerging zoonotic diseases of significant health importance. Knowledge of the ecology for several species, particularly fruit bats (Pteropodidae) is lacking and this limits our understanding of the role bats play in ecosystem functioning, disease transmission and hinders their management and conservation. The overall aim of this study was to describe the ecology of fruit bats in Ghana with particular reference to *Epomophorus gambianus*, and the role fruit bats play in possible emergence and transmission of zoonotic diseases. Specifically, this study sought to document the distribution of fruit bats in Ghana, determine demographic parameters and reproductive characteristics and describe aspects of the roosting and feeding ecology of *E. gambianus*. The study also focused on providing further serological evidence for prevalence of zoonotic viruses in fruit bats in Ghana and identifies human bat interactions that can serve as potential routes for zoonotic disease transmission. The study used direct field observations involving roost searches and mapping, mist netting, radio-tagging, faecal collection and plant phenological studies, as well as an innovative citizen science approach and questionnaire administration to collect empirical and biological data to address the aims of the study. Ten of the 13 species of fruit bats reported for the West African sub-region were recorded in this study. These were *Epomophorus gambianus*, *Eidolon helvum*, *Nanonycteris veldkampii*, *Epomops franqueti*, *Epomops buettikoferi*, *Hypsignathus monstrosus*, *Lissonycteris angolensis*, *Megaloglossus woermanni*, *Rousettus aegyptiacus* and *Micropteropus pusillus*. Roosts belonging to five species of fruit bats were identified in 74 different locations across the country. This is the first study that has attempted the nationwide description of the distribution of roost sites for fruit bats in Ghana. Most of the colonies identified occurred

in close proximity to humans and in densely populated places. Majority of the roosts identified belonged to *E. helvum* and *E. gambianus* and several roosts were identified for the first time, although they had been occupied or used intermittently by bats for ten or more years. Trapping of bats at eleven different sites showed that *E. gambianus* and *E. helvum* were the most common fruit bat species in Ghana. Out of the 6,132 bats captured the two species accounted for 75%. By analyzing faecal and ejecta pellets collected under day roosts and from captured bats over a two year period, *E. gambianus* was found to utilise fruits and flowers from 35 plant species, including some economically important ones. Monthly monitoring of plants for fruit and flower abundance indicated that fruits were relatively available throughout the year but in varying quantities, with peaks during the rainy seasons. Flowers were mostly abundant during the dry season and potentially contributed up to 79% of the diet of bats during this season. Roost selection analysis showed that *E. gambianus* was more likely to select trees species such as *Magnifera indica*, *Ficus* sp., *Azadirachta indica*, and *Polyalthia longifolia* trees for roosting, and showed preference for bigger, taller trees. Roosting sites were also more likely to be closer to buildings and less likely to occur in areas with high tree densities. Roosts with higher number of bats, and were more frequently occupied by bats were more likely to be utilised as maternal roosts. Radio-tracking of 60 bats suggested a fission-fusion roosting system in *E. gambianus*. Female bats used a relatively smaller roosting area compared to males. Based on the proportion of adult females detected to be pregnant and lactating for each month, the reproductive rate of *E. gambianus* was estimated to vary between 0.56-1.0 offspring per female per reproductive season, while that for *M. pusillus* varied between 0.80 to 1.0 offspring per female per reproductive season. This study confirmed the reported reproductive chronology of *E. gambianus* and *M. pusillus* as continuous bimodal polyoestry, with post partum oestrus in Ghana. There

was strong synchrony in parturition among most of the fruit bat species that were assessed in this study. The overall sex ratio for *E. gambianus* was male biased but varied for each age class and over different years. Capture-recapture analysis gave an estimated monthly survival of 0.81 (95% CI-0.74-0.86) for *E. gambianus* with slight variation between sexes and age groups. Monthly survival for *M. pusillus* varied between 0.92 (95% CI-0.62-0.99) for adult males to 0.77 (95% CI-0.65-0.86) for immature females. This is the first study to provide estimates of these important demographic parameters for a colony of *E. gambianus* and *M. pusillus* in Africa. Females of *E. gambianus* attained sexual maturity at 6 months, while males matured after about 11 months. Juveniles that were born and grew through the rainy seasons were significantly bigger (forearm length:  $77 \pm 4$  mm vs.  $74 \pm 4$  mm;  $p < 0.0001$ ) and heavier (weight:  $67 \pm 12$  g vs.  $59 \pm 12$  g;  $p < 0.0001$ ) than those that were born and grew through the dry seasons. A cross-sectional serosurvey conducted for 1,047 blood samples from six species of fruit bats that were sampled during this study indicated the presence of antibodies to Hendra virus, Nipah virus and Cedar virus in several of these species of fruit bats. Seroprevalence of henipaviruses were highest in *E. Helvum*, with evidence of sex and age effect on seroprevalence rates. Hunting of bats, fruit collection, contact with bat urine and faeces under roosts were identified as some of the common potential human-bat interaction pathways that could facilitate spillover of zoonotic pathogens from bats. The findings of this study are important in bridging the knowledge gap about the ecology of fruit bats and provide important estimates which can be incorporated in future analysis of infection and spillover dynamics in bats and how bat ecology can influence and drive disease dynamics.

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Dr. Richard Suu-Ire and Mr. Meyir Ziekah from the Veterinary Services Department and the Wildlife Division of the Forestry Commission of Ghana assisted with the routine blood sampling from the bats captured.

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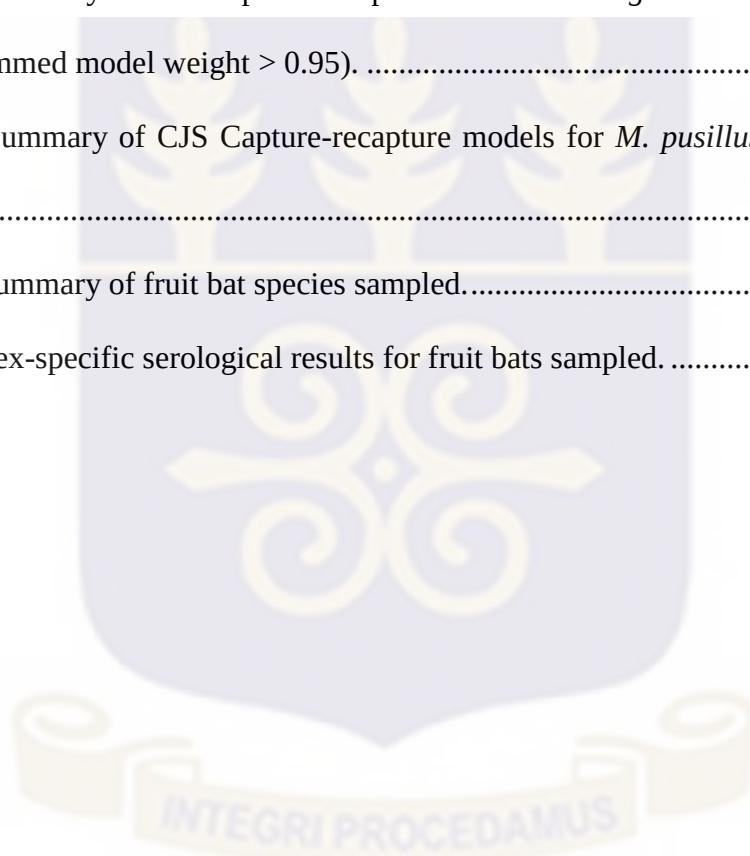


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## LIST OF ABBREVIATIONS

|        |                                                          |
|--------|----------------------------------------------------------|
| AD     | Adult                                                    |
| AIC    | Akaike Information Criterion                             |
| AICC   | Akaike Information Criterion corrected for small samples |
| CedV   | Cedar virus                                              |
| CedV-G | Cedar virus protein G                                    |
| CI     | Confidence interval                                      |
| CJS    | Cormack-Jolly-Seber                                      |
| cm     | Centimetre                                               |
| CMR    | Capture-Mark-Recapture                                   |
| COSHH  | Control of Substances Hazardous to Health                |
| DBH    | Diameter at breast height                                |
| DRC    | Democratic Republic of Congo                             |
| EID    | Emerging Infectious Disease                              |
| FA     | Forearm                                                  |
| g      | Gram                                                     |
| GHC    | Ghana Cedi                                               |
| GMT    | Greenwich Mean time                                      |
| GOF    | Goodness-of-fit                                          |
| GPS    | Global positioning system                                |
| h      | Hour                                                     |
| H'     | Shannon Index                                            |
| ha     | Hectare                                                  |
| HeV    | Hendra virus                                             |

|          |                                                                                |
|----------|--------------------------------------------------------------------------------|
| HeV-F    | Hendra virus protein F                                                         |
| HeV-G    | Hendra virus protein G                                                         |
| HIV/AIDS | Human immunodeficiency virus infection and acquired immune deficiency syndrome |
| IoZ      | Institute of Zoology                                                           |
| IQR      | Inter quartile range                                                           |
| ITCZ     | Inter-tropical convergent zone                                                 |
| IUCN     | International Union for Conservation of Nature                                 |
| Juv      | Juvenile                                                                       |
| k        | number of parameters                                                           |
| KAM      | Kofi Amponsah-Mensah                                                           |
| km       | Kilometre                                                                      |
| LCL      | Lower confidence interval                                                      |
| ln       | Natural log                                                                    |
| m        | Metre                                                                          |
| mAb      | Monoclonal antibody                                                            |
| MCP      | Minimum Convex Polygon                                                         |
| MFI      | Median fluorescence intensity                                                  |
| MHz      | Megahertz                                                                      |
| ml       | Millilitre                                                                     |
| mm       | Millimetre                                                                     |
| NiV      | Nipah virus                                                                    |
| NiV-F    | Nipah virus protein F                                                          |
| NiV-G    | Nipah virus protein G                                                          |
| °C       | Degree Celsius                                                                 |

|          |                                                    |
|----------|----------------------------------------------------|
| PA       | Protected Area                                     |
| PC       | Personal Computer                                  |
| PIT      | Passive Integrated Transponder                     |
| RFID     | Radio frequency Identification                     |
| RNA      | Ribonucleic acid.                                  |
| SARS-CoV | Severe acute respiratory syndrome coronavirus      |
| SD       | Standard deviation                                 |
| SI       | Sexually Immature adult                            |
| SPSS     | Statistical Package for the Social Sciences        |
| UCL      | Upper confidence interval                          |
| UENR     | University of Energy and Natural Resources         |
| UK       | United Kingdom                                     |
| USA      | United States of America                           |
| USAID    | United States Agency for International Development |
| USD      | United States Dollar                               |
| w        | Model weight                                       |
| ZSL      | Zoological Society of London                       |





## CHAPTER ONE

### 1.0 INTRODUCTION

#### 1.1 Background

Globally, life forms are very diversified and there is a great number of wild animals spread across varying landscapes and habitats (Sahney *et al.*, 2010). Within each of these landscapes and habitats, there exists an extensive array of niches, macro and micro-habitats. These support species and each taxon, in turn, supports a much greater diversity of micro and macro-parasites and pathogens (Bengis *et al.*, 2004). Occasionally, these pathogens jump from their animal and wildlife origins and break the animal/wildlife barrier to humans and successfully cause zoonotic infections in humans.

Bats (Order Chiroptera) are a taxonomically and ecologically diverse group of animals that make up over 20% of all mammal species (Simmons, 2005; Happold & Happold, 2013). Bats have several unique characteristics that make them important providers of ecosystem services and also increase their propensity to serve as hosts of several zoonotic pathogens (Calisher *et al.*, 2006; Wong *et al.*, 2007; Drexler *et al.*, 2012; Luis *et al.*, 2013).

Bats play vital roles in ecosystem service provisioning, with different species playing varying roles at different trophic levels in pollination of plants including economically important species (Mosley, 1879; Fujita & Tuttle, 1991; Mickleburgh *et al.*, 1992), seed dispersal (Muscarella & Fleming, 2007; Kunz *et al.*, 2011) and insect control (Kunz *et al.*, 2011). These roles have earned bats keystone species status in some ecosystems (Mickleburgh *et al.*, 2002). Of particular focus in this study are bats of the family Pteropodidae, which are commonly referred to as flying foxes or fruit bats.

Fruit bats occur extensively in African ecosystems and are well represented in West Africa (Rosevear, 1965; Yeboah, 2008). They feed exclusively on plants. Fruit bats are also hunted as food across most of their range (Mickleburgh *et al.*, 2009; Kamins *et al.*, 2015). Most species of fruit bats are considered either threatened, vulnerable or endangered on the IUCN Red List (Mickleburgh *et al.*, 1992;2002). Key threats to fruit bat species include hunting and other anthropogenic causes such as habitat degradation and loss of suitable habitat (Lacki & Baker, 2007; Mickleburgh *et al.*, 2009).

The increase in emergence of zoonotic diseases has been linked to several factors. Most of these factors are anthropogenic in nature and often result from increasing contact between humans and wildlife. In the past years, there has been persistent expansion into, and encroachment on wildlife habitats as a result of increasing human population, causing people to come into contact more frequently with wild animals and their pathogens (Morse, 1995; Daszak *et al.*, 2000; Aluwong & Bello, 2010; Hayman, 2011). Encroachment into wildlife habitats may have played a key role in the emergence of diseases such as Marburg and Ebola in Africa (Daszak *et al.*, 2000; Aluwong & Bello, 2010). Rapid population increase and the need for increase in food production have also led to rapid agricultural expansion. Agricultural expansion usually brings people and/or domestic animals into contact with pathogens or their reservoir hosts and often changes the ecological conditions to favour the increased population of the pathogen or host (Morse, 1995). Another impact of the increased human population is the demand for natural resources including bushmeat. Hunting is one of the primary routes for human-wildlife interaction, bringing people into contact with wild animals with increased risk of zoonotic infection (Wolfe *et al.*, 2005). Other factors include increased international travel and globalization of trade, climate change and environmental changes that alter the

distribution of wild hosts and vectors, thereby enhancing the chances of transmission of infectious agents (Morse, 1995; Daszak *et al.*, 2000; Bengis *et al.*, 2004).

Fruit bats have been implicated in some of the most serious outbreaks of viral diseases of zoonotic origin, particularly, viruses of the family Paramyxoviridae (paramyxoviruses) and Filoviridae (Filoviruses). These viruses cause diseases with high fatality rates in both humans and domestic animals (Drexler *et al.*, 2009; Clayton *et al.*, 2013; Pigott *et al.*, 2014). Fruit bats are known to have caused outbreaks of Nipah virus in Malaysia, India and Singapore (Drexler *et al.*, 2009; Clayton *et al.*, 2013) and Hendra virus outbreaks in Australia (Murray *et al.*, 1995; Plowright *et al.*, 2011). Fruit bats are also suspected to be the likely host and cause of several Ebolavirus disease outbreaks including the outbreak in West Africa in 2014 (Pigott *et al.*, 2014; Chiappelli *et al.*, 2015).

Bats are numerous and diverse in species and are found almost everywhere. Their widespread distribution increases their chances of exposure to a wide variety of pathogens which they can transmit to humans and other animals. Bats occupy several niches and habitats including man-made structures which get them into frequent contact with humans and domestic animals. The flight ability in bats implies that they have the potential for rapid widespread dispersal. Hence bats can easily carry and transmit pathogens between otherwise very distant and disconnected habitats. The ability to fly also allows for continual connectivity between otherwise isolated groups which can help maintain infections among dispersed populations. Infections have the potential to persist longer within bats because of the high longevity of bats; when adjusted for body mass, bats have the highest longevity among mammals (Calisher *et al.*, 2006).

In evolutionary terms, bats have existed in their current forms for a very long time. This has led to a long evolutionary and ecological relationship between bats and several

viruses, with possible co-evolution between them (Calisher *et al.*, 2006; Drexler *et al.*, 2012). Several species of bats also have highly gregarious social structures such as the formation of large dense roosts, which provide suitable conditions for the exchange of viruses and pathogens among individuals (Bennett, 2006; Klug *et al.*, 2011). Parturition between many bat species are often synchronised, resulting in periods of high influx of vulnerable young and this can easily affect disease dynamics within populations (Hayman *et al.*, 2013).

Despite the important roles of bats in the ecosystem and public health, there is limited knowledge on the ecology of bats. Several species, representing about 60% of all fruit bat genera remain to be assessed properly (Calisher *et al.*, 2006). Because of the costs of zoonotic Emerging Infectious Diseases (EIDs) on public health and national economies, a better understanding of bat distribution and ecology to improve our ability to forecast where and how future emergence of bat transmitted zoonotic diseases will occur and reduce the risks of infection is essential.

This is the context within which this study is set, with the aim of contributing to the knowledge about the ecology of fruit bats that occur in Ghana and their role in zoonotic disease transmission.

## **1.2 Justification**

There is a general recognition of bats as reservoirs and potential reservoirs of several infectious agents (Calisher *et al.*, 2006; Clayton *et al.*, 2013; Hayman *et al.*, 2013; Luis *et al.*, 2013). Bats exhibit several behavioural and ecological characteristics that enable them to be suitable hosts for many viruses, and according to Luis *et al.* (2013) bats harbour more viruses than even rodents.

Globally, the cost of zoonotic disease outbreaks in which bats have been implicated run into millions of dollars. However, despite the great concern of the role of bats in zoonotic disease transmission, very little is known about most bat species, especially aspects of their biology and ecology (Limpert *et al.*, 2007; Richter & Cumming, 2008). Because of the disastrous outcome of emerging zoonotic diseases on human health and wildlife conservation, it is critical that we improve our perception of how bat ecology may drive disease dynamics (Hayman *et al.*, 2013). There has been no recorded outbreak of a zoonotic disease from bats in Ghana to date, but Ghana has been identified as a hotspot for risk of disease emergence from bats (Pigott *et al.*, 2014; Brierley *et al.*, 2016). Thirteen fruit bat species occur in Ghana and evidence of circulation of zoonotic viruses in several species of fruit bats have been reported (Leroy *et al.*, 2005; Hayman *et al.*, 2008a; Hayman *et al.*, 2008b; Wright *et al.*, 2010) with spillover to some domestic animals highlighted (Hayman *et al.*, 2011).

Demographic parameters of bats can be vital in understanding disease dynamics and in predicting infections in populations, but such information is largely lacking (Hayman *et al.*, 2013). For instance, in a very common and widely studied species such as the Straw coloured fruit bat *Eidolon helvum*, a key demographic parameter such as adult survival rate, was only recently estimated by Hayman *et al.* (2012a) and was the first for any Pteropodidae. Demographic parameters for instance survival and birth rates, can help to determine the dynamics of wild animal populations and can also help to predict periods of infections in populations and how infections persist (Hayman *et al.*, 2013). Ecological parameters such as species' reproduction, synchronised parturition, sex differences in distribution and species' sympatry influence disease dynamics (Streicker *et al.*, 2010; Wood *et al.*, 2012; Hayman *et al.*, 2013), hence the need for better documentation and quantification of such parameters. Knowledge of the feeding ecology of fruit bats (e.g.



food sources and feeding sites) can help to inform how bats influence and contribute to local ecosystem functioning. Availability of such knowledge will increase understanding of how rapid anthropogenic land use practices will influence bat behaviour and populations and help to identify points of bat interactions with humans and livestock, particularly where resources are shared (Wood *et al.*, 2012).

Some fruit bat roosts have been documented in Ghana especially large roosts in cities (e.g. 37 Hospital roost in Accra) and rural areas. These are mostly roosts of *Eidolon helvum* and information on distribution of roosts of other species (e.g. *Epomophorus gambianus*) remains scanty. Even for *E. helvum*, some roosts remain to be located and documented especially those that may be occupied only seasonally or used as stopovers during this species' migratory movements.

Our ability to understand, properly predict and investigate zoonotic disease emergence and spillover events depends to a large extent on our knowledge of the ecological strategies of the host (in this case bats). Host ecological strategies are important drivers of disease emergence and dynamics (Hayman *et al.*, 2013). Additionally, to prevent spillover of viruses from bats, an understanding of the linkage between bat habitat use and human/livestock activity is vital in predicting and explaining patterns of emergence (Hahn *et al.*, 2014). Knowledge of bat ecology is also required to deploy appropriate measures that ensure safe co-existence of humans and bats without exposing humans to risks of disease spillover or compromising on bat conservation. An uninformed or wrong perception of bats and disease transmission can lead to eradication efforts that may cause the loss of important bat ecosystem services and may end up increasing spillover risks (Wood *et al.*, 2012).

This study focuses on aspects of the ecology of fruit bat species in Ghana and their role in zoonotic disease transmission. The results of this study will increase knowledge on bat ecology to better inform zoonotic disease and spillover dynamics and help in the future predictions of disease emergence and prevention. The results will inform also, future directions for the conservation of fruit bat species in Ghana.

### **1.2.1 Aims and objectives**

The overall aim of this study was to describe the ecology of fruit bats in Ghana with particular reference to the Gambian epauletted fruit bat *Epomophorus gambianus*, and the role fruit bats play in the transmission of zoonotic diseases.

The specific objectives of this study were to:

- Document the distribution and estimate the population of fruit bats in Ghana
- Determine the diet of *E. gambianus* and describe seasonal variations in food availability;
- Investigate the roosting behaviour and site selection of *E. gambianus*;
- Determine demographic parameters of fruit bats in Ghana
- Provide further serological evidence for prevalence of zoonotic viruses in fruit bats in Ghana and identify human bat interactions that can serve as potential routes for zoonotic disease transmission.



## CHAPTER TWO

### 2.0 LITERATURE REVIEW

#### 2.1 Bats (Order Chiroptera)

The order Chiroptera is a unique mammalian order as its members have their forearms modified into wings and thus, are the only mammals that are capable of true and sustained flight. With over 1,116 species in 18 families and 202 genera, the order Chiroptera is the second largest order of mammals, and constitutes 20% of all mammal species (Simmons, 2005; Happold & Happold, 2013). About 221 species of bats are reported to occur in Africa (Happold & Happold, 2013).

The order Chiroptera traditionally had two sub-orders, Megachiroptera and Microchiroptera (Dobson, 1875). Megachiroptera comprised bats usually referred to as 'megabats' or old world fruit bats and Microchiroptera included insectivorous bats often described as 'microbats'. Recent molecular genetics however proposed the suborders Yinpterochiroptera to include the "megabats" and three families of "microbats", and Yangochiroptera to include the rest of the "microbat" families (Giannini & Simmons, 2003; Van Den Bussche & Hofer, 2004). This recently proposed classification is slowly replacing the traditional classification of Microchiroptera and Megachiroptera in some recent literature. In this study, the traditional classification of Microchiroptera and Megachiroptera is used.

Generally, the head of bats are more varied than those of other mammalian orders. Typical "megabats" have dog-like heads with simple muzzles, simple erect ears and very large eyes, while "microbats" have astounding heads, smaller eyes, large variations in external ears and the presence of fleshy nose-leaves in some species. The bones in the

forearm of bats are very similar to that of other mammals, but with some modifications; the humerus is reduced, the ulna is fused to the radius with greatly elongated metacarpals and phalanges. The thumb is short and bears a claw and in "megabats", the second finger also has a claw. The wing membrane is vascularised and also supplied with nerves and muscles. Wings vary greatly in shape and size in bats, with marked differences between families and less pronounced differences between species in the same genus. Differences in shape and size of wings define the speed and manoeuvrability of different bat species (Norberg & Rayner, 1987; Happold & Happold, 2013).

"Megabats" have excellent night and colour vision which enables them to detect food (fruits and flower products) at close range and an acute sense of smell for detecting food from afar. "Microbats" on the other hand have poorly developed eyesight and perceive their surroundings mainly by using echolocation. Echolocation occurs only in one genus in "megabats", *Rousettus*, which uses clicks made with their tongues to navigate in total darkness in the caves in which they roost.

### **2.1.1 Family Pteropodidae**

The family Pteropodidae currently contains 186 species of bats in 42 extant genera, of which 28 species in 14 genera occur in Africa (Simmons, 2005; Kunz *et al.*, 2011). Members in this family that occur in Africa are commonly described as fruit bats as they almost exclusively depend on plants for food, feeding on nectar, fruits, floral parts and pollen (Rosevear, 1965; Marshall, 1985; Kunz *et al.*, 2011; Happold & Happold, 2013). Pteropodid bats differ from "microbats" (sub-order Microchiroptera) by having a claw on the index finger and on the thumb. They have a simple external ear, no tragus (a small structure inside the ear) or nose leaf (dermal outgrowths above the nostrils or on the lips

which most microchiropterans possess). The inter-femoral membrane and the tail is either well reduced or mostly entirely absent (Happold & Happold, 2013). The head is dog-like with an elongated muzzle. In pteropodids, the eyes are generally large and adapted for improved night vision; orientation in this group is by smell and sight (Rosevear, 1965; Mickleburgh *et al.*, 1992). The teeth are simple and modified for crushing fruit with dental formula of usually  $^{2121}_{2132}=28$  or  $^{2132}_{2133}=34$  (Happold & Happold, 2013). The tongue is usually long and the cheeks are large and expansible, enabling pteropodids to carry whole fruits or large chunks of fruit in the cheeks.

Fruit bats in Africa show great variation in size across species with forearm lengths ranging from 38-163mm. Within the Pteropodidae, males often show secondary sexual dimorphism. Secondary sexual characters in adult males include epaulettes (long white or yellowish hairs found on each shoulder and usually hidden in a pouch and displayed during courtship) or ruffs (greasy rigid mantles) and modifications of the head skull and larynx (Bergmans, 1989; Happold & Happold, 2013). The pelage in fruit bats is typically brown or grey and soft with some species having pelage markings or contrasting coloured mantles across the neck or shoulders. Most species show sexual dimorphism in size, although this may not be very obvious. Males are usually larger than females especially in larger species. In the smaller species females are often larger than the males.

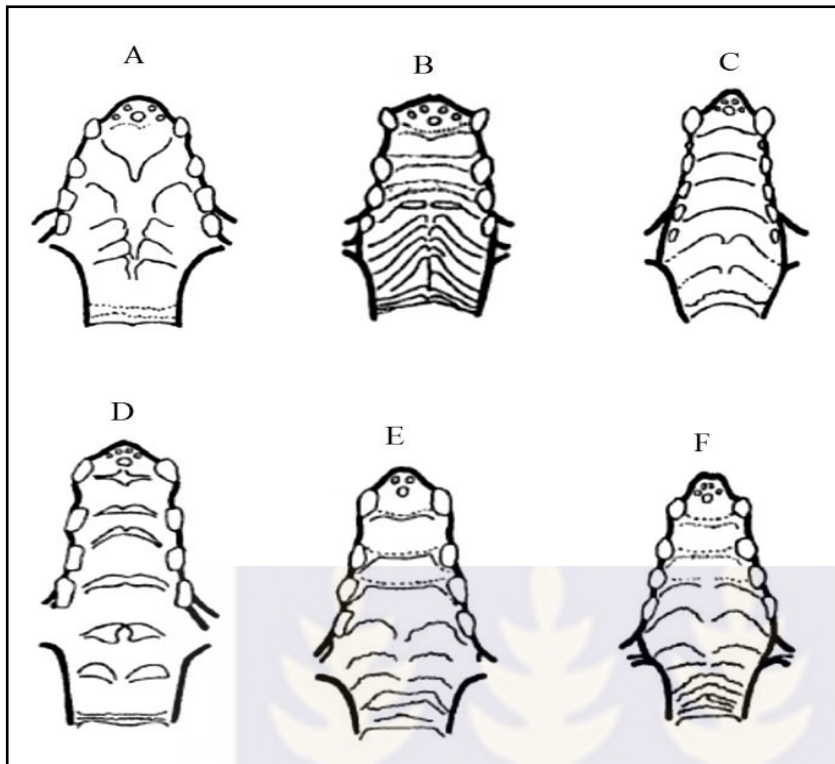
Distinguishing between species of fruit bats can pose a challenge, particularly among similar-sized epauletted bats. Pelage markings on the head are important in identifying species and often include white patches on the rostrum or tuft of white pelage at the base of the ears (Rosevear, 1965; Happold & Happold, 2013). The hammer-headed bat *Hypsignathus monstrosus* is clearly distinguished from other fruit bats by its large size

and hammer-shaped head. The head is massive with an enlarged humped muzzle which ends in a blunt flat fleshy plate formed by the upper and lower lips (Rosevear, 1965; Happold & Happold, 2013). The species shows the greatest form of sexual dimorphism in bats, with males weighing twice as much as females; males also have a massive larynx and have much larger and monstrous muzzle. The females look much smaller and have an epomophorine appearance (Bradbury, 1977).

The palate in fruit bats has ridges with well defined patterns which differ between species (Plate 2.1). The patterns of the palatal ridges can be used to differentiate very similar species when other features are too similar (Rosevear, 1965; Happold & Happold, 2013). The palatal ridges refer to number and shape of the ridges that lie across the roof of the mouth from side to side. Rosevear (1965) and Happold and Happold (2013) provide very good descriptions and identification keys that can be used as guides for differentiating species.

## **2.2 Occurrence and distribution of fruit bats in Ghana**

In West Africa, the 11 genera of African fruit bats that occur are *Eidolon*, *Epomophorus*, *Micropteropus*, *Epomops*, *Nanonycteris*, *Lissonycteris*, *Megaloglossus*, *Rousettus*, *Scotonycteris*, *Hypsignathus* and *Myonycteris*. Four of these genera (*Hypsignathus*, *Nanonycteris*, *Lissonycteris*, and *Megaloglossus*) are monotypic groups and the others are polytypic groups in Africa. With the exception of the genera *Scotonycteris* and *Epomops*, both of which have two species each occurring in Ghana, all the other genera that are polytypic in Africa are represented by single species in Ghana. Together, 13 species of African fruit bats are known to occur in Ghana.

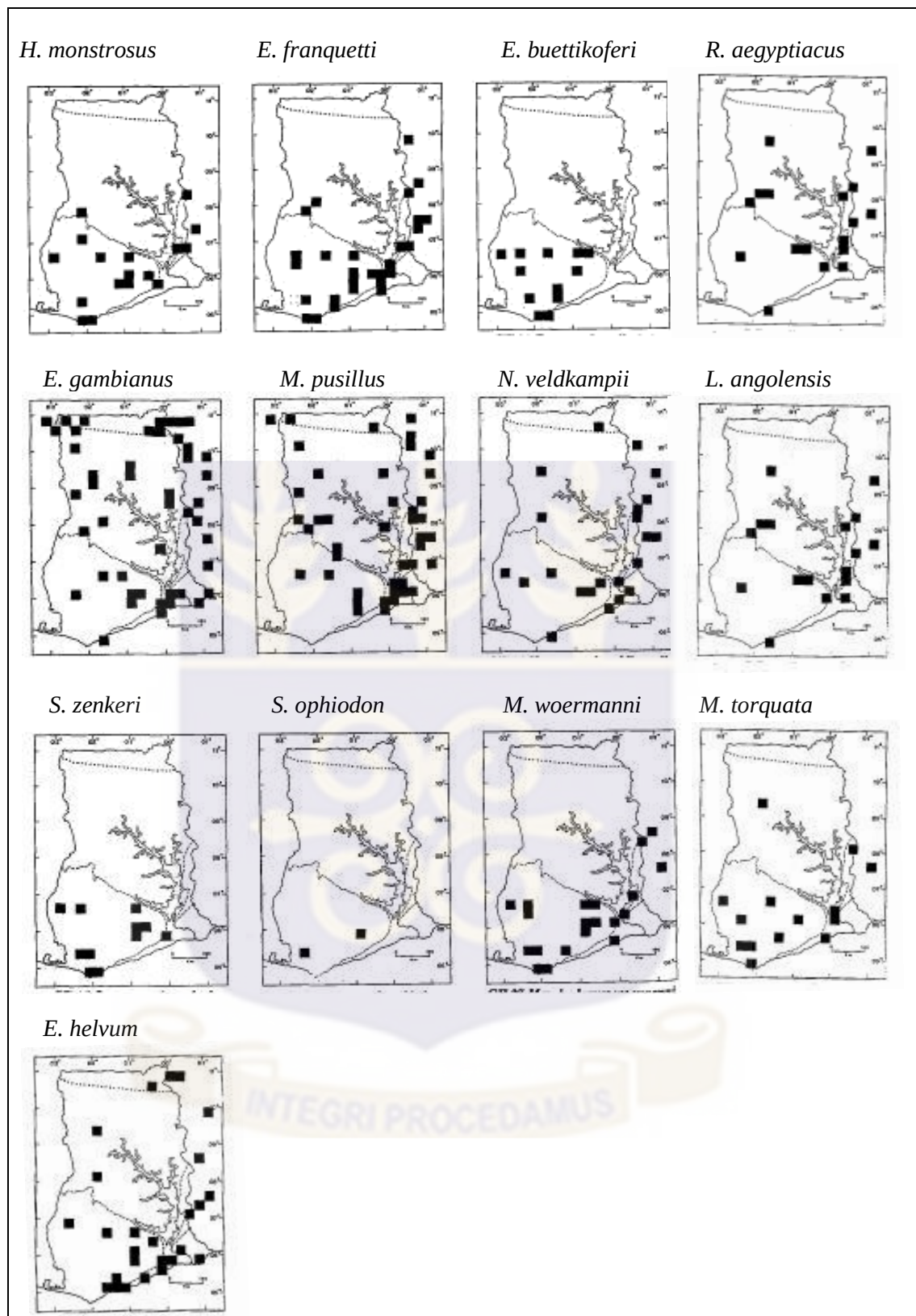


**Plate 2.1 Diagrammatic representation of palatal ridges of some fruit bats in Ghana.**

Source: Rosevear (1965). **A-** *Micropteropus pusillus*; **B-** *Nanonycteris veldkampii*; **C-** *Megaloglossus woermanni*; **D-** *Epomophorus gambianus*; **E-** *Epomops franqueti*; **F-** *Epomops buettikoferi*.

To date, Grubb *et al.* (1998) provides the only distribution maps for bats in Ghana (Plate 2.2). Other species occurrence records have been reported in the country subsequent to the work of Grubb *et al.* (1998) but mainly as records from Rapid Assessment Programmes [e.g. Decher and Fahr (2007); Weber and Fahr (2007)], or from individual bat species studies. Other distribution records are mostly from museum records, personal observations made by mammalogists and from other bat related studies.





**Plate 2.2 Fruit bat distribution in Ghana.**

Source: Grubb et al. (1998).

*Eidolon helvum* is very common and widespread species in West Africa and Ghana (Rosevear, 1965; Thomas & Michaël, 2013a). The species is very adaptable and occurs in a variety of habitats including moist and dry tropical rain forest, evergreen forests, coastal forests (including mangrove) and riverine forests, as well as moist and dry savannah mosaics. The species also persists in modified habitat and often forms large roosts in urban areas. In Ghana several large roosts have been reported at Adumnya sacred grove (Decher, 1997), Tanoboase and 37 Military Hospital Accra (Hayman *et al.*, 2012a), Wli Falls (Grubb *et al.*, 1998), Kumasi zoo and Abgasiagba Island on Lake Volta (Kamins *et al.*, 2011). *E. helvum* is a relatively more studied species than all the other fruit bats.

*E. gambianus*, on the other hand, is generally described as a woodland savannah species and is rarely associated with forests (Rosevear, 1965; Boulay & Robbins, 1989). It may however utilise forest edges and mosaics or cleared patches in forests (Happold, 2013). There are some records of *E. gambianus* from Atewa forest in Grubb *et al.* (1998). However, Weber and Fahr (2007) suggest that these records could have been misidentifications or could have been that the species was trapped within highly degraded parts and portions of the forest edge. They argue that the species rather occurs within more wooded savannah habitats and not in forests. The distribution provided by Grubb *et al.* (1998) indicates that *E. gambianus* is common and occurs in all the ecological zones in Ghana.

The distribution of *Micropteropus pusillus* appears to be very similar to that of *E. gambianus* (Plate 2.2). Thus, *M. pusillus* is often recorded alongside *E. gambianus* during bat captures from similar habitats. However, *M. pusillus*, is suggested to penetrate



forests and has been recorded from forest areas including Atewa and Ajenuja forest reserve (Yeboah, 2001).

*Nanonycteris veldkampii* utilizes a wide variety of habitats due to its migratory movements and may appear rare or uncommon because of its migratory behaviour. The species is often recorded from secondary forests, farmlands, mangroves and coastal forests and rarely occurs in the Dahomey gap and undisturbed forests (Grubb *et al.*, 1998; Fahr, 2013a). In Ghana, it has been recorded commonly from the Volta and Western regions (Plate 2.2)

The distribution of *Rousettus aegyptiacus* and *Lissonycteris angolensis* are somehow restricted by their requirements of caves for roosting. Hence, they are distributed mostly around areas where caves suitable for roosting occur (Rosevear, 1965; Happold & Happold, 2013). In Ghana, *R. aegyptiacus* has been recorded from Mole National Park (Marshall & McWilliam, 1982), Ajenjua and Bosomtwe forest reserves (Yeboah, 2001) and Buoyem (Anti *et al.*, 2015). Booth (1959) reported the species roosting in caves at Krobo Hills where he describes the species to be restricted to the Accra plains. The distribution of *Lissonycteris* overlaps with that of *R. aegyptiacus* in Ghana according to maps by Grubb *et al.* (1998).

The two members of the genus *Scotonycteris* are among the rarest of the fruit bat species in Ghana (Weber & Fahr, 2007). These species occur only in forest regions. *S. ophiodon* has a very small, restricted and disjunct range within the rainforest zone in West Africa where it is known from only 15 locations in five countries (Fahr, 2013b). A single museum record for this species exists for Ghana from a collection made at Oda (Hayman, 1945; Bergmans, 1973). Decher and Fahr (2007) suggest the species might occur within the forest reserves located in the Western Region of Ghana but the

distribution map by Grubb *et al.* (1998) shows the occurrence in only two locations, one at Oda and a second location in the Western Region (Plate 2.2).

On the other hand, *S. zenkeri* has been recorded from disturbed forests, forest edges and gardens, but usually found very close to forests (Happold & Happold, 2013). Records from locations in Ghana include Atewa (Weber & Fahr, 2007) and Pampramase (Western Region) in a garden edge near a high forest (Jeffrey, 1975). Museum records indicate samples taken from Cape-Coast, Kade, Oda, Prestea, Ahiriso and Nkawkaw (Van-Cakenberghe & Seamark, 2013).

*H. monstrosus* is reported from only the forest zone in Africa and rarely occurs outside this zone. In Ghana, *H. monstrosus* is known from several locations in the forest zone with records from forests including Krokosua Hills (Jeffrey, 1975), Mammang Forest Reserve (Yeboah, 2008) and Atewa (Abedi-Lartey & Guba-Kpelle, 2005; Weber & Fahr, 2007). Yeboah (2001) also recorded this species from four other forest reserves in the Western Region. Hayman *et al.* (2008b) report trapping a few individuals of this species in forested habitat at Pra, Kibi, Adoagyiri, and Oyibi. Other earlier records and general distribution are shown in Plate 2.2.

The two species of the genus *Epomops* that occur in Ghana show similar distribution patterns. However, *Epomops buettikoferi* shows preference for rainforest and forest-savannah mosaic. There are some records of the species from moist savannah and lowland forest and the species is often associated with disturbed forests, secondary bush, cultivated lands and edges of closed forests (Thomas & Michaël, 2013b). The distribution map for the species based on Grubb *et al.* (1998) shows records from the forest region mostly in the Western Region of Ghana. *Epomops franqueti* also occurs in similar forest vegetation as *E. buettikoferi* but with slight extensions into the Guinea

savannah zones (Happold & Happold, 2013). Records from Accra, Bimbila, Leklegbi (Van-Cakenberghe & Seamark, 2013) confirm that in Ghana, this species extends into savannah and woodland areas than its closely related species *E. buettikoferi*.

*Myonycteris torquata* occurs within forests and forest savannah mosaics in West Africa. In Ghana, most records are from the south western parts of the country, but some records from Mole National Park suggests that the species extends far north (Grubb *et al.*, 1998).

### **2.3 Roosting ecology and habitat selection in bats**

Bats utilise a wide variety of both natural and man-made structures as roosts. Bats can be described as lithophilic or phytophilic based on their choice of roosts. Lithophylic species utilise natural day roosts found in caves, rock crevices or under rocks or boulders. Phytophilic bats roost in trees or shrubs by hanging freely from branches or foliage, in hollow tree trunks or inside furled leaves. Both groups can also utilise man-made structures which have features similar to naturally occurring roosts (Happold & Happold, 2013). Over 50% of all known bat species utilise different types and forms of trees as roosts (Kunz *et al.*, 2003). Roosts of most Microchiropteran bats are in closed spaces whereas most Megachiropterans roost in open spaces on branches in trees (Brooke *et al.*, 2000). Bat roosts may consist either of single individuals, groups of a few individuals, to hundreds or aggregations of large numbers up to a million individuals in some species. Some species hang freely or in contact with a surface while others do not hang but cling to exposed surfaces or hide in crevices. Other species may hang apart with no contact with other bats or huddle together in large clusters.

Bats, like all mammals, require and select shelter to provide rest, adequate protection (e.g. against predators and environmental conditions) and to satisfy other social needs

(Kunz, 1982; Altringham *et al.*, 1996; Tan *et al.*, 1999). Because bats spend a good part of their time at roosts, roosts are vital to their survival and reproductive success (Richter *et al.*, 1993; Zahn, 1999; Kunz *et al.*, 2003) and therefore they select roost sites that provide optimum benefits and increase their survival and fitness. In several species of bats, roost selection has been shown to be non random, with different species having specific requirements for roosting (Gumal, 2004; Stier & Mildenstein, 2005; Lacki & Baker, 2007; Limpert *et al.*, 2007; Hahn *et al.*, 2014). Roost selection has been suggested to occur in a hierarchical manner at different scales (i.e. roost, plot and landscape scales) (Limpert *et al.*, 2007). At the roost level, several tree roosting species of bats have been shown to select specific tree species. For example, *Pteropus giganteus* selects roosts in tree species like bamboo, *Albizia* spp., and Eucalyptus, but avoid other tree species which are more common (Hahn *et al.*, 2014). Other characteristics of roosts commonly selected by bats include size of tree (DBH), height of roosting tree, plot basal area and habitat type (Gumal, 2004; Stier & Mildenstein, 2005; Lacki & Baker, 2007; Limpert *et al.*, 2007).

The choice of roosting sites can also be influenced by factors such as temperature, noise levels (disturbance), proximity to food and humidity. In *Pteropus* for example, roost selection is suggested to be influenced by the availability and proximity to food resources. This was suggested as a possible explanation for their occurrence very close to human settlements where fruiting trees in backyard gardens are common (Palmer & Woinarski, 1999; Hahn *et al.*, 2014). Other species may be more tolerant and adapted to a variety of factors and can utilise different roosts. According to Lacki and Baker (2007), species that have wide distribution are more likely to have varying roost selection criteria in different habitats across their range. Different bat species that have similar roosting requirements may co-roost. In some species of bats that co-roost in caves, species groups

are formed in different parts of the cave according to similarities in their requirement for environmental variables such as light, temperature and humidity.

## **2.4 Roosting in fruit bats**

The dependence of fruit bats on plants is not only for food but also for shelter. Most fruit bats utilise trees as day roosts and are either concealed by foliage or hang in the open. According to Santana *et al.* (2011), there is an evolutionary relationship between the roosting ecology of species and the development of adaptive pelage markings. These pelage markings help to conceal bats in trees, especially those that roost singly. Fenton (1992) suggests that the brown colouration of most fruit bats gives them a cryptic appearance when roosting.

Fruit bats roost either singly or form small loose groups to very large colonies. *E. helvum* forms clusters of between 8-100 individuals huddled together in colonies of up to ten million individuals as recorded in Zambia (Richter & Cumming, 2008). In West Africa, colonies can reach between 300,000 to 1 million (Rosevear, 1965; DeFrees & Wilson, 1988; Hayman *et al.*, 2012a). In Ghana, the Accra colony is reported to hold up to 1 million bats (Hayman *et al.*, 2012a). *R. aegypticus* typically, also forms large colonies of up to 4,000 individuals in caves. It is suggested that such large aggregations may offer better protection from predators through the predator dilution effect (Wilkinson & South, 2002; Santana *et al.*, 2011). The predator dilution effect predicts that the chances of each individual being preyed upon are much lower among individuals that form larger colonies. Other species either roost singly or form small loose groups of a few individuals. Some species like *L. angolensis* also form maternity roost (Happold & Happold, 2013).



## 2.5 Roost fidelity and lability in bats

Different species of bats show varying degrees of roost fidelity (Fenton *et al.*, 1985; Lewis, 1995). Some species may use the same roosts repeatedly for several years, while others may show high lability, switching roosts almost every day. Several factors may affect roost fidelity and lability in bats. Kunz (1982;2013) suggested that roost fidelity is influenced by factors such as the availability and permanency of roost, proximity to food resources, predator pressure and human disturbance.

In an analysis of roost fidelity in forty-five species of bats, Lewis (1995) found that high roost availability was negatively associated with roost fidelity, but high roost permanence was positively associated with roost fidelity. Generally, cavity and cave dwelling bats exhibit stronger fidelity to roost sites than foliage and tree roosting bats. Foliage and tree roosting bats often show fidelity to a home area, rather than a single specific roosting site, and often switch between several alternative roosts (Vonhof & Barclay, 1996; Gumal, 2004). Roost fidelity may also vary depending on reproductive condition, sex and age of an individual bat. For instance, females may exhibit high roost fidelity during pregnancy and lactation periods due to the high energetic costs involved in switching roosts, but may show lower roost fidelity after weaning of the young ones (Lewis, 1995).

A high degree of roost fidelity may be beneficial in several ways. Bats that show high roost fidelity may benefit by avoiding the energetic cost associated with searching for other roosts, especially if roosts differ in quality or are highly dispersed. High roost fidelity also helps in the maintenance of beneficial social relationships as individuals are more likely to cooperate with others they are familiar with through repeated interactions (Rothstein & Pierotri, 1988; Lewis, 1995; Lewis, 1996). Another advantage of high roost



fidelity is that it reduces exposure to predation (e.g. from raptors) that may arise when searching for new sites (Lewis, 1996). Roost switching may be detrimental to individuals, for example, in Big brown bats (*Eptesicus fuscus*) females showed reduced reproductive success when forced to change roosts prior to parturition (Brigham & Fenton, 1986).

Despite the benefits of maintaining high roost fidelity, several species of bats are known to be very labile and switch roosts very often (Thomas & Fenton, 1978; Lewis, 1995; Sedgeley & O'Donnell, 2004; Willis & Brigham, 2004). According to Lewis (1995), individuals that readily switch roosts do so because the benefits of switching roosts surpass or at least balance the costs of switching roosts. Roost lability may be in response to disturbance (either natural or anthropogenic). Roost lability directly correlates with disturbance as predicted by the disturbance hypothesis which states that there is a direct correlation between disturbance and site fidelity where undisturbed animals will have a high site fidelity and increasing disturbance leads to lower site fidelity (Lewis, 1995). Lability could also be in response to adverse changes in microhabitat conditions. For instance, cavity roosting bats may abandon roosts that become too cold while foliage roosting species may switch roosts when current roosts become defoliated (Findley & Wilson, 1974; Kunz, 1982). Roost switching also occurs in response to changing locations of food resources in order to reduce travelling distances to foraging sites (Lewis, 1995).

Roost switching may also be a strategy to avoid predators that would become familiar and attracted to repeatedly used or conspicuous roosts (Wilkinson, 1985). For instance, *E. helvum* and *R. aegyptiacus* that are known to show high fidelity to roosting sites are very vulnerable and predictable to hunters (Mickleburgh *et al.*, 2009). The decision of

bats to show high roost fidelity or be very labile, could be the outcome of the tradeoffs between the benefits of roost fidelity and that of switching roosts (Lewis, 1995).

## **2.6 Movement in bats**

Movement in bats is achieved mainly by flight, a trait which in mammals is unique only to this order. Bats show great diversity in their flight ability. The mode of flight usually correlates with the morphology and feeding strategy employed by the bat species (Norberg & Rayner, 1987). For instance, insectivorous bats require more agility and manoeuvrability to capture insects compared to frugivorous bats. Fast and long range insect hawkers have high wing loading, long and pointed wing tips, together with short high aspect ratio that are adaptations for agility at high speeds while most fruit bats have sustained flights at relatively slower speeds (Norberg & Rayner, 1987).

Movement in bats can also be achieved by crawling or scurrying across surfaces using forearms, tightly folded wings and hind limbs (Rosevear, 1965) and by swimming when the need arises (Craft *et al.*, 1958; Rosevear, 1965). Several species can easily climb shrubs or trees especially to gain enough height off the ground for take-off after being grounded. Once suspended in the normal upside-down posture, bats can make rapid sideways movements on rough surfaces, a technique that is well executed in *Taphozous mauritanus*. Happold and Happold (2013) describe three major movements in bats; namely, localized movements, nomadic movements and migration.

### 2.6.1 Localized and nomadic movements

Localized movements describe movements made within the bat's home range and feeding range and are often for a limited time period. This includes commuting movements made between day roosts and from day roosts to foraging sites. Depending on the size of the species' home range, some species, for example *E. helvum*, can travel beyond 50 km from day roosts to foraging sites in a single evening (Richter & Cumming, 2006). Nomadic movements however, are often non predictable, irregular movements in response to unpredicted habitat changes or food availability. Such movements can occur at any time or season and in any direction, with the extent of movement usually being determined by the prevailing local conditions (Happold & Happold, 2013).

### 2.6.2 Migration

Migration describes the predictable mass movement of species from one habitat to another, and back, usually along a predefined route in response to changes in climatic conditions, food or other resources availability (Happold & Happold, 2013). Bat migration has long been known to occur as happens for birds and other mammals. Banding methods were used in earlier studies to establish migration in bats, and advancements in research methodology (e.g. use of radio and satellite telemetry) is increasing knowledge on bat migration (Hedenström, 2009; Popa-Lisseanu & Voigt, 2009). Although both bats and birds have similar flight ability, migration in bats occurs in relatively fewer species compared to birds. Unlike birds, several bat species rather undergo hibernation to avoid extreme changes in temperature in the temperate regions rather than undertake migration (Hedenström, 2009; Popa-Lisseanu & Voigt, 2009). Some bat species also migrate to slightly warmer areas where conditions are more

suitable for hibernation (Happold & Happold, 2013; Moussy *et al.*, 2013), for example *Lasiurus* sp. (Cryan, 2003).

In the tropics, bats migrate for different reasons, but mainly because of seasonal fluctuations and widely spaced availability of their food resources (Popa-Lisseanu & Voigt, 2009; Happold & Happold, 2013). Migration could also be triggered by the need to find mates or gather information on other parts of a species' geographical range as described in the Grey-headed flying fox (*Pteropus poliocephalus*) (Tidemann & Nelson, 2004). Migration in response to food availability has been shown especially for the family Pteropodidae (Tidemann & Nelson, 2004; Richter & Cumming, 2006). In West Africa, *E. helvum*, *N. veldkampii* and *M. torquata* are known to migrate from the rainforest to savannah zones and back again in response to seasonal fluctuations in food supply (Thomas, 1983; Fleming *et al.*, 2003; Happold & Happold, 2013). Migration in *E. helvum* in particular, is relatively well known and studied than in any other fruit bat species on the African continent. It is reported that the species can cover distances exceeding 2000km in just a few months during the migratory periods of this species, which is synchronised with rainfall patterns and corresponding food availability (Richter & Cumming, 2008).

Migration in bats appears to be more flexible with some variations among species (Popa-Lisseanu & Voigt, 2009). Across the range of some species, there can be both migratory and non migratory populations (e.g. *Nyctalus* sp.) (Ibáñez *et al.*, 2009). In some species, sex biased migrations also exists, for example *Tadarida brasiliensis* (Russell *et al.*, 2005). Partial migration occurs in some species such as *Perimyotis subflavus* (Fraser *et al.*, 2012), while other species may also exhibit different migratory behaviour when their populations are isolated (Moussy *et al.*, 2013). For example, mainland populations of *E.*

*helvum* undergo long distance annual migrations whiles island populations do not migrate (Juste *et al.*, 2000).

## **2.7 Reproduction in bats**

Most small mammals have life histories characterised by rapid reproduction and high mortality and hence they "live fast and die young" (Promislow & Harvey, 1990). Bats are an exception, having a unique life history characterized by high longevity, low mortality rates and multiple reproduction events with small litter sizes (Gaisler, 1989; Barclay *et al.*, 2003). The low mortality rate in bats is attributed to the evolution of nocturnal flight. The ability to fly and be active at night reduces mortality through the avoidance of diurnal predators. It also implies that young ones have to be large enough and ready for flight before the weaning age (Pomeroy, 1990; Barclay, 1994). Longer and energetically costly lactation periods are required for young ones to be weaned at a very large size. Generally, because of the high energetic cost of reproduction and the costs on female body condition, animals have to decide on timing of reproduction based on their body condition and availability of resources to meet the energy demands (Thompson, 1992). In this perspective, the Order Chiroptera, have evolved reproductive strategies that are more varied than in any other mammalian order (Crichton & Kruttsch, 2000).

### **2.7.1 Reproductive strategies in bats**

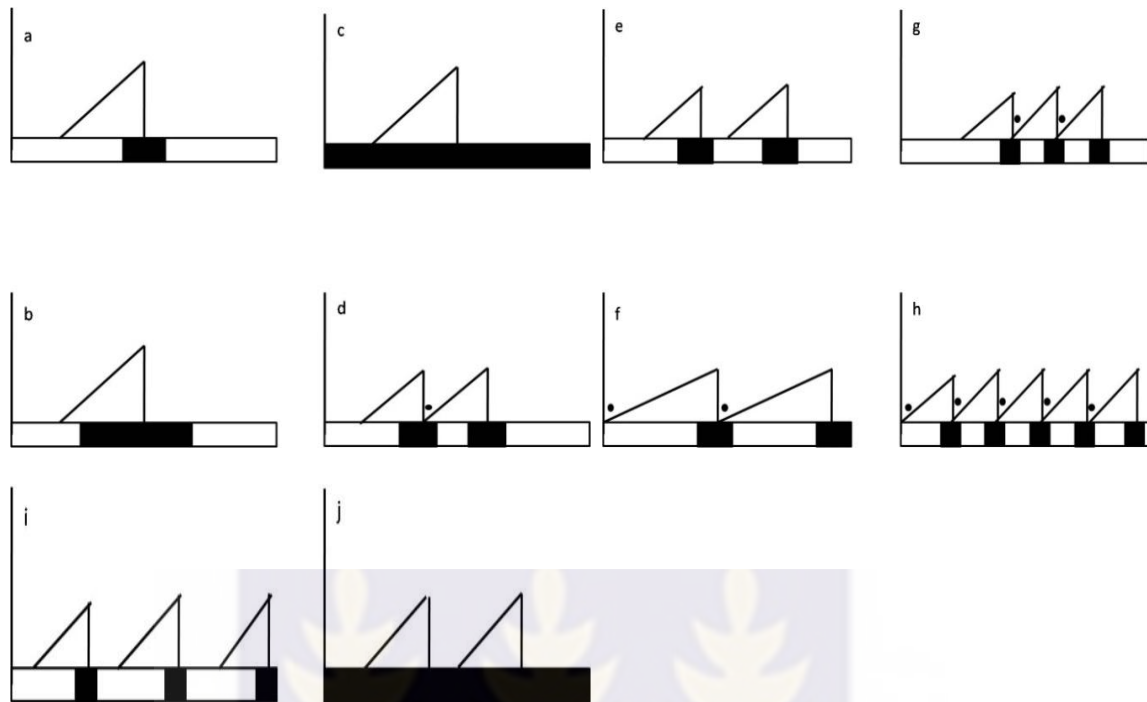
The reproductive strategies adopted by bats depend on the litter size and the reproductive chronology that a particular species exhibits (Happold & Happold, 2013). Several bat species are monotocous, giving birth to one young per litter; a few species are polytocous, with litter size of more than one (Racey, 1982; Tuttle & Stevenson, 1982;

Happold & Happold, 2013). In monotocous species however, twinning may occur but are rare incidents (Happold & Happold, 2013). Information on litter size is known for 103 species of African bats, out of which 83% are monotocous (Happold & Happold, 2013).

Reproductive chronologies are also defined by the number of litters produced per year and the timing of the reproductive events (seasonal or aseasonal) (Happold & Happold, 2013). In the order Chiroptera, most species that have been well studied are known to be monoestrous, reproducing once in a year with a few being polyoestrous with two or more births in a year (Jerrett, 1979; Oxberry, 1979). In African fruit bats, most species are monotocous (one offspring per birth) and polyoestrous (each female gives birth more than once in a year). Polyoestry has been suggested as a primitive strategy in bats with monoestry evolving as an adaptive strategy in more seasonal zones (especially at higher altitudes) where conditions are only favourable for reproduction once a year (Cumming & Bernard, 1997). Happold and Happold (1990), however, show that some species exhibit flexibility in reproduction depending on the environment they find themselves across their geographic distribution. In Africa, ten reproductive chronologies have been identified in bats (Figure 2.1).

Table 2.1 summarizes information on reproductive chronologies, parturition periods and litter sizes of fruit bats that occur in Ghana. With the exception of *H. monstrosus*, *E. franqueti* and *E. buettikoferi*, very little is known about the social structure and mating system of fruit bats (Happold & Happold, 2013). These three species are known to exhibit lek mating systems where males aggregate in special arenas called leks and carry out displays of calls and wing beating to attract females for mating (Bradbury, 1977; Happold & Happold, 2013).





**Figure 2.1 Illustrations of the reproductive chronologies in African fruit bats.**

Source: (Happold & Happold, 1990; Happold & Happold, 2013).

*Horizontal lines cover a 12 month period; sloped lines indicate pregnancy of one individual; vertical lines indicate parturition in the same individual; black bars indicate the season of parturition in one population as a whole; black circles indicate post-partum oestrus.*

*(a) Restricted seasonal monoestry (b) extended seasonal monoestry (c) aseasonal monoestry (d) seasonal bimodal polyoestry with post partum oestrus after first parturition (e) seasonal bimodal polyoestry without post partum oestrus (f) continuous bimodal polyoestry (with post partum oestrus after both parturitions) (g) seasonal multimodal polyoestry with post partum oestrus after all but last parturition in the season (h) continuous multimodal polyoestry with post partum oestrus (i) continuous multimodal polyoestry without post partum oestrus and j) aseasonal polyoestry.*

**Table 2.1 Reproductive chronology and parturition periods of fruit bats that occur in Ghana.**

| Species                | Litter size | Reproductive Chronology                                                                      | Birth periods      | Reference                                             |
|------------------------|-------------|----------------------------------------------------------------------------------------------|--------------------|-------------------------------------------------------|
| <i>E. helvum</i>       | one; 2 rare | Restricted seasonal monoestry with delayed implantation                                      | Feb-Mar            | (Fayenuwo & Halstead, 1974; Happold & Happold, 1990)  |
| <i>H. monstrosus</i>   | one         | Continuous bimodal polyoestry with post partum oestrus                                       | Jan-Feb, Jun-Jul   | (Bradbury, 1977)                                      |
| <i>E. franqueti</i>    | one         | Continuous bimodal polyoestry with post partum oestrus                                       | Mar, Sept          | (Okia, 1974a)                                         |
| <i>E. buettikoferi</i> | one         | Continuous bimodal polyoestry with post partum oestrus                                       | Feb-Mar, Aug-Sept  | (Thomas & Marshall, 1984; Kofron & Chapman, 1994),    |
| <i>N. veldkampii</i>   | one         | *Aseasonal or extended seasonal polyoestry with post partum oestrus at least in some females | Uncertain          | (Fahr, 2013a)                                         |
| <i>M. pusillus</i>     | one         | Continuous bimodal polyoestry with post partum oestrus                                       | Apr-Mar, Sep-Oct   | (Marshall & McWilliam, 1982; Thomas & Marshall, 1984) |
| <i>S. ophiodon</i>     | one         | *extended seasonal monoestry                                                                 | *Nov-Dec           | (Fahr, 2013b)                                         |
| <i>S. zenkeri</i>      | one         | *Seasonal bimodal polyoestry                                                                 | Uncertain          | (Fahr, 2013c)                                         |
| <i>E. gambianus</i>    | one         | Continuous bimodal polyoestry with post partum oestrus                                       | Apr, Oct           | (Thomas & Marshall, 1984)                             |
|                        |             | Continuous bimodal polyoestry with post partum oestrus                                       | Mar, Sept          | (Mutere, 1967b; Okia, 1974b)                          |
| <i>R. aegyptiacus</i>  | one; 2 rare | Restricted seasonal monoestry                                                                | Nov-Dec            | (Penzhorn & Rautenbach, 1988)                         |
|                        |             | seasonal bimodal polyoestry without post partum oestrus                                      | Mar, Sept          | (Mutere, 1967b)                                       |
|                        |             | extended seasonal monoestry                                                                  | Oct-Dec            | (Jacobsen & DuPlessis, 1976)                          |
| <i>L. angolensis</i>   | one         | *Probably polyoestry                                                                         | uncertain          | (Happold & Happold, 2013)                             |
| <i>M. woermanni</i>    | one; 2 rare | *Bimodal polyoestry or aseasonal polyoestry                                                  | *Jan, Sep          | (Okia, 1987; Happold & Happold, 2013)                 |
| <i>M. torquata</i>     | one         | *Seasonal bimodal polyoestry                                                                 | *Feb-Mar, Aug-Sept | (Thomas & Michaël, 2013c)                             |

\* Suspected and requires further confirmation

### 2.7.2 Timing of Reproduction in bats

Reproduction is an energetically costly process, thus, the availability of food tends to play an important role in the timing of reproduction in animals (Bronson, 1985; Loudon & Racey, 1987). In areas where food is available throughout the year, animals may reproduce at any time, but where food availability is seasonal, animals may time their reproduction such that it coincides with peaks in food availability in order to meet the energetic requirements for pregnancy and lactation (Racey & Entwistle, 2000). In species with long gestation periods, single events or multiple events of reproduction are timed such that they occur during periods when food is most abundant. In bats for example, most species reproduce seasonally, with reproduction timed such that the most energetically demanding period coincides with peak food abundance (Racey, 1982; Heideman, 1995).

According to Cumming and Bernard (1997), gestation in most African bats start about 2-3 months prior to significant increase in food abundance. This implies that reproduction is timed such that peak food availability coincides with weaning periods. They argue that the post weaning needs of young ones may be far more important than the need to meet energy demands of lactating mothers. Fleming *et al.* (1972) shared similar views based on similar observations.

In Africa, it has been shown that food availability for bats is constrained by rainfall. Peaks in insect and fruit abundance are tied to peaks in rainfall (Rautenbach *et al.*, 1988; Happold & Happold, 1990; Cumming & Bernard, 1997). Parturition generally takes place at the beginning of the rains and lactation occurs during the peak of the rainy season (Racey, 1982; Thomas & Marshall, 1984; Cumming & Bernard, 1997).

Intraspecific variation in the timing of reproduction has been shown to occur in some species of bats. This is however more common in insectivorous bats and rare in fruit bats and has been attributed to the fact that fluctuations in insect abundance are often large enough to impose significant selective pressure on reproductive strategies of insectivorous species (Happold & Happold, 1990). Conversely, fluctuations in fruit abundance are often too small to have any significant selective pressure on reproduction.

Bat species that specialize in feeding on specific food types often show differences in their timing of reproduction. For such species, reproduction may rather be timed with food availability and not with climatic factors such as rainfall. For instance, fruit phenology studies indicate that peaks in fruiting occurs during the peak rainy season, with flowering occurring in the preceding dry period (Janzen, 1967; Frankie *et al.*, 1974). Hence, reproduction in obligate nectarivores would be restricted to the dry season rather than during the rains. With insectivorous bats, abundance of aerial insects peaks with rainfall while peaks in ground dwelling arthropods occurs after peaks in rainfall (Cumming & Bernard, 1997); hence insectivorous bats that specialize in feeding on ground dwelling arthropods may time their reproduction to coincide rather with peaks in ground dwelling arthropod abundance after rains and not with rainfall (Rautenbach *et al.*, 1988; Racey & Entwistle, 2000). Also factors such as nutritional value and water content of fruits may vary seasonally, so in species which depend on particular fruits reproduction may not correlate well with rainfall. According to Racey and Entwistle (2000), observed differences in timing of reproduction in some bats highlight the importance of food availability as the major factor that determines the timing of reproduction in bats in the tropics, rather than climatic factors like rainfall.

## 2.8 Foraging in bats

Within the order Chiroptera, there is a clear distinction between the feeding methods employed by the two major groups of bats as implied by their descriptors, "insect eating bats" (Microchiroptera) and "fruit eating bats" (Megachiroptera). Although there is an almost strict adherence to these feeding modes by species belonging to each group, there are a few deviations (Rosevear, 1965). There are morphological adaptations in each group of bats that enables them to successfully utilise the food type exploited. Insectivorous bats respond to the challenge of pursuing insects which are flying constantly, may be camouflaged and may have to be located in darkness through echolocation. Conversely, in fruit eating bats, food sources are just sitting targets in trees and once discovered can be consumed easily. Fruit bats overcome the challenge of detecting fruits at a distance by having an acute sense of smell and sight (Rosevear, 1965).

The differences in the types of food utilised also has implications on the modes of flight in the two groups. Insectivorous bats are very swift, agile and have a keen sense of perception which enables them to pursue and catch swift moving insects. In fruit eating bats, simple and continuous flight is usually needed to reach foraging areas.

In tropical Africa, insects appear, relatively, to be available throughout the whole year than fruits (Cumming & Bernard, 1997). Peaks of fruiting may last for very short periods and trees or even whole landscapes could be devoid of fruits shortly after such peaks. The spatio-temporal variation in fruit abundance across landscapes leads to long distance nomadic and night-time feeding movements in fruit bats (Cumming & Bernard, 1997).

In the selection of prey or food items, most fruit bats are seen as generalist and feed on what is available. Very few species have modifications for specialized diets such as

nectarivory (Rosevear, 1965; Kunz *et al.*, 2011). In insectivorous species, however, there are different views about prey selection; some studies suggest selective predation on prey while others suggest opportunistic-generalist-predation, consuming whatever is available within preferred habitats (Kunz *et al.*, 2011).

Differences in foraging strategies may also exist between sexes of the same bat species (Barclay, 1989; Barclay & Jacobs, 2011). Female bats may have longer foraging times or may forage on different food sources compared to males. This may happen especially in response to nutrient and energy demands during pregnancy and lactation (Wilkinson & Barclay, 1997; Barclay & Jacobs, 2011). Also, differences in sizes of sexes due to sexual dimorphism may lead to differential foraging in species as energy demands may be higher in the larger sex, hence the need to feed more or on more nutritious food resources (Barclay & Jacobs, 2011).

### **2.8.1 Food sources for fruit bats**

African fruit bats are almost entirely phytophagous, and they feed on a wide variety of plant resources. Fruit bats feed on no less than 188 genera in 16 families of plants (Marshall, 1983). Pteropodids utilise three major plant food sources; fruits, flower resources and leaves (Rosevear, 1965; Marshall, 1985). Appendix 1 provides a list of plant families and genera that are known to be utilised as food by fruit bats that occur in West Africa. Most fruit bats visit plants for their soft fleshy fruits. Feeding usually involves carrying whole fruit or large chunks of fruit from the parent tree to a feeding roost where the fruits are crushed and the juice is extracted by pressing the crushed pulp against the palate using the tongue. The extracted juice is then swallowed while the remaining solid matter made up mostly of fibre and seeds are discarded in a spat



(Marshall, 1985; Thomas, 1991; Picot *et al.*, 2007). Occasionally very small seeds are swallowed with the juice and pass out through the faeces. According to Marshall (1985), bats are not seed predators so seeds ingested are unintentional. Nogueira and Peracchi (2003) however, describe seed predation in Phyllostomid bats.

Bats in general are reported to have a very short gut retention time and in fruit bats, ingested liquids pass out shortly after ingestion (Wolton *et al.*, 1982; Stier & Mildenstein, 2005). According to Rosevear (1965), this implies that digestion in fruit bats is so quick that it is almost impossible to identify a bat's meal from the stomach content or faeces, except when seeds of the last fruit eaten are ingested. However, several studies to identify diet of fruit bat species have used faecal collections, including those without seeds to identify correctly food sources of fruit bats (Stier & Mildenstein, 2005; Picot *et al.*, 2007).

Fruits usually have very low protein content so fruit bats consume large quantities of fruits in order to acquire sufficient amounts of proteins (Thomas & Marshall, 1984). In a study by Thomas (1991), *M. pusillus* (weighing 18 to 32 g) was recorded to consume food up to twice its body weight in captivity while *E. buettikoferi* (weighing 160 to 200 g) consumed up to 240 g of fruit per night.

Fruit bats visit flowers either for the nectar, pollen or to consume whole flowers or their buds. Specialized morphological modifications are required to feed effectively on nectar and pollen. Such modifications include elongated snouts and tongues. Hence, not all pteropodids are able to utilise nectar and pollen resources successfully. Only 15 species of the family Pteropodidae are known to be specialised for feeding on nectar and pollen (Kunz *et al.*, 2011). However, other species are able to exploit pollen and nectar opportunistically. This is done either by consuming whole flowers, or licking pollen

which sticks to their fur when they visit flowers. According to Rosevear (1965) the eating of fleshy flowers and flower buds occurs as an alternative to fruit eating, especially during times of limited fruit or in an attempt to obtain nectar or pollen from flowers. There are very few reports of fruit bats feeding on pollen. In Madagascar, several food items eaten by *Pteropus rufus* and *Eidolon dupreanum* were identified from pollen in the faeces of these bats. This suggests that the contribution of pollen and nectar to the diet of fruit bats may have been underestimated previously (Andriafidison *et al.*, 2006).

## **2.9 Ecological and socio-economic importance of bats.**

### **2.9.1 Ecosystem services**

Bats are known to play key roles in ecosystem service provisioning and functioning, mostly as a result of their feeding. Since the first speculation by Mosley (1879) of pollination by fruit bats, several studies have explored and confirmed the important role that fruit bats play in the pollination of flowers. It is now known that about 528 species of plants in 67 families and 28 orders of angiosperms are pollinated by bats (Mickleburgh *et al.*, 1992; Kunz *et al.*, 2011). Fruit bat species that feed on nectar and floral parts contribute largely to pollination of plants by carrying pollen on their bodies from one flower to another during foraging. This contributes to the promotion and maintenance of genetic diversity of flowering plants (Kunz *et al.*, 2011). Through evolutionary time, some plants have become exclusively pollinated by bats and this has produced some form of mutualistic interactions between some plants and bats and has resulted in extensive co-evolution between plants and their pollinators (Kunz *et al.*, 2011).

Seed dispersal is another one of the vital ecological services essential for plant regeneration, recruitment and succession in tropical ecosystems (Balcomb & Chapman, 2003; Muscarella & Fleming, 2007). The role of frugivorous bats in seed dispersal is enormous because of their large numbers and diversity, and also due to the fact that an estimated 50-90% of all tropical trees produce fleshy fruits which may be consumed by vertebrates (Howe & Smallwood, 1982). Part of the success of frugivorous bats as effective seed dispersers is due to their feeding habits. Fruits are carried away from the parent tree before they are eaten and in the process the bulk of the seeds are spat out. The few seeds that are swallowed pass through the gut quickly and are dispersed through faecal droppings (Happold & Happold, 2013).

Due to the high mobility of fruit bats (Bergmans, 1990; Webb & Tidemann, 1996; Roberts *et al.*, 2012) and their ability to travel long distances during foraging bouts, seeds that are retained in their gut may be carried up to 100 km away from parent trees, thus enabling dispersal over very long distances (Djossa *et al.*, 2008; Kunz *et al.*, 2011). Oleksy *et al.* (2015) illustrated the important role of the Madagascan Flying fox (*Pteropus rufus*) in restoration of degraded forest in Madagascar. GPS tracking showed that the bats could travel up to 19 km in 84 minutes during night time feeding and in the process dispersed fig seeds as they moved across cleared areas and agricultural fields.

Bats play an important role in the regeneration process of degraded lands. They have the ability to transport and disperse seeds of plants which are usually not found in the immediate surroundings of degraded habitats (Duncan & Chapman, 1999). According to Silva *et al.* (1996) and Duncan and Chapman (1999), bats are important seed dispersers in early succession stages in degraded areas, even before other seed dispersers like birds begin to move to the area to aid in the succession process. Bats disperse mostly seeds of

pioneer species like figs that are important for early succession. Seeds passed through the gut of bats and into faeces may be dropped in flight or at roost sites and contribute extensively to soil seed banks, plant regeneration and introduction of plants to disturbed areas (Muscarella & Fleming, 2007; Kelm *et al.*, 2008; Kunz *et al.*, 2011). The ability to fly also gives bats a wider foraging area in both continuous and fragmented forests, thereby helping to maintain genetic connection between fragmented plant populations (Kunz *et al.*, 2011).

Fruit handling by bats has also been described to have a positive effect on germination of seeds. For example, it has been shown that handling of Shea fruits *Vitellaria paradoxa*, (Djossa *et al.*, 2008) and *Antiaris toxicaria* (Kankam & Oduro, 2012) enhances seed germination.

### **2.9.2 Socio-economic importance of bats**

The difficulty in quantifying the economic value of the ecosystem services provided by bats makes it difficult to appreciate the importance of bats in the ecosystem (Kunz *et al.*, 2011). Very few studies have attempted to quantify the economic value of the benefits provided by bats. Fujita and Tuttle (1991) provide one of the earliest attempts to measure the economic importance of bats by quantifying the economic values of some of the products obtained from plants that are pollinated and dispersed by bats in the Neotropics. A total of 289 Old-World tropical plants were identified as either pollinated or dispersed by bats in that study. From these, 448 bat dependent products including food provision, timber and other wood products and medicinal values were identified.

The study estimated the sawn timber export value of *Palagium* spp., a bat pollinated timber species to be over USD 5 million in a single year. Silk cotton fibre exports from

Indonesian plantations and oil produced from seeds were also estimated to be worth USD 5 million annually. Also the sale of Durian fruit of south-east Asia was estimated to yield at least USD 120 million annually, while the seeds of *Parkia*, which is eaten as a vegetable, yields USD 15 million annually in sales in peninsular Malaysia alone.

Insectivorous bats feed on a wide variety of insect species and in doing so act as biological control agents for agricultural pests. Herbivorous arthropods destroy up to 50% of agricultural crops worldwide, with estimated costs running up to billions of dollars in loss of agricultural products and cost of controlling these pests (Kunz *et al.*, 2011). In the Big brown bat (*Eptesicus fuscus*), it has been estimated that a colony of 150 individuals can consume over a million individuals of four species of insect pests annually (Whitaker, 1995).

In the engineering field, studies of bat flight and movement dynamics have stimulated the engineering of bat-inspired micro aerial vehicles that imitate the flight dynamics of bats for use in military and surveillance purposes (Bunget & Seelecke, 2008). Extensive studies of flight in birds, bats and insects revealed bats as the best model for such designs due to their ability to fly at varying speeds and high agility and manoeuvrability even in very small spaces while avoiding obstacles (Bunget & Seelecke, 2008).

In some countries, bat watching is a recreational activity. Visitors to bat emergence sites are reported to pay up to USD 12 in some places to watch bats as they emerge at dusk from the caves in which they roost. Up to USD 3 million was estimated as tourist related expenditures per year at the Avenue Bridge in Texas which houses over million Brazilian free tailed bats (Ryser & Popovici, 1999). In Ghana bat watching is not very common, but appears to be an added attraction for packages to sites where bats occur and are

advertised together with the main attractions. Thus, bat watching contributes directly or indirectly to income generated from tourism in Ghana.

Despite the positive value of bats, they are also known to cause negative economic impacts. For instance, fruit bats feed on commercially cultivated fruits and cause significant economic losses. In Mauritius, the Mauritian fruit bat (*Pteropus niger*) was alleged to cause the loss of about 50,000 kg of litchis every year (Oleksy, 2015). In Australia, orchid farmers have been dealing with the problem of flying fox damage in orchards for decades, while the Greater short nosed fruit bat (*Cynopterus sphinx Vahl*) is also known for the severe damage it causes to grapes in India (Verghese, 1998). Other fruits often destroyed include bananas, mango and guava. Apart from the damage caused, mitigation methods are often very labour-intensive and expensive and often bats are killed by farmers. In Ghana, cashew farmers have complained about fruit bats carrying whole fruits away from their farms and causing the loss of cashew nuts (Ohemeng *et al.*, 2017). Fujita and Tuttle (1991) however, suggest that bats are often blamed for damage caused by other animals, while the actual damage caused by bats is often exaggerated.

Vampire bats are also significant pests of livestock responsible for transmitting rabies which is estimated to cause the deaths of about 100,000 cattle annually with an economic loss of around USD 30 million (Hutson & Mickleburgh, 2001). Diseases caused by bats also cause substantial loss of human lives and domestic animals with huge global economic costs (Morens *et al.*, 2004; Hayman, 2011).

### **2.9.3 Bats as bushmeat**

Bats are commonly hunted for bushmeat and their meat forms a source of protein in the diet of local communities in several places, while the sale of bat meat provides income.



A number of studies including Fujita and Tuttle (1991); Mickleburgh *et al.* (2009); Kamins *et al.* (2011), have reported the use of bats as bushmeat.

According to Kamins *et al.* (2011), larger fruit bats are hunted, smoked and sold in markets in Ghana. Insectivorous bats are avoided as they are described as smelly and distasteful. *E. helvum* is the commonly hunted species in Ghana and provides an additional and probably seasonal meat source in some communities. Income from trade in bat bushmeat is reported as an additional source of income to supplement other income sources for hunters and traders. Kamins *et al.* (2011) estimated a daily income of USD 2.2 from the sale of ca. 30 bats and an annual income of USD 11,660. In a recent study, Ohemeng *et al.* (2017) reports of a single bat being sold for USD 0.30 in a rural town in Ghana. MacDonald *et al.* (2011) reports bats being sold for about USD 1.63 and USD 10.6 per kilogram (depending on whether they were fresh or smoked) in rural markets in Cameroon and Nigeria. In Malaysia, larger flying foxes were sold for USD 2.50 to 3.30 with vendors reportedly making sales between USD 200 to 300, per person per season. Also, in Jakarta, *Pteropus vampyrus* sold for as much as USD 10 per bat (Fujita & Tuttle, 1991). Culturally, bats are used in local and traditional medicine preparations and used in the treatments of physical ailments and spiritual diseases and may also be hunted for this purpose.

## **2.10 Conservation status of bats and threats to bat populations**

Bats face numerous threats which have led to decline of the populations of several species. The IUCN Red list of Threatened Species lists over 20% of known bat species as threatened. Table 2.2 summarizes the IUCN categories and population trends of fruit bat species that occur in Ghana.

**Table 2.2 Conservation status of fruit bats that occur in Ghana.***Source: IUCN (2015).*

| Species                | Population Trend                             | Major Threats                    | IUCN Category   |
|------------------------|----------------------------------------------|----------------------------------|-----------------|
| <i>E. helvum</i>       | Decreasing                                   | Hunting                          | Near threatened |
| <i>H. monstrosus</i>   | Presumed large and wide distribution         | Hunting, Habitat loss            | Least concern   |
| <i>E. franqueti</i>    | Stable                                       | Possibly deforestation           | Least concern   |
| <i>E. buettikoferi</i> | Decreasing                                   | Deforestation                    | Least concern   |
| <i>N.veldkampii</i>    | Unknown                                      | Possibly deforestation           | Least concern   |
| <i>M. pusillus</i>     | Stable, presumed large and wide distribution | No major threats listed          | Least concern   |
| <i>S. ophiodon</i>     | Decreasing                                   | Habitat loss                     | Vulnerable      |
| <i>S. zenkeri</i>      | Decreasing                                   | Habitat loss                     | Least concern   |
| <i>E. gambianus</i>    | Presumed large and wide distribution         | Hunting, habitat loss            | Least concern   |
| <i>R. aegyptiacus</i>  | Stable                                       | Hunting, cave disturbance        | Least concern   |
| <i>L. angolensis</i>   | Decreasing                                   | Habitat loss                     | Least concern   |
| <i>M. woermanni</i>    | Presumed large and wide distribution         | Habitat loss, forest degradation | Least concern   |
| <i>M. torquata</i>     | Presumed large and wide distribution         | Habitat loss, logging            | Least concern   |

Bats are viewed in many cultures with disgust and/or fear and are commonly depicted as vectors of diseases, demons, dark magic, agents of misfortune and blood sucking animals (Mickleburgh *et al.*, 2002; Kunz *et al.*, 2011). These perceived attributes and risks

associated with bats often lead to intentional persecution involving cruel and destructive elimination of bats from roosts, especially those in the proximity of humans (Mickleburgh *et al.*, 2002; Kunz *et al.*, 2011). Local people in many areas do not hesitate to cut roost trees to drive away bats or kill bats on sight because of perceptions that they are either dangerous or evil.

Apart from destruction, bats face other major threats of anthropogenic origins emerging from human population increases with increase in demand for land and other natural resources. Degradation and loss of suitable habitat are among the leading threats to bat populations worldwide (Lacki & Baker, 2007).

Tree roosting bats are particularly vulnerable to habitat fragmentation which presents a two sided problem; the loss of roosting sites and loss of suitable foraging habitat (Hayes & Loeb, 2007). Several of the fruit bat species in Africa are threatened in one way or another by deforestation and habitat loss. Agricultural practices like slash and burn and pesticide usage (e.g. Dichlorodiphenyltrichloroethane) have also been implicated in bat population declines (Mickleburgh *et al.*, 1992;2002; Kunz *et al.*, 2011). Deforestation in tropical areas has led to the loss of vital food resources for many species and caused declines in populations of many species (Mickleburgh *et al.*, 1992; Kunz *et al.*, 2011).

Hunting and trading of bats as bushmeat poses a major threat to bat populations especially those of larger fruit bat species like *E. helvum*. The overexploitation of bats for food has led to the decline of populations and has endangered several bat species. Since these bats often roost in large colonies in rural and urban centres, it makes them very conspicuous and very easy targets for hunters (Mickleburgh *et al.*, 2002; Mickleburgh *et al.*, 2009; Kamins *et al.*, 2011). *E. helvum* which is the preferred bat meat in Ghana, is listed as threatened on the IUCN Red list, (IUCN, 2015), with hunting as the

primary cause of decline of this species' population. Current extraction levels of *E. helvum* across the country is estimated to be far above maximum sustainable yields (Kamins *et al.*, 2011). Overexploitation usually interacts with other factors such as habitat loss and the low reproductive rate of bats to cause drastic population declines (Mickleburgh *et al.*, 2002).

Other practices such as the removal of dead trees and pruning of dead branches as a management practice can also affect populations of cavity dwelling bats. The overexploitation of bat guano, mining in caves and the use of environment near caves for tourism or religious purposes where bats roost in large colonies could all threaten bat populations particularly of cave dwelling bats.

### **2.11 Bats and emerging zoonotic diseases**

Globally, infectious diseases present a significant threat to ecosystems and public health and remain the leading cause of mortality in the world (Daszak *et al.*, 2001; Morens *et al.*, 2004; Jones *et al.*, 2008). An estimated 75% of all infectious diseases in humans are zoonotic in origin and majority of these are derived from wildlife (Wolfe *et al.*, 2005; Jones *et al.*, 2008; Luis *et al.*, 2013). Emerging infectious diseases (EID's) are infectious diseases with increasing occurrence following first introduction, or newly occurred in new areas where it was previously absent (Cleaveland *et al.*, 2001; Engering *et al.*, 2013). There has been a steady rise in the occurrence of emerging infectious diseases in recent decades with most EID's being caused by viral and bacterial pathogens (Jones *et al.*, 2008). The incidence of EID's of zoonotic origin is increasing over time (Jones *et al.*, 2008) and this has been attributed to several causal factors, the key one being the increasing contact rates between humans and wildlife hosts, mainly as a result of

anthropogenic factors (Wolfe *et al.*, 2005; Cunningham *et al.*, 2012; Wang & Crameri, 2014).

Bats are an important source of emerging zoonotic viruses. Over the past decade, research and publications that focus on bats as reservoirs of several viruses have more than doubled (Wang & Crameri, 2014). According to Wang *et al.* (2011), the increase in research that focuses on bats and viruses, is due to the recent occurrence of high profile viral diseases that have been proven to be of bat origin, and secondly because of advancements in technology that has enabled the discovery of novel bat viruses. Most bat related viruses are of global concern and include viruses such as lyssaviruses (Rabies and rabies-like viruses), filoviruses (e.g. Ebola and Marburg viruses), paramyxoviruses (henipaviruses) and coronaviruses (e.g. Severe Acute Respiratory Syndrome). Several recent publications address the enormous diversity of bat viruses (Calisher *et al.*, 2006; Wong *et al.*, 2007; Kuzmin *et al.*, 2009; Drexler *et al.*, 2012). These viruses cause diseases that have high case fatalities in both humans and domestic animal populations.

A central theme that runs across bat-viruses related research is that bats have a unique ecology and biology that enables them to be reservoirs of numerous emerging and re-emerging viruses. Aspects of their ecological diversity, taxonomic diversity, evolution and their biology are often cited as rationales for their ability to serve as reservoirs of viruses. Luis *et al.* (2013), Wang *et al.* (2011), Calisher *et al.* (2006) and Hayman *et al.* (2013), provide extensive reviews on what makes bats "special" in their ability to serve as reservoirs of viruses.

### 2.11.1 Human bat interactions and zoonotic spillover

Anthropogenic factors that increase contact rates between humans and wildlife hosts of zoonotic pathogens increases the risk of spillover and emergence of zoonotic diseases (Wolfe *et al.*, 2005; Cunningham *et al.*, 2012; Wang & Crameri, 2014). Thus, human activities that enhance exposure to bats will increase potential transfer and spillover of diseases between humans and bats or to intermediate hosts (Hayman *et al.*, 2013). In Ghana, known interactions between humans and bats include the hunting of bats for bushmeat, contact with urine and faeces as a result of the presence of roosts in towns and cities close to human habitation, visiting bat caves for tourism and religious practices, collection and consumption of fruits partly eaten by bats (Mickleburgh *et al.*, 2009; Kamins *et al.*, 2011; Anti *et al.*, 2015; Lawson *et al.*, 2016; Ohemeng *et al.*, 2017). These may present multiple opportunities for spillover from bats to humans or to domestic animals.

Different human demographic parameters have been shown to have different implications on the risk levels associated with transmission of wildlife zoonosis to humans [e.g. Wolfe *et al.* (2005); Subramanian (2012)]. Recent studies by Lawson *et al.* (2016), shows that in Ghana, there are social determinants of risk levels and potential spillover of diseases from bats. Bat hunting and consumption of bat meat, for instance, were identified to be done mostly by men. Bat hunting and consumption was also significantly higher in rural areas and the less educated were more likely to participate in these activities. Hence, disease risks may be higher in men or in rural than urban areas and among less educated people. Human-bat interactions are likely to be high in places with high bat populations.



Previous outbreaks of zoonotic diseases from bats suggests a direct linkage between occurrence and proximity of bats to humans (Hahn *et al.*, 2014). However, the occurrence of bats alone may not necessarily imply a higher risk of disease spillover. Usually, human behaviour and practices play a role in the spillover of diseases from bats and other wildlife (Hahn *et al.*, 2014). In the case of the spillover of Nipah virus in Bangladesh, the human practice of drinking date palm left uncovered overnight and contaminated by bats led to the spillover of the disease and not mere exposure to bat excreta under roosts. Also in the Malaysian outbreak of Nipah virus, the practice of keeping pig farms near fruit orchards brought foraging fruit bats close to animal pens which exposed pigs to bat ejecta pellets and faeces and led to the outbreak (Pulliam *et al.*, 2012). Other practices such as the degradation and fragmentation of natural feeding and roosting habitats for bat species may be causing fruit bats to roost near humans or cause them to feed in backyard gardens, fruit orchards and in agricultural landscapes (Hahn *et al.*, 2014; Plowright *et al.*, 2015). This further suggests that anthropogenic factors play a major role in human bat interaction and spillover from bats.

#### **2.11.2 Zoonotic infections in fruit bats that occur in Ghana**

In Ghana, several fruit bat species occur and in large numbers, creating the potential for disease spillover and occurrence. Hayman *et al.* (2008b) detected antibodies against Nipah virus in 1% *E. gambianus* sampled, 23% *E. helvum* and 6% *H. monstrosus* in Ghana. Drexler *et al.* (2009) subsequently identified and confirmed the presence of some of these henipaviruses in fruit bat species in Ghana. Hayman *et al.* (2012b) reported Ebola virus antibodies in 37% of *E. franqueti* sampled, 37.8% of *E. gambianus*, 43.7% of *H. monstrosus* and 25% of *N. veldkampii* in Ghana. Wright *et al.* (2010), provides

evidence of Lagos bat virus in *E. helvum* bat populations in some cities in Ghana. Serological investigations by Hayman *et al.* (2011) revealed potential spillover of henipaviruses to domestic animals in some villages and cities in Ghana in close proximity to large bat roosts and this indicates potential risk of outbreaks of diseases caused by these pathogens. A summary of viral pathogens identified from African fruit bats that occur in Ghana is provided in Table 2.3.

The purpose of this review was to assess available published information and research on bats, particularly fruit bats in Ghana, in relation the aims and objectives of this study. This review started with a taxonomic and morphological description of bats, then an assessment of the information available for fruit bats that occur in Ghana, with sections that reviewed information available for aspects of the biology and ecology of bats including roosting ecology, feeding ecology and their reproduction. Other sections reviewed the socio-economic and ecological importance and conservation issues about bats, and concluded with a section on bats and zoonotic disease transmission.

While a lot of work has been done and published in literature, there are significant gaps in information available. Most bat research do focus on temperate insectivorous species with very little research and information available for tropical African bat species. Where information is available, they are often outdated with little or no updates. Recent literature on bats does focus on disease transmission, with very little focus on their ecology.

The overall aim of this study was to describe the ecology of fruit bats in Ghana with focus on *Epomophorus gambianus* and the role of fruit bats in zoonotic disease transmission. Results from this study should improve knowledge of the ecology of fruit bats and help to understand disease transmission from bats.

**Table 2.3 Zoonotic Viruses identified from African fruit bats which occur in Ghana.**

| Species                | Virus                              | Location                       | Reference                                                                                 |
|------------------------|------------------------------------|--------------------------------|-------------------------------------------------------------------------------------------|
| <i>E. helvum</i>       | Mastadenovirus                     | Ghana                          | Baker <i>et al.</i> (2013a)                                                               |
|                        | SARS-CoV                           | Kenya                          | Tong <i>et al.</i> (2009)                                                                 |
|                        | Ebolavirus                         | Ghana                          | Hayman <i>et al.</i> (2010)                                                               |
|                        | Pegivirus                          | Kenya, DRC, Nigeria            | Quan <i>et al.</i> (2013)                                                                 |
|                        | Herpesviruses                      |                                | Baker <i>et al.</i> (2013a)                                                               |
|                        | Papillomaviruses                   |                                | Baker <i>et al.</i> (2013a)                                                               |
|                        |                                    |                                | (Hayman <i>et al.</i> , 2008b; Drexler <i>et al.</i> , 2009; Hayman <i>et al.</i> , 2011) |
|                        | Henipaviruses                      | Ghana                          | (Canuti <i>et al.</i> , 2011; Baker <i>et al.</i> , 2013a)                                |
|                        | Family Parvoviridae                | Ghana                          | (Hayman <i>et al.</i> , 2008a; Kuzmin <i>et al.</i> , 2008; Peel <i>et al.</i> , 2012)    |
|                        | Lagos bat virus                    | Ghana, Kenya, Nigeria, Annobon | (Baker <i>et al.</i> , 2013b)                                                             |
| <i>H. monstrosus</i>   | Achimota virus                     | Ghana                          | (Müller <i>et al.</i> , 2007)                                                             |
|                        | SARS-CoV                           | DRC                            | (Leroy <i>et al.</i> , 2005; Pourrut <i>et al.</i> , 2009; Hayman <i>et al.</i> , 2012b)  |
|                        | Ebolavirus                         | Gabon, DRC, Ghana              | (Hayman <i>et al.</i> , 2008b; Drexler <i>et al.</i> , 2012)                              |
|                        | Henipaviruses                      | Ghana                          | (Pourrut <i>et al.</i> , 2007; Hayman <i>et al.</i> , 2012b)                              |
| <i>E. franqueti</i>    | Ebolavirus                         | Ghana, Congo                   | (Hayman <i>et al.</i> , 2008a)                                                            |
| <i>E. buettikoferi</i> | Lagos bat virus                    | Ghana                          | (Hayman <i>et al.</i> , 2012b)                                                            |
| <i>N. veldkampii</i>   | Ebolavirus                         | Ghana                          | (Hayman <i>et al.</i> , 2012b)                                                            |
| <i>M. pusillus</i>     | Lagos bat virus                    | African Central Republic       | (Sureau <i>et al.</i> , 1980)                                                             |
|                        | MokolaVirus                        | African Central Republic       | (King <i>et al.</i> , 1990)                                                               |
| <i>E. gambianus</i>    | Ebolavirus                         | Ghana                          | (Hayman <i>et al.</i> , 2012b)                                                            |
|                        | Lyssavirus                         | Ghana                          | (Hayman <i>et al.</i> , 2008a)                                                            |
|                        |                                    |                                | (Leroy <i>et al.</i> , 2005; Hayman <i>et al.</i> , 2008b; Drexler <i>et al.</i> , 2012)  |
|                        | Hendra and Nipah                   | Ghana, Congo, Gabon            | (Müller <i>et al.</i> , 2007; Tong <i>et al.</i> , 2009)                                  |
| <i>R. aegyptiacus</i>  | SARS-CoV                           | South-Africa, DRC, Kenya       | (Towner <i>et al.</i> , 2007; Kuzmin <i>et al.</i> , 2011)                                |
|                        | Marburg                            | Gabon, Uganda, Kenya           | (Kuzmin <i>et al.</i> , 2008; Kuzmin <i>et al.</i> , 2011)                                |
|                        | Lagos bat Virus, Shimoni bat virus | Kenya                          | (Drexler <i>et al.</i> , 2012)                                                            |
|                        | Henipavirus                        | Gabon, Congo                   | (Müller <i>et al.</i> , 2007)                                                             |
| <i>L. angolensis</i>   | SARS-CoV                           | DRC                            | (Quan <i>et al.</i> , 2013)                                                               |
| <i>M. woermanni</i>    | Pegivirus                          | DRC                            | (Drexler <i>et al.</i> , 2012)                                                            |
|                        | Paramoxivirus                      |                                | (Müller <i>et al.</i> , 2007)                                                             |
| <i>M. torquata</i>     | SARS-CoV                           | DRC                            | (Leroy <i>et al.</i> , 2005; Pourrut <i>et al.</i> , 2007)                                |
|                        | Ebolavirus                         | DRC, Gabon                     |                                                                                           |
|                        | Henipavirus                        | Gabon, Congo, DRC              | (Drexler <i>et al.</i> , 2012)                                                            |

## CHAPTER THREE

### 3.0 GENERAL METHODOLOGY

#### 3.1 Study areas.

Data for this study were collected from several locations across Ghana, West Africa from August 2012 to August 2016. Ghana lies within latitude  $4^{\circ}44'N$  and  $11^{\circ}11' N$  and  $3^{\circ} 11'W$  and  $1^{\circ}11' E$  and is bordered to the north by Burkina Faso, on the East by Togo and on the West by Côte d'Ivoire (Figure 3.1). Ghana has a total land area of 238533 km<sup>2</sup> and estimated population of 24,658,823 (Ghana Statistical Service, 2012). The terrain is generally flat with over 50% of the country with altitudes below 150 m; the highest point reaching 885 m.



**Figure 3.1 Map of West Africa showing Ghana and the Upper Guinea Forest Block (dark green).**

*Courtesy Global Forest Watch*

The country experiences alternate wet and dry seasons which is controlled by the movement of the Intertropical Convergence Zone (ITCZ) (Borrow & Demey, 2010). The southern parts of the country experiences two major rainy seasons; one in March-July (peaking in May/June) and the second in September/October-November. Both rainfall seasons are separated by a short dry season in July/August-September, and a major dry season from December to February. The mean annual rainfall exceeds 2000 mm with rains generally falling throughout the year (Borrow & Demey, 2010). The south-western part of the country is generally hot and humid with the south-eastern part which forms part of the Dahomey Gap being much drier (mean annual rainfall 700-900 mm). The northern part experiences a single rainy season which extends from April to October (mean annual rainfall 900-1300 mm). Average temperatures in the south are around 26 °C (maximum of 29 °C), and around 29 °C in the north, reaching up to an annual mean maximum temperature of 34 °C (Borrow & Demey, 2010).

One of Africa's major lowland forest block, the Upper Guinea forest block, extends into Ghana and covers a major part of the south-western part of the country (Figure 3.1). However, this block has suffered deforestation and most of the vegetation has been degraded into mosaics of cultivated land, farm bush and secondary forest. Very little true primary forest remains in the country as most parts have undergone anthropogenic modification. The little forest that remains is mostly in protected areas. Based on physiognomy, environmental and geographical criteria, Hall and Swaine (1981), identified seven major forest types: wet evergreen, moist evergreen, upland evergreen, moist semi-deciduous, dry semi-deciduous, southern marginal and south-east outlier forest. The northern two-thirds of the country is mostly Guinea savannah, with only a small part of the extreme north-east corner being Sudan savannah. Characteristic of these two vegetation types is fire adapted grasses and trees, which are taller and much denser

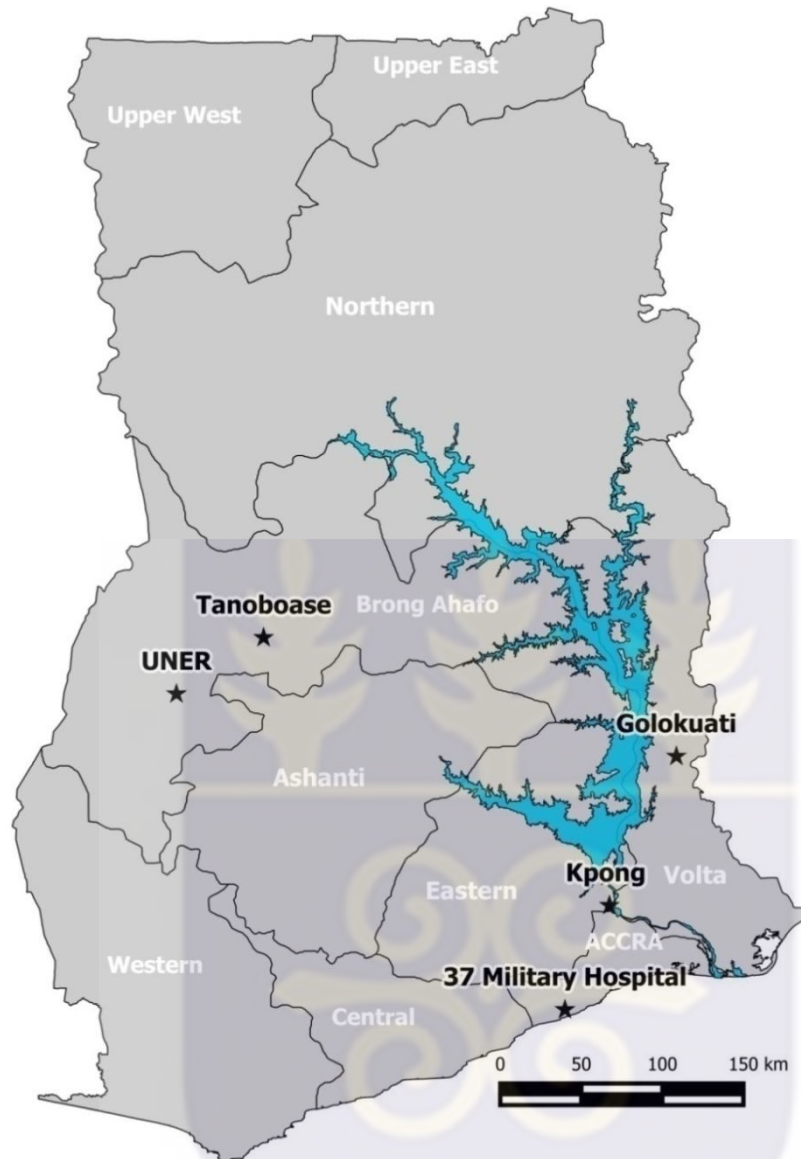


in the Guinea savannah. Gallery forest may occur around water-courses. Along the coast, the vegetation is mainly scrub with grasses and scattered trees; mangroves (most of which are degraded) are found mostly around the delta of the Volta River and in the west within the Amansure River catchment.

While the data on bat distribution were collected all over Ghana, the intensive field data collection and bat sampling were carried out at three main sites where colonies of the focal species had been identified. These are Ve-Golokuati in the Volta Region, 37 Military Hospital in Accra and Tano Sacred Grove in Techiman district (Figure 3.2). The bat colonies at two additional sites, Kpong and University of Energy and Natural Resource (UENR) campus, Sunyani were also monitored.

Ve-Golokuati is located on Lat 7.00107 °, Lon 0.43604 ° along the Tema-Jasikan road and is the capital of the Afadzato South District in the Volta Region. Ve-Golokuati is located within the forest-savannah transitional ecological zone of Ghana and receives annual rainfall totals ranging between 1016 mm and 1210 mm (Ghana Statistical Service, 2014a). Within the town is a large colony of epauletted bats (mostly *E. gambianus*) which was located and reported for the first time during the initial search for bat colonies in Ghana as part of this study. The occurrence of this large colony made it a suitable site to conduct several of the detailed ecological studies on the focus species, *E. gambianus*. Several of the inhabitants are farmers, growing mainly vegetable crops, but a few rice farms could be found in the swampy areas around the town.





**Figure 3.2 Map of Ghana showing study sites.**

*Study sites are indicated by black star.*

The 37 Military Hospital site (Lat 5.587418<sup>o</sup>; Lon -0.185147<sup>o</sup>) is located in Accra, the capital of Ghana. A huge *Eidolon helvum* colony has been associated with the 37 Military Hospital for many years. The 37 Hospital colony is one of the largest reported *E. helvum* colonies in the country with up to a million bats recorded (Hayman *et al.*, 2012a). The bats can be seen roosting on the Mahogany (*Khaya senegalensis*) and Neem

(*Azadirachta indica*) trees within the hospital compound and surrounding areas. The vegetation of the coastal belt within which Accra is situated is mainly coastal scrub and grassland; the average annual rainfall is around 730mm, and is distributed mainly between two rainy seasons. The landscape is mainly urban with a mosaic of smaller settlements and farming patches on the outskirts.

The Tano Sacred Grove, located on Lon 7.66281 °, Lat -1.85904° is found in the town of Tanoboase in the Techiman Municipality of the Brong Ahafo Region. The Sacred Grove has an area of ca.300 ha and is a site of historical and cultural importance to the people of the Brong Ahafo Region. The grove was also one of fourteen sites that was selected for development under the Community Based Ecotourism Project in 1996 (USAID, 2014). This sacred grove arguably has the largest bat population in the country with an estimated population of over 2 million bats. The colony is relatively less studied and was reported in the scientific literature for the first time by Hayman *et al.* (2012a).

Tano Sacred Grove lies within the forest/savannah transition zone and experiences both semi-equatorial and savannah climates, characterized by moderate to heavy rainfall. The mean annual rainfall in the area is between 1660 mm and 1260 mm with a single pronounced dry season occurring from November to March each year (Ghana Statistical Service, 2014b).

### 3.2 Study species

This study focused generally on fruit bats (Family, Pteropodidae) in Ghana. Thirteen fruit bat species have been recorded in Ghana (Yeboah, 2008; Happold & Happold, 2013). However, the detailed ecological studies concentrated on the three most common species that occurred at the study sites; *Epomophorus gambianus*, *Eidolon helvum* and

*Micropteropus pusillus* with the intensive feeding, roosting and reproductive ecology studies focusing on *E. gambianus*. Special focus is given to *Epomophorus gambianus* in this study as this species is a common species in West Africa (Boulay & Robbins, 1989) but relatively not very well studied compared to another common species like *Eidolon helvum*. This species is also of public health concern because of its links to potential zoonotic disease-causing pathogens (Hayman *et al.*, 2008a; Hayman *et al.*, 2012b).

### **3.3 Mapping of the distribution of bat colonies in Ghana**

To identify and map out fruit bat colonies in Ghana, a nationwide search for bat roosts was conducted using two approaches. The first approach involved travelling along selected transects across the country and interacting with people in towns and villages to identify bat roosts. The local people in the towns and villages were asked also about locations of other places that they knew to have bat roosts, using the snowball effect. The second method involved a citizen science approach where the general public was engaged to report places that they knew bat roosts occurred. Reported sites were visited for confirmation of roost occurrence and identification of the species of bat(s) involved.

#### **3.3.1 Roost size estimation**

For all identified roosts, the size was estimated by counting or estimating the number of bats that made up the roost. Roost size estimation was done by visual counting between 0800-1630h during which time bat activity and movement within the roost is minimal so as to prevent obvious double counting and missing large numbers of individuals (Hayman *et al.*, 2012a).

*E. helvum* typically forms clusters of about 8-100 individuals (DeFrees & Wilson, 1988; Hayman *et al.*, 2012a) and these aggregations make it impossible to count every individual precisely. Colony size estimation for the species was done using a modified method employed by Hayman *et al.* (2012a) in estimating *E. helvum* populations in Ghana. In this method, an arbitrary reference branch on a roost tree was selected and bat numbers forming different cluster sizes on the branch was estimated. This was repeated for each branch on the roost tree, moving in a clockwise direction from the reference branch to avoid double counting or missing some branches. Counts were done for each roost tree within the entire colony. For the other species (*E. gambianus* and *M. pusillus*) that roost in trees with individuals well spaced (except mothers and pups), roost counts were made by counting individual bats per branch (in a clockwise manner from an arbitrary reference branch) for each roost tree within the colony using a handheld tally counter. The monthly roost counts were done at the Ve-Golokuati, 37 Military Hospital, Tano Sacred Grove, the UENR campus and the Kpong sites.

### **3.4 Mapping of trees used by bats as roosting sites**

The locations of all identified roosts were taken using a Garmin eTrex 20 GPS device. For the sites where repeated or monthly colony counts were carried out and where individual trees were accessible on foot, all trees that were identified to support bats at the roost site were mapped at the beginning of the study using GPS. Each roosting tree was given a unique identification number which was used in the monthly counts. Subsequently, newly identified roosting trees were added as and when they were observed. This allowed for the monitoring of each roost tree and changes in the number of bats roosting on it throughout the study period.

### 3.5 Bat trapping and sampling

Bats were caught using ground mist nets (Plate 3.1) (3-5m high, 6-18m long) or canopy mist nets erected in tree tops depending on the species occurring at the study site, the vegetation of the site and convenience. Bats were trapped between 18:00h and 06:00h GMT; nets were checked at least 30-45 minute intervals and any bats trapped were carefully removed. Each bat caught was kept in a separate cloth bag and transported to the processing station where they were identified, sexed, aged and the weight and forearm length were measured. Processing stations were usually set up close to the trapping locations. This ensured that bats were not kept in bags for long periods during movement from net sites to processing stations.



**Plate 3.1 Mist netting of bats.**

*A- Mist net used in trapping bats. B-Removal of trapped bats from mist nets*

Bat species were identified using field guides (Rosevear, 1965; Happold & Happold, 2013). The sex was determined by examining external genitalia. The age and breeding status were determined by direct observation of morphological features and categorised into neonate, juvenile, sexually immature adult or adult groups. Unfused epiphyses,



typical of juvenile bats (Anthony, 1988) was used together with morphological characteristics to distinguish juveniles from sexually immature individuals. Sexual maturity was determined based on development of testes or mammary glands (DeFrees & Wilson, 1988; Hayman *et al.*, 2012a) or through other secondary sexual characteristics such as shoulder epaulettes, fur colourations or ruff of stiff hairs, if present for the species. Pregnancy in females was determined by abdominal palpation and lactation was detected by the expression of milk from nipples. Every bat caught was marked with either a thumb band (Tidemann, 1999; Hayman *et al.*, 2012a) or a Trovan® RFID nano transponder (Trovan Electronic Identification Systems, UK) before being released.

With the exception of individuals kept for blood sampling, all bats were processed as quickly as possible and released immediately. Bats sampled for blood were kept in a 1x1x1m flight cage and provided with fruits (mango, pawpaw, and banana) and processed within 12 hours of capture. All bats that were sampled for blood were given glucose solution *ad libitum* before their release.

### **3.6 Blood sampling**

Periodic blood sampling from *E. gambianus* and other sympatric fruit bat species was done at selected sites. All blood sampling events were done by certified veterinary personnel from the Wildlife Division of Ghana Forestry Commission. Blood collection was done by taking between 0.2-1.0 ml of blood (less than 1% of bat's body weight) from an occluded propatagial vein using a 28 gauge needle and a 1 ml syringe into labelled tubes (Plate 3.2). Blood samples were transported on ice from the field to the laboratory where the blood was centrifuged (6000 revolutions per minute for 15 minutes) to separate serum and blood cells.



The separated blood serum was then heat-treated at 56°C for 30 minutes to inactivate RNA viruses and remove complement before freezing and transporting (under license) at -80°C for serological studies by Luminex® assays (Baker, 2012; Baker *et al.*, 2013b) at the Institute of Zoology (IoZ) laboratory in the UK. With the exception of blood centrifuging, which was done at the Techiman Veterinary Investigation farm laboratory (for samples taken near Techiman), all other blood preparation procedure, prior to final transportation to the UK, were done at the National Veterinary Laboratory in Accra.



**Plate 3.2 Blood sampling from *Epomophorus gambianus*.**

### **3.7 Luminex serology testing**

Sera collected from bats were tested for the presence of anti-hendra (HeV), Nipah (NiV), and Cedar (CedV) viruses which are all viruses in the family *Paramyxoviridae*. Tests were performed using a highly sensitive multiplexed immunoassay against soluble

glycoproteins (that were coupled to beads) of these viruses. The antibodies of these viruses were quantified against titration of a cross-reactive potentially-neutralizing antiviral monoclonal antibodies (mAb102.4, mAb 5D2 and mAb 2B8) and positive and negative control sera.

The beads (coupled to soluble titrimetric forms of the glycoproteins of the viruses) were used as the antigen base for the immunoassays. Beads of each analyte were initially blocked in skimmed milk powder before incubation with diluted sera. The beads were then incubated with Biotinylated Protein A (ProA) before incubation with Streptavidin conjugated phycoerythrin as the reporter molecule. The resulting solution in the microplate wells were analysed by the Luminex system which reports the Median Fluorescence Intensity (MFI) of  $\geq 100$  beads for each analyte for each sample and the results were interpreted as positives or negatives for each sample.

### **3.8 Data handling and statistical analysis**

Data handling, organisation and manipulation was done in Microsoft Excel (Microsoft®), SPSS, or R (R Core Team). Specific methods and statistical analyses for each data set are described for each chapter.

### **3.9 Ethics**

Ethical clearance was obtained for this study from the Ethical Approval committee of the Noguchi Memorial Institute for Medical Research, Ghana (CPN:002/13-14). All bat sampling techniques were done safely and all bats captured were treated humanely.

### **3.10 Risk assessment**

Prior to beginning of this work, all personnel involved in the direct handling of bats were vaccinated against rabies and tetanus which are likely to occur from accidental bat bites during trapping and handling of bats. Protective gear (e.g. leather gloves) was worn when handling bats to prevent and/or reduce incidence of bites from bats. Laboratory work (serology testing of blood samples using Luminex® assays) was conducted under UK Control of Substances Hazardous to Health (COSHH) regulations and Zoological Society of London (ZSL) laboratory safety regulations.



## CHAPTER FOUR

### 4.0 DISTRIBUTION OF FRUIT BATS AND PEOPLES'

#### PERCEPTION OF BATS IN GHANA

##### 4.1 Introduction

Bats have a global distribution, occurring almost everywhere with the exception of a few locations where the climate is unsuitable. Throughout Africa, bats appear to be absent only in the more distant and arid desert areas. In West Africa, bats are known to occur in all the different vegetation zones, from forests, mangrove swamps to the sub-desert regions. Generally, bats seem to show no special preference for any particular vegetation zone however, individual species may be more adapted and suited to one type of vegetation than another (Rosevear, 1965). Thus, only few species occur in all habitats.

Fruit bats (family Pteropodidae) occur extensively throughout much of Africa within a variety of habitats. While many species rely on different types of forests, a few species are able to utilise savannah areas. Within suitable vegetation the local distribution and abundance of different bat species may be influenced by factors such as roosts availability, competition, food abundance and predators (de Jong & Ahlén, 1991). Roost availability is an important factor in predicting the distribution of cave dwelling bats (Kunz, 1982).

Eleven genera of fruit bats are known to occur in West Africa and all of these genera are represented by at least one species in Ghana. Information about the distribution of bats in Ghana is scanty. The few studies on distribution include Booth (1956;1959), Decher (1997), while studies on relative abundance include Decher and Fahr (2007), Yeboah (2001), Weber and Fahr (2007). Earlier works by Grubb *et al.* (1998) provide the only

distribution maps for bats in Ghana which were based mostly on museum specimens and on literature records (Plate 2.2). A few other species' occurrence records in Ghana that have been made subsequent to the work of Grubb *et al.* (1998) are mainly records from Rapid Assessment Programmes or from a few individual bat species studies.

Most fruit bat distribution studies are based on mist netting of bats at night with very little records of roosting sites for bats. Roost locations, however is important in assessing threats to bat populations at roosts, monitoring population of species, planning and setting up conservation measures for species of concern, and assessing risk of zoonotic disease exposure to humans due to interactions at roost sites.

This chapter provides the distribution of roosts for several fruit bat species in Ghana and the relative abundance of fruit bat species at several locations in Ghana. Additionally, this study also provides information on the general perceptions that people have about bats.

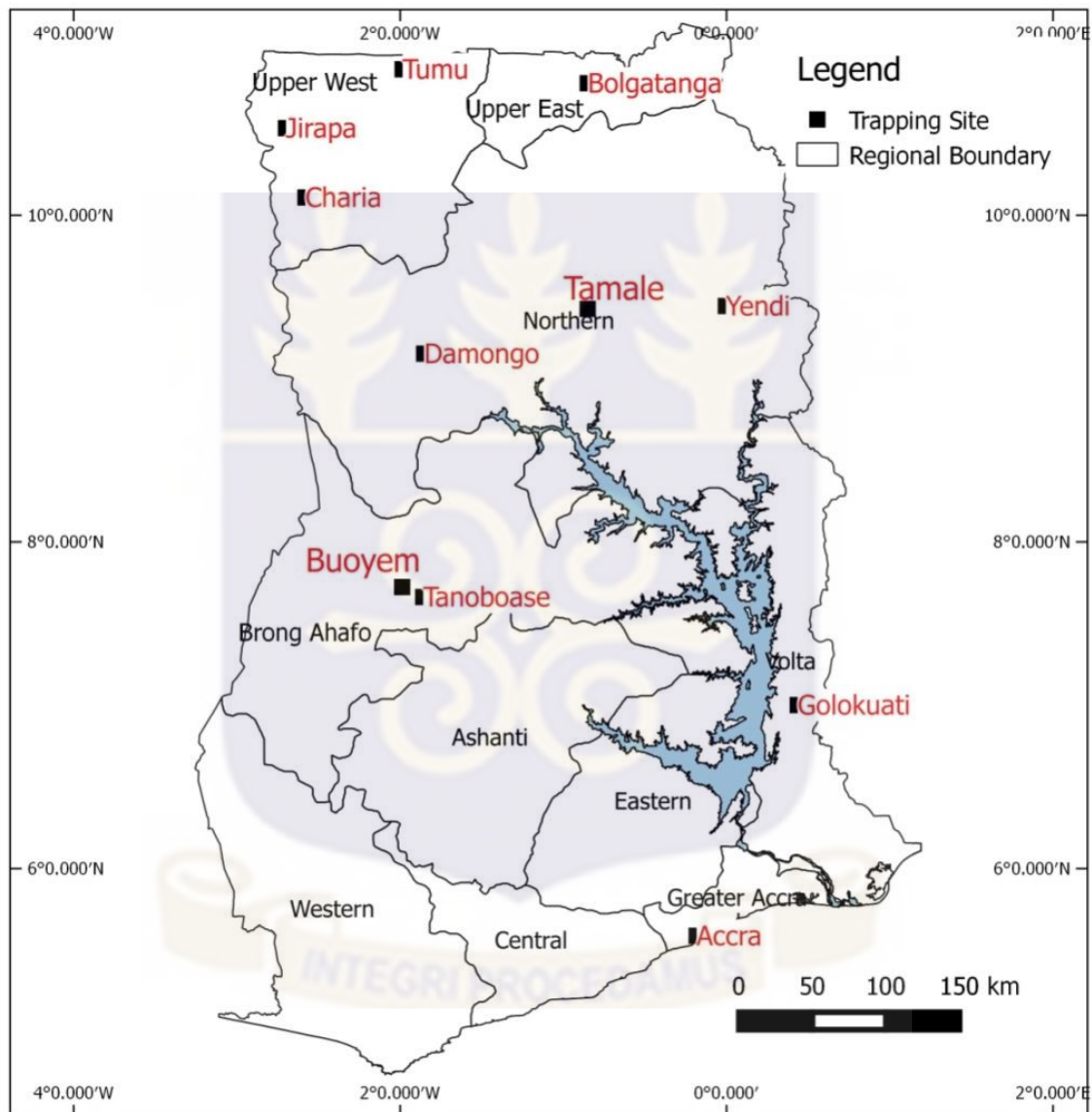
## **4.2 Methodology**

### **4.2.1 Study sites**

Figure 4.1 provides details of the specific locations where bat trapping was done, namely, Accra, Ve-Golokuati, Buoyem, Tanoboase, Bolgatanga, Tumu, Jirapa, Charia, Yendi, Tamale and Damongo (see Appendix 2 for the coordinates of the trapping sites). However, the information on bat roost occurrence was collected nationwide. The Accra, Ve-Golokuati and Tanoboase sites are described in Chapter three (Section 3.1). Buoyem is located in the Techiman North district of the Brong-Ahafo region, where the vegetation is transition between the semi-deciduous forest type and the Guinea Savannah. Damongo, Tamale and Yendi are all located in the Northern Region of Ghana



where the vegetation is Guinea savannah. Tumu, Jirapa and Charia are in the Upper West region of Ghana also in the Guinea savannah vegetation. Bolgatanga is the capital of the Upper East Region, and falls within the Sudan savannah vegetation.



**Figure 4.1 Map showing trapping sites.**



#### **4.2.2 Bat trapping**

Bats were trapped using mist nets as described in Chapter three (Plate 3.1). Due to different net lengths used and variation in trapping times at the different sites, capture effort was standardised as number of bats of each species caught per net hour; where one net hour is defined as a 6 m net length opened for one hour. Capture success, calculated as the number of bats caught per unit effort was used as a proxy for species abundance across all sites sampled, with the assumption that all species have an equal chance of being captured if present within the sampling area.

#### **4.2.3 Roost sites search and colony size estimation**

Roost identification and mapping were conducted between August 2012 and July 2016 across the whole country. A three step approach was used starting with literature search to compile reported bat roosts and visiting those to confirm current occurrence of bats at those sites. This was followed by surveys along specific road transects across the country to locate bat roosts. Ten road transects were selected; 1-Accra to Yendi using the Eastern corridor road, 2-Yendi to Tamale; 3-Accra to Tamale through Kumasi; 4-Tamale to Wechiau through Wa in the Upper West region; 5-Wa to Bolgatanga in the Upper East region; 6-Accra to the Wli falls in the Volta region along the Tema-Jasikan road; 7-Accra to Ve-Golokuati through Ada, using the Tema motorway; 8-Accra to Aburi; 9-Accra to Cape-coast; 10-Accra to Akosombo. Whiles driving along these road transects, intermittent stops were made in towns/villages to interact with locals to help locate bat roosts using a snowball effect where a person interacted with within one town/village would direct the researcher to another town/village where they knew a bat roost to occur. Thirdly, an innovative citizen science approach was used to expand the bat roost

identification. Using two insertions of newspaper advertisements, the general public was engaged to report locations of bats. Roost sites that were reported were visited to confirm their existence and to identify the bat species occurring. The GPS locations of confirmed roosts were taken using a Garmin eTrex 20 GPS device.

A few reported roost sites (n=10) were not visited, but were deemed credible because of multiple reporting of these roost sites and the confirmation of the bat species occurring at those roost sites using photographs. These were added to the data. For these roosts, the geographical location of the town or village where respondents reported the roosts was used. Other reports from the general public which were not deemed credible enough were not included in the findings.

At each roost site visited, the number of bats of each species identified was estimated by visual counting where possible (detailed methodology described in Chapter two). At one colony of *Eidolon helvum*, the bats roosted on the surface of the rocks of the Wli waterfalls in the Volta region so the population was estimated from counts of bats as they flew out at dusk from the roost to forage.

#### **4.2.4 Perceptions and knowledge of bats among local communities**

At each particular locality where a bat colony was identified and was visited, at least one key informant was selected and interviewed using a simple questionnaire (Appendix 3) to obtain information such as seasonality of occupancy of the roost, length of occupancy and general perceptions of the importance and problems associated with bats. The selection of key informants targeted elderly people (at least 30 years old) who had lived near identified roosting sites for ca. 5 years or more and were aware of the presence of the bat roosts. Such people were expected to be in the best position to provide

information required. Questionnaire interviews were conducted for small groups (2-3 informants) or individuals. A total of 87 group and individual key informant interviews were conducted. For the few reported sites that could not be visited but were deemed credible (n=10), respondents to the newspaper adverts were selected as key informants and interviewed on phone using the same questionnaire.

#### **4.2.5 Data analysis**

Bat trapping data is presented as number of each species that was trapped at each trapping site. A sample based rarefaction curve was calculated using the "Mao Tau" function (Colwell *et al.*, 2004) and a species accumulation curve, rescaled by number of individuals, was generated using Estimate S, version 9.10 (Colwell, 2005). This was done for pooled bat capture data across all sampling sites. Forearm and weight measurements for the different bat species captured, are reported as means and their standard deviations. Data from questionnaire interviews was analysed using SPSS and results of responses are reported as frequencies (percentages).

### **4.3 Results**

#### **4.3.1 Species recorded and relative abundance**

A total of 6,132 individuals of 10 species of fruit bats were captured from 11 trapping sites. Plate 4.1 shows some of the species of bats commonly recorded in the study. The total sampling effort across all sites was 13,745 net hours with an average capture success for all species combined of 0.4 bats per net hour (Table 4.1). Capture success for Charia and Jirapa however, were relatively very high. This was because bat trapping at

these sites was done close to *E. gambianus* roost which resulted in very high capture rates within a short period.

*Epomophorus gambianus* was the most common and abundant species, captured at all trapping sites (Table 4.1). *Eidolon helvum* and *Micropteropus pusillus* were each caught at four sites with *E. helvum* being more abundant than *M. pusillus*. These three species together accounted for 90% of all individuals trapped. *Hypsignathus monstrosus* was trapped from Buoyem and Tanoboase sites only, while *Rousettus aegyptiacus* was trapped from Buoyem and Ve-Golokuati only. *Megaloglossus woermanni* was the least common species with only a single individual recorded across all trapping sites. Nine different species of fruit bats were recorded at Ve-Golokuati and Buoyem, 8 species at Tanoboase, 2 at Accra and Charia with only one species trapped at each of the remaining six sites (Table 4.1). The combined species accumulation curve is shown in Figure 4.2. The species accumulation curve almost reaches an asymptotic plateau which indicates that sampling of fruit bats for this study was almost adequate but suggests that there were still some species to be encountered.







*Eidolon helvum*



*Epomophorus gambianus*



*Micropteropus pusillus*



*Lissonycteris angolensis*



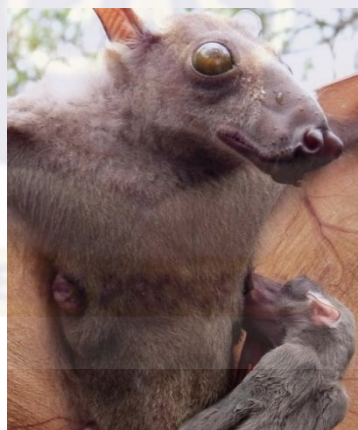
*Nanonycteris veldkampii*



*Epomops franqueti*



*Epomops buettikoferi*



*Hypsignathus monstrosus*



*Rousettus aegyptiacus*

(Credit: Michael Abedi-Lartey)

**Plate 4.1 Fruit bats commonly recorded in the study.**

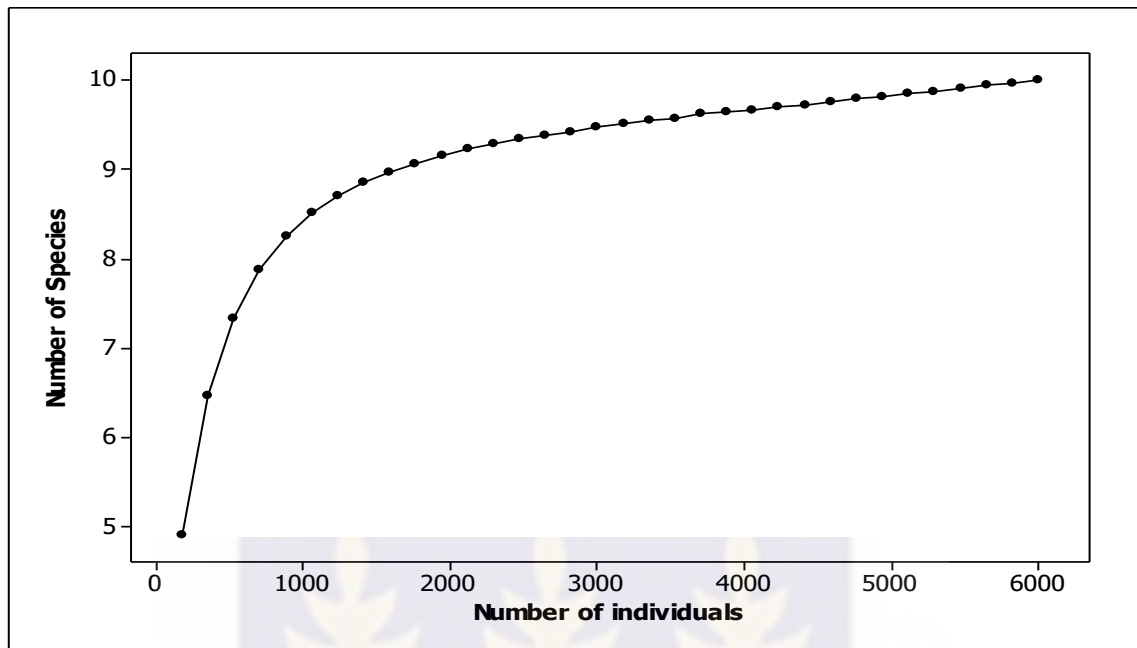
**Table 4.1 Summary of the species and individuals of fruit bats captured at the various trapping sites.**

*One net hour equals a 6 m net opened for one hour.*

| Species                                      | Trapping location |            |            |             |            |             |            |            |            |             |            | TOTAL       |
|----------------------------------------------|-------------------|------------|------------|-------------|------------|-------------|------------|------------|------------|-------------|------------|-------------|
|                                              | a                 | b          | c          | d           | e          | f           | g          | h          | i          | J           | k          |             |
| <i>E. helvum</i>                             | 668               |            | 3          |             |            |             |            | 483        |            | 9           |            | 1163        |
| <i>E. gambianus</i>                          | 257               | 25         | 147        | 25          | 17         | 25          | 20         | 221        | 25         | 2665        | 21         | 3448        |
| <i>E. buettikoferi</i>                       |                   |            | 8          |             |            |             |            | 19         |            | 29          |            | 56          |
| <i>E. franqueti</i>                          |                   |            | 17         |             |            |             |            | 8          |            | 114         |            | 139         |
| <i>H. monstrosus</i>                         |                   |            | 1          |             |            |             |            | 18         |            |             |            | 19          |
| <i>L. angolensis</i>                         |                   |            | 18         |             |            |             |            | 11         |            | 9           |            | 38          |
| <i>M. woermanni</i>                          |                   |            |            |             |            |             |            |            |            | 1           |            | 1           |
| <i>M. pusillus</i>                           |                   |            | 37         | 5           |            |             |            | 9          |            | 851         |            | 902         |
| <i>N. veldkampii</i>                         |                   |            | 2          |             |            |             |            | 11         |            | 35          |            | 48          |
| <i>R. aegyptiacus</i>                        |                   |            | 317        |             |            |             |            |            |            | 1           |            | 318         |
| <b>TOTAL</b>                                 | <b>925</b>        | <b>25</b>  | <b>550</b> | <b>30</b>   | <b>17</b>  | <b>25</b>   | <b>20</b>  | <b>780</b> | <b>25</b>  | <b>3714</b> | <b>21</b>  | <b>6132</b> |
| <b>N(SPECIES)</b>                            | 2                 | 1          | 9          | 2           | 1          | 1           | 1          | 8          | 1          | 9           | 1          | 10          |
| <b>NET UNITS</b>                             | 178.3             | 5.5        | 294.5      | 2.5         | 2.0        | 2.5         | 6.5        | 274.8      | 2.5        | 567.3       | 4.5        | 1341.0      |
| <b>NET HOURS</b>                             | 2007.8            | 10.8       | 3250.3     | 2.5         | 22.0       | 2.5         | 53.8       | 2976.8     | 20.0       | 5358.1      | 40.5       | 13745.1     |
| <b>CAPTURE<br/>SUCCESS<br/>(bats/net Hr)</b> | <b>0.5</b>        | <b>2.3</b> | <b>0.2</b> | <b>12.0</b> | <b>0.8</b> | <b>10.0</b> | <b>0.4</b> | <b>0.3</b> | <b>1.3</b> | <b>0.7</b>  | <b>0.5</b> | <b>0.4</b>  |

*a*-Accra, *b*-Bolgatanga, *c*-Buoyem, *d*-Charia, *e*-Damongo, *f*-Jirapa, *g*-Tamale, *h*-Tanoboase, *i*-Tumu, *j*-Ve-Golokuati, *k*-Yendi





**Figure 4.2 Smoothed species accumulation curve for bats captured across all sites.**

Sample based rarefaction curve, rescaled by number of individuals [“Mao Tau” curve, Colwell et al. (2004)].

#### **4.3.2 Morphometrics of bat species captured.**

The summary of morphometric measurements of all captured species are shown in Table 4.2. The sizes of species trapped varied from the very large *H. monstrosus* (FA 117 mm, Wt=231g) and *E. helvum* (FA-119-120 mm, wt=225 g) to the smallest species *M. woermanni*, (FA=43 mm, wt=16 g). No adult male *H. monstrosus* was captured but males can reach twice the size of females at sexual maturity. The average morphometrics (forearm and body mass) for the species trapped in this study are similar to those previously published (Rosevear, 1965; Happold & Happold, 2013). Sexual size dimorphism was evident in *E. gambianus*, *E. franqueti* and *E. buettikoferi* with males larger than females. Conversely, in the smaller species (*M. pusillus* and *N. veldkampii*) females were slightly larger than males.

**Table 4.2 Measurements of species trapped from all sites.***Based on measurements of adults.*

| Species                | Male                 |                       | Female                |                       |
|------------------------|----------------------|-----------------------|-----------------------|-----------------------|
|                        | Forearm<br>(mm)      | Weight (g)            | Forearm<br>(mm)       | Weight (g)            |
| <i>E. helvum</i>       | 119.40±4.28<br>n=595 | 255.20±30.11<br>n=601 | 120.00± 5.97<br>n=142 | 255.56±36.03<br>n=144 |
| <i>E. gambianus</i>    | 93.40±13.27<br>n=383 | 130.40±13.84<br>n=367 | 84.79 ± 3.24<br>n=679 | 104.78±12.56<br>n=652 |
| <i>E. franqueti</i>    | 87.23±5.42<br>n=13   | 113.73±8.60<br>n=11   | 83.17 ± 3.11<br>n=35  | 86.85±10.95<br>n=34   |
| <i>E. buettikoferi</i> | 83.24±8.90<br>n=5    | 119.20±49.16<br>n=5   | 83.59±4.78<br>n=25    | 91.6±15<br>n=25       |
| <i>H. monstrosus</i>   |                      |                       | 117.591± 3.65<br>n=9  | 231.44±20.98<br>n=9   |
| <i>L. angolensis</i>   | 71.55±1.90<br>n=12   | 66.92±5.40<br>n=12    | 72.04±1.56<br>n=8     | 69.86±7.20<br>n=8     |
| <i>M. pusillus</i>     | 51.00±1.25<br>n=118  | 29.65 ±3.12<br>n=127  | 52.35±1.70<br>n=184   | 30.72±3.93<br>n=195   |
| <i>N. veldkampii</i>   | 46.98±1.54<br>n=11   | 24.25±8.77<br>n=12    | 50.7±1.267<br>n=9     | 24.89±7.99<br>n=9     |
| <i>R. aegyptiacus</i>  | 96.31±3.08<br>n=112  | 138.00±14.82<br>n=112 | 95.38±3.32<br>n=70    | 126.65±16.12<br>n=71  |
| <i>M. woermanni</i>    |                      |                       | 43.2<br>n=1           | 16<br>n=1             |

#### 4.3.3 Bat distribution across Ghana

At each locality visited, several trees were often observed to have bats. Within a particular locality, each tree identified with bats on it was referred to as a roost, while the total of all roost trees with bats within that particular locality was referred to as a colony for a particular bat species. Hence, a total of 82 colonies made up of five species of bats were identified in 74 different localities across all ecological zones in Ghana. In eight of these locations, colonies shared by two different bat species were recorded. Within all the colonies, roosts were found in over 2,900 trees and two caves (Table 4.3;

Appendix 4); one *E. helvum* colony was found on the surface of a cliff.

*E. gambianus* and *E. helvum* colonies were the most dominant, accounting for 91% of all colonies identified. *E. gambianus* was recorded in 398 roosts and a total population of 28,538 was estimated, while *E. helvum* was recorded in 2,524 roosts with an estimated population of over 3 million. Colony sizes for *E. gambianus* ranged from one to 5,842 bats while *E. helvum* colony sizes ranged from 1,500 to about 1 million bats (Table 4.3).

Four *M. pusillus* colonies were recorded and were made up of 30 roosts and a total of 222 bats while the two colonies of *H. monstrosus* recorded were made up of 17 bats in two roosts. Two *R. aegyptiacus* roost caves were identified but population numbers could not be estimated from these caves due to poor accessibility to parts of the cave where this species was roosting. Both caves were however assumed to be utilised by bats from the same colony because of the proximity of both caves and the ability of this species to switch between caves close to each other. Based on population size estimates from identified and reported colonies, over three million bats occurred in the 82 colonies identified across the country.

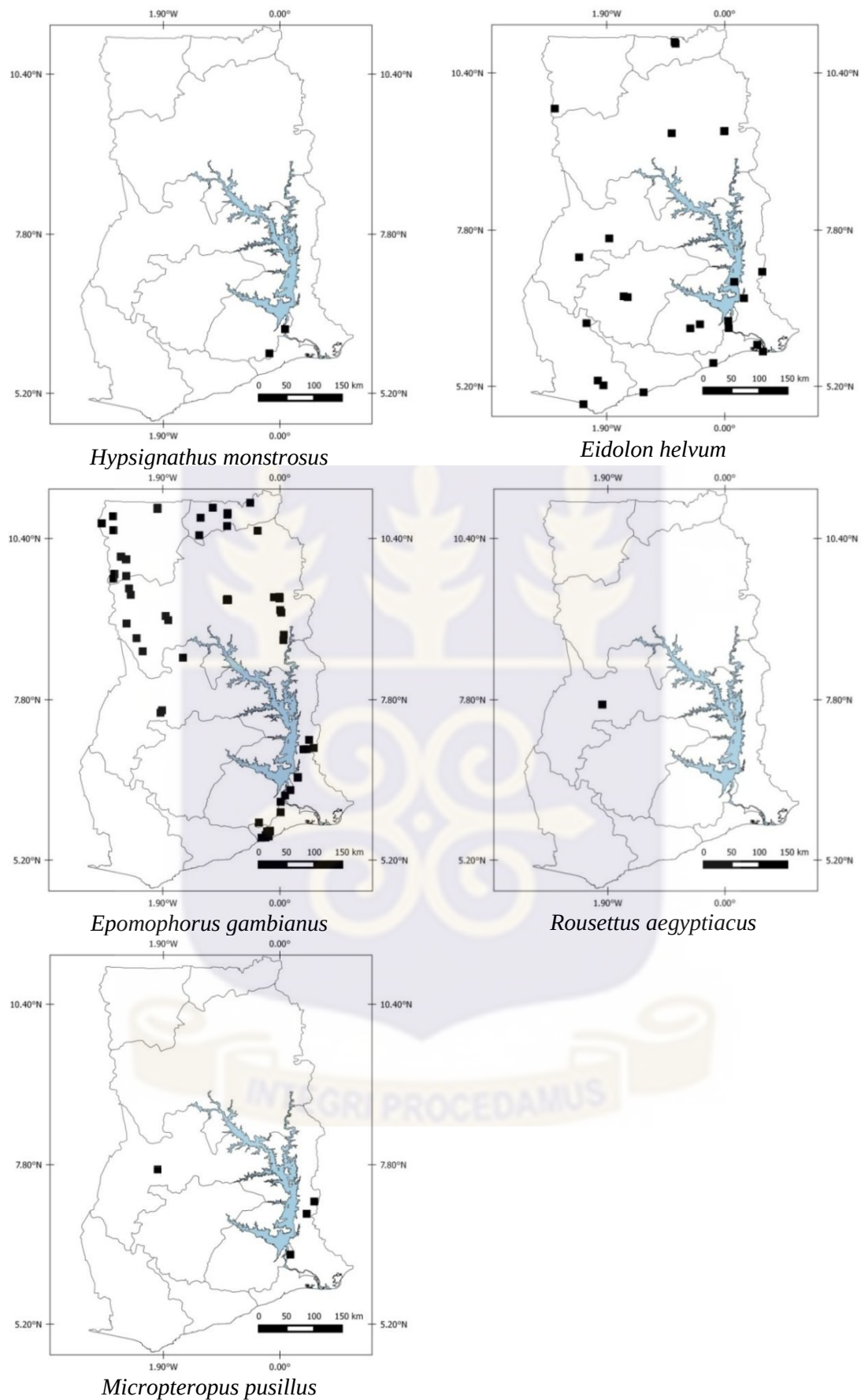
**Table 4.3 Population estimates and attributes of bat colonies identified.**

| <b>Bat Species</b>    | <b>Number of colonies</b> | <b>Number of roosts</b> | <b>Total population estimated</b> | <b>Colony size range</b> |
|-----------------------|---------------------------|-------------------------|-----------------------------------|--------------------------|
| <i>E. gambianus</i>   | 51                        | 398                     | 28,538                            | 1 -5,842                 |
| <i>R. aegyptiacus</i> | 1                         | 2                       | *                                 |                          |
| <i>E. helvum</i>      | 24                        | 2,524                   | 3,028,443                         | 1,500 -1 million         |
| <i>M. pusillus</i>    | 4                         | 30                      | 222                               | 5-174                    |
| <i>H. monstrosus</i>  | 2                         | 2                       | 17                                | 6- 11                    |
| <b>TOTAL: N=5</b>     | <b>82</b>                 | <b>2,956</b>            | <b>3,057,220</b>                  |                          |

\*Population numbers could not be estimated from roost caves due to poor accessibility.

Figure 4.3 shows the distribution maps of bat colonies identified for the various fruit bat species. Maps are based on confirmed bat colonies identified from the citizen science reports, and bat colony searches from this study. *E. gambianus* colonies were found in 51 locations in seven regions of Ghana, while *E. helvum*, colonies occurred in 24 locations with at least one colony occurring in each of the ten regions in Ghana. *M. pusillus* roosts were recorded in four regions and two *R. aegyptiacus* roost caves were identified at Buoyem in the Brong-Ahafo region. Two *H. monstrosus* roosts were identified, both in the Eastern region (Figure 4.3). Seventy-three out of the 82 colonies identified (89%) are reported for the first time in this study (see

Appendix 4). Roosts trees were found very close to human habitations and were typically found in school compounds, hospitals, homes and homesteads, trees that provided shade in markets and other public places (Plate 4.2).



**Figure 4.3** Distribution maps for fruit bat colonies identified during the study.





**Plate 4.2 Typical bat roosting sites.**

#### **4.3.4 Roost occupancy**

The results from the 87 questionnaire interviews with key informants at roost sites showed that 75 percent of colonies visited have been occupied continuously or intermittently for 10 years or more. Sixty-five percent of the colonies identified were reported to be occupied throughout the whole year, with temporal variations in numbers in some cases. Fourteen colonies were described as seasonal; 72% of the seasonal

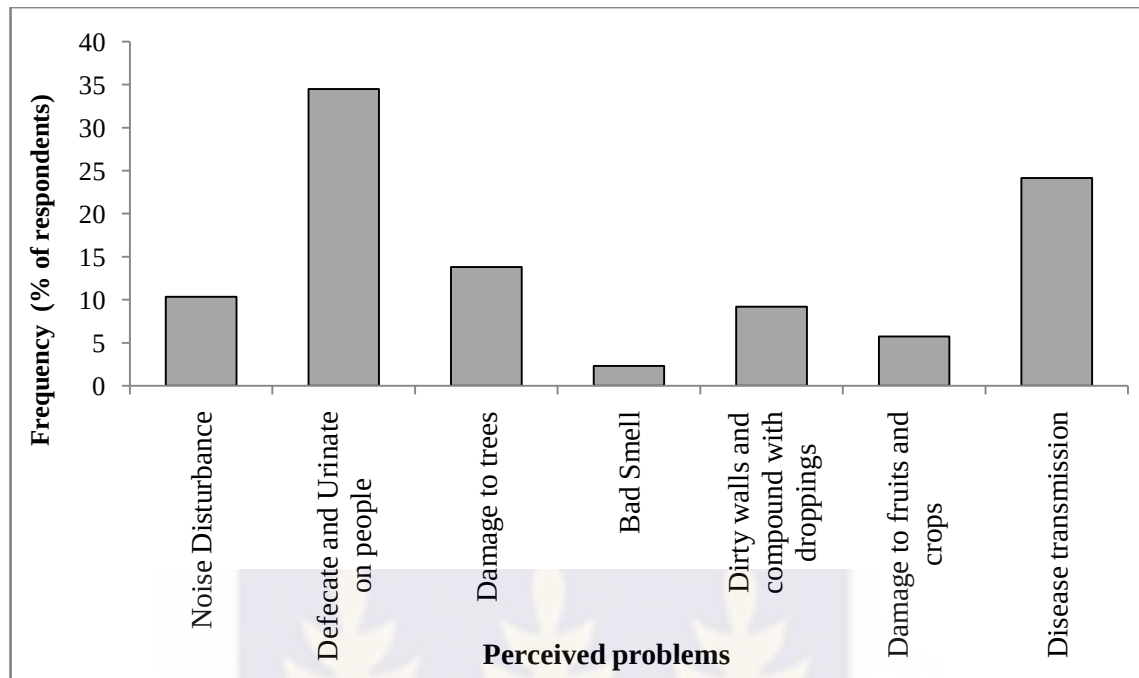


colonies were occupied during the dry season. Fifty-five percent of colonies were reported to show increases in bat numbers during the dry season and 45% of colonies were described to have peak numbers coinciding either with the rainy season or the fruiting period for Figs (*Ficus* sp.) and Mango (*Mangifera indica*).

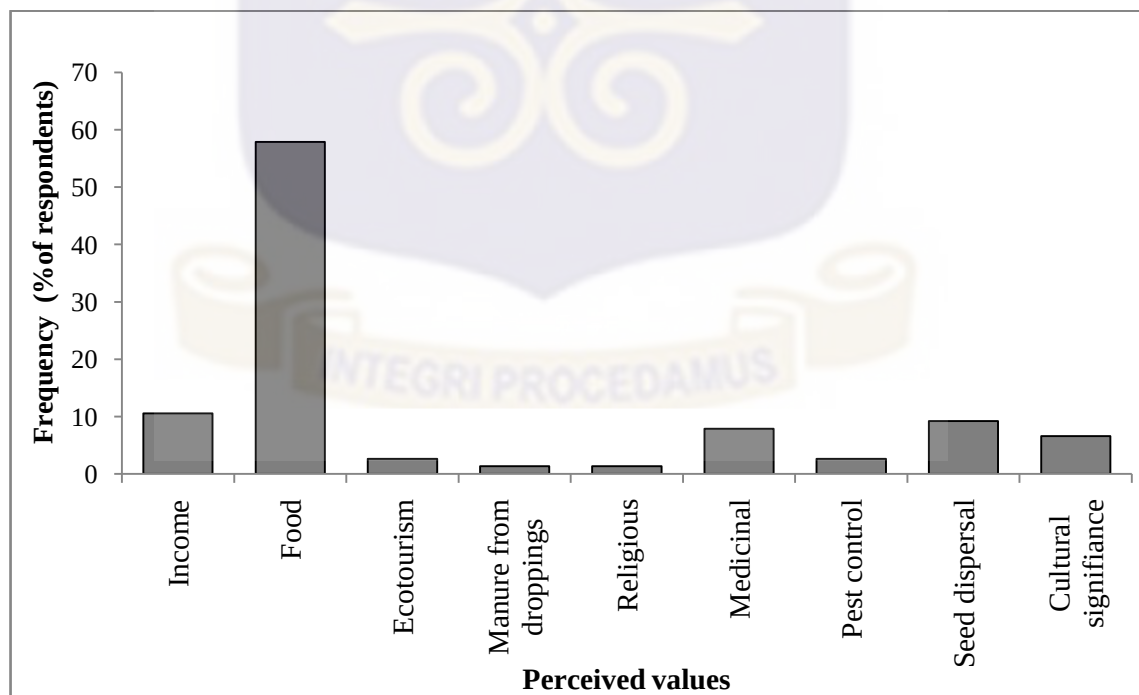
#### **4.3.5 Perceptions about bats**

The respondents to the questionnaires administered at bat colonies expressed both negative and positive views on bats. Of the problems perceived to be caused by bats, contact with bat faeces and urine was the highest, stated by 35% of respondents (Figure 4.4). Twenty four percent of respondents associated bats with the problem of disease transmission of which they knew or had heard about. It is important to note that all the 21 respondents who perceived problem of disease transmission by bats were interviewed after and/or during the 2014 Ebola outbreak in West Africa. Before the outbreak, none of the 44 persons interviewed associated bats with disease transmission. Other perceived problems associated with bats were noise disturbance, damage to trees from large aggregations, bad smell, dirtying of compounds and houses with faeces and damage to fruits and crops (Figure 4.4).

A majority of the respondents (58%) valued bats as a source of food, while 11% considered bats as a source of income from the sale of bat meat. The perception of the ecological importance of bats was generally very low among respondents; only 9.2% valued bats as seed dispersers while 2.6% valued bats as natural insect pest control. Eight percent of respondents valued bats for their use in preparation of local medications. Some respondents (7.8%) indicated a cultural or religious significance of bats. Other values described included bats as a source of ecotourism attraction and a source of organic manure from droppings (Figure 4.5).



**Figure 4.4 Perceived problems associated with bats.**



**Figure 4.5 Values placed on bats.**

## 4.4 Discussion

### 4.4.1 Fruit bat distribution in Ghana

Ten species of bats out of the 13 previously reported for Ghana were recorded in this study. These were *Eidolon helvum*, *Epomophorus gambianus*, *Hypsignathus monstrosus*, *Epomops franqueti*, *Epomops buettikoferi*, *Micropteropus pusillus*, *Nanonycteris veldkampii*, *Lissonycteris angolensis*, *Rousettus aegyptiacus* and *Megaloglossus woermanni*. The most abundant of these are *E. helvum* and *E. gambianus*, accounting for over 75% of all bats trapped.

The distribution of *R. aegyptiacus* and *L. angolensis* is restricted by the requirements of caves for roosting (Rosevear, 1965; Happold & Happold, 2013). The records of some individuals of both species at Ve-Golokuati suggest the possibility of colonies around the area. This area lies close to the part of the Akwapim-Togo range along the eastern part of Ghana where several hills with rock formations occur and may create suitable caves around the area that could be utilised by these two species. Previous records in the Bosomtwe Forest Reserve and, Ajenjua Forest Reserve (Yeboah, 2001), Krobo hills, (Booth, 1959) show that these species may occur in several other places in the country with similar habitats. *H. monstrosus* is known to occur mostly in closed forests with known records reported from the forests zones of Ghana (Grubb *et al.*, 1998; Yeboah, 2001; Decher & Fahr, 2007). Captures of reproductively active individuals of this species was made in the forest- savannah transition zone and implies that this species extends into the zone and can thrive in similar habitats or extends slightly into wooded savannah habitats.

The three species, *Scotonycteris ophiodon*, *Scotonycteris zenkeri* and *Myonycteris torquata* were not encountered during this study. *Scotonycteris zenkeri* and *S. ophiodon*

are both very rare species and not often encountered during trapping. The distributions of these species are also more or less restricted to the forest zones in the south-western parts of the country which was not sampled during this study. *Myonycteris torquata* occurs mainly in the forest zones in the south-western part of Ghana but previous records also show that it also occurs in the northern savannahs (Grubb *et al.*, 1998; Decher & Fahr, 2007). Sampling efforts in the northern savannahs were however too low and may explain why the species was not encountered.

This study is the first that has attempted to describe the nationwide distribution of fruit bat roosts in Ghana. Several colonies identified from this study were unreported prior to this study even for a relatively well studied species like *E. helvum*. Prior to this study, the only nationwide distribution maps for bats in Ghana are those provided by Grubb *et al.* (1998) which was based on museum specimens and literature records. These results support the assertion that there is a general lack of knowledge about this important group of mammals even in a relatively small and well studied country like Ghana (Weber & Fahr, 2007; Hayman *et al.*, 2012a). Seventy-one of the bat colonies recorded in this study are reported for the first time, thus providing additional data to update the distribution maps produced by Grubb *et al.* (1998).

Fruit bats are known to show high levels of roost fidelity and maintain the same roosts or switch between several roosts within a roosting area (Fenton *et al.*, 1985; Gumal, 2004). Majority of the bat roosts identified by this study have been occupied continuously or intermittently for ten years or more. The findings from this study are consistent with these observations of high roost fidelity in bats reported by other studies.

Majority of the colonies identified in this study belong to *E. helvum* and *E. gambianus*. Of the fruit bat species that are recorded in Ghana, these two species form relatively

large roosts compared to the other tree roosting fruit bats. The two species are very common and abundant and have been recorded across all vegetation types. *E. helvum* typically forms very large unmistakeable aggregations in colonies that are very conspicuous and easily noticed with numbers up to 10 million individuals recorded in Zambia (Richter & Cumming, 2008). In West Africa, colonies can reach between 300,000 to 1 million (Rosevear, 1965; DeFrees & Wilson, 1988; Hayman *et al.*, 2012a). *E. gambianus* also forms roosts of up to 100 individuals (Rosevear, 1965; Boulay & Robbins, 1989). Hence these two species may be more conspicuous and easily identified than other species that roost singly or in relatively smaller groups.

The records of these two species across the varying range of habitat types including forested woodlands and urban centres further confirm the reported ability of these two species to persist in varying habitats and to withstand highly modified habitats (such as the city centre in Accra) which may be unsuitable to most other species. The distribution of *E. gambianus* and *E. helvum* is also likely to be influenced by food availability. Hahn *et al.* (2014) established that *Pteropus giganteus* selected roosts that were close to homesteads and suggested that the maintenance of home gardens in Bangladesh was providing a wide variety of food which was absent in natural forests for bats. In Australia, the absence of food resources in natural habitats has been associated with bat movements and increased formation of roosts of bats in urban and peri-urban areas in pursuit of alternate food sources (Plowright *et al.*, 2015). Similarly, a common practice among several Ghanaian households is the planting and maintenance of varieties of fruiting trees within their compounds. These may be creating oasis of fruit availability and variety within vast degraded lands and could be attracting *E. gambianus* and *E. helvum* to utilise areas closer to humans.

#### 4.4.2 Perceptions and knowledge about fruit bats

Bats are generally perceived in a negative sense and often associated with dark magic, evil or depicted as agents of misfortune and blood sucking animals in several communities and cultures, and are among the least likeable animals (Ayensu, 1974; Mickleburgh *et al.*, 2002; Kunz *et al.*, 2011; Mahmood-ul-Hassan *et al.*, 2011). Such negative perceptions associated with bats contribute to their persecution and subsequently to declines in populations of several species (Toop, 1995; Mickleburgh *et al.*, 2002).

Knowledge of the ecological importance of bats among respondents in this study was very poor with less than 12% of respondents indicating awareness of the role of bats in seed dispersal and insect pest control and other ecological services. Similar findings were made by Kamins *et al.* (2015) among bat bushmeat actors in Ghana, where respondents valued bats mostly as a source of meat and income, with very little knowledge about their ecological importance. Similar observations have been made in Northern Pakistan where bats were deemed useless animals among 98% of respondents interviewed in a study (Mahmood-ul-Hassan *et al.*, 2011). Similarly, in a study in Fort Collins, USA, residents admitted knowing nothing to very little about bat ecology (Sexton & Stewart, 2007).

According to Kunz *et al.* (2011) and Mickleburgh *et al.* (2002) most people are ignorant of the biology, ecology and the important roles bats play in ecosystem functioning and this accounts for the negative perceptions that people have about bats. People's education level and their ecological knowledge are vital in shaping their biophilic or biophobic attitudes (Kellert & Westervelt, 1984; Mahmood-ul-Hassan *et al.*, 2011). Sexton and Stewart (2007), observed a positive correlation between residents' level of knowledge



about bats and their beliefs and attitudes, where people with higher knowledge about bats had a more positive attitude towards bats. Educated respondents were also less likely to kill bats on sight compared to illiterates (Mahmood-ul-Hassan *et al.*, 2011). Appropriate education about the biology, ecology and importance of bats could be the key to promoting bat conservation in Ghana.

Despite the increasing knowledge about the role of bats in zoonotic disease transmission, awareness still remains low among Ghanaian communities. A number of recent studies including Kamins *et al.* (2015), Lawson *et al.* (2016), Ohemeng *et al.* (2017) and Leach *et al.* (2017) also reported low perception of disease risk associated with bats especially in rural areas where education was lower. The incidence of the 2014 Ebola outbreak in West-Africa sparked education campaigns mostly about role of bats in disease transmission across the country, but such campaigns may not have been adequate especially in rural areas. While educational campaigns about the role of bats in disease transmission is critical (Lawson *et al.*, 2016; Ohemeng *et al.*, 2017), such campaigns if not carefully managed, may create misguided thoughts about bats and trigger eradication of bats and cutting down of roosts which will threaten bat conservation and possibly also lead to increasing potential for disease spillover (Wood *et al.*, 2012). The lack of people placing any importance on bats could lead to their persecution and affect their conservation (Mickleburgh *et al.*, 2002; Kunz *et al.*, 2011). Educational programmes should not only focus on the role of bats in disease transmission but also highlight their importance in ecosystem functioning and provide guidance to limit human interaction with bats.

## CHAPTER FIVE

### 5.0 SEASONAL VARIATION IN FOOD AVAILABILITY AND RELATIVE USE OF DIETARY ITEMS IN *EPOMOPHORUS* *GAMBIANUS*

#### 5.1 Introduction

Dietary studies can provide understanding of the interrelationships between species and their environment and how individual species affect and contribute to their ecosystems (Stier & Mildenstein, 2005). Fruit bats (Pteropodidae) are almost exclusively phytophagous, relying extensively on fruits, flowers and leaves as dietary materials (Marshall, 1985). Through their feeding interactions with plants, fruit bats provide vital ecosystem services that make many of them keystone species in some communities. The distribution and timing of food availability varies across landscapes and seasons, and this influences the biology of bats (Marshall, 1985), particularly reproduction and migration (Cumming & Bernard, 1997). The timing of fruiting/flowering in plants is often irregular across landscapes which makes it difficult to generalize findings (such as reproductive synchrony with food abundance) obtained from one landscape to others (Cumming & Bernard, 1997). The utilisation of food resources is also not uniform among fruit bats and some studies for example Baker and Harris (1957); Marshall and McWilliam (1982); Barclay and Jacobs (2011), have shown inter- and intraspecific variations in food utilisation.

Very few studies, however, have explored the relative use and importance of different food items in the diet of fruit bats (Marshall, 1985; Stier & Mildenstein, 2005). Several studies that explore the dietary resources of fruit bats fail to quantify the relative use of

identified dietary resources, but mainly provide lists of food items and assume equal use (Stier & Mildenstein, 2005). The current lack of knowledge about the relative use of food items limits efforts to assign trophic roles to fruit bats (Marshall, 1985). Hence, the important roles of fruit bats in the functioning of ecosystems has been inadequately characterised, and this limits our understanding of how bats impact ecosystems at local scales and how changing land use and habitat modifications affect bat populations (Stier & Mildenstein, 2005; Wood *et al.*, 2012). Improved knowledge in this area is vital in setting up conservation and management strategies for bats and will provide better understanding of the infection dynamics of zoonotic diseases in bats. (Wood *et al.*, 2012).

The aim of this component of the thesis was to identify the diet of *E. gambianus* and describe seasonal variations in availability and relative use of different food items.

## 5.2 Methodology

The study was conducted at Ve-Golokuati, a town in the Afadzato South district in the Volta region of Ghana (see Chapter two for full description of study site). To investigate and identify the food sources utilised by bats, several methods were used:

1. Regular collection of faecal and ejecta pellets dropped by bats under day roosts and feeding roosts;
2. Direct observations for plants visited by foraging bats at night;
3. Opportunistic collection of ejecta/faecal pellets and whole or remnants of food items dropped by captured bats;
4. Literature search and documentation of indigenous knowledge of plants known to be eaten by bats in the study area.

### 5.2.1 Faecal collection

Nine species of fruit bats were known to occur within the study site from captures during night-time foraging. Two of these species *E. gambianus* and *M. pusillus*, were observed to share some roosting trees within the area. Both species however were usually separated within roost trees; *M. pusillus* were often found in groups on small branches at the extremities and were hardly observed to mix with *E. gambianus*. Hence, it was possible to collect faecal samples specifically from *E. gambianus*. Also *E. gambianus* was far more abundant (97%) than *M. pusillus* at these roosts, hence in the case of mixed faecal collection from both species, a significant portion could be safely assumed to be coming from *E. gambianus*.

Faecal collection was done by placing 1.5 x 1 m plastic sheets directly under day roosts of *E. gambianus* during the early hours of the day (0500 h-0800 h) to collect faeces excreted by bats. To avoid repeated collection of faecal samples from same individuals that could arise from splatters or discontinuous deposition, faecal material that were within 5 cm and had same characteristics (colour, texture) of already collected ones were ignored (Stier & Mildenstein, 2005). Fresh ejecta pellets were also collected under feeding roosts within the study area. All feeding and day roost used were identified during a concurrent study that was monitoring bat population within the same study area.

Each faecal/ ejecta sample was placed into a separate plastic zip loc bag for later processing. Collections were done on 2-3 consecutive days in each sampling month for 21 months (January 2014 to December 2015).

### 5.2.2 Direct observations

The study area was monitored for plants that were fruiting or flowering. Identified fruiting and flowering plants were visited at night and observed using headlamps to confirm if bats were visiting these trees to feed. Additionally, these trees were also observed for signs of feeding activity such as bats dropping fruits with bite or claw marks and partly eaten fruits under these trees to confirm feeding activity.

### 5.2.3 Opportunistic observations

Bat trapping sessions were ongoing concurrently during this study's period in the study area. This presented the opportunity to collect additional data on dietary sources from *E. gambianus*. Bats trapped were checked for presence of pollen on their nostrils or wings, or for remnants of food materials in their mouths. An assumption made here was that the occurrence of pollen on the body of bats was taken as evidence that the bats had visited flowers to feed on pollen or nectar. Occasionally, some captured bats were observed to have seeds in their mouths and others excreted faeces with seeds during removal from nets and handling. Bats often excreted into sacs in which they were being transported and kept before processing. Occasionally, some bats were found together with whole fruits in the nets in which they were caught. All these records were added to faecal and ejecta samples for the determination of dietary resources.

### 5.2.4 Literature and indigenous knowledge

Plants that are known to be utilised as food sources by fruit bats in West Africa are well documented in literature (Marshall, 1985). Interactions with local people and farmers facilitated the identification and location of some of these plants that were likely to occur

within the study area. The local people and farmers were chosen impulsively and approached informally. The local people were also asked to identify plants that they knew bats fed on. Plants identified from indigenous knowledge were subsequently followed up through direct observations for additional evidence and confirmation of utilisation as a food source by bats.

#### **5.2.5 Identification of food items from ejecta and faecal pellets**

Ejecta and faecal pellets collected were washed through a 0.3 mm sieve and examined with a magnifying glass for seeds, flower parts, and other food particles (Stier & Mildenstein, 2005). Seeds and fruit particles collected were identified using a reference collection. The reference collection was prepared from dry collections of seeds (kept in envelopes). This also included notes and field lexicons that were developed to describe the characteristics of fruit (colour, smell, texture) samples collected from the study area. The reference collection was developed at the beginning of the study to provide a means for comparing and matching the samples collected (Stier & Mildenstein, 2005; Picot *et al.*, 2007; Djossa *et al.*, 2008).

Seeds collected from bat faeces and ejecta pellets that were not readily identifiable through the reference collection were germinated in black plastic bags filled with soil and kept until they were grown enough to be identified. Plants and trees from which fruits and seeds were collected were identified using field guide (Hawthorne & Gyakari, 2006). Others were identified at the Herbarium at the Plant Biology and Environmental Science Department of University of Ghana.

Pollen and flower parts retrieved from bat samples could not be identified to species level; these were pooled together as "flower resources" in the analysis of faecal /ejecta



samples. Samples from possibly 5 different species of figs (*Ficus* sp.) were also grouped together as "*Ficus* sp." due to the difficulty in distinguishing between seeds. All other plants were identified to species level where possible.

A total of 1,503 samples of faecal and ejecta pellets were collected and analysed. This comprised 455 faecal, ejecta and food remnants collected opportunistically from trapped bats, 505 ejecta pellets and 543 faecal samples collected under day roosts. This translates to an average of nearly 72 faecal and/or ejecta samples per month over the 21 months sampling period. A total of 39 faecal samples that were collected but could not be identified as they were without seeds or did not fit descriptions of the reference collection were not included in the analysis as these formed less than 3% of all samples collected from *E. gambianus*.

Dietary materials identified from samples were expressed as monthly relative abundance or as a percentage of total samples collected. Each dietary item that was detected in a particular faecal/ejecta/opportunistic sample was recorded to occur once in that sample. All dietary materials were assumed to be equal with no difference in calorimetric or energetic content.

#### **5.2.6 Estimation of food resource availability and abundance**

To estimate availability and seasonal variations in food resources available to fruit bats at the study site, plants that were identified to be utilised by fruit bats were monitored monthly between January 2014 and December 2015 for fruiting and flowering abundance. The estimation of fruit abundance of tropical trees by visual estimation is a fairly accurate technique (Chapman *et al.*, 1992) and this method was employed and was done by a single observer (KAM) to maintain consistency and increase internal validity.

Fruit/Flower abundance was estimated by a modification of the method described by Devineau (1999).

Bats feed on ripe and overripe fruits and may avoid immature and unripe fruits and visit flowers which are matured and open for pollen and nectar. This implies that fruits and flowers may be available but may not be utilised until they are ripe or matured, or avoided when they are dry. Based on this, flowering and fruiting were categorized into 4 stages (0 to 3) with corresponding phenology scores of 0, 0.09, 0.5 and 1; that is;

- Stage 0- no flower/no fruit -score=0
- Stage 1- flower buds with less than 10% of open flowers/early fruit setting with less than 10% of mature sized fruits; - score = 0.09
- Stage 2- flower buds present and 10 to 50% of open flowers/10 to 50% of mature sized fruits; -score = 0.5
- Stage 3- over 60% up to 100% Peak flower bloom/peak of fruit maturity or any stage beyond this where most flowers /fruits on the tree are matured or ripe but not dried; score = 1

In addition to the flowering/fruiting stages described, the total number of fruits and flowers at any of these stages was estimated in each month for each plant that was monitored. Monthly fruit/flower abundance per plant was then estimated as the product of the total number of fruits/ flowers estimated and the phenology score for that month.

Due to unequal numbers of individual trees per each species that was monitored, monthly fruit/flower abundance was expressed as mean abundance of fruits/flowers per tree for each species.

### 5.2.7 Timing of flowering and fruiting of food plants in relation to rainfall

To determine the timing of flower and fruit abundance to rainfall within the study area, the estimated mean monthly fruit and flower abundances were related to the mean monthly rainfall for the study area. Rainfall data used was obtained from the Ghana Meteorological Agency ([www.meteo.gov.gh](http://www.meteo.gov.gh)). Due to gaps in the rainfall data obtained, the mean monthly rainfall data used were compiled from monthly rainfall data from 2009-2014 for the study area.

## 5.3 Results

### 5.3.1 Food composition

A total of 35 species of plants belonging to at least 17 plant families were identified (from faecal samples, ejecta pellets, indigenous knowledge and personal observations) to be utilised as dietary sources by bats within the study area (Table 5.1). Out of this, seven were utilised for their flowers only, 23 for their fruits and four for both fruits and flowers. *E. gambianus* was observed feeding on flowers of the Forest ordeal tree (*Erythrophleum suaveolens*) and on fruits of Paper mulberry (*Broussonetia papyrifera*) and Shea tree (*Vitellaria paradoxa*) outside the study area; these records were added to the list of dietary resources utilised by the bat species.

**Table 5.1 Plant families and species identified as dietary resources for fruit bats.**

| Plant Family  | Species                           | Common name                              | Food resource | Source |
|---------------|-----------------------------------|------------------------------------------|---------------|--------|
| Anacardiaceae | <i>Spondias mombin</i>            | Yellow mombin, Hog plum                  | FR            | a,b,c  |
|               | <i>Anacardium occidentale</i>     | Cashew                                   | FR            | b,c    |
|               | <i>Mangifera indica</i>           | Mango                                    | FR            | a,b,c  |
| Annonaceae    | <i>Polyalthia longifolia</i>      | Indian mast tree, False Ashoka           | FR            | a,b,c  |
|               | <i>Annona muricata</i>            | Soursop                                  | FR            | b,c    |
| Bignoniaceae  | <i>Spathodea campanulata</i>      | African tulip tree                       | FL            | a,b    |
| Bombacaceae   | <i>Bombax buonopozense</i>        | Red silk-cotton; Red cotton tree         | FL            | b      |
|               | <i>Ceiba pentandra</i>            | Silk Cotton, Kapok                       | FL            | a,b    |
| Caricaceae    | <i>Carica papaya</i>              | Pawpaw, Papaya                           | FR            | a,b,c  |
| Combretaceae  | <i>Terminalia catappa</i>         | Indian almond                            | FR            | a,b,c  |
| Cucurbitaceae | <i>Melothria</i> sp.              | Mouse melon                              | FR            | a      |
|               | <i>Daniellia oliveri</i>          | African copal balsam, West African copal | FL            | a,b    |
| Fabaceae      | <i>Parkia biglobosa</i>           | African locust bean                      | FL            | a,b    |
|               | * <i>Erythrophleum suaveolens</i> | Forest ordeal tree                       | FL            | a      |
| Gentianaceae  | <i>Anthocleista vogelii</i>       | Cabbage tree                             | FR, FL        | a,b    |
| Malvaceae     | <i>Adansonia digitata</i>         | Baobab                                   | FL            | b      |
|               | <i>Sterculia rhinopetala</i>      | Brown sterculia                          | FR            | a      |
| Meliaceae     | <i>Azadirachta indica</i>         | Neem                                     | FR, FL        | a,b,c  |
| Moraceae      | <i>Antiaris toxicaria</i>         | False iroko, Antiaris, Bark cloth tree   | Fr            | a,b    |
|               | <i>Ficus</i> sp. (6 species)      | Figs                                     | FR            | a,b,c  |
|               | <i>Milicia excelsa</i>            | Iroko, Odum                              | FR            | a,b,c  |
| Musaceae      | * <i>Broussonetia papyrifera</i>  | Paper mulberry                           | FR            | a,b    |
|               | <i>Musa</i> sp.                   | Banana                                   | FR, FL        | a,c    |
| Myrtaceae     | <i>Psidium guajava</i>            | Guava                                    | FR            | a,b,c  |
|               | <i>Syzygium</i> sp.               |                                          | FR            | a,b    |
| Sapotaceae    | * <i>Vitellaria paradoxa</i>      | Shea                                     | FR            | a,b,c  |
| Solanaceae    | <i>Solanum</i> sp.                | Potato tree.                             | FR            | a,b    |
| Verbenaceae   | <i>Vitex doniana</i>              | Black plum                               | FR            | a,b,c  |
| **            |                                   | Unidentified                             | FR, FL        | a      |

**FR**=Fruit; **FL**=Flower; **a**-personal observation; **b**-literature [Marshall and McWilliam (1982); Marshall (1985)]; **c** indigenous knowledge; \*- identified outside study area; \*\*- unidentified trees

### 5.3.2 Relative abundance of food resources based on faecal and ejecta samples analysis

*E. gambianus* utilised between three to ten different food items in each month (Table 5.2). Flower resources together with fruits from three plant species, Black plum (*Vitex doniana*), Cabbage tree (*Anthocleista vogelii*), Figs, (*Ficus* sp.) and the Indian mast tree (*Polyalthia longifolia*), constituted over 80% of all dietary items identified for *E. gambianus*.

The genus *Ficus* (Figs), was the most common plant species recorded in the samples collected, recorded in all but one sampling month (20 out of 21 months sampled) and occurring in 40.6% of all samples collected from *E. gambianus* (Table 5.2). Fruits of the Potato tree (*Solanum* sp.) and Mouse melon (*Melothria* sp.) were also frequently encountered, recorded in 14 and 10 sampling months respectively. These two species however occurred in only 3.1% and 1.7% of all collected samples respectively. Fruits of *V. doniana*, occurred most frequently in the diet of *E. gambianus* from August to October when the number of food sources was relatively low. Similarly, *A. vogelii* and *P. longifolia* fruits formed a high proportion of dietary items during March/April and May/June respectively.

Flower resources were recorded in 10% of all samples collected. Flower resources were mostly recorded as part of the diet of *E. gambianus* from November to February. Insect parts were recorded in only one faecal sample.

**Table 5.2 Monthly relative use (percentage) of dietary items identified from *E. gambianus* faecal and ejecta pellets.**

| Dietary Item                 | Month/ Frequency of occurrence (%) |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |     |      | % of total |
|------------------------------|------------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|-----|------|------------|
|                              | Jan                                | Feb  | Mar  | Apr  | May  | Jun  | Jul  | Aug  | Nov  | Dec  | Feb  | Mar  | Apr  | May  | Jun  | Jul  | Aug  | Sep  | Oct  | Nov  | Dec |      |            |
|                              | 2014                               |      |      |      |      |      |      |      |      |      |      | 2015 |      |      |      |      |      |      |      |      |     |      |            |
| <i>Anthocleista vogelii</i>  |                                    |      | 46.6 | 60.9 | 18.1 | 5.3  |      |      |      |      |      | 39.1 | 10.6 | 8.6  | 24.4 | 3.7  |      |      |      |      |     | 10.7 |            |
| <i>Antiaris toxicaria</i>    |                                    |      |      |      |      |      |      |      |      |      | 5.9  |      |      |      |      |      |      |      |      |      |     | 0.1  |            |
| <i>Azadirachta indica</i>    |                                    |      |      |      |      | 24.6 | 4.0  |      | 1.6  |      |      | 3.1  | 3.6  | 8.0  |      | 7.4  | 1.9  |      |      |      |     | 3.1  |            |
| <i>Carica papaya</i>         |                                    |      |      |      |      |      |      |      | 6.3  | 1.4  |      |      |      |      |      |      |      |      |      |      |     | 0.3  |            |
| <i>Ficus</i> spp.            | 23.8                               | 18.4 | 26.2 | 34.8 |      | 22.8 | 38.0 | 21.6 | 43.8 | 52.2 | 61.8 | 18.8 | 75.2 | 54.0 | 17.8 | 66.7 | 34.3 | 11.8 | 38.1 | 37.5 | 24  | 40.7 |            |
| Flower resources             | 52.4                               | 78.9 |      |      |      | 3.5  |      |      | 34.4 | 40.6 | 26.5 |      |      |      |      |      |      |      |      | 12.5 | 59  | 10.3 |            |
| Insect parts                 |                                    |      |      |      |      | 1.8  |      |      |      |      |      |      |      |      |      |      |      |      |      |      |     | 0.1  |            |
| <i>Mangifera indica</i>      |                                    |      |      |      | 2.8  | 15.8 |      |      |      |      |      | 32.8 | 4.3  | 14.7 |      |      |      |      |      |      |     | 4.6  |            |
| <i>Melothria</i> sp.         | 9.5                                |      |      |      | 2.8  | 5.3  | 2.0  | 5.9  | 3.1  | 1.4  |      |      |      |      | 6.7  |      |      | 7.1  |      | 6.3  |     | 1.7  |            |
| <i>Milicia excelsa</i>       |                                    |      | 3.9  | 4.3  |      |      |      |      |      |      |      | 1.6  |      |      |      |      |      |      |      |      |     | 0.4  |            |
| <i>Musa</i> sp.              |                                    |      |      |      |      |      |      | 3.9  |      |      |      |      |      |      |      |      |      |      |      |      |     | 0.1  |            |
| <i>Polyalthia longifolia</i> |                                    |      |      |      | 69.4 |      | 36.0 |      |      |      |      |      | 6.3  | 12.3 | 46.7 | 3.7  |      |      |      |      |     | 8.6  |            |
| <i>Psidium guajava</i>       |                                    |      | 11.7 |      |      |      |      | 19.6 |      |      | 2.9  | 4.7  |      |      |      | 3.7  | 5.6  |      |      |      |     | 2.2  |            |
| <i>Solanum</i> sp.           |                                    | 2.6  |      |      | 6.9  | 7.0  | 2.0  | 2.0  | 4.7  | 4.3  | 2.9  |      |      |      |      | 7.4  | 6.5  | 3.5  | 4.8  | 31.3 | 15  | 3.1  |            |
| <i>Spondias mombin</i>       |                                    |      |      |      |      | 5.3  | 4.0  |      |      |      |      |      |      |      |      |      |      |      |      |      |     | 0.3  |            |
| <i>Sterculia rhinopetala</i> |                                    |      |      |      |      |      |      |      |      |      |      |      | 0.6  |      |      |      |      |      |      |      |     | 0.1  |            |
| <i>Vitex doniana</i>         |                                    |      |      |      |      |      | 4.0  | 47.1 | 6.3  |      |      |      |      |      |      | 7.4  | 47.2 | 77.6 | 52.4 | 12.5 | 2.9 | 10.9 |            |
| others                       | 14.3                               |      | 11.7 |      |      | 8.8  | 10.0 |      |      |      |      |      |      | 1.8  | 4.4  |      | 4.6  |      | 4.8  |      |     | 2.6  |            |
| No. of dietary items         | 4                                  | 3    | 5    | 3    | 5    | 10   | 8    | 6    | 7    | 5    | 5    | 6    | 5    | 7    | 5    | 7    | 6    | 4    | 4    | 5    | 4   |      |            |

No data were collected in September and October 2014, and in January 2015.

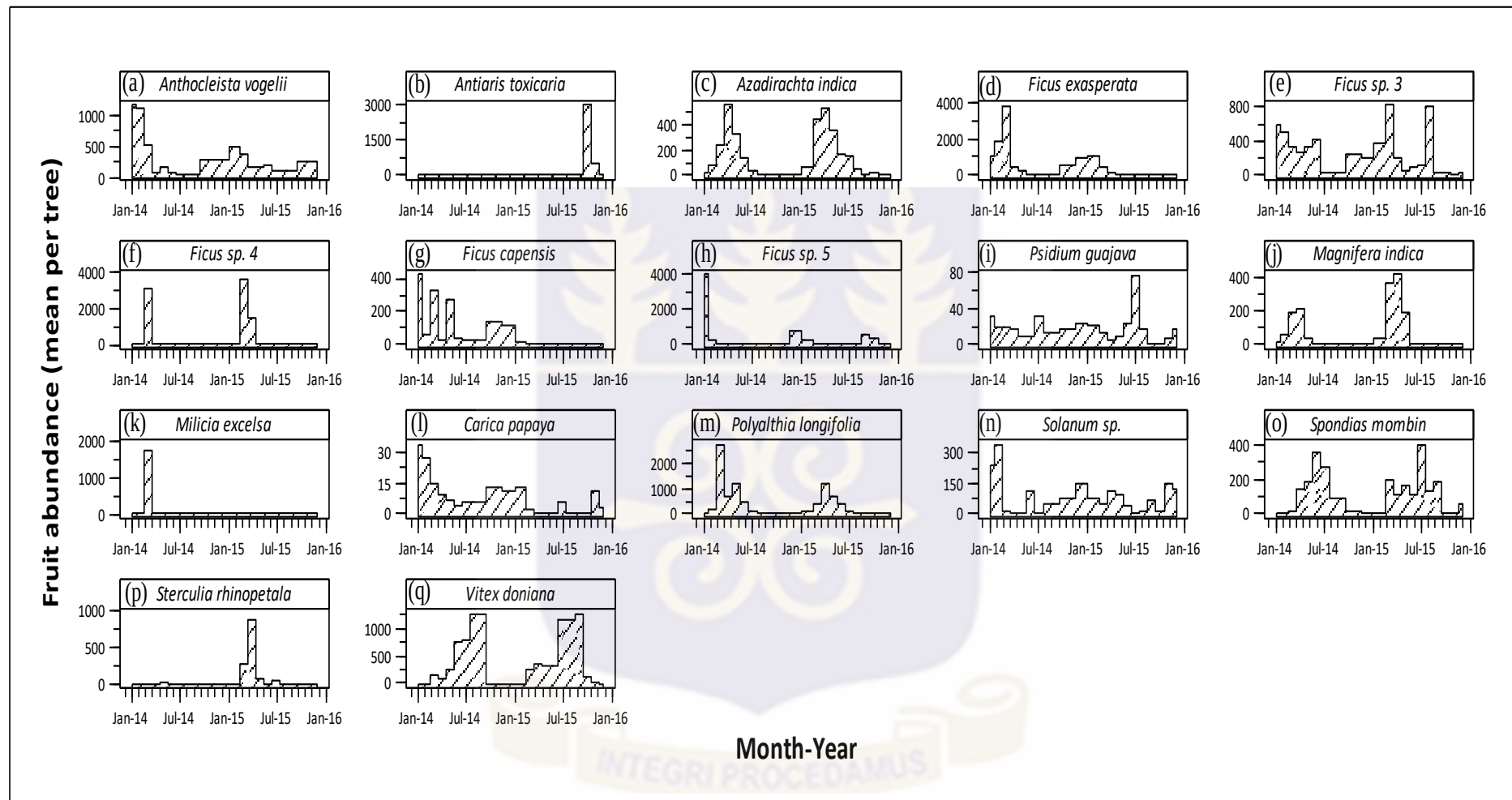


### 5.3.3 Timing of food resource abundance in relation to rainfall

A total of 17 plant species including five species of Figs were monitored for timing of fruiting and fruit abundance. Fruits were generally available throughout the study period although most species showed a clear seasonal pattern in fruit abundance. The fruiting of *Antiaris* (*Antiaris toxicaria*), *Odum* (*Milicia excelsa*), and *Brown sterculia* (*Sterculia rhinopetala*), however, appeared patchy (Figure 5.1 b, k, p). Fruits of Cabbage tree (*A. vogelii*), an unidentified Fig species (*Ficus* sp. 3), *Guava* (*Psidium guajava*) and *Potato tree* (*Solanum* sp.) were in season throughout the sampling period but with varying abundance at different times of the year (Figure 5.1 a, e, i, n).

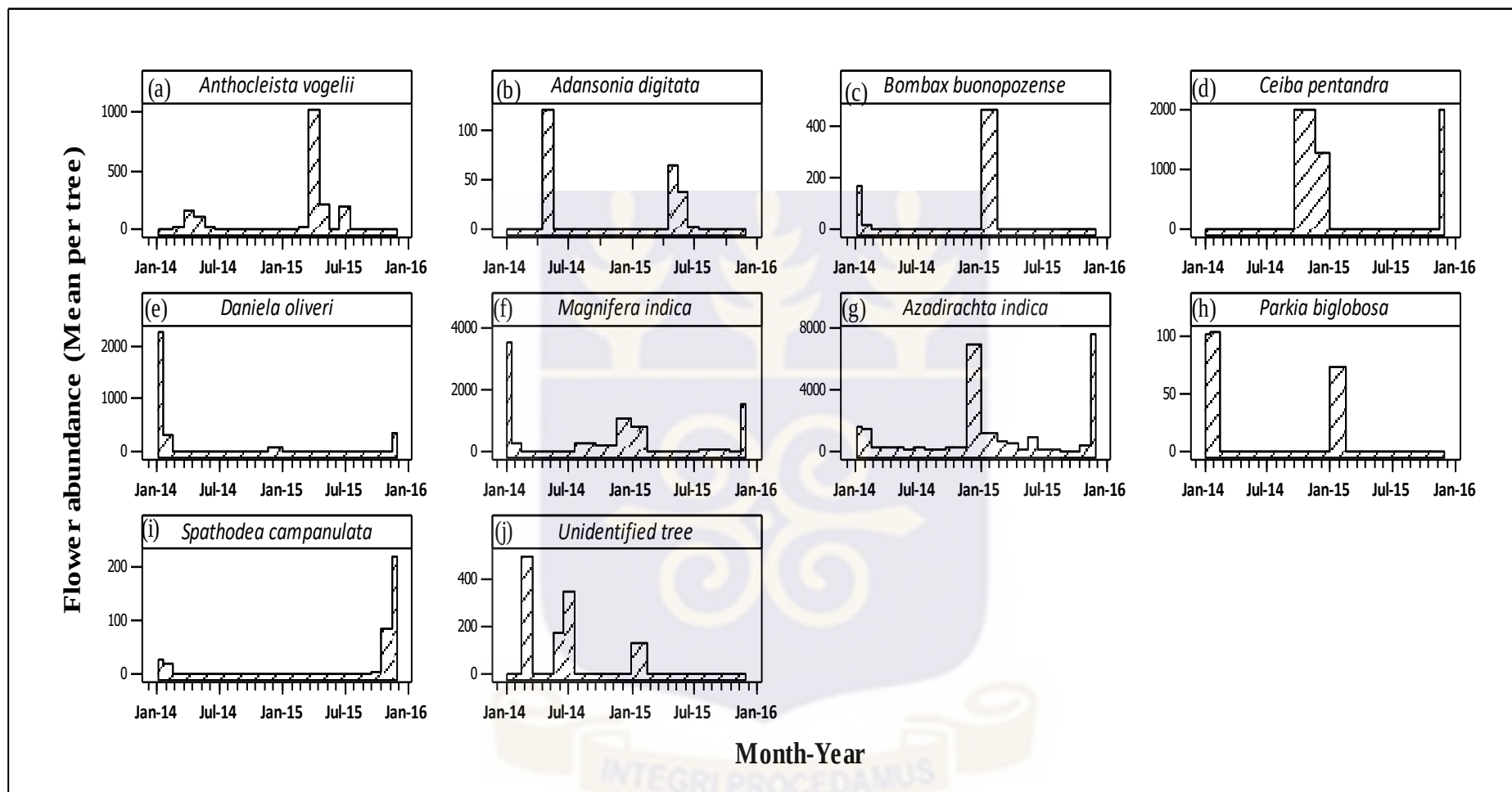
Several of the plants whose flowers were exploited by bats flowered once in a year around December/January. A few plants like *Mango* (*Mangifera indica*) and *Neem* (*Azadirachta indica*) had two flowering periods; a major one in December/January and minor one in June/July (Figure 5.2 f, g). Flowers lasted for short periods and most flowering plants were devoid of flowers within a month of flowering.

Fruit and flower abundance both showed bimodal distributions in a year. Peaks in fruit abundance occurred after peaks in flower abundance (Figure 5.3). There was one pronounced period of flower abundance that occurred during the dry season from November to February with a peak in December. A lower incidence of flowering occurred from April through to August with minimum flower abundance around September-October. Fruits were relatively more abundant throughout the year compared to flowers. A major peak in fruit abundance occurred in March and a minor peak occurred in October.



**Figure 5.1** Estimated monthly fruiting abundance per species.

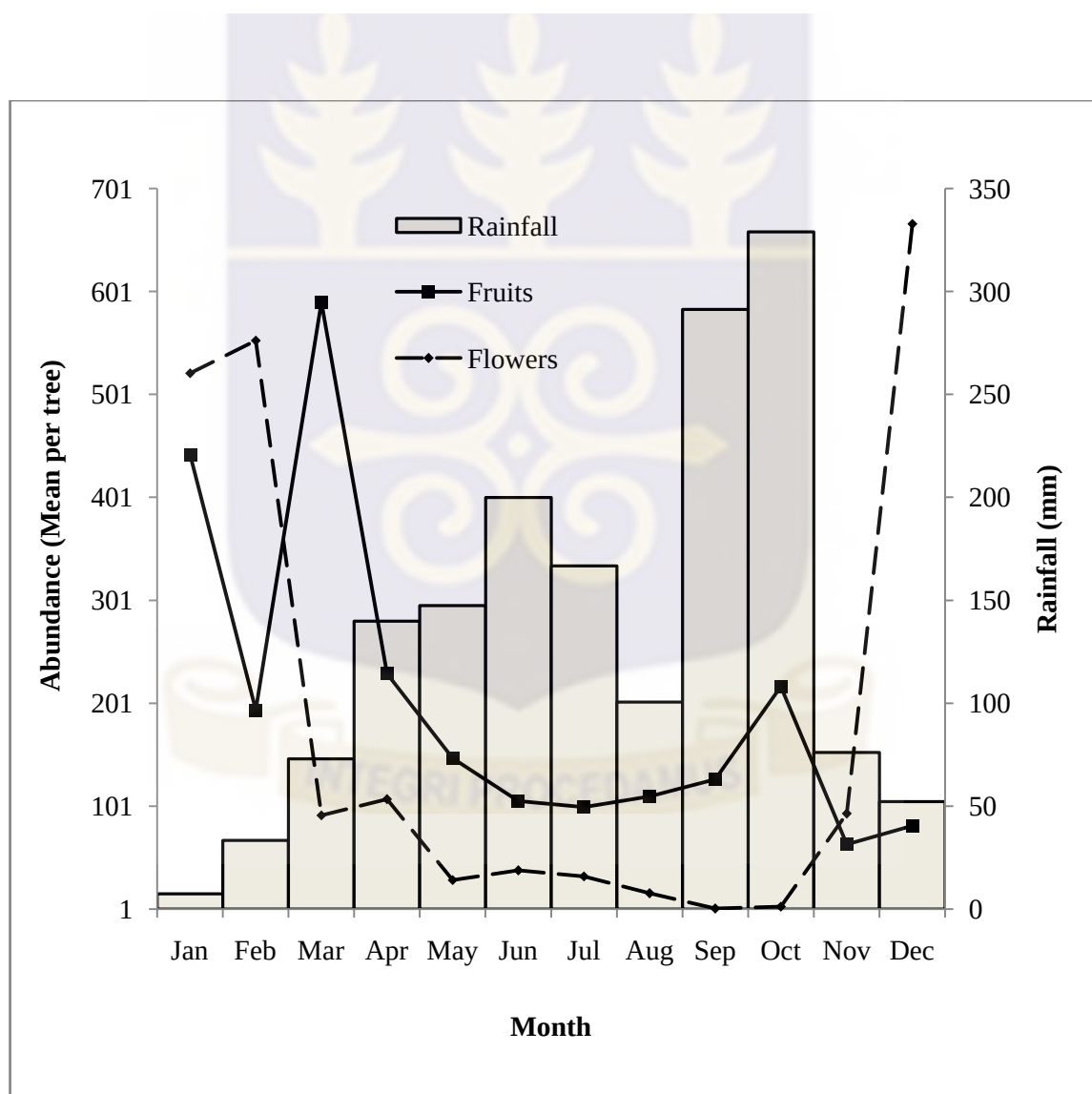
*Abundance = total number of fruits X monthly phenology score per tree. Mean abundance for each species was used.*



**Figure 5.2 Estimated monthly flowering abundance.**

Only plants identified to be utilised by bats are shown.

There was a clear relationship between flowering and fruiting of plants and rainfall patterns in the study area. Rainfall is bimodal in distribution with peaks occurring in June and October. These two peaks in rainfall are separated by a short period of reduced rain in August and a long dry season after the October peak in rainfall. The main peak in flowering occurred during the dry period of the year (November to February) while the first peak in fruiting occurred towards the end of the dry season in March and the second peak occurred during the second rainy season in October (Figure 5.3).



**Figure 5.3 Timing of flowering and fruiting in relation to rainfall.**

Changes in fruiting abundance appeared to occur a month after changes in flowering abundance. This suggests a one month lag between flowering and fruiting abundance. Because data for some months were missing from the original rainfall data obtained (particularly the months when phenology and food abundance data were collected) the correlations between monthly rainfall and the corresponding flower and fruit abundance were not explored any further.

## 5.4 Discussion

### 5.4.1 Dietary composition

In this study, *E. gambianus* utilised a wide variety of food items, with up to ten different food items being utilised during certain periods of the year. This species is generally an opportunistic feeder with a catholic diet as with several West African fruit bats (Marshall & McWilliam, 1982; Marshall, 1985; Boulay & Robbins, 1989). A total of 35 plants species from at least 17 families were identified in the diet of *E. gambianus* of which sixteen are known to provide food for bats in West Africa (Rosevear, 1965; Marshall & McWilliam, 1982; Marshall, 1985; Mickleburgh *et al.*, 1992).

Mouse melon (*Melothria* sp.; family Cucurbitaceae) was identified in the diet of *E. gambianus*, constituting about 2% of all dietary items and was utilised in 10 out of the 21-months that data was collected. There are no records of fruit bats in West Africa feeding on plants of this genus. However, Marshall (1985) lists the fruits and leaves of another member of the family Cucurbitaceae, *Sechium* sp. as a food source for the bat genus *Cynopterus* in parts of Asia. This observation provides an addition to the large range of plant species and families utilised by fruit bats of West Africa.

The utilisation of several food items appeared to be linked to seasonal availability of the plants within the study area. Fruits of Mango, Black plum, and the Indian mast tree were largely utilised during periods of peak abundance so their utilisation was predicted by their abundance. Although seasonal availability may dictate the use of food resources in fruit bats, preferential diet selection has been suggested in some bat species when options are available. Baker and Harris (1957) describe the preference for flowers of Silk cotton (*Ceiba pentandra*) by *E. helvum* rather than *Parkia clappertoniana* even when both were in flower in Ghana. In the current study, Guava fruits were available almost every month but were detected in the diet of *E. gambianus* in just six out of the 21 months duration of this study. Fruits of Potato tree, and Mouse melon were identified in the diet of *E. gambianus* in several months. However, their overall relative abundance in the diet of *E. gambianus* for the entire duration of the study was less than 5%. This may suggest preference for certain dietary items over others or use in hierarchical manner where some may only be used as supplementary to more preferred ones. This would support Marshall's suggestion that most fruit bats could be spatio-temporal "sequential specialists" with preference for a few species among those available, rather than generalists (Marshall, 1985).

#### **5.4.2 Relative importance of food of different plant items in the diet of *E. gambianus***

Figs were represented in over 40% of all samples and recorded in all but one month in this study, suggesting that figs constitute an important component of the diet of *E. gambianus*. The genus *Ficus* is perhaps the most important source of food to frugivorous animals throughout the world (Mickleburgh *et al.*, 1992), providing food to an estimated



1274 bird and mammal species (Shanahan *et al.*, 2001). Within the family Pteropodidae, Figs provide a staple diet in over 20 genera of bats (Shanahan *et al.*, 2001; Barclay & Jacobs, 2011) and it is therefore not surprising that it dominated the diet of *E. gambianus* in this study.

Figs are particularly important fruit bat dietary item for two major reasons. Firstly, Figs have an asynchronous fruiting phenology with several species producing fruits almost every six to twelve months (Mickleburgh *et al.*, 1992), creating a year-round availability of fruits (Shanahan *et al.*, 2001; Barclay & Jacobs, 2011). This is consistent with observations in this study as Fig fruits were always available throughout the study period.

Figs are also important to bats for their high levels of calcium (O'Brien *et al.*, 1998) and provide a vital nutrient in an otherwise low calcium frugivore diet. Figs may be of much significance in the diet of lactating mothers because of the high calcium requirement to ensure that young ones have well developed bones to fly on their own after weaning and increase their fitness (Barclay & Jacobs, 2011). If the overall survival of a population was dependent on the fitness of young ones, then females (and young ones) could feed differentially and selectively more on Figs to ensure proper development of young ones. The loss of Figs due to increasing habitat degradation within foraging habitats could then affect bat survival and have serious consequences on fitness of populations, particularly those already in decline.

Palmer *et al.* (2000) and Barclay and Jacobs (2011) suggested that selective feeding on Figs may occur in fruit bats. In the current study selective feeding on figs could not be assessed since all faecal and ejecta samples that were collected were pooled together making it impossible to distinguish between samples for males and females. More

advanced methods such as the use of steroid concentrations in faecal analysis as suggested by Stier and Mildenstein (2005) could help quantify and assess differential use of figs by fruit bats in future studies.

Other fruits that may play vital roles in the diet of *E. gambianus* include Black plum and Cabbage tree fruits. These fruits accounted for high proportions of the diet of *E. gambianus* when they were available and this suggests preferential selection of these fruits over other food items. Black plum fruits have a higher protein content (72.8-82.4 g/kg ) (Agbede & Ibitoye, 2007; Vunchi *et al.*, 2011), compared to Guava and figs (22.2 g/kg and 24.6 g/kg respectively) (Ruby *et al.*, 2000) and may be preferred over other available fruits because of its higher protein content. Additionally, Black plum and Cabbage tree fruits were highly abundant and were utilised in high proportions during periods that coincided with late pregnancy and parturition periods for *E. gambianus* in this study. Thus, these two species together with Figs could be important dietary items during such vital stages in the reproduction of *E. gambianus*.

While fruit bats may feed mostly on fruits, flowers also constitute important dietary items (Marshall, 1985). However, very few studies have assessed the extent of use of flowers as a dietary source in fruit bats. From this study, flower resources contributed to over 10% of the dietary items identified for *E. gambianus* and in the dry "lean" fruiting seasons in particular, contributed up to 79% of dietary items for this species, assuming all dietary items are equal with no difference in calorific or energetic content. At least 10 plant species were identified to be exploited for their flowers within the study area and all these have been reported to be utilised by *E. gambianus* and other fruit bat species in West Africa (Baker & Harris, 1957; Marshall & McWilliam, 1982; Marshall, 1985; Mickleburgh *et al.*, 1992).

Because flowering and fruiting periods of most plants did not occur simultaneously, this provided justification for the assumption that bats carrying pollen on their bodies had visited plants solely because of their flowers and to feed on nectar and/or their pollen. Peak flowering and use of flower resources occurred during the dry season when fruit abundance was minimal. This suggests that the use of flower resources play a major subsistence role in the diet of *E. gambianus* rather than a supplementary one. For instance, flowers of Silk cotton is reported to be an important food source for bats in Madagascar during the dry season (Andriafidison *et al.*, 2006). Flowers from a single Silk cotton tree can produce about 200 litres of nectar and an estimated 30 kg of sugars during a five week flowering period (Gribel *et al.*, 1999) which can sustain a large community of bats.

The use of flowers may also have an added nutritional benefit to fruit bats. Fruits are very low in protein content and this vital nutrient is often lacking in the diet of frugivorous bats (Marshall, 1985; Ruby *et al.*, 2000; Stier & Mildenstein, 2005; Barclay & Jacobs, 2011). Flowers and leaves can provide considerable high amounts of protein to bats (Law, 1992; Nelson *et al.*, 2000; Ruby *et al.*, 2000). Although leaves were not detected as part of the diet of *E. gambianus*, observations of flower parts in dietary materials may indicate the consumption of parts or whole flowers.

The use of pollen as a dietary item in *E. gambianus* is uncertain. Boulay and Robbins (1989) states that there is no evidence to support *E. gambianus* feeding on pollen. This assertion was based on the absence of pollen in the gut contents of the species in the study by Baker and Harris (1957). However according to Marshall (1985), within the family Pteropodidae, pollen may be licked from anthers directly during feeding or ingested during grooming of fur dusted with pollen. Pollen consumption is suggested to

occur in some Pteropodidae genera like *Pteropus* (Marshall, 1985; Mickleburgh *et al.*, 1992).

Although *E. gambianus* was observed to visit flowering trees and several trapped bats were covered in pollen, the current study cannot confirm if the bats visiting flowers were actively eating pollen, nectar or both. The poor reporting of pollen in the diet of bats could be due to a surveillance bias. Andriafidison *et al.* (2006) reports that in Madagascar, over 40 percent of the 118 plant taxa that have been identified to be utilised by *Pteropus rufus* and *Eidolon dupreanum* were identified from pollen in the faeces of these fruit bats. The contribution of pollen and nectar to the diet of fruit bats may be largely underestimated especially when macroscopic analysis of faeces as a method to identify dietary items is used (Andriafidison *et al.*, 2006). This study was not equipped to carry out microscopic analysis of pollen in samples collected. Further studies that utilize microscopic pollen analysis from faecal samples of fruit bats are needed to confirm the importance of the use of pollen as a dietary material in fruit bats

#### **5.4.3 Timing of food resources**

In Africa, food availability for bats has been shown to be constrained by rainfall. Fluctuations in insect and fruit abundance are tied to rainfall patterns (Rautenbach *et al.*, 1988; Happold & Happold, 1990; Cumming & Bernard, 1997). Peaks in flowering have been shown to occur during peak rainfall or shortly after peak rains (Hepburn & Radloff, 1995). Some fruit phenology studies show peak fruiting during the peak rainy season with flowering occurring in the preceding dry period (Janzen, 1967; Frankie *et al.*, 1974); this is supported by the findings of this study. Fruits were relatively available

throughout the year with two peaks in fruiting which occurred with the rains. Each fruiting period occurred one to two months after a flowering period. Two peaks in flowering were also observed; a minor one around June-July and a major and more prominent peak during the major dry season. In Africa, seasonality in fruiting and flowering however may be more pronounced particularly in drier areas where strong seasonal variations in rainfall occur. In such drier regions, fruits may be less seasonally available throughout the year (Cumming & Bernard, 1997).

The timing and seasonality of food abundance is particularly important to the timing of reproduction in fruit bats (Happold & Happold, 1990; Cumming & Bernard, 1997). Reproduction in fruit bats is reported to be timed such that food is available for young ones after they are weaned (Fleming *et al.*, 1972; Cumming & Bernard, 1997).

In West Africa, parturition in *E. gambianus*, is reported to occur twice; in April/ May and in October/November, with gestation lasting about 6 weeks (Thomas & Marshall, 1984). The first post-weaning period occurs around June/July. This period coincides with the rainy season which according to this study is a period when both flowers and fruits are relatively abundant. The second post-weaning period for this species occurs around December/January which coincides with the major peak in flower abundance observed in this study. Racey and Entwistle (2000) however, propose that in the tropics, reproduction in some species of bats may be rather timed to coincide with the availability of some particular food resources, in which case climatic factors like rainfall may not correctly predict reproduction.

#### 5.4.4 Ecosystem services: importance of foraging habits of *E. gambianus*

Through the feeding on flowers and fruits of specific plants, it is expected that *E. gambianus* pollinates and disperses seeds of these plants. *E. gambianus* potentially provides important ecological services through the dispersal of food plants. Figs, which formed a major part of the diet of *E. gambianus* are keystone plants in tropical ecosystems as they contribute largely to ecosystem biomass and provide food to other birds and mammals (Shanahan *et al.*, 2001; Kunz *et al.*, 2011). The seeds of some fruits that are eaten by bats have been found to have improved germination rates after passing through the gut of bats (Djossa *et al.*, 2008; Kankam & Oduro, 2012). Hence, by feeding on these plants *E. gambianus* may contribute to the successful germination of these food plants.

Several of the dietary items for *E. gambianus* such as Red silk-cotton (*B. buonopozense*) several fig species, African tulip tree (*S. campanulata*) and Silk cotton are important pioneer species of original forest vegetation (Hawthorne & Gyakari, 2006). Other species like Potato tree, Figs and the Cabbage tree are also important and abundant species during early succession stages of primary and secondary forests (Swaine & Hall, 1983). This highlights the important role *E. gambianus* plays in maintenance and regeneration of the natural forest vegetation, especially in the midst of current levels of habitat loss and forest degradation.

Aside these ecological values, there are several direct and indirect benefits to humans. Some of the plants that are likely to be pollinated and dispersed by *E. gambianus* are of very high economic importance. Tree species like *M. excelsa*, *B. buonopozense*, *S. rhinopetala*, *C. pentandra* and *E. suaveolens* are exploited in Ghana for timber and are of economic importance (Hawthorne & Gyakari, 2006). *M. excelsa*, commonly referred to



as Odum, in particular, is heavily exploited and threatened by overexploitation in Ghana (Taylor *et al.*, 1999; Hawthorne & Gyakari, 2006). Through its feeding activities and consequently pollination and dispersion, *E. gambianus* contributes to the continuous persistence of these plant species.

Fruits of Black plum, Yellow mombin (*S. mombin*), *Syzygium* sp., and Guava, are sold and consumed locally and contribute to diet and income of people, especially rural dwellers. Even though plants like Mango, Guava and Cashew are cultivated on large scales, and may no longer rely on bats for their dispersal or pollination, bats are still relevant in maintaining the genetic diversity of their wild types (Kunz *et al.*, 2011). The services provided by *E. gambianus* through its foraging highlights the importance of this species (and fruit bats in general) to the ecosystems in which they occur and this calls for the need to ensure their persistence and conservation.



## CHAPTER SIX

### 6.0 ROOST SITE SELECTION AND ROOSTING BEHAVIOUR OF *EPOMOPHORUS GAMBIANUS*

#### 6.1 Introduction

A significant proportion of the lives of bats is spent at their day roosts (Kunz *et al.*, 2003). Roosts are important as they provide shelter, protection from predators and avenues for social interactions between individuals. By selecting an optimum roosting site, bats achieve better protection from adverse weather and predators, enhance their chances of better mating, better maternal care, reduced energetic costs in commuting to foraging sites and increased social interactions (Kunz, 1982; Tan *et al.*, 1999; Neuweiler, 2000; Kunz *et al.*, 2003). Because of these important provisions, roosts play vital roles in the fitness, reproductive success and overall survival of bats (Vonhof & Barclay, 1996; Kunz *et al.*, 2003).

Roost selection depends largely on some basic characteristics of the structure being utilised, such as availability, physical structure and reliability, among others (Kunz *et al.*, 2003). Manley *et al.* (1993) suggest that resource selection occurs in a hierarchical manner, beginning with the geographic range of the species, to home ranges of individuals, their use of broad features within the home range, and the selection of particular elements within the broad features. Hence, factors that determine habitat selection in animals may vary depending on the scale; as such, selection and use is best studied at a multi scale in order to obtain accurate depiction and description of how a particular habitat may be selected and used (Limpert *et al.*, 2007; Lucas, 2009).

Ecological studies on bats are often very challenging because of their behaviour and thus, basic knowledge about several bat species are lacking (Limpert *et al.*, 2007). Advancements in radio-tracking and telemetry has helped to gain insight into some aspects of the ecology of several bat species, particularly their habitat use (Kalcounis-Rüppell *et al.*, 2005; Mildenstein *et al.*, 2005), but much remains to be discovered.

*Epomophorus gambianus* is a widespread and very common fruit bat in Ghana and much of Africa. The species utilizes a wide variety of natural habitats, including wooded savannah, forest edges and mosaics or cleared patches in forests. The species also thrives well in anthropogenically modified landscapes and are common in cultivated areas, orchards, rural and urban areas with mosaics of fruiting trees. However, very little knowledge exists on roost selection and roosting behaviour of this species. The aim of this study was to determine roost site selection and roosting behaviour of *Epomophorus gambianus* in a rural landscape within the forest-savannah transition ecological zone of Ghana; specifically, to:

- determine roosting behaviour in *E. gambianus* using radiotelemetry;
- describe roost selection across roost tree and plot spatial scales;
- determine the tree and plot scale variables that are important for roosting in *E. gambianus*.

## 6.2 Methodology

### 6.2.1 Study location

The study was conducted at Ve-Golokuati in the Volta region of Ghana (see Chapter two for full description of the study site). This site was selected for this study because of the presence of a large *E. gambianus* colony that occurs in the town. The extent of this

colony was used to define the specific study area within the town for data collection. Hence, all data for this study were collected within an 82.6 hectare area in the Ve-Golokuati town.

### **6.2.2 Location of roosts**

Bat roosts were located using two methods: tree searches and radiotelemetry. Trees within the Ve-Golokuati town were searched for the presence of bats. For each tree identified to be occupied by bats, the location was taken using a hand-held Garmin GPS e-Trex 20 device and the number of bats occupying each tree was recorded. These trees were subsequently monitored monthly over a three-year period for changes in bat population and for frequency of occupancy of roost trees. During the population monitoring period, any tree that was newly occupied was noted and added to the roost trees already identified. Roosts that were observed to have at least one female bat carrying a young were delineated as maternal roost trees. Some roost trees were also identified from tracking radio-tagged bats to their specific day roosts.

### **6.2.3 Bat capture and radio-tracking**

Bat capture, species identification and determination of age and sex followed methodology described in Chapter three. Candidates for radio-tagging were selected based on their weights. Tags weighed between 5.0 to 6.3 g (mean  $5.7 \pm 0.3$  g). According to Aldridge and Brigham (1988), tag weights for telemetry studies should not exceed 5% of the body weight of bats, especially for bats that weigh  $<70$  g. Hence for this study, minimum weights of 100-126 g were required for candidate bats to be radio-tracked and bats that did not meet this minimum weight category (particularly juvenile and sexually

immature bats) were not selected for radiotagging. Tags weighed averagely  $5.1 \pm 0.5\%$  (range 4.0-6.8%) of the total body weight of selected bats. Only a few bats were fitted with tags that slightly exceeded the 5% weight threshold. It was assumed that a slight increase (up to 1.8 g) above the suggested 5% weight threshold would not significantly affect the roosting behaviour of such bats since they weighed  $\geq 100$  g.

A total of 60 SOM 2190 HWSC radio-transmitters (Wildlife Materials International, Inc, Murphysboro, Illinois) were fitted to adult and sexually immature adult *E. gambianus* using collars (Plate 6.1). Tags were tuned to emit frequencies with the range of 150.000-150.999 MHz with each tag emitting a unique frequency within this range. Twenty tags were fitted in October 2015 and 40 tags were fitted in February 2016. In total, 18 females (17 Adults, 1 sub-adult) and 42 males (14 adults and 28 sexually immature adults) were fitted with radio-tags. All roost trees identified in the study area were easily accessible and tagged bats were subsequently tracked on foot during the day to their roosts at least once a month over a period of 10 months using a TRX- 1000S, receiver and a 3-element directional Yagi antenna (Wildlife Materials International, Inc).

To locate a specific tag, the receiver was tuned to the tag's unique frequency. The 3-element Yagi antenna (connected to the receiver) was held above the head and rotated slowly in a 360 degree arc until the receiver tuned in the transmitter's beeping signal; the direction at which the loudest signal was obtained indicated the direction of the tagged bat. Once the transmitter's beeping signal was detected, the location of the bat was further narrowed down by moving in the general direction of the detected signal while making slight directional adjustments with the antenna. Moving closer to the transmitter increased the signal strength, hence the location closest to the tagged bat was identified as the point where the loudest signal was obtained and beyond which the signal strength



dropped. Once at the location where the strongest signal was obtained, efforts were made to visually confirm the presence of the tagged bats at its specific roost tree. This was to ensure that signals from tags traced to roosts were coming from tags that were still attached to bats and not tags that had fallen under roosts.



**Plate 6.1 Radio-tagging and radio-tracking of *E. gambianus*.**

**A-** *E. gambianus* fitted with radio-tag prior to release      **B-** A radio-tagged bat tracked to its roost.

#### **6.2.4 Characteristics of roost trees.**

To determine roost selection by *E. gambianus*, roost selection was tested at two scales; tree scale and plot scale. For each identified roost tree, measurements of the height, diameter at breast height (DBH) and the crown diameter were measured. Each roost tree species was also identified. Heights were measured in meters to the nearest 0.1 m using a Nikon® Forestry Pro laser rangefinder. DBH was measured at 1.3 m above the ground



and crown diameter was measured as the ground distance between the extents of the crown of each tree using a tape measure.

In order to test roost site selection in *E. gambianus*, comparison trees were selected within the extent of the roosting area. Comparison trees were defined as all trees with DBH >10 cm that were not used as roosts within the study area. All comparison trees were assessed for similar characteristics as done for roost trees. This minimum DBH criterion was chosen because this was the minimum DBH that was recorded for all roost trees. The GPS locations of all comparison trees within the study area were also taken. The basal area of each tree was calculated from the DBH measured. Additionally, all houses, homesteads and buildings within the study area were also mapped out for further assessments of the factors that influence *E. gambianus* roost selection.

#### **6.2.5 Spatial Analysis**

All GPS coordinates captured for roost and non-roost trees, and all buildings were downloaded using PC-GPS software Garmin BASECAMP version 4.6.2 (Garmin Ltd). All spatial analysis was conducted in Quantum GIS software (QGIS version 2.12.2-Lyon). All measured characteristics of each tree were linked to each tree's GPS coordinates. The locations points and complete information of all trees were merged into one shapefile in Quantum GIS (QGIS version 2.12.2-Lyon). To obtain comparison plots, a 25m buffer (ca 0.19 ha area) was created for each tree in QGIS. Buffers that were created around roost trees were classified as roost plots whereas those created around non-roost trees were classified as comparison plots. Within each 0.19 ha plot created the total tree density was calculated. The total number of trees occurring within each plot was estimated using the "points in polygon" feature in QGIS to give an estimate of tree

density per plot (number of trees /ha). Building density (number of buildings /ha) was also estimated for each roost and non-roost plot using a similar approach. Inter tree distances for roost and non-roost trees were estimated using the linear distance matrix in QGIS. Nearest neighbour analysis were also conducted to extract distances for nearest roosts and non-roost trees, and for distances to nearest buildings for roost and non-roost trees. Using the QGIS field calculator, the sum of the basal area of all trees occurring within each plot was estimated to give the total basal area for each plot. Total basal area for each plot was estimated as the sum of basal area for all trees that occurred within each plot.

To enable comparisons between maternal roost trees and non maternal roost trees, point shape file for roost trees was split into two point files: maternal roost trees and non maternal roost trees. Measurements of inter roost distance, distance to nearest roost tree, distance to nearest building were extracted for maternal roost trees and non maternal roost trees. Additionally, tree density, building density and basal area per plot were calculated for each maternal and non maternal roost trees.

### **6.3 Statistical analysis**

#### **6.3.1 Comparison of tree characteristics.**

All data were tested for normality using Anderson-Darling test for normality at  $p=0.05$ . Data were not normally distributed and most were not transformed successfully. Hence, comparisons for differences in tree and plot characteristics between categories (roost vs. non-roost trees and maternal vs. non maternal roost trees) were made using non parametric 2 independent sample Mann-Whitney *U* tests. Tests Results are presented as Median values with Inter-Quartile ranges (IQR) and *p* values. Data for roost

characteristics are presented as means  $\pm$  SD and their ranges (min-max). Frequency of occupancy for roosts was calculated as a percentage of the number of times a roost was occupied to the number of times it was monitored for bats.

### 6.3.2 Roost use in radio-tagged bats

Roost use in radio-tagged bats are presented as number of times bats were located, the number of different roosts they utilised and the number of times they switched roosts and the means  $\pm$  1 SD of these measures. In addition to these measures, roost fidelity was estimated for bats that were tracked and identified at their roosts for  $\geq 4$  times (n=19).

The Shannon index was used as a measure of both the number of roosts used by an individual bat (Richness) and the relative contribution made by each roost to the overall time spent at all roosts (Evenness). This method reduces the biases that possibly arise from unequal differences in number of times an individual was tracked (unequal sampling effort) and differences in success of locating roosts of individuals (sampling success) (Trousdale *et al.*, 2008). The Shannon diversity is given by:

$$H' = -\sum p_i \log p_i$$

Where  $p_i = n_i/N$ , and is the contribution (proportion) of a particular species to the total number of individuals of all species.

In this analysis,  $p_i = n_i/N$ ,

where:  $n_i$  is the number of times a bat was located at a particular roost

$N$  is the total number of times the bat was located at any roost during the radio-tracking period (Trousdale *et al.*, 2008).

Individuals with high H' score would be those that used relatively large number of roosts evenly and those with a low H' would be those that used a few number of roosts and spent a large portion of roosting time at one roost.

To calculate roosting area covered by tagged bats, Minimum Convex Polygons (MCP) was calculated for tagged bats that utilised  $\geq 3$  different roosts. MCP calculations were done using the Convex hull function in QGIS. Differences in measures of roost use, fidelity and MCP of tagged bats were compared between male and female groups and between age groups using non parametric Mann-Whitney-Wilcoxon tests.

To test for preference of tree species used as roosts in bats, binomial exacts tests (Minitab statistical package Vs 16.1) were used to compare the relative use of each tree species that was identified. Results from binomial exact tests were used to classify trees as "Selected", "Avoided" or used at "Random". If the proportion of a tree species used was significantly greater than what was expected based on its availability, the species was described as "Selected". If a tree species' use was significantly less than expected based on its availability, it was considered as "Avoided". However if there was no significant difference in relative use and availability, the species was described to be used at "Random" (Neu *et al.*, 1974; Sedgeley & O'Donnell, 2004; Hahn *et al.*, 2014). All statistical tests were done at a 95% confidence interval ( $\alpha=0.05$ ) in Minitab.

To model *E. gambianus* roost selection within the study area, logistic regression was used to determine which variables at tree and plot scales best differentiated roost trees from non-roost trees. Variables considered in the models included tree species, height of tree, DBH, crown diameter, plot basal area, plot tree density, plot building density and distance of tree to nearest building. All the variables listed above were included in the logistic regression modelling as initial multicollinearity tests indicated that none of the

variables were strongly correlated (correlations at  $r \geq 0.7$  would be considered as strongly correlated).

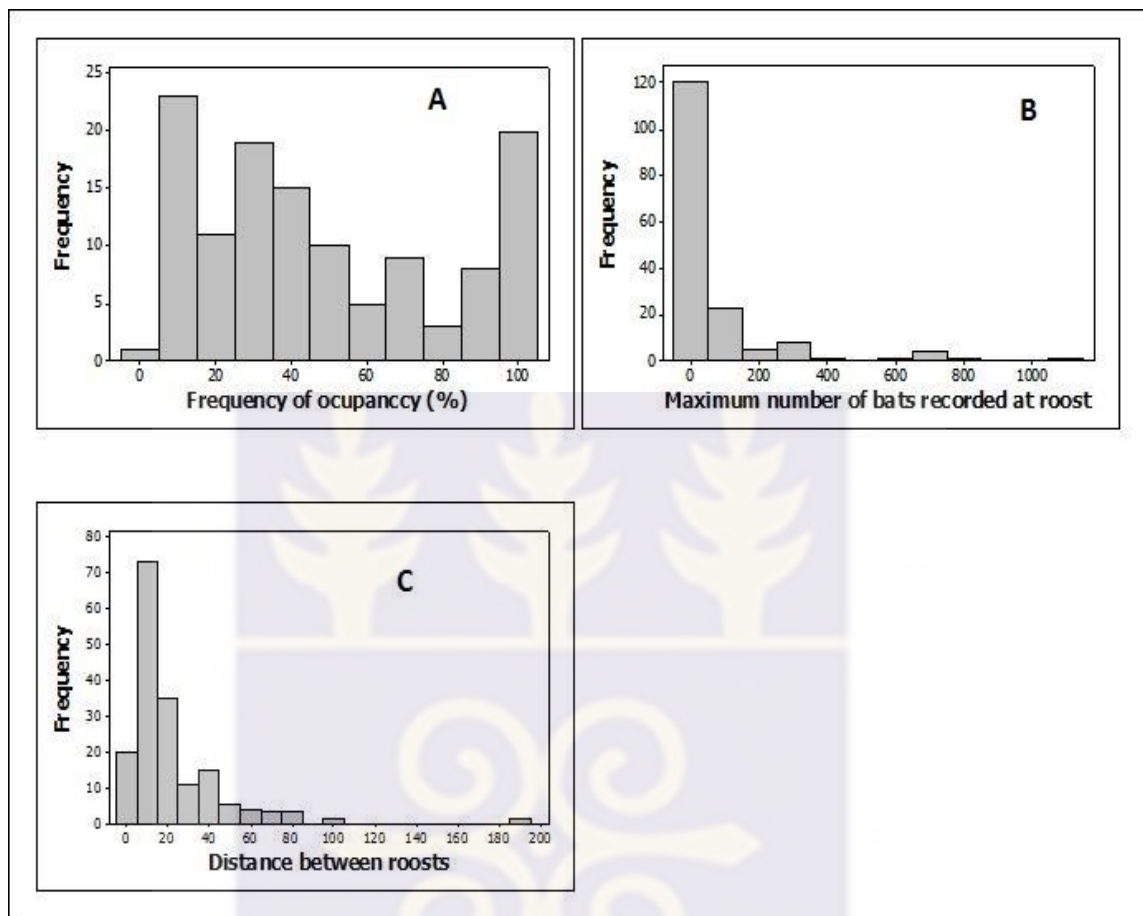
Because a large number of tree species were recorded that were not used as roosts, these trees were combined as a single tree species and one of the frequencies was manually assigned a value of 1 to ensure model convergence. All variables were entered into the initial model (full model) and variables were assessed for their significance to the model. Assessment of significance of parameters to the models were done using Likelihood ratio statistic ( $p < 0.05$ ). Variables that were not significant were removed from the initial models, and the models were then re-run with remaining variables to obtain candidate models. Final selection of the best model was done using Akaike's Information Criterion (AIC). The contribution of variables in the final model was assessed using Likelihood ratio tests [R, Package "aod", Lesnoff and Lancelot (2012)] and the overall assessment of the final model was done using the Hosmer and Lemeshow goodness of fit test [R, Package "ResourceSelection", Lele *et al.* (2013)]. Some roost trees were lost (cut) before some assessments could be completed and were not used in the calculations.

## **6.4 Results**

### **6.4.1 Roosting behaviour**

A total of 178 roost trees were identified. Of the total roosts that were identified, 92.7% were from roost searches while only 7.3% were identified from tracking radio-tagged bats to their roosts. Forty-four percent of these roost trees were utilised as maternal roost. The number of bats per roosts ranged between single individuals up to a maximum of 1,122 bats, with an average number of 80 bats per tree. Roosts were averagely occupied 48% of the time and this varied from 3.1% up to 100% among roosts (Figure 6.1). Roosts

were typically made up of a mix of both males and females. *E. gambianus* was observed to share twenty six of these roosts with *Micropteropus pusillus*.



**Figure 6.1 Characteristics of identified *E. gambianus* roosts.**

**A-** Frequency of occupancy at roosts **B-** Maximum number of bats recorded at roosts; **C-** Distance between roost trees.

Out of the 60 bats that were tagged, only 19 were detected on four or more occasions and were used for analysis. Out of these, 6 were adult females and 13 were males (6 Adults, 7 sexually immature). Radio-tagged bats utilised between 2 to 6 different roosts with a mean of  $3.26 \pm 1.05$  roosts per individual (Table 6.1). Bats switched roosts between 1-6 times, averagely  $2.63 \pm 1.42$  times.

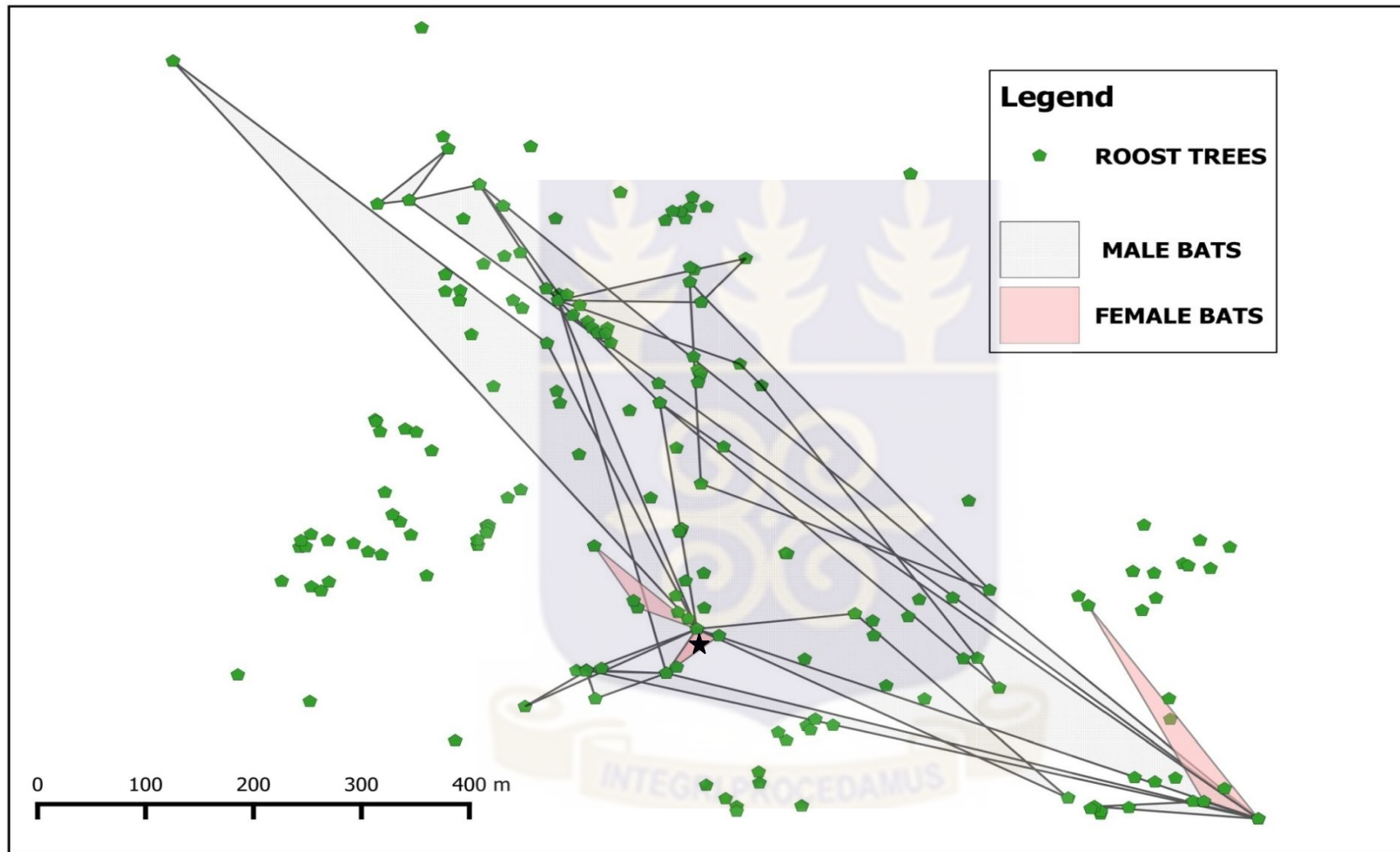


**Table 6.1 Number of detections, roosts used, roost switches and roost diversity for radio-tagged *E. gambianus*.**

*Data for bats detected  $\geq 4$  times were used in calculations. AD-Adult; SI-Sexually immature adult; F-female; M-male*

| Bat ID      | Sex | Age | Number of detections | Number of roosts used             | Number of Roost switches          | H'                                |
|-------------|-----|-----|----------------------|-----------------------------------|-----------------------------------|-----------------------------------|
| 0.065       | M   | AD  | 10                   | 5                                 | 6                                 | 0.68                              |
| 0.105       | M   | SI  | 5                    | 4                                 | 4                                 | 0.58                              |
| 0.135       | M   | SI  | 10                   | 3                                 | 2                                 | 0.39                              |
| 0.155       | M   | SI  | 4                    | 2                                 | 2                                 | 0.24                              |
| 0.165       | M   | AD  | 6                    | 3                                 | 2                                 | 0.38                              |
| 0.195       | M   | AD  | 7                    | 6                                 | 6                                 | 0.76                              |
| 0.255       | M   | AD  | 5                    | 3                                 | 3                                 | 0.46                              |
| 0.285       | F   | AD  | 8                    | 3                                 | 3                                 | 0.32                              |
| 0.354       | F   | AD  | 6                    | 3                                 | 2                                 | 0.44                              |
| 0.435       | F   | AD  | 5                    | 4                                 | 3                                 | 0.58                              |
| 0.455       | F   | AD  | 5                    | 3                                 | 2                                 | 0.41                              |
| 0.465       | F   | AD  | 4                    | 2                                 | 1                                 | 0.30                              |
| 0.515       | M   | SI  | 4                    | 2                                 | 1                                 | 0.24                              |
| 0.655       | M   | AD  | 4                    | 4                                 | 3                                 | 0.60                              |
| 0.715       | M   | SI  | 4                    | 3                                 | 2                                 | 0.45                              |
| 0.725       | M   | AD  | 4                    | 2                                 | 1                                 | 0.24                              |
| 0.735       | M   | SI  | 4                    | 3                                 | 2                                 | 0.45                              |
| 0.835       | M   | SI  | 4                    | 3                                 | 2                                 | 0.45                              |
| 0.885       | F   | AD  | 5                    | 4                                 | 3                                 | 0.58                              |
| <b>Mean</b> |     |     |                      | <b>3.26 <math>\pm</math> 1.05</b> | <b>2.63 <math>\pm</math> 1.42</b> | <b>0.45 <math>\pm</math> 0.15</b> |

Tagged bats were tracked to 51 different roosts. Out of this, 19 roosts were found to be used by more than one radio-tagged bat within the period. Roost sharing among radio-tagged bats was very common. Up to a maximum of 7 radio-tagged bats were identified to be sharing the same roosts at the same time. Several bats had overlapping roosting ranges and two female bats had completely overlapping MCP's (Figure 6.2).



**Figure 6.2** Minimum convex polygons for radio-tagged male and female *E. gambianus*. Completely overlapping MCP's for two female bats indicated by black star.

MCP's were calculated for 18 bats which used  $\geq 3$  different roost sites. The average MCP was  $1.18 \pm 1.61$  ha and ranged between 0.05 ha to 5.85 ha. (Table 6.2).

**Table 6.2 Minimum convex polygon (MCP) of roost area for radio-tagged bats.**

*MCP was calculated for bats that used  $\geq 3$  roosts. AD-Adult; SI-Sexually immature adult; F-female; M-male*

| Bat ID        | Sex | Age | MCP(ha)         |
|---------------|-----|-----|-----------------|
| 0.065         | M   | AD  | 2.76            |
| 0.165         | M   | AD  | 0.11            |
| 0.195         | M   | AD  | 2.45            |
| 0.255         | M   | AD  | 0.79            |
| 0.285         | F   | AD  | 0.13            |
| 0.354         | F   | AD  | 0.06            |
| 0.435         | F   | AD  | 0.42            |
| 0.455         | F   | AD  | 0.06            |
| 0.655         | M   | AD  | 1.58            |
| 0.685         | M   | AD  | 0.07            |
| 0.764         | M   | AD  | 3.15            |
| 0.105         | M   | SI  | 0.05            |
| 0.135         | M   | SI  | 0.48            |
| 0.246         | M   | SI  | 2.78            |
| 0.715         | M   | SI  | 0.11            |
| 0.735         | M   | SI  | 5.85            |
| 0.835         | M   | SI  | 0.07            |
| 0.885         | M   | SI  | 0.31            |
| Mean $\pm$ SD |     |     | $1.18 \pm 1.61$ |

There were no significant differences between the number of roosts used by males (median = 3.0) and females (median =3.0; w=129.5, p=1.0) and also for adult males (median =3.5) and sexually immature males (Median=3.0; w=50.5, p=0.23). No difference was also observed between number of roost switches made by the two sex groups and the two male age groups (Table 6.3). Roost fidelity did not differ between gender and age groups.

**Table 6.3 Comparisons of *E. gambianus* roost and non-roost tree characteristics.**

Data are presented as medians and inter quartile ranges. Comparisons were made using Mann-Whitney U tests. Significant tests are shown in bold.

|                                          |                   | MALES |        |            |         | FEMALES |        |            |             |
|------------------------------------------|-------------------|-------|--------|------------|---------|---------|--------|------------|-------------|
|                                          |                   | N     | Median | IQR        | P value | N       | Median | IQR        | P value     |
| <b>Number of roosts used</b>             | Adult             | 6     | 3.5    | 2.8-5.3    | 0.2     |         |        |            |             |
|                                          | Sexually immature | 7     | 3.0    | 2.0-3.0    |         |         |        |            |             |
|                                          | TOTAL             | 13    | 3.0    | 2.5-4.0    |         | 6       | 3.0    | 2.8-4.0    | 1.0         |
| <b>Number of roost switches observed</b> | Adult             | 6     | 3.0    | 1.8-6.0    | 0.2     |         |        |            |             |
|                                          | Sexually immature | 7     | 2.0    | 2.0-2.0    |         |         |        |            |             |
|                                          | TOTAL             | 13    | 3.0    | 2.5-4.0    |         | 6       | 2.5    | 1.8-3.0    | 0.1         |
| <b>H'</b>                                | Adult             | 6     | 0.5    | 0.3-0.7    | 0.2     |         |        |            |             |
|                                          | Sexually immature | 7     | 0.5    | 0.2-0.5    |         |         |        |            |             |
|                                          | TOTAL             | 14    | 0.5    | 0.3-0.6    |         | 6       | 0.4    | 0.3-0.6    | 0.8         |
| <b>Minimum Convex Polygon area (ha)</b>  | Adult             | 7     | 1.6    | 0.1-2.8    | 0.5     |         |        |            |             |
|                                          | Sexually immature | 7     | 0.3    | 0.06-2.8   |         |         |        |            |             |
|                                          | TOTAL             | 14    | 0.63   | 0.09-2.77  |         | 4       | 0.10   | 0.05-0.4   | 0.1         |
| <b>Distance between roosts (m)</b>       | Adult             | 45    | 181.5  | 87.0-412.4 |         |         |        |            |             |
|                                          | Sexually immature | 32    | 129.8  | 59.0-239.8 | 0.09    |         |        |            |             |
|                                          | TOTAL             | 77    | 163.4  | 68.2-394.9 |         | 17      | 78.2   | 55.2-138.3 | <b>0.02</b> |

Median MCP for adult males was 1.58 ha compared to 0.31 ha for sexually immature males but this was not statistically significant ( $p=0.5$ ). Median MCP for male bats was 0.63 ha and larger than that of female bats (0.1 ha;  $p=0.1$ ). The distance between roost trees used by males was significantly longer (median= 163 m) compared to the distance between roost trees used by female bats (median=78.2 m;  $p=0.02$ ; Table 6.3).

#### 6.4.2 Roost characteristics

A total of 1,177 trees of 85 species belonging to over 25 plant families were identified and assessed within the 82.6 ha study area. *E. gambianus* roosted in a total of 177 trees of 30 species belonging to a minimum of 12 plant families. Characteristics of roost trees differed significantly from non-roost (comparison) trees (Table 6.4). Roost trees were significantly taller ( $p<0.0001$ ), had significantly larger DBH ( $p<0.0001$ ) and had larger crown diameters ( $p<0.0001$ ) compared to non-roost trees. Roost plots had lower tree density per ha ( $p<0.0001$ ) and lower total basal area ( $p=0.009$ ) compared to non-roost plots. Trees utilised by bats were also closer to buildings than non-roost trees ( $p<0.001$ ).

Of the roosts trees that were identified, 43.8% were used by maternal females. Maternal females used roost trees that had higher number of bats per tree ( $p<0.0001$ ; Table 6.5) compared to roosts that were not used by maternal bats and this was still significantly different after excluding six of the maternal trees with the highest number of bats per tree. Maternal roosts were frequently occupied by bats when compared to non maternal roosts ( $p=0.0001$ ). Roost tree characteristics were not significantly different between maternal roosts and non maternal roosts. At the plot scale, maternal roost plots had fewer trees per ha ( $p=0.02$ ). Plot basal area and building density did not differ between the two. Maternal roosts were closer to each other compared to non maternal roosts ( $p<0.0001$ ).

**Table 6.4 Comparisons of *E. gambianus* roost and non-roost tree characteristics.**

Data are presented as medians and inter quartile ranges. Comparisons were made using Mann-Whitney U tests. Significant tests are shown in bold.

| Variable                         | Roost characteristics |        |           | Non-roost characteristics |        |           | P value           |
|----------------------------------|-----------------------|--------|-----------|---------------------------|--------|-----------|-------------------|
|                                  | N                     | Median | IQ range  | N                         | Median | IQR       |                   |
| Tree height (m)                  | 146                   | 10.4   | 8.8-12.4  | 992                       | 7.8    | 6-9.8     | <b>&lt;0.0001</b> |
| Tree DBH (m)                     | 148                   | 0.5    | 0.4-0.7   | 1000                      | 0.3    | 0.2-0.5   | <b>&lt;0.0001</b> |
| Tree crown diameter (m)          | 146                   | 10.2   | 7.5-13.0  | 998                       | 7.5    | 5.26-9.74 | <b>&lt;0.0001</b> |
| Tree density (trees/ha)          | 174                   | 30.6   | 20.4-50.9 | 1000                      | 45.8   | 25.5-71.3 | <b>&lt;0.0001</b> |
| Basal area (m <sup>2</sup> /ha)  | 166                   | 5.4    | 3.0-8.5   | 1000                      | 6.1    | 3.0-10.4  | <b>0.009</b>      |
| Building density (buildings/ha)  | 175                   | 10.2   | 5.1-20.4  | 1000                      | 5.1    | 0.0-15.3  | <b>0.001</b>      |
| Distance to nearest building (m) | 174                   | 13.5   | 7.2-22.8  | 1000                      | 17.0   | 10.3-26.9 | <b>&lt;0.0001</b> |



**Table 6.5 Differences in characteristics of maternal and non-maternal roosts.**

*Data are presented as medians and inter quartile ranges. Comparisons were made using Mann-Whitney U tests. Significant tests are shown in bold.*

| Variable                              | Maternal roosts |        |              | Non-maternal Roosts |        |              | P value           |
|---------------------------------------|-----------------|--------|--------------|---------------------|--------|--------------|-------------------|
|                                       | N               | Median | IQR          | N                   | median | IQR          |                   |
| Number bats per tree                  | 73              | 42     | 150-170.5    | 91                  | 13     | 4.0-30.0     | <b>&lt;0.0001</b> |
| Frequency of occupancy (%)            | 73              | 50     | 27.9-86.6    | 51                  | 25     | 12.5-50.0    | <b>0.001</b>      |
| Tree height (m)                       | 71              | 10.6   | 9-12.6       | 76                  | 10.3   | 8.5-12.4     | 0.37              |
| Tree DBH (m)                          | 71              | 0.53   | 0.4-0.8      | 78                  | 0.46   | 0.3-0.7      | 0.079             |
| Tree crown diameter (m)               | 71              | 11     | 8-13.2       | 76                  | 9.8    | 7-12.8       | 0.13              |
| Distance to nearest roost (m)         | 78              | 20.2   | 11.9-38.3    | 97                  | 18.93  | 11.6-41.3    | 0.61              |
| Tree density (trees/ha)               | 78              | 30.6   | 15.3-45.8    | 98                  | 40.73  | 20.4-56      | <b>0.02</b>       |
| Total basal area (m <sup>2</sup> /ha) | 76              | 4.9    | 3.2-7.8      | 91                  | 6.46   | 3.11-9.4     | 0.19              |
| Plot building density (buildings/ha)  | 78              | 10.2   | 5.1-20.4     | 98                  | 10.18  | 5.1-20.4     | 0.42              |
| Distance to building (m)              | 78              | 13.7   | 7.5-21.4     | 98                  | 12.93  | 6.0-23.3     | 0.80              |
| Distance between roosts (m)           | 3003            | 350.0  | 213.9 -507.0 | 4851                | 388.01 | 240.1 -572.5 | <b>&lt;0.0001</b> |

Roost selection with respect to tree species was not at random. Bats showed preference for some tree species and avoided others. Bats selected Neem (*Azadirachta indica*), Mango (*Mangifera indica*), Fig trees (*Ficus sp.*), Indian mast tree (*Polyalthia longifolia*) and African tulip tree (*Spathodea campanulata*). These selected species made up only 31% of trees assessed in the study area but constituted 57% of all roost trees (Table 6.6). Bats avoided Oil palm trees (*Elaeis guineensis*) and did not use 57 other tree species that occurred in the study area. Twenty-four species of trees were used but their use appeared to be random rather than preferred (Table 6.6). Species that were present in the study area but were not used as roosts by bats are shown in Appendix 5.

#### **6.4.3 Modelling Roost selection**

Eight variables were entered into a logistic regression model to determine the characteristics that best differentiated between roosts and non-roost (comparison) sites. The final model selected (best fit model) had six variables that best explained most of the variation between roost sites from non-roost (comparison) sites (Table 6.7). The Hosmer and Lemeshow goodness of fit test showed that the best model selected fitted the data well ( $\chi^2=5.1$ ,  $df = 8$ ,  $p\text{-value} = 0.74$ ).

*E. gambianus* was more likely to use trees that belonged to particular species, had larger DBH and were taller (Table 6.8). Roost trees were also more likely to be within plots with lower tree densities and closer to buildings. Unit increments in height and DBH of a tree increased the odds of being utilised as a roost by 1.42 and 24.75 respectively. Unit decrements in the tree density of a plot and distance of a tree to buildings increased the odds of being utilised by 0.99 and 0.94 respectively. Likelihood ratio tests showed that all these variables contributed significantly to the final model (Table 6.8).

**Table 6.6 *E. gambianus* roost tree selection showing selected and avoided species.**

*Based on the use of a tree species as a roost compared to abundance of the tree species within the study area. Tests are based on binomial exact tests.*

| Tree species                 | Plant family     | Prop. of all trees | Prop. of roost trees | p-value           | Preference |
|------------------------------|------------------|--------------------|----------------------|-------------------|------------|
| <i>Anogeissus leiocarpus</i> | Combretaceae     | 0.001              | 0.006                | 0.2               | Random     |
| <i>Antiaris toxicaria</i>    | Moraceae         | 0.003              | 0.006                | 0.5               | Random     |
| <i>Azadirachta indica</i>    | Meliaceae        | 0.065              | 0.136                | <b>0.008</b>      | Selected   |
| <i>Blighia sapida</i>        | Sapindaceae      | 0.003              | 0.006                | 0.5               | Random     |
| <i>Ceiba pentandra</i>       | Malvaceae        | 0.003              | 0.006                | 0.5               | Random     |
| <i>Delonix regia</i>         | Caesalpinioideae | 0.038              | 0.023                | 0.4               | Random     |
| <i>Elaeis guineensis</i>     | Arecaceae        | 0.102              | 0.006                | <b>&lt;0.0001</b> | Avoided    |
| <i>Ficus</i> sp.             | Moraceae         | 0.024              | 0.073                | <b>0.01</b>       | Selected   |
| <i>Gliricidia sepium</i>     | Fabaceae         | 0.037              | 0.017                | 0.3               | Random     |
| <i>Gmelina arborea</i>       | Lamiaceae        | 0.042              | 0.062                | 0.3               | Random     |
| <i>Mangifera indica</i>      | Anacardiaceae    | 0.202              | 0.282                | <b>0.03</b>       | Selected   |
| <i>Milicia</i> sp            | Moraceae         | 0.006              | 0.011                | 0.3               | Random     |
| <i>Millettia thonningii</i>  | Fabaceae         | 0.005              | 0.017                | 0.1               | Random     |
| <i>Morinda lucida</i>        | Rubiaceae        | 0.004              | 0.006                | 0.6               | Random     |
| <i>Newbouldia laevis</i>     | Bignoniaceae     | 0.037              | 0.045                | 0.6               | Random     |
| <i>Polyalthia longifolia</i> | Annonaceae       | 0.016              | 0.051                | <b>0.04</b>       | Selected   |
| <i>Senna siamea</i>          | Caesalpinioideae | 0.076              | 0.085                | 0.7               | Random     |
| <i>Spathodea campanulata</i> | Bignoniaceae     | 0.006              | 0.023                | <b>0.04</b>       | Selected   |
| <i>Spondias mombin</i>       | Anacardiaceae    | 0.035              | 0.028                | 0.8               | Random     |
| <i>Sterculia rhinopetala</i> | Malvaceae        | 0.003              | 0.006                | 0.4               | Random     |
| <i>Syzygium</i> sp.          | Myrtaceae        | 0.002              | 0.006                | 0.3               | Random     |
| <i>Tamarindus indica</i>     | Fabaceae         | 0.001              | 0.006                | 0.2               | Random     |
| <i>Tectona grandis</i>       | Lamiaceae        | 0.042              | 0.04                 | 0.9               | Random     |
| Unknown a                    |                  | 0.001              | 0.006                | 0.2               | Random     |
| Unknown b                    |                  | 0.001              | 0.006                | 0.2               | Random     |
| Unknown c                    |                  | 0.001              | 0.006                | 0.2               | Random     |
| Unknown d                    |                  | 0.001              | 0.006                | 0.2               | Random     |
| Unknown e                    |                  | 0.001              | 0.006                | 0.2               | Random     |
| Unknown f                    |                  | 0.007              | 0.017                | 0.2               | Random     |
| <i>Vitex doniana</i>         | Verbenaceae      | 0.007              | 0.011                | 0.6               | Random     |

**Table 6.7 AIC values, Aikaike weights and likelihood for candidate models that explained differences between roost sites of *E. gambianus* and non-roost sites.**

| Model                                                                                                                 | AIC    | $\Delta$ AIC | Aikaike weight | Model likelihood |
|-----------------------------------------------------------------------------------------------------------------------|--------|--------------|----------------|------------------|
| Tree species + Height+ DBH+ Plot tree Density+ Distance to Building                                                   | 577.85 | 0.00         | 0.62           | 1.00             |
| Tree species+ Height+ DBH+ Tree Density+ Building Density+ Distance to building                                       | 579.65 | 1.80         | 0.25           | 0.41             |
| Tree species+ Height + DBH+ Plot basal area+ Plot tree density+ Building density+ Distance to Building                | 581.64 | 3.80         | 0.09           | 0.15             |
| Tree species+ Height+ DBH+ Crown Diameter +Plot Basal area+ Plot Tree density+ Building density+ Distance to building | 583.30 | 5.45         | 0.04           | 0.07             |

**Table 6.8 Coefficient estimates, odds ratios and Likelihood ratio statistic for parameters in the best fit model for roost selection in *E. gambianus*.**

| Variable             | Estimate | Odds ratio | df | Pr > $\chi^2$ |
|----------------------|----------|------------|----|---------------|
| Tree Species         |          |            | 22 | <0.0001       |
| Height               | 0.350    | 1.419      | 1  | <0.0001       |
| DBH                  | 3.209    | 24.754     | 1  | <0.0001       |
| Tree density         | -0.015   | 0.985      | 1  | <0.0001       |
| Distance to Building | -0.067   | 0.935      | 1  | <0.0001       |

## 6.5 Discussion

### 6.5.1 *E. gambianus* roosting behaviour and roost selection at different spatial scales.

This study is the first to describe roost selection in *E. gambianus*. This bat species preferred to roost in bigger and taller trees of the species of *A. indica*, *M. indica*, *P. longifolia*, *Ficus* sp. and *S. campanulata* that were closer to buildings in areas with fewer tree densities. Univariate analysis of variables measured showed significant differences between roost and non-roost trees/plots for all these variables. Logistic regression however, indicated that only five of these variables (Tree species, DBH, Tree height, plot tree density and Distance to nearest building) were the most important factors that explained most of the variation between roost and non-roost trees and determined roost selection in *E. gambianus*.

Although the logistic regression showed that variables at the tree scale explained most of the variation, variables from other spatial scales were also important and represented in the final model. This suggests that *E. gambianus* selects roosts by considering factors from different spatial scales. The study thus provides support to the view that resource selection occurs in hierarchical manner and is best studied at multi-scale approach (Manley *et al.*, 1993; Limpert *et al.*, 2007; Lucas, 2009; Lucas *et al.*, 2015). The study area was small, hence the landscape was comparatively homogenous and not many variables could be measured at this scale. At a much larger scale, effects of some other landscape variables (e.g. distance to water bodies, distance to varying habitat patches) could be assessed for their effects on the roosting ecology of this species. Extrapolating these results to the entire range of this widely distributed species should be done with caution, especially where the landscape differs from that of this study.

*E. gambianus* is often described to form loose colonies of a few individuals, with large colonies containing up to a few hundred individuals (Rosevear, 1965; Thomas & Fenton, 1978; Marshall & McWilliam, 1982; Boulay & Robbins, 1989). For this study, roost sizes varied from single individuals to over a thousand individuals (average of 80 bats per roost) and the total numbers in the study area was estimated to be over 5,000 individuals. This suggests that *E. gambianus* can form larger colonies than previously assumed. *E. gambianus* was also observed to share roosts with *M. pusillus*. There is a record of *E. gambianus* roosting in a tree with *M. pusillus* (Boulay & Robbins, 1989). In another site, *E. gambianus* was also observed sharing roosts with *Eidolon helvum*. In both cases however, *E. gambianus* was always spatially separated from the other species within the same tree and never mixed.

Roosts trees differed significantly from non-roost trees by having larger DBH, and greater heights. The selection of trees with larger DBH and greater height is very common in tree roosting bats; e.g. *Pteropus giganteus* (Hahn *et al.*, 2014), *Pteropus vampyrus natunae* (Gumal, 2004), *Corynorhinus rafinesquii* (Lucas *et al.*, 2015) and in several *Myotis* species (Kalcounis-Rüppell *et al.*, 2005). In tree cavity roosting bats, trees with larger DBH and greater heights are selected because they are usually old enough to develop numerous suitable cavities for roosting (Sedgeley & O'Donnell, 1999; Sedgeley & O'Donnell, 2004), and also provide better insulation (Sedgeley, 2001). In large, foliage roosting bats such as *E. gambianus*, it has been suggested that larger trees provide enough room to accommodate more bats in a single tree, especially in colonial and social bats (Gumal, 2004). Others have suggested that such larger and taller trees provide enough room for easier free fall to take-off during flight (Pierson & Rainey, 1992). Roosting in taller trees also offer high roosting positions that minimize their vulnerability to disturbance and to predation, especially by ground-dwelling predators



(Kunz, 1982; Lumsden & Bennett, 2006). Presumably, these characteristics (larger size, greater height) imply that these are older trees which have stronger branches that are less likely to break under the bats' weight compared to younger trees. Alternatively, the preference of older trees as roosts could be as a result of consistent usage in the past, thus known to be reliable and offer better conditions for roosting. Such roosts therefore could be selected because of historical philopatry.

Roost trees occurred in plots that had fewer tree density but higher building density and were closer to buildings than plots that had no roost trees. The advantage of roosting in plots with lower tree density is that it allows bats to scan for predators which enhances the chances of detecting an approaching predator from far off (Limpert *et al.*, 2007).

Several pteropodid species form roosts that are in close proximity to humans. *Eidolon helvum* and several *Pteropus* species form very large colonies in rural and urban centres (Rosevear, 1965; Pierson & Rainey, 1992; Hahn *et al.*, 2014). According to Hahn *et al.* (2014), fruit bats may also roost closer to human settlements because household backyard gardens offer an oasis of fruit diversity, especially as rapid habitat loss and agricultural intensification has led to the loss of foraging sites for fruit bats across their range of occurrence. *E. gambianus* may be roosting very close to buildings because most of these tree species that were preferred for roosting are usually planted near buildings. These tree species are commonly planted as ornamental trees and to provide shade within compounds of houses of several households.

The general utilisation of roosts closer to humans could be as a result of loss of suitable bat roosting and feeding habitat or the encroachment of humans into suitable bat habitat. The loss of suitable habitat has been identified as one of the leading problems bats face globally (Mickleburgh *et al.*, 1992;2002; Kunz *et al.*, 2011). This has driven several

species into rapid population declines and may be causing them to utilise areas that are closer to humans. Diminishing food resources in natural habitats may cause increased formation of roosts of bats within urban and peri-urban centres where they may obtain alternate food sources (Plowright *et al.*, 2015). In the event of loss of roosting and feeding sites in the natural habitat, backyard trees, gardens or ornamental trees may be providing the only alternate sources of both feeding and roosting options for bats. In accordance with Kunz (1982)'s assertion that bats use spatial familiarity and environmental cues to locate roosts, these bats may be roosting close to human habitations because several artificial cues (e.g. roads, electric pylons, street lights, buildings) make it easier for bats to return to roosts after foraging and migratory movements.

Roost tree species selection by *E. gambianus* was non random; the species selected Neem, Mango, African tulip tree, Indian mast tree, and Fig trees over other tree species within the area even though these selected species made up less than 32% of all trees within the area. The Oil palm tree was avoided and several other species were never used during the study. While a few studies have made observations of tree species that *E. gambianus* utilizes as roosts, there is very little documentation on details about selection of tree species for roosting by this species. In other parts of Ghana, *E. gambianus* has been reported to roost in Neem, Fig trees and Mahogany (*Khaya senegalensis*), (Baker & Harris, 1957; Ayensu, 1974; Marshall & McWilliam, 1982) and elsewhere, in *Kigelia Africana* and *Cola* sp. (Rosevear, 1965; Thomas & Fenton, 1978). This suggests that in different ecological zones, different tree species may be selected and roost selection may vary.

Marshall and McWilliam (1982) described *E. gambianus* roosting high up in "umbrella shaped trees" and Boulay and Robbins (1989) also described the species hanging from branches in trees well shaded by foliage. Specific species of trees may be preferred because of their morphology and characteristics that offer suitable protection, roosting space and suitable concealment. Other morphological features of these trees, in addition to those measured in this study, may influence their selection. For instance, parameters like leaf density and canopy cover, even though they were not measured, may be important selection criteria for this species to provide shade for protection against sunlight and for concealment. Foliage roosting species are known to abandon roosts when leaf cover is lost, hence tree species that lose their leaves often/seasonally may be avoided or less preferred (Kunz, 1982). The tree species that were identified to be preferred and selected by *E. gambianus* in this study are evergreen /semi evergreen species that can provide enough cover and concealment for bats over different seasons. This may further explain their preference over deciduous species.

#### **6.5.2 Sex, and reproduction related differences in roosting behaviour, and roost selection in *E. gambianus***

Sexual segregation was not evident from this study. There was no sexual segregation in roosting, and aggregation of females was not evident, but two females used completely overlapping roosting areas. The results from this study however suggest sex differences in roosting area in *E. gambianus*. Females used a relatively smaller roosting area with significantly shorter distances between roosts compared to males. A possible reason is that these areas offer the best conditions for the survival of their young, thus female bats may be restricting their roosting to limited suitable areas.

Males on the other hand can use other roosts which may be less suitable for females. The need to search for suitable mates and/ or the need to enhance the chances of procreating may also cause males to utilise larger roosting areas. Although the reproductive behaviour of *E. gambianus* is unknown, males of this species are known to perform piping calls with epaulet displays away from roosts (proposed to be a courtship display to attract females during mating periods) (Happold & Happold, 2013). This behaviour also occurs in other similar species (*Epomophorus wahlbergi*, *Epomophorus scriptus* and *Epomops franqueti*) which are known to be polygamous and exhibit multi male/multi female mating systems with mating that occur away from roosts; *E. gambianus* may exhibit a similar mating system. For such a mating system, males usually use calling roosts that are dispersed and may be competed for. Hence, *E. gambianus* males may be using larger roosting areas so as to enhance their overall chances of reaching these calling roosts and their chances of finding mates.

The use of a smaller roosting area by females is a strategy that can reduce the energetic constraints in carrying young ones across roost trees during roost switching (Henry & Kalko, 2007). This observation is further supported by the finding that maternal roosts had significantly shorter distances between them compared to non maternal roosts. Utilizing a smaller roosting area and travelling shorter distances between roosts may also reduce the risk of detection from predators, especially during roost switching in the event of disturbance at one roost. Although the extent of predation was not assessed during this study, some observations were made of Pied crow (*Corvus albus*) attacking juvenile bats at roosts. Also the Yellow-billed kite (*Milvus migrans*) and Shikra (*Accipiter badius*) attacked some bats in flight when roosts were disturbed. The extra weight of carrying a young one can reduce the agility and manoeuvrability needed to evade an aerial attack from predators and can make females more vulnerable to predation. Lucas (2009) noted

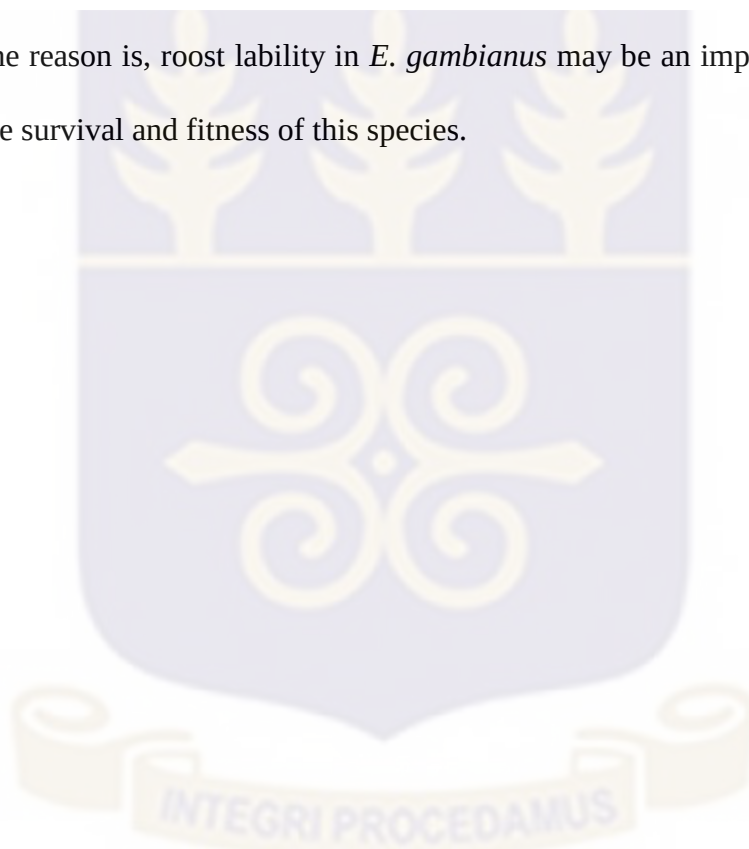
that the use of roosts that are closer to each other (clustered) in maternal females enables females to expose their young ones to several roosts in case maternal roosts are dissolved or the young ones become independent. Studies exploring the possibility of such sex differences in roosting behaviour in this species are lacking and future studies are needed to explore this possibility.

Maternal roosts differed from non-maternal roosts by having a higher number of bats per tree, were more frequently occupied and were closer to other maternal roosts. The selection of roosts that have more individuals and are frequently occupied by maternal bats may lead to better protection from predation. The chances or risk of predation on a single individual is reduced when individuals are in a larger group according to the predation dilution effect (Wilkinson & South, 2002) or the selfish herd theory (Hamilton, 1971). Selection of such roosts also may be advantageous as they offer the opportunity for young bats to learn and socialize with other bats.

### **6.5.3 Roost lability in *E. gambianus***

*E. gambianus* is a very labile species, and switches roosts very often. In a review of site fidelity in bats by Lewis (1995), *E. gambianus* was listed as one of the species that changed roosts frequently. In this study, radio-tagged bats used averagely three roosts and switched frequently between these roosts, at least 2.68 times over the observation period. Thomas and Fenton (1978) also reported two *E. gambianus* utilizing five different roosts and switching roosts almost each day. Generally, roost lability is known to be high among tree roosting bats (Kunz, 1982; Menzel *et al.*, 1998), and has been documented for several species, including, *Epomophorus wahlbergi* (Fenton *et al.*, 1985), *Hypsignathus monstrosus* (Bradbury, 1977), *Myotis thysanodes* (Lacki & Baker,

2007), *Nyctophilus geoffroyi* (Lumsden & Bennett, 2006), *Eptesicus fucus* (Vonhof & Barclay, 1996), *Pteropus vampyrus natunae* (Gumal, 2004), *Cynopterus sphinx* (Storz *et al.*, 2000). Fidelity to a diurnal home area, rather than single roost trees, is common among foliage roosting species (Kunz, 1982; Vonhof & Barclay, 1996; Gumal, 2004; Hein *et al.*, 2008). Reasons proposed to explain roost lability in bats include; to minimize commuting distances to foraging sites (Kunz, 1982), predator avoidance and to avoid large ectoparasite loads (Kunz, 1982; Lewis, 1996). This study does not provide evidence that supports any of the above reasons for roost lability in *E. gambianus*. Whatever the reason is, roost lability in *E. gambianus* may be an important strategy that is vital to the survival and fitness of this species.





## CHAPTER SEVEN

### 7.0 DEMOGRAPHY OF FRUIT BATS IN GHANA

#### 7.1 Introduction

Demographic parameters are important to the understanding of the dynamics of populations and for addressing a variety of ecological questions (Pryde *et al.*, 2005; Skalski *et al.*, 2005; O'Shea *et al.*, 2011). Parameters such as survival, population sizes and birth rates are major determinants of the growth or decline and the overall viability of populations (Schorcht *et al.*, 2009). For demographic research to be successful, the population under study should be easily observable and monitored over time (Humphrey & Oli, 2015). However, in wild animals this is often very challenging and makes demographic studies very difficult (Manning & Goldberg, 2010).

Among mammals, bats in particular are very difficult to monitor and observe because of their cryptic nature, difficulty in capturing and counting them, as well as their nocturnal behaviour (O'Shea *et al.*, 2003; O'Shea *et al.*, 2004). Recent advancements in technology such as (e.g. radiotelemetry) and development of sophisticated models and flexible software (Lebreton *et al.*, 1992; Cooch & White, 2006) have facilitated the study of complex dynamics in wildlife populations. Particularly, capture–mark–recapture (CMR) models have been very instrumental in the study of population dynamics, especially of cryptic animals such as bats (Burnham, 1987; Pollock *et al.*, 1990; Lebreton *et al.*, 1992). Despite the availability of such methods and the long history of bat research, very few studies have provided robust demographic estimates for bats (Sendor & Simon, 2003; Papadatou *et al.*, 2009; Schorcht *et al.*, 2009; O'Shea *et al.*, 2010; O'Shea *et al.*, 2011; Humphrey & Oli, 2015). Although some notable efforts have been made to improve this knowledge gap, most of these studies focused on insectivorous bat species that have life

history traits such as high roost fidelity and formation of small stable populations that enable high recapture rates. Such studies and estimates are largely lacking for fruit bats. For instance, the first robust estimates of demographic parameters such as survival for any pteropodidae was provided only recently by Hayman *et al.* (2012a).

Substantial evidence shows rapid population declines for several fruit bat species across their range of occurrence (Mickleburgh *et al.*, 2002). The need for studies that provide demographic information is increasing as several pteropodidae are threatened, critically endangered, endangered, vulnerable or data deficient (Mickleburgh *et al.*, 1992) and the ultimate success of conservation measures will depend on an understanding of their population dynamics (Beissinger & Westphal, 1998). Fruit bat species are also of interest to zoonotic disease and public health scientists because of their links to emerging zoonotic diseases (Calisher *et al.*, 2006; Drexler *et al.*, 2012) hence, demographic information will be vital to the understanding of aspects of management and disease dynamics (O'Shea *et al.*, 2011).

The aim of this component of the study was to estimate demographic parameters, particularly population size, survival, sex ratios and birth rates in fruit bats that occur in Ghana.

## 7.2 Methodology

Data for this study were collected from October 2012 to October 2015, and from a total of six sites, these were: Ve-Golokuati, Accra, Tanoboase, Buoyem, Kpong and University of Energy and Natural Resources campus (UENR), Sunyani. Site descriptions, bat trapping and processing procedures are described in Chapter three. Bat trapping was carried out at four sites (Ve-Golokuati, Accra, Tanoboase and Buoyem);

trapping sessions at each site typically lasted three nights each month resulting in a total of 13,593 net hours across all sites. All data presented for *E. gambianus* and *M. pusillus* were based on the single colony at Ve-Golokuati where both species were sympatric at roosting sites. Trapping of *E. helvum* was carried out at two sites (Accra and Tanoboase) and data for other species were based bat trapping at Ve-Golokuati, Tanoboase and Buoyem..

### **7.2.1 Colony size estimates.**

Monthly colony size estimates and population monitoring for the three focal species, *E. gambianus*, *M. pusillus*, and *E. helvum* was carried out over two years at five sites (Ve-Golokuati, Accra, Tanoboase, Kpong and UENR, Sunyani) depending on the species abundance at the various sites. *E. gambianus* and *M. pusillus* typically roosts in trees with individuals well spaced (except mothers and pups) so monthly estimates of population size were made by visually counting all bats at each identified day roost in the study area using a hand-held trip counter. *Eidolon helvum* roosted in large aggregations of individuals clustered together; the estimates were carried out as described in Chapter three (section 3.31). For the sites where the vegetation was impenetrable or the landscape prevented direct access to individual trees, roost counts were done along access paths or selected observation points within the roosting site. In such cases, the same observation points or access paths were used on successive occasions for uniformity.

### **7.2.2 Sex and age ratios.**

Following trapping, individuals were categorised into one of three age classes; adult, sexually immature adults and juveniles as described in Chapter three (Section 3.5). Age-

specific sex ratios were calculated for *E. gambianus* and *M. pusillus* only. These were the only species for which significant numbers of each age-class were obtained for the analysis. For *M. pusillus* however, due to difficulty in clearly distinguishing juvenile bats from sexually immature adult bats, these two groups were merged and termed "immature bats". Hence, individual *M. pusillus* were categorized into adult or immature groups.

Assuming an equal chance of catching individuals across all ages and sexes, sex ratios (with 95% confidence intervals) were calculated for each of the age classes. The sex ratio was expressed as a ratio of number of females to the number of males for multiple sampling with replacement following methodology by Skalski *et al.* (2005) using the equation:

$$\hat{R}_{F/M} = \frac{\sum_{i=1}^k f_i}{\sum_{i=1}^k m_i} = \frac{\bar{f}}{\bar{m}}.$$

With variance:

$$\widehat{\text{Var}}(\hat{R}_{F/M}) = \frac{\sum_{i=1}^k (f_i - \hat{R}_{F/M} m_i)^2}{k \bar{m}^2 (k-1)},$$

Where  $f_i$  = number of females observed in the  $i$ th survey ( $i = 1, \dots, k$ );

$m_i$  = number of males observed in the  $i$ th survey ( $i = 1, \dots, k$ );

$\bar{m}$  = average number of males observed across all samples.

$k$  = number of surveys (Skalski *et al.*, 2005).

Based on this approach, sex ratios  $<1$  were male biased, whereas a sex ratio  $>1$  was female biased and a sex ratio of 1 implied equality of both sexes. Sex ratios were assessed to determine if there was variation from a 1:1 ratio among the different age

classes and within the overall colony, using chi square goodness of fit tests. Equality test was also performed for the overall age ratios within the colony.

### **7.2.3 Birth, lactation periods and reproductive chronology**

All sexually matured adult females that were trapped were assessed for pregnancy and lactation. The proportions of adult females that were either lactating or pregnant together with evidence from female bats that were trapped with neonate bats clinging to them were used to determine the parturition periods for the different species.

For *E. gambianus*, suckling young could easily be seen attached to their mothers at day roosts during the lactation period. During monthly colony estimates for *E. gambianus*, counts of the number of females that were observed to be carrying young ones at day roosts were also made. This, together with monthly trends in the proportions of females that were detected to be lactating or pregnant, was used to assign birth periods, lactation periods and weaning periods for *E. gambianus* to specific months.

Birth periods were chosen as the months when the first observations of females carrying young ones at day roosts were made or the first time a lactating female was observed after the peak pregnancy periods. Weaning periods were also chosen as the months where lowest proportion of lactating adult females was recorded or when no females were seen carrying young ones at day roosts following the previous birth period.

### **7.2.4 Estimation of birth rates**

Monthly trapping of *E. gambianus* and *M. pusillus* at the Ve-Golokuati colony allowed the estimation of birth rates for these two species. For the other species of fruit bats that

were trapped, sample sizes were too low for the estimation of birth rates. Both *E. gambianus* and *M. pusillus* are reported to breed twice in a year with females normally giving birth to one young per reproductive season (Thomas & Marshall, 1984; Boulay & Robbins, 1989). To confirm this, females of both species that were caught during monthly trapping sessions were examined for pregnancy by abdominal palpation and lactation by expression of milk from the nipples. This allowed for both pregnancy and lactating rates for the same reproductive period to be estimated from the proportion of females that were detected as pregnant or lactating during peak pregnancy and lactation periods. Birth rates were estimated from pregnancy rates and lactation rates. Assumptions made were that, all pregnancies that were detected led to successful live births and all females that were detected to be lactating had successfully given birth following pregnancy. Chi-square tests and Fisher's exact test were used where appropriate, to test for differences in reproductive rates between seasons and years.

#### **7.2.5 Capture-Mark-Recapture analysis and estimation of survival rates**

CMR analysis was carried out for *E. gambianus* and *M. pusillus* only. Other species were either captured in very low numbers or recapture rates were too low for any analysis to be carried out. For both species, each individual trapped was tagged with a 1.25 mm radio frequency identification device (RFID) passive integrated transponder (PIT) (Trovan Ltd.), which was subcutaneously implanted in the dorsum. These RFID, PIT tags allowed each individual to be identified with a unique number, which could be detected electronically by scanning using a handheld transponder scanner on subsequent recapture encounters.



Data from a total of 287 individuals of *M. pusillus* that were trapped and marked over 29 months was used in the CMR analysis for this species. Initially, PIT tags that were used to mark *E. gambianus* bats resulted in very low recapture rates of less than 3% out of over 2,300 tagged bats. Hence radiotelemetry was used to mark and relocate bats. A total of 60 Adult and sexually immature adult bats were fitted with SOM 2190 HWSC radiotransmitters (Wildlife Materials International, Inc, Murphysboro, Illinois). Attempts were made to relocate tagged bats at least once a month over a period of 10 months. Tag fixing and relocation of tagged bats followed the same procedure as described in Chapter six. All tags were double tested; initially before fixing on the bats and after fixing on bats prior to release.

Recapture data were converted to encounter histories for estimation of apparent monthly survival and recapture probabilities for both species. For *E. gambianus*, only data for the first 8 months of radio-tracking were used because beyond this point, the battery life of the first group of tags were too low to distinguish between bats present and those absent from the study area.

Capture-mark-recapture (CMR) data were analysed using the programme Mark (White & Burnham, 1999) by fitting Cormack-Jolly-Seber (CJS) model to the data. The CJS model allows the estimation of apparent survival and recapture probabilities in open populations provided that the data meet specific assumptions which can be tested using a Goodness-of-fit (GOF) test (Lebreton *et al.*, 1992). Each individual bat was categorized under one of two sex classes (male and female) and into one of two age classes (adult and sexually immature adult for *E. gambianus*; adult and immature bats for *M. pusillus*). Hence four groups were obtained for each species; adult males, adult females, sexually immature adult males and sexually immature adult females for *E. gambianus*; adult

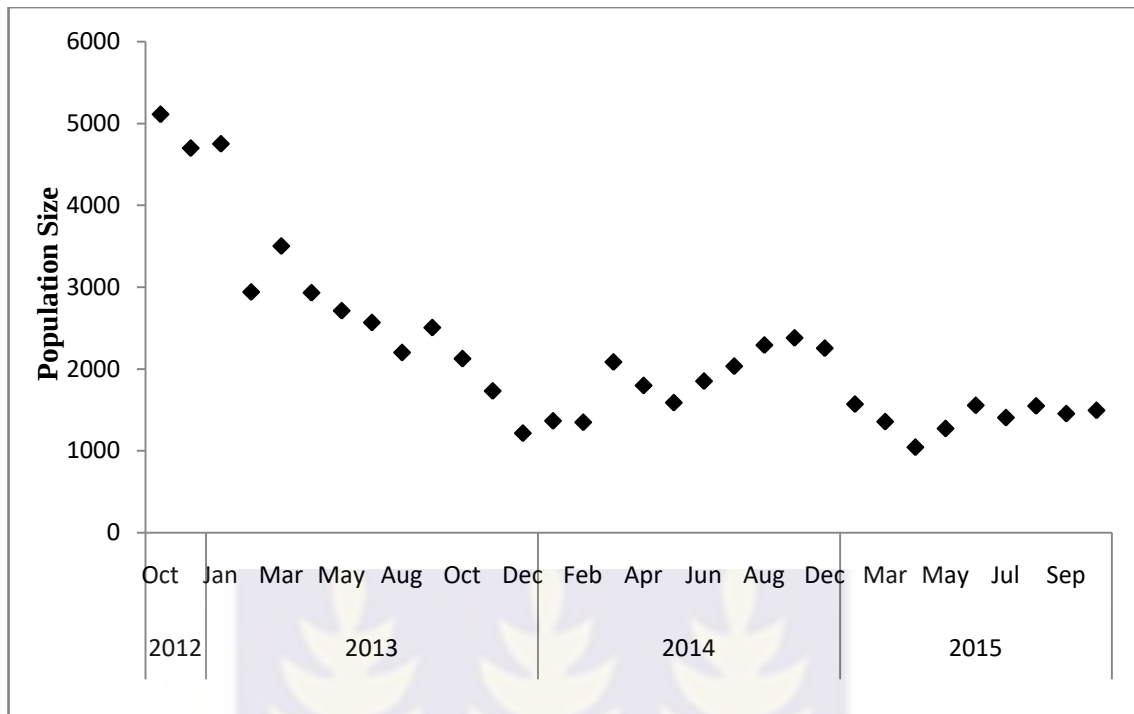
males, adult females, immature males and immature females for *M. pusillus*. Models were used to test for possible effect of age and sex groups on apparent survival probability assuming constant survival over time. Additionally, the effect of these groups and time on recapture probability of bats was tested. An initial GOF test was performed for the global model for each species using the programme RELEASE. The GOF test showed no indication of lack of fit of data for both species (*E. gambianus*:  $\chi^2=10.77$ , df=12 p=0.5; *M. pusillus*:  $\chi^2=6$ , df=26, p=1.00) but data for both species were under-dispersed (*E. gambianus*: TEST 1+TEST 2/df=0.89; *M. pusillus*: TEST 1+TEST 2/df=0.3). Hence, a variance inflation factor (C-hat) of 1 was maintained for the analysis (Cooch & White, 2006). Model selection was based on Akaike information criterion adjusted for small samples (AICc). To account for model uncertainty, weighted model averaging for candidate models was used to provide robust parameter estimates and their unconditional 95% confidence intervals (Burnham & Anderson, 2002) in the event where no particular model received significant Akaike weight.

### 7.3 Results

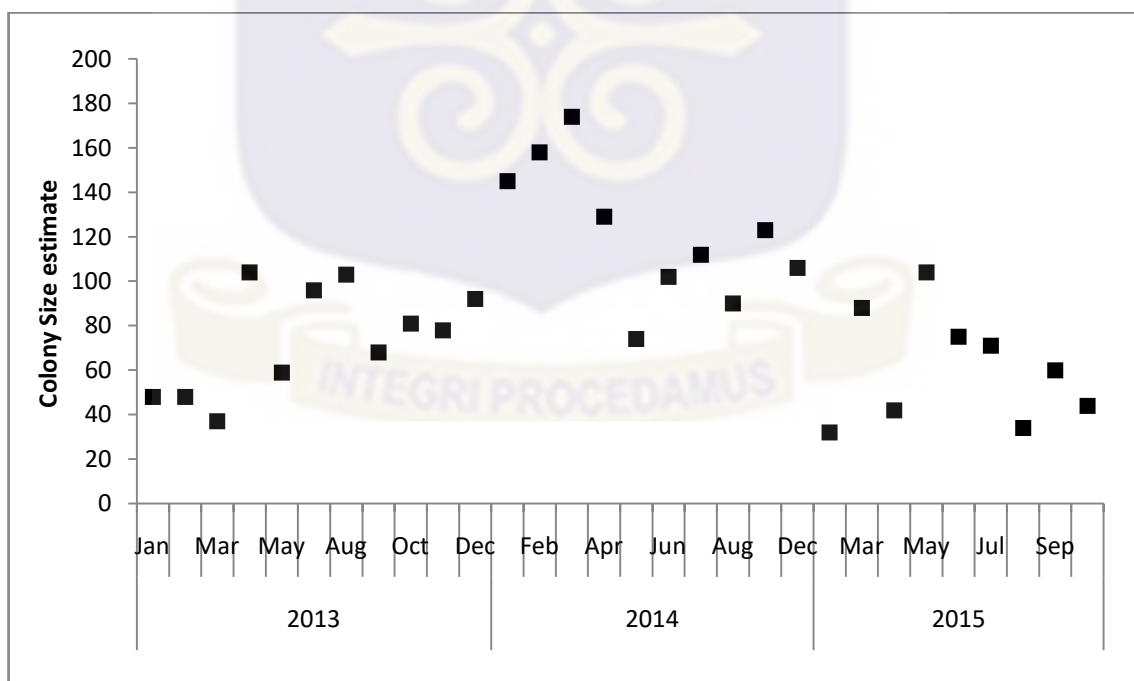
#### 7.3.1 Estimates of colony sizes

Estimates of the *E. gambianus* colony size varied between a maximum of around 5,000 to a minimum of about 1,000 bats. The initial population of this colony declined over the 32-month monitoring period to approximately 1,500 individuals, with peak numbers occurring in March and September (Figure 7.1).

*Micropteropus pusillus* population estimates varied between 174 and 32 individuals across the three year period. Two peaks in numbers were observed each year and appeared to occur around March/April and June/July (Figure 7.2).

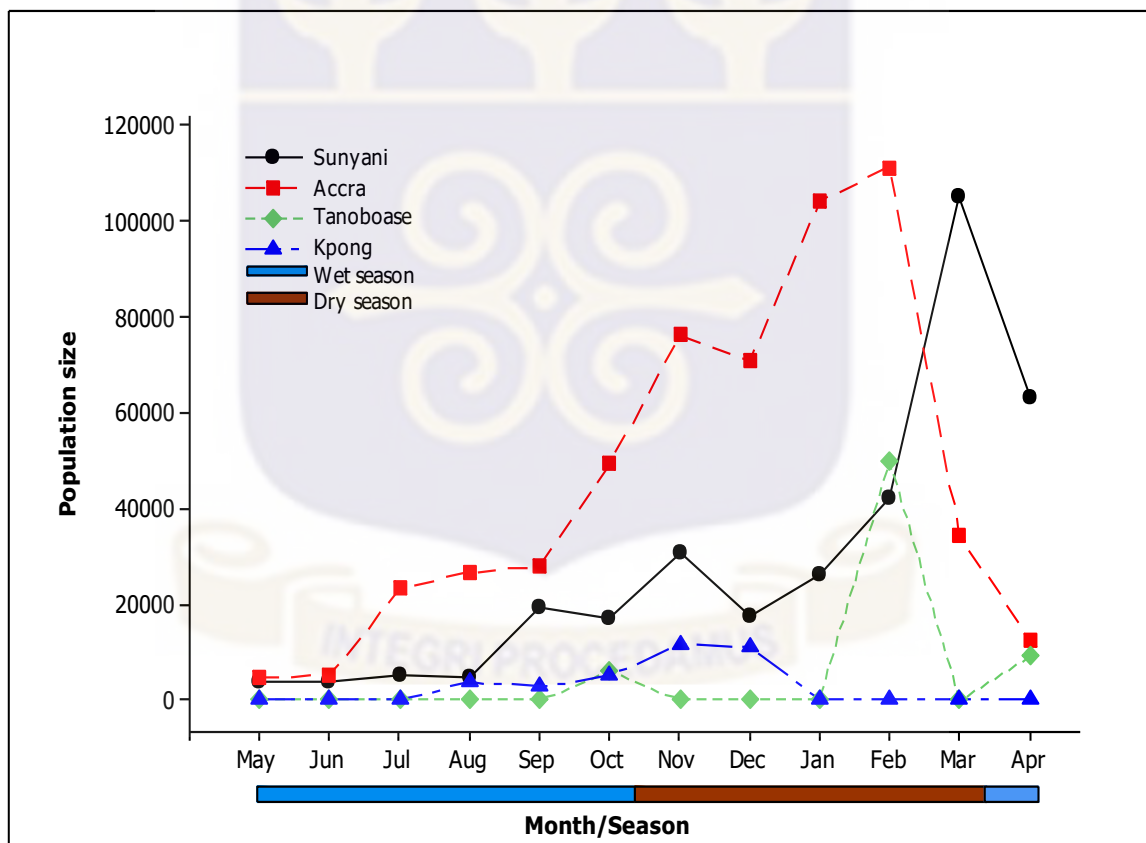


**Figure 7.1 *E. gambianus* population trends based on monthly manual counts.**



**Figure 7.2 *M. pusillus* population trend based on monthly manual counts.**

Generally across all monitored colonies, *E. helvum* numbers were from April to July with peaks in numbers around February/March each year. Colony sizes varied across the different sites with the Accra colony being the largest with an estimated 110,000 bats recorded at peak times (Figure 7.3). The smallest colony was the Kpong colony which contained up to a tenth of the Accra population at peak time. The Accra and Sunyani colonies were always occupied throughout the year while the Kpong colony was only occupied from August to December each year. The Tanoboase colony however appeared to be sporadic.



**Figure 7.3** *Eidolon helvum* population trend across selected colonies in Ghana.

### 7.3.2 Age-specific sex ratios and age structure of the *E. gambianus* colony

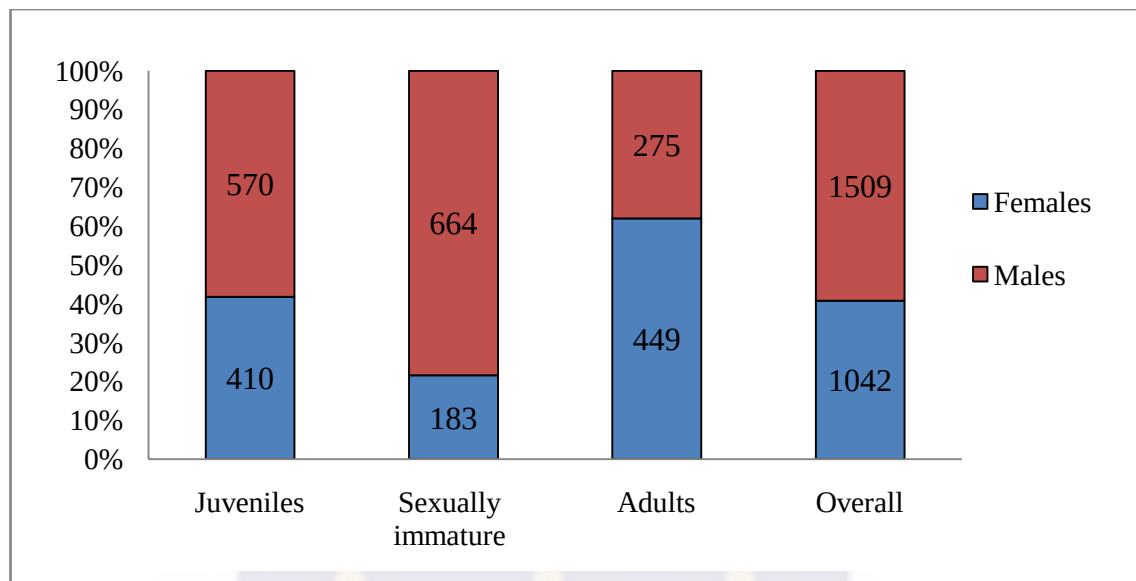
Assessments of sex and age ratios for the *E. gambianus* colony were based on a total of 2,551 individuals that were trapped. The overall sex ratio for the colony was significantly male biased ( $\chi^2 = 85$ ,  $df=1$   $p<0.0001$ ), with a sex ratio of 0.69 (95% CI:0.64-0.75: Table 7.1). There was no difference in proportions of males and females between years ( $\chi^2 = 2.4$ ,  $df = 2$ ,  $P = 0.3$ ). Proportions of males and females however differed significantly between the three age classes ( $\chi^2 = 264$ ,  $df = 2$ ,  $P<0.0001$ ) with sex ratios differing from a 1:1 ratio for each age class.

Over the study period, juvenile female : male sex ratio for *E. gambianus* was estimated at 0.72 (95% CI: 0.61-0.84) while the female: male sex ratio for sexually immature adults was estimated at 0.28 (95% CI: 0.21-0.36: Table 7.1); i.e., both with significantly male biased sex ratios. Fifty-eight percent of all juveniles of *E. gambianus* captured were males ( $\chi^2 = 26$ ,  $df=1$ ,  $p<0.0001$ ) while over 78% of 847 sexually immature adults were males (Figure 7.4).

**Table 7.1 Age specific sex ratios of *E. gambianus* colony at Ve-Golokuati.**

*Sex ratios expressed as proportion of females to males*

| Age Category            | Sex Ratio   | 95% LCL     | 95% UCL     |
|-------------------------|-------------|-------------|-------------|
| Juvenile                | 0.72        | 0.61        | 0.84        |
| Sexually immature adult | 0.28        | 0.21        | 0.36        |
| Adult                   | 1.63        | 1.22        | 2.18        |
| Overall                 | <b>0.69</b> | <b>0.64</b> | <b>0.75</b> |



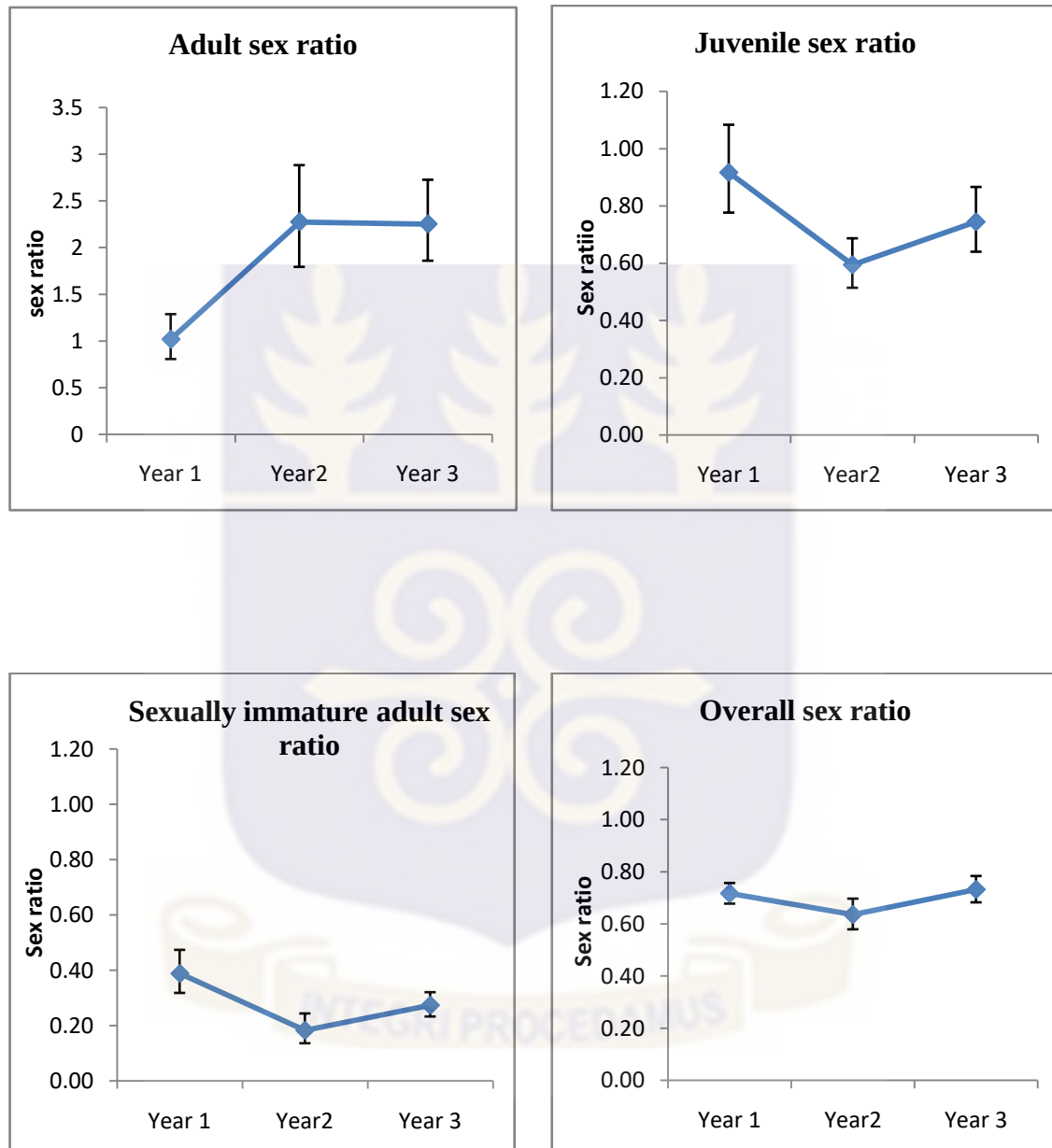
**Figure 7.4 Percentage of male and female *E. gambianus* within the different age-classes.**

*Numbers within bars indicate number of individuals of either sex.*

Adult sex ratio for *E. gambianus* was however significantly female dominated with a sex ratio of 1.63 (95% CI: 1.22-2.18), with 62% of all adults assessed being females ( $\chi^2 = 42$ ,  $df=1$   $p < 0.0001$ ). A significant variation in the sex ratios for *E. gambianus* was detected between years for each age-class (Juveniles-  $\chi^2 = 7.3$ ,  $df = 2$ ,  $p = 0.03$ ; Sexually immature adults  $\chi^2 = 13.7$ ,  $df = 2$ ,  $p = 0.001$ ; Adults-  $\chi^2 = 26$ ,  $df = 2$ ,  $p < 0.0001$ ). Juvenile sex ratio was male dominated throughout the three years but varied from 0.92 (95% CI: 0.78-1.08) in the first year to 0.59 (95% CI: 0.51-0.69) in the second year to 0.75 (95% CI: 0.64-0.87) in the third year (Figure 7.5). Similarly sex ratio for sexually immature adults was also male dominated throughout the study period but varied from 0.39 (95% CI: 0.26-0.59) in the first year to 0.18 (95% CI: 0.05-0.67) in the second year to 0.27 (95% CI: 0.13-0.58) in the third year. Adult sex ratio also varied from an approximately 1:1 ratio



in the first year (1.02, 95% CI: 0.81-1.29) to significantly female biased sex ratio of 2.28 (95% CI: 1.80-2.89) in the second year and 2.25 (95% CI: 1.86-2.73) in the third year.



**Figure 7.5 Annual variations in age-specific sex ratios for *E. gambianus*.**

Vertical lines are 95% confidence intervals.

Figure 7.6 shows the age structure of the *E. gambianus* population at the study site based on captured individuals. The proportions of individuals belonging to the three age classes differed significantly ( $\chi^2 = 37$ ,  $df=2$ ,  $p<0.0001$ ). The colony was made up of more juveniles (38.4%) than sexually immature adults (33.2%) and adults (28.4%).



**Figure 7.6** Age structure of the *E. gambianus* colony at Ve-Golokuati.

### 7.3.3 Sex ratios for *M. pusillus* and other fruit bat species encountered

Assessments of age-class specific sex ratios for *M. pusillus* were based on a total of 867 individuals that were trapped and assessed at Ve-Golokuati. The overall sex ratio for *M. pusillus* at this site was significantly female biased ( $\chi^2 = 12$ ,  $df=1$ ,  $P<0.001$ ) with a sex ratio of 1.3 (95% CI-1.1-1.5) (Table 7.2). Adult sex ratio also differed from a 1:1 ratio ( $\chi^2=16$ ,  $df=1$ ,  $p<0.001$ ) with a female biased sex ratio of 1.6 (95% CI-1.3-2.0). Sex ratio for sexually immature individuals appeared to be slightly female biased with a sex ratio

of 1.1 (95% CI-0.9-1.3) but this did not differ significantly from a 1:1 ratio ( $\chi^2=1.6$ ,  $df=1$ ,  $P=0.2$ ).

**Table 7.2 Age specific Sex ratios of *M. pusillus* colony at Ve-Golokuati.**

| Age Category      | Sex Ratio | 95% LCL | 95% UCL | Test statistic                   |
|-------------------|-----------|---------|---------|----------------------------------|
| Adult             | 1.6       | 1.3     | 2.0     | $\chi^2=16$ , $df=1$ , $p<0.001$ |
| Sexually Immature | 1.1       | 0.9     | 1.3     | $\chi^2=1.6$ , $df=1$ $P=0.2$    |
| Overall           | 1.3       | 1.1     | 1.5     | $\chi^2=12$ , $df=1$ $P<0.001$   |

For the other species, the numbers trapped at different sites were merged to increase sample sizes for sex ratio estimation. Initial tests showed that proportions of males and females did not differ between sites for each of these species. Sex ratios for *E. helvum* and *R. aegyptiacus* were both significantly male biased, while ratios for *E. buettikoferi* and *H. monstrosus* were highly female biased (Table 7.3). Sex ratio for *E. franqueti* was slightly skewed towards females but was not significant. Similarly, sex ratios for *N. veldkampii* and *L. angolensis* did not differ from 1:1 ratio although they appeared slightly male biased.

**Table 7.3 Estimated sex ratio for other fruit bat species in Ghana.**

Degrees of freedom for all tests =1, significant tests are shown in bold.

| Species                | Sex ratio | 95%<br>LCL | 95%<br>UCL | Test statistic ( $\chi^2$<br>value, p value) | Trapping<br>site |
|------------------------|-----------|------------|------------|----------------------------------------------|------------------|
| <i>E. helvum</i>       | 0.33      | 0.29       | 0.39       | <b>281, p&lt;0.001</b>                       | 2, 4             |
| <i>E. franqueti</i>    | 1.18      | 0.77       | 1.81       | 0.9, p=0.3                                   | 1, 2,3           |
| <i>E. buettikoferi</i> | 4.88      | 2.81       | 8.45       | <b>20.4, p&lt;0.001</b>                      | 1, 2             |
| <i>H. Monstrosus</i>   | 3.50      | 2.44       | 5.02       | <b>5.6, p=0.02</b>                           | 2                |
| <i>N. veldkampii</i>   | 0.67      | 0.38       | 1.18       | 1.8, p=0.2                                   | 1, 2             |
| <i>R aegyptiacus</i>   | 0.61      | 0.53       | 0.71       | <b>18.4, p&lt;0.001</b>                      | 3                |
| <i>L. angolensis</i>   | 0.59      | 0.25       | 1.37       | 1.8, p=0.2                                   | 1,3              |

1-Ve-golokuati, 2-Tanoboase, 3-Buoyem, 4-Accra

### 7.3.4 Birth rates and gestation in *E. gambianus*

A total of 371 *E. gambianus* adult females were assessed during peak pregnancy and lactation periods for signs of pregnancy or lactation. Pregnancy rates for *E. gambianus* were estimated for six reproductive seasons while lactation rates was estimated for five reproductive seasons, as no sampling was done during the peak lactation period for the second reproductive season of the second year.

Detection rates for pregnancy in *E. gambianus* did not vary between the six reproductive seasons (Fishers exact test  $p=0.2$ ) but detection rates for lactation varied across the five reproductive seasons for which lactation rate was assessed (Fishers exact test,  $p=0.003$ ). This difference in lactation rates was contributed largely by a low lactation rate recorded

in the second reproductive season of the first year of this study. Excluding the lactation rate for that season resulted in a non significant difference in the lactation rates (Fisher's exact test,  $p=0.9$ ). During the second reproductive season of the first year, the proportion of lactating females was significantly lower compared to the proportion of females that were detected to be pregnant in that same reproductive season (fisher's exact,  $p=0.001$ ). Pregnancy and lactation rates in *E. gambianus* for all the other reproductive seasons were not different.

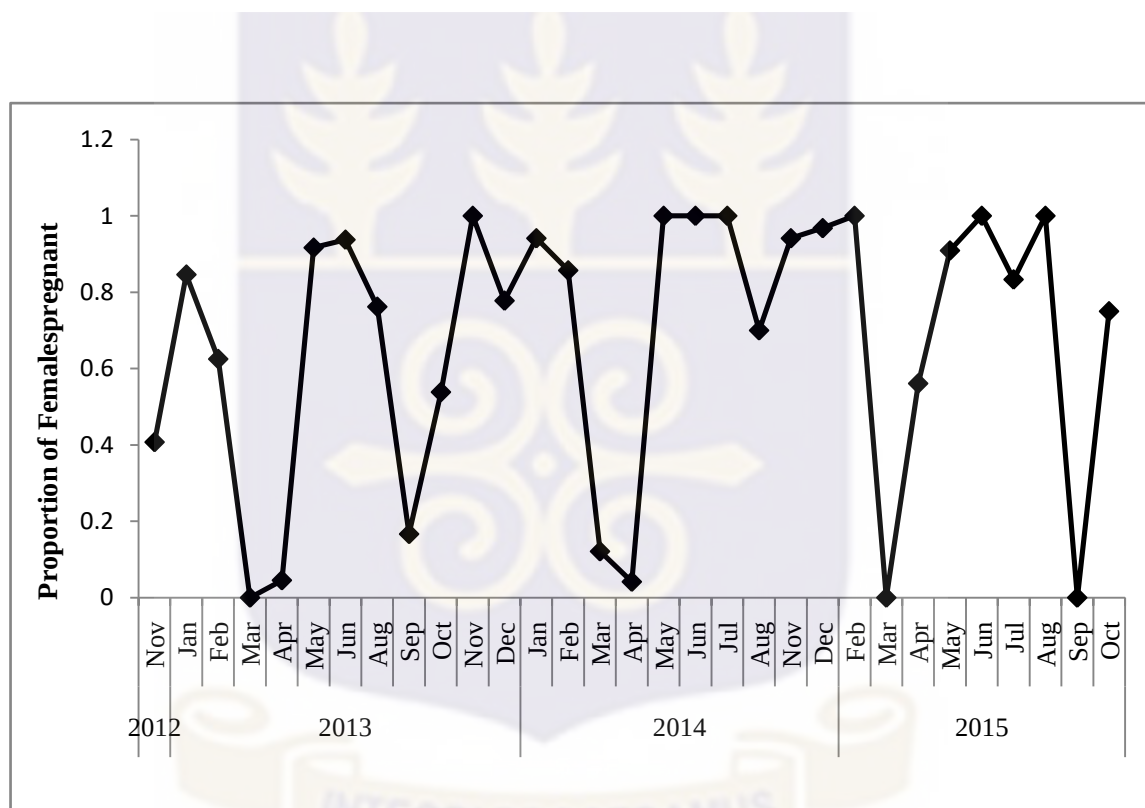
The estimates of birth rates for *E. gambianus* using pregnancy rates as a proxy ranged from 0.85 to 1.0 offspring per female per reproductive season, while the birth rates estimated from lactation rates varied from 0.56 to 0.92 offspring per female per reproductive season across the three years (Table 7.4).

**Table 7.4 Seasonal proportions of total *E. gambianus* adult females sampled that were observed to be pregnant and lactating.**

*Figures in parentheses indicate total number of females sampled during peak pregnancy /lactation period.*

| Reproductive Season | Proportion of Females | Year      |           |           |
|---------------------|-----------------------|-----------|-----------|-----------|
|                     |                       | Year 1    | Year 2    | Year 3    |
| 1                   | Pregnant              | 0.85 (13) | 0.90 (31) | 0.98 (44) |
|                     | Lactating             | 0.92 (25) | 0.91(57)  | 0.88 (50) |
| 2                   | Pregnant              | 0.93 (40) | 1.00 (27) | 0.96 (23) |
|                     | Lactating             | 0.56 (25) | -         | 0.86 (36) |

*E. gambianus* reproduced twice in each year, with births followed almost immediately by another embryonic development and pregnancy. For the first reproductive season in each year, pregnancy occurred around April and peaked in June with births occurring in August-September. Pregnancy for the second reproduction season occurred around October, peaked in January and births occurred around February-March (Figure 7.7). Newly formed foetus could be detected in *E. gambianus* females roughly a month after giving birth.

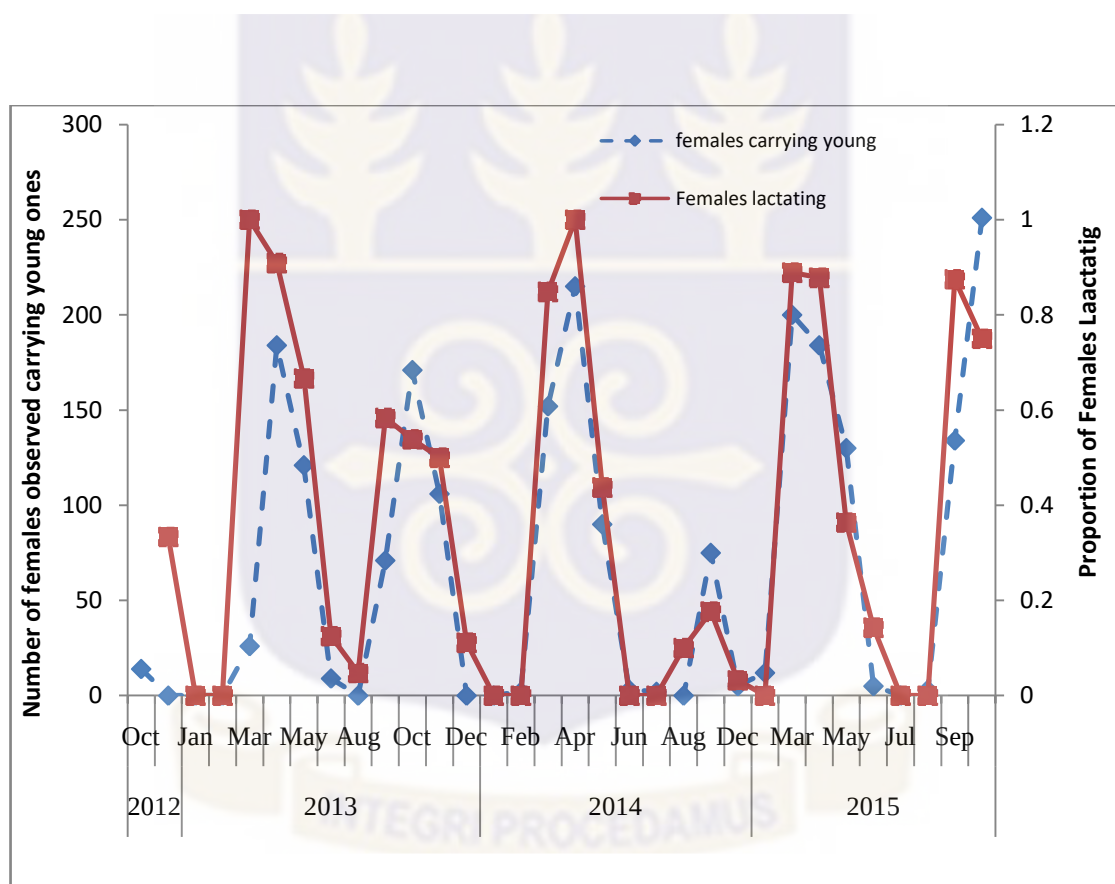


**Figure 7.7** Gestation cycle for *E. gambianus* indicating pregnancy periods.

Lactation in *E. gambianus* peaked around March and September (Figure 7.8). Lactation lasted for a period of three to four months during which females were observed carrying their young ones at day roosts. There was a period of about 2 months prior to weaning

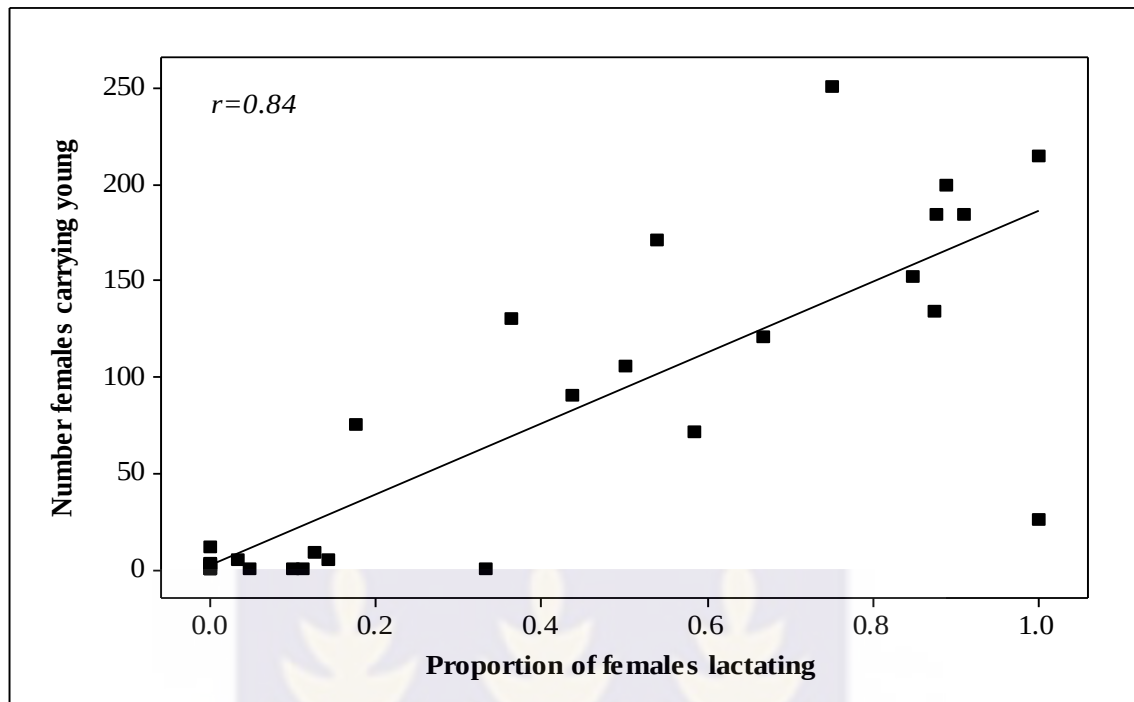


(May/June and October/November) when pregnancy could be detected in females while they were still lactating. This was observed in 75 females. Lactation in this species lasted for four months on average and weaning occurred in January and June each year. The proportion of females that were detected to be lactating correlated strongly and positively with monthly estimates of the number of females that were observed to be carrying their offspring at roost (Figure 7.9), hence the latter provided good support for estimates of lactation rates and periods.



**Figure 7.8 Lactation cycle for *E. gambianus*.**

Showing monthly proportions of females detected to be lactating (red solid lines) and the corresponding monthly number of females observed to be carrying offspring at roosts (blue dashes).

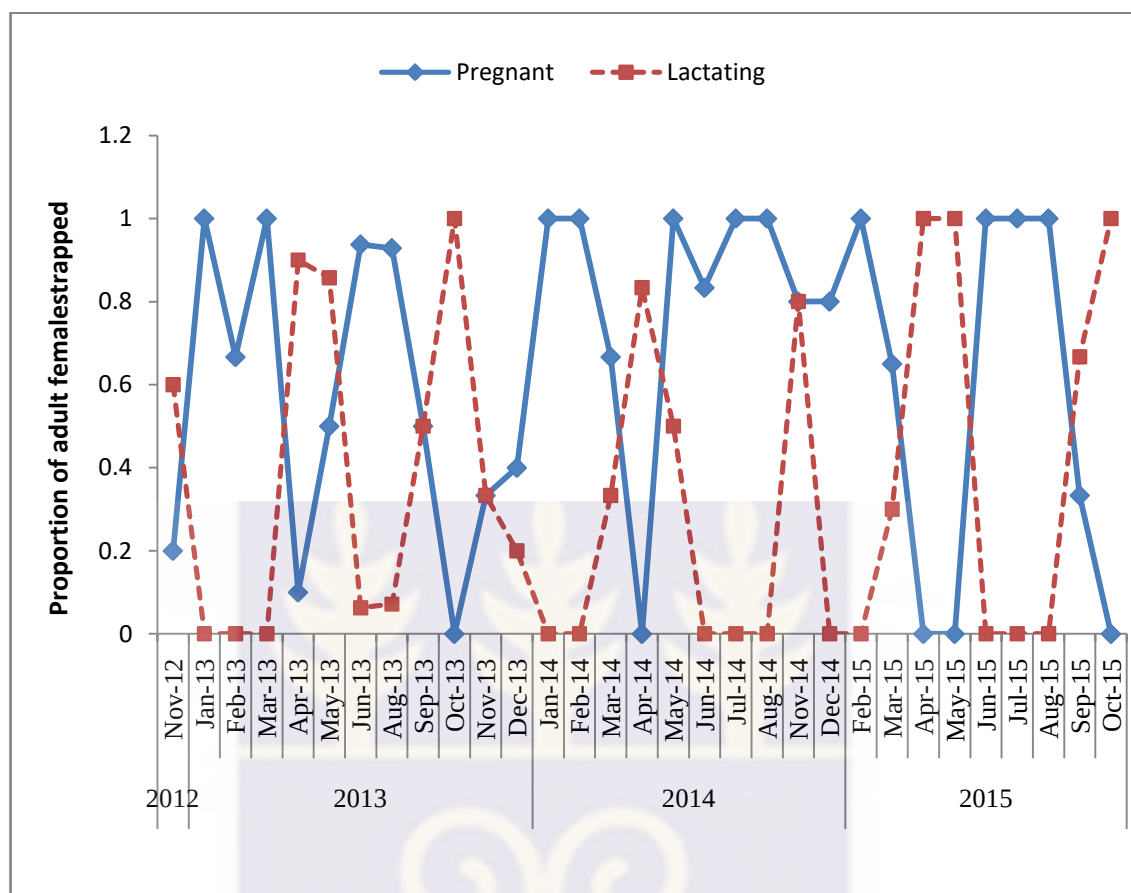


**Figure 7.9 Correlation of estimates of monthly proportion of females lactating with monthly counts of females observed carrying offspring at roosts.**

*Counts of females carrying their young at roosts provided good support and confirmation for estimates of lactation rates and periods.*

### **7.3.5 Birth rates, gestation and reproductive chronology in *M. pusillus* and other fruit bat species**

*M. pusillus* reproduced twice in a year and gestation periods lasted about 5 months. Females carrying neonates were captured in late March and late September suggesting that births occurred from late March to early April and late September to early October each year (Figure 7.10). Births in *M. pusillus* were followed immediately by post partum oestrus and immediate pregnancy in females; several females could be detected to be pregnant and lactating concurrently, shortly after births. Lactation in *M. pusillus* was rather very short, lasting just about 2-3 months and weaning occurred around June and January each year.



**Figure 7.10 Pregnancy and lactation trends for *M. pusillus*.**

Detection rates for pregnancy and lactation in *M. pusillus* did not vary between years. ( $\chi^2 = 0.03$ , df = 2, p-value = 1.0) or between reproductive seasons ( $\chi^2 = 0.04$ , df = 1, p= 0.9). For each reproductive season, pregnancy rates and lactation rates did not differ significantly. Estimates of *M. pusillus* birth rates based on pregnancy rates varied between 0.9 to 1.0 offspring per female season per reproductive while birth rates based on lactation rates varied between 0.8 to 1.0 offspring per female per reproductive season (Table 7.5).

**Table 7.5 Seasonal proportions of *M. pusillus* adult females detected to be pregnant and lactating.**

*Figures in parentheses indicate total number of females sampled during peak pregnancy/lactation periods.*

| <b>Reproductive</b> |                | <b>Proportion of</b> |               |               |
|---------------------|----------------|----------------------|---------------|---------------|
| <b>Season</b>       | <b>Females</b> | <b>Year 1</b>        | <b>Year 2</b> | <b>Year 3</b> |
| <b>1</b>            | Pregnant       | 0.9 (11)             | 1.00(17)      | 0.9 (8)       |
|                     | Lactating      | 0.9 (24)             | 0.8 (12)      | 1.0 (9)       |
| <b>2</b>            | Pregnant       | 0.9 (30)             | 0.9 (13)      | 1.0 (12)      |
|                     | Lactating      | 1.0 (2)              | 0.8 (5)       | 0.8 (4)       |

For both species within the genus *Epomops*, most females that were caught during March and August/September were lactating suggesting bimodal polyoestry in these species (Table 7.6). A female *E. franqueti* carrying a neonate was caught in August indicating that some births occur around this period. Some females that were caught in October and November were detected to be pregnant and lactating simultaneously, which indicated post-partum oestrus and polyoestry in these species.

In *Lissonycteris angolensis*, females caught in early March were heavily pregnant or lactating, and a female carrying a young one was captured in March indicating that births occurred in late March / early April. By June - July, females of *L. angolensis* were detected pregnant again and some individuals were simultaneously pregnant and lactating indicating post partum oestrus after births. A single female caught in October was lactating suggesting a second birth period was around this month.

**Table 7.6 Timing of reproduction in other fruit bat species in Ghana**

P=Pregnancy; L= Lactation

| Species                | Month / Reproductive condition |     |        |     |        |        |        |        |        |        |        |        |
|------------------------|--------------------------------|-----|--------|-----|--------|--------|--------|--------|--------|--------|--------|--------|
|                        | Jan                            | Feb | Mar    | Apr | May    | Jun    | Jul    | Aug    | Sep    | Oct    | Nov    | Dec    |
| <i>E. buettikoferi</i> | P                              |     | P<br>L | L   | P      | P      |        |        | P<br>L | P<br>L |        | P<br>L |
| <i>E. franqueti</i>    | P                              |     | L      | L   |        | P      | P      | P<br>L |        | P<br>L | P<br>L | P      |
| <i>N. veldkampii</i>   |                                |     |        |     |        | P      |        |        | P      | P      | P      |        |
| <i>L. angolensis</i>   |                                |     | P<br>L |     |        | P<br>L | P<br>L |        |        | L      |        |        |
| <i>M. woermanni</i>    |                                |     |        |     |        |        |        |        | P      |        |        |        |
| <i>E. helvum</i>       | P                              | P   | P      |     | L      |        |        |        |        | L      |        | P      |
| <i>H. monstrosus</i>   |                                |     | P<br>L |     |        |        | P      |        |        | L      |        | P<br>L |
| <i>R. aegyptiacus</i>  | P<br>L                         |     | P<br>L |     | P<br>L |        | P      | L      |        | P      |        | P<br>L |

*Nanonycteris veldkampii* adult females were detected pregnant in June and in September to November. Females were in their early pregnancies in September and October. In *Megaloglossus woermanni*, the single female caught in September was heavily pregnant. In *E. helvum*, pregnancy was detected in females from December to March. Lactating was detected in females captured in May, suggesting that births occurred around this period. A single female was detected pregnant in June and another female was lactating in October. Parturition in *H. monstrosus* seemed to occur in March and October. Females carrying neonates were captured in October and March suggesting births occurred twice in a year in these months.

Several female *R. aegyptiacus* were detected to be in their early pregnancy in May. Pregnancy in this species was also detected in October while majority of females were lactating in December. This suggests a birth period around November/ December. Females trapped in January were either pregnant, lactating or both, suggesting post partum oestrus and polyoestry in *R. aegyptiacus*. Majority of females sampled in mid March were pregnant but a single female carrying a suckling young was also trapped in March suggesting that most births occurred in late March or early April.

### 7.3.6 Growth to sexual maturity of *E. gambianus*

After births, *E. gambianus* females carried and flew with very young (neonate) pups and a few were trapped together. Neonate bats (presumed to be a few days old) that were trapped together with females were averagely  $20.6 \pm 5.0$  g ( $n=3$ ) with forearm length  $39.5 \pm 5.1$  mm (Table 7.7). Juveniles became newly volant, about when they attained 45% of average adult body mass and forearms were 83% of that of adult females. These newly volant juvenile bats first appeared in the flying population in April (for cohort born in March) and October (for cohort born in September) each year. At the time of weaning, juvenile bats had attained 57% of average adult body mass and their forearms were 88% that of adults.

A newly volant juvenile female bat (ca 1 month old; forearm=74.5 mm) which was caught in September, 2013 was recaptured five months later and was detected to be in its first pregnancy (primiparous). Males ( $n=4$ ) which were also captured about a month after birth were recaptured between 7-11 months later but showed no signs of male secondary sexual features such as epaulettes, scrotal testes, implying they had not reached sexual maturity. One male was however recaptured as sexually matured after eleven months

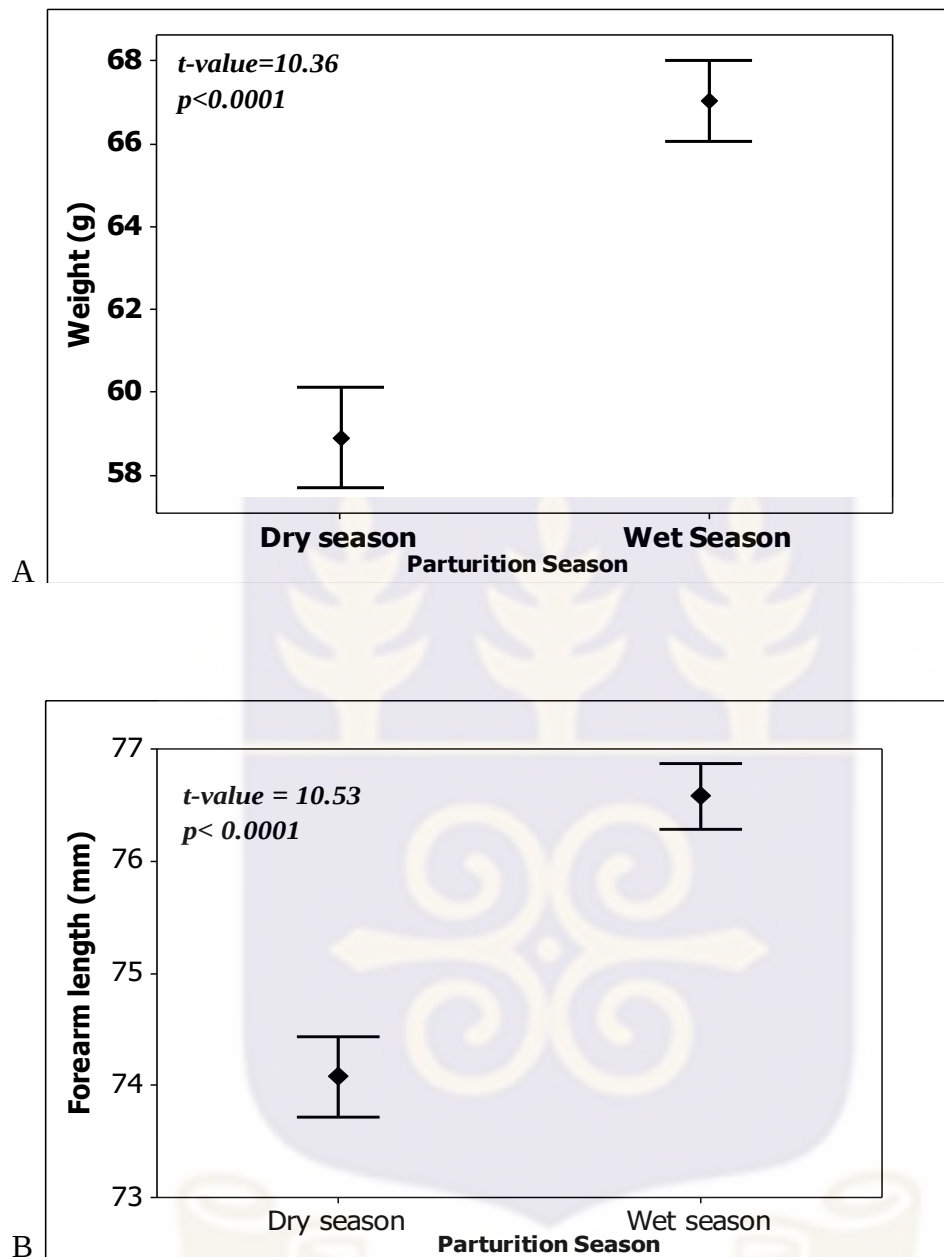


since first being caught as a newly volant juvenile (forearm=71 mm). This suggests that males do not attain sexual maturity until they are about twelve months, while females may reach sexual maturity when they are about six months old.

**Table 7.7 Morphometrics of adult and juvenile *Epomophorus gambianus*.**

| Age-class               | Weight (g)       |     | Forearm (mm)    |     |
|-------------------------|------------------|-----|-----------------|-----|
|                         | Mean ( $\pm$ SD) | N   | Mean $\pm$ (SD) | N   |
| Neonate                 | 21 $\pm$ 5       | 3   | 40 $\pm$ 5      | 3   |
| Juvenile (Newly Volant) | 50 $\pm$ 7       | 146 | 72 $\pm$ 3      | 173 |
| Juvenile (Weaning age)  | 65 $\pm$ 8       | 206 | 76 $\pm$ 3      | 209 |
| Female Adult            | 103 $\pm$ 13     | 434 | 84 $\pm$ 3      | 465 |
| Male Adult              | 130 $\pm$ 15     | 276 | 90 $\pm$ 3      | 291 |

Based on the mean weights and forearm lengths for the different age classes, it was possible to identify juvenile bats belonging to each cohort before they became indistinguishable from sexually immature adult bats. This allowed for comparisons between the growth (weights and forearm lengths) of juvenile bats that were born during the March birth period (growing through the wet season) and those that were born during the September birth period (and grew through the dry season) for each year. Juvenile bats that were born and grew through the wet season were significantly heavier and had longer forearms (mean weight- 67 $\pm$ 12 g; mean forearm length-77 $\pm$ 4 mm) than those that were born and grew through the dry season (mean weight-59 $\pm$ 12 g, forearm length 74 $\pm$ 4 mm; Figure 7.11A,B).



**Figure 7.11 Interval plots for differences in growth for juvenile bats born during the wet and dry seasons.**

*Vertical lines are 95% confidence intervals. Tests are based on two sample t-tests at 95% confidence intervals.*

### 7.3.7 Survival rates and recapture probabilities for *E. gambianus*

For the radio-tracking, 38% of *E. gambianus* bats that were tagged were never detected again from the morning after their release the previous night. From the CMR analysis, none of the models for *E. gambianus* received large support (top model Akaike weight 0.19). As a result, model averaging was used to generate robust parameter estimates to account for model uncertainty. There was moderate support for both sex and age-class differences in survival probability (summed Akaike weight=0.76) in *E. gambianus*. All of the best models showed no effect of varying time on recapture probability for *E. gambianus* (Table 7.8) so only a single estimate was provided for each group.

Model averaged parameter estimates indicated that monthly survival for *E. gambianus* adult males (0.91: 95% CI: 0.75-0.97), was not significantly higher than that of adult females (0.82: 95% CI: 0.67-0.91). Survival estimates in adults were higher than that of sexually immature adults (males: 0.74- 95% CI: 0.62-0.84; females: 0.32- 95% CI: 0.03-0.89). However, due to the very low sample size of sexually immature female adults (n=2), parameter estimates for this group should be viewed with some reservations. Recapture probability in *E. gambianus* was very similar among groups (Figure 7.12). Males however, appeared to have relatively lower recapture probabilities than females.

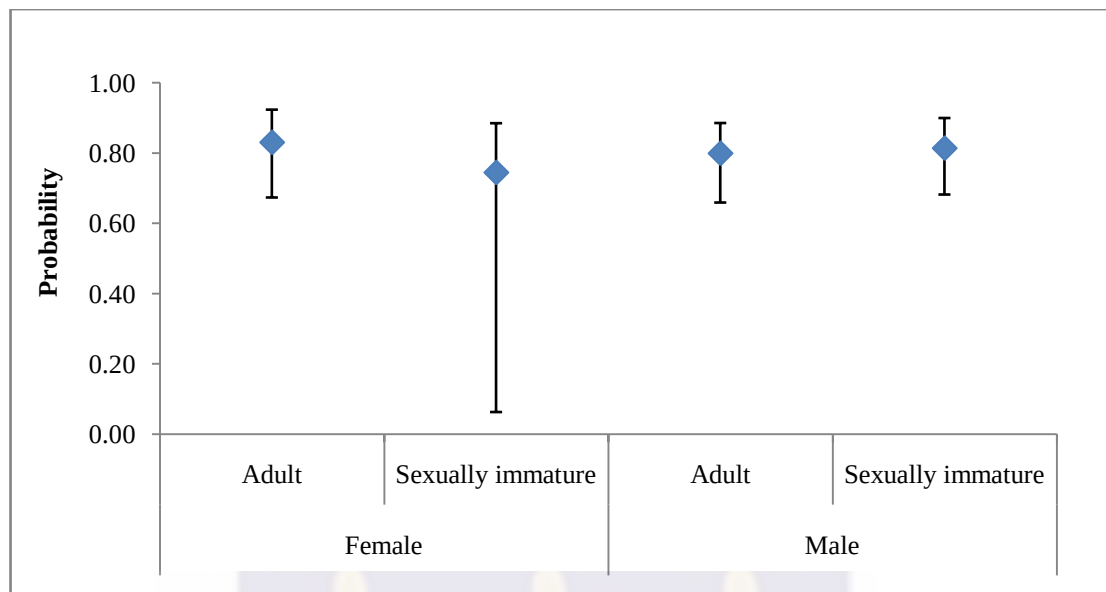
### 7.3.8 Survival rates and recapture probabilities for *M. pusillus*

The best model from CJS-CMR analysis had very little support (w=0.4) so model averaging across the top 8 models with a total weight >0.9 (Table 7.9) was done to provide estimates of model parameters. There was very weak support of constant survival (Summed w=0.1) but there was good support for time varying recapture probability (summed weights =0.9).

**Table 7.8 Summary of CJS Capture-recapture models for *E. gambianus* showing the best models (summed model weight > 0.95).**

| <b>Model</b>                                                        | <b>AICc</b> | <b><math>\Delta</math>AICc</b> | <b>w</b> | <b>Deviance</b> | <b>k</b> |
|---------------------------------------------------------------------|-------------|--------------------------------|----------|-----------------|----------|
| $\phi(\text{Ageclass} * \text{Sex})p(.)$                            | 269.051     | 0.000                          | 0.190    | 88.022          | 5        |
| $\phi(\text{Ageclass} + \text{Sex})p(.)$                            | 269.430     | 0.379                          | 0.157    | 90.534          | 4        |
| $\phi(\text{Ageclass} * \text{Sex})p(\text{Sex})$                   | 270.535     | 1.483                          | 0.090    | 87.344          | 6        |
| $\phi(\text{Ageclass} + \text{Sex})p(\text{Sex})$                   | 270.831     | 1.779                          | 0.078    | 89.802          | 5        |
| $\phi(\text{Ageclass})p(.)$                                         | 271.086     | 2.035                          | 0.069    | 94.296          | 3        |
| $\phi(\text{Ageclass} * \text{Sex})p(\text{Ageclass})$              | 271.161     | 2.109                          | 0.066    | 87.970          | 6        |
| $\phi(\text{Ageclass} + \text{Sex})p(\text{Ageclass})$              | 271.486     | 2.435                          | 0.056    | 90.457          | 5        |
| $\phi(\text{Ageclass})p(\text{Ageclass} * \text{Sex})$              | 272.257     | 3.206                          | 0.038    | 89.067          | 6        |
| $\phi(\text{Ageclass} + \text{Sex})p(\text{Ageclass} * \text{Sex})$ | 272.282     | 3.230                          | 0.038    | 86.901          | 7        |
| $\phi(\text{Ageclass} * \text{Sex})p(\text{Ageclass} + \text{Sex})$ | 272.282     | 3.230                          | 0.038    | 86.901          | 7        |
| $\phi(\text{Ageclass} + \text{Sex})p(\text{Ageclass} + \text{Sex})$ | 272.316     | 3.265                          | 0.037    | 89.125          | 6        |
| $\phi(\text{Ageclass})p(\text{Sex})$                                | 273.038     | 3.987                          | 0.026    | 94.142          | 4        |
| $\phi(\text{Ageclass})p(\text{Ageclass})$                           | 273.166     | 4.114                          | 0.024    | 94.270          | 4        |
| $\phi(.)p(\sim \text{Ageclass} * \text{Sex})$                       | 273.688     | 4.637                          | 0.019    | 92.659          | 5        |
| $\phi(.)p(.)$                                                       | 273.996     | 4.944                          | 0.016    | 99.284          | 2        |
| $\phi(\text{Ageclass} * \text{Sex})p(\text{Ageclass} * \text{Sex})$ | 274.501     | 5.450                          | 0.012    | 86.901          | 8        |

*Models are ranked by ascending AiCc values. AiCc is Akaike information criterion corrected for small samples k is the number of parameters, w is Akaike weights of the models,  $\Delta$ AICc denotes the difference between the AIC value of each model and that of the most parsimonious model. "+" indicates additive effects, "\*" indicates interactive effects, "." indicates constant.*



**Figure 7.12 CJS model averaged estimates for recapture probability in *E. gambianus*.**

*Vertical bars are 95% confidence intervals*

Model averaged parameter estimate for monthly survival for *M. pusillus* adult males was 0.9 (95% CI: 0.6-1.0) and for immature males was 0.9 (95% CI: 0.7-1.0). Monthly survival estimates for males were higher than estimates for females. Monthly survival of adult females was 0.8 (95% CI: 0.6-0.9) and immature females was 0.8 (95% CI: 0.6-0.9). However, the unconditional 95% confidence intervals overlap considerably. Generally, recapture probability was very low (0.02; 95%CI: 0.01-0.04) but varied with time and between age and sex classes. Recapture probability was high on encounter occasions 3, 6, 9, 12, 15 and 19 (Figure 7.13). Recapture probability was lowest in adult males and highest in immature females.

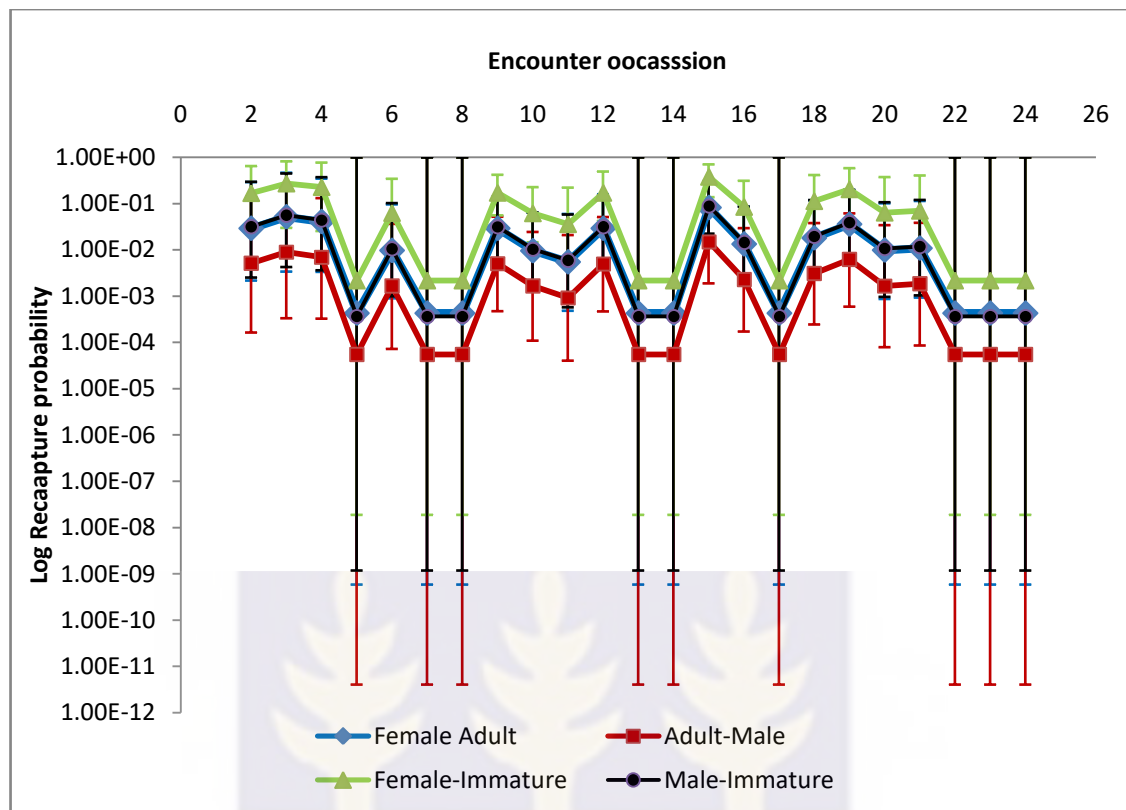
**Table 7.9 Summary of CJS Capture-recapture models for *M. pusillus* showing the best models.**

*Summed model weights of best models > 0.95.*

| Model                                                                             | AICc  | $\Delta AICc$ | w     | Deviance | k  |
|-----------------------------------------------------------------------------------|-------|---------------|-------|----------|----|
| $\phi(\text{Ageclass} + \text{Sex})p(\text{Ageclass} + \text{Sex} + \text{time})$ | 371.2 | 0.0           | 0.4   | 154.3    | 29 |
| $\phi(\text{Sex})p(\text{Ageclass} + \text{Sex} + \text{time})$                   | 372.0 | 0.8           | 0.2   | 157.5    | 28 |
| $\phi(.)p(\text{Ageclass} + \text{Sex} + \text{time})$                            | 373.6 | 2.4           | 0.1   | 161.5    | 27 |
| $\phi(\text{Ageclass} * \text{Sex})p(\text{Ageclass} + \text{Sex} + \text{time})$ | 373.6 | 2.4           | 0.1   | 154.3    | 30 |
| $\phi(\text{Ageclass})p(\text{Ageclass} + \text{Sex} + \text{time})$              | 374.3 | 3.1           | 0.08  | 159.9    | 28 |
| $\phi(\text{Ageclass} + \text{Sex})p(\text{Ageclass} * \text{Sex})$               | 377.3 | 6.1           | 0.02  | 210.1    | 7  |
| $\phi(\text{Sex})p(\text{Ageclass} * \text{Sex})$                                 | 378.1 | 6.9           | 0.01  | 213.0    | 6  |
| $\phi(.)p(\text{Ageclass} + \text{time})$                                         | 378.6 | 7.4           | 0.009 | 168.9    | 26 |

*Models are ranked by ascending AiCc values. AiCc is Akaike information criterion corrected for small samples k is the number of parameters, w is Akaike weights of the models,  $\Delta AICc$  denotes the difference between the AIC value of each model and that of the most parsimonious model. "+" indicates additive effects, "\*" indicates interactive effects, "." indicates constant.*





**Figure 7.13 Model averaged estimates of time dependent recapture probability of *M. pusillus*.**

Vertical bars are 95% CI.

## 7.4 Discussion

### 7.4.1 Survival rates in *E. gambianus* and *M. pusillus*

This is the first study to provide estimates of demographic parameters for a colony of *E. gambianus* and *M. pusillus*, and one of few studies that estimates age and sex specific survival rates for fruit bats (Pteropodidae). Survival rate is an important demographic parameter that is useful in predicting the health of populations and also in assessing how populations can fare under different stress conditions. In tree roosting fruit bats this is particularly difficult because in open populations, capture mark recapture methods such as banding or PIT tags provide very few recaptures, (Towner *et al.*, 2009). In *M. pusillus*

where PIT tags were used as a CMR method, recapture rates were however very low across all groups (at best 0.015 for immature females) and estimates of survival could have been largely underestimated. These extremely low recapture rates highlights one of the major problems in CMR studies that uses methods which require physically recapturing individual bats.

The use of radio-tags appears to be a more appropriate solution to this problem, particularly in large tree roosting fruit bats. However, radio-tracking also has its problems. In order to track animals usually over long periods (to provide robust estimates), tags need to have longer battery life (lasting several months) and this usually means extra added size and weight. Again, radiotagging as a CMR method does not distinguish between tag loss/failure, actual death and emigration of an individual. In this study, extra efforts were made to visually confirm all bats that were tagged to ensure they were alive and still carrying tags to reduce underestimation of parameters due to tag loss.

Recapture rates from radio tagging CMR analysis compared to initial estimates from PIT tags (<6% of over 2000 marked individuals) is suggestive that *E. gambianus* may have avoided areas where they were initially caught. Hence future studies aimed at estimating survival using CMR (or any other studies that require individual bats to be recaptured) could either use radio-tags or consider frequent switching of netting sites to improve recapture rates.

A monthly survival of 0.81 (95% CI: 0.74-0.86) was estimated for *E. gambianus*. CMR analyses showed sex and age differences in survival rates with males having higher survival probability than females of similar ages, while adults also have a higher survival rates than sexually immature adults. Similar to monthly survival estimates of *E.*

*gambianus*, adult survival in *M. pusillus* was higher than sexually immature individuals while males had a relatively higher survival than females. For *M. pusillus*, there was strong evidence of sex and temporal variation in recapture probability. Peaks in recapture probability for *M. pusillus* however occurred in the months of March, June/July and November/December which coincided with peaks in fruiting and flowering abundance in the study area (Chapter five). Periods of low food abundance within the study area may cause bats to forage further away from roost sites thereby reducing capture rates, whereas peaks in food abundance may increase encounter and recapture rates of bats. Such variations in food availability have been shown to cause temporal variations in the abundance of fruit bats in an area (Hodgkison *et al.*, 2004). Future studies using marking methods such as banding or the use of PIT tags should consider intensive seasonal trapping sessions especially during peak food abundance when recapture rates are likely to be higher.

Survival rates frequently vary between sexes and age classes (Lebreton *et al.*, 1992) with juvenile survival often lower, but increases towards a stable survival at adulthood (Loery *et al.*, 1987). Survival probabilities are often lower in females possibly due to extra energetic constraints associated with pregnancy and lactation (Kurta & Matson, 1980; Perry *et al.*, 2010). Alternatively the larger size of *E. gambianus* adult males may confer reduced predator attacks compared to females and may infer higher survival in adult *E. gambianus* males than females.

Several of the *E. gambianus* individuals that were radio-tagged (38%) were not detected within the colony after their release. All tags used were tested to be working prior to their deployment. It is therefore unlikely that these tags had failed or the bats had died overnight. Rather, this suggests that either these bats had emigrated from the study area

or were bats that did not belong to this colony, but were only trapped during nomadic foraging bouts. Hence, the apparent survival estimates for *E. gambianus* in this study could be substantially underestimated as possible permanent emigration of these bats was not distinguishable from death in the CMR analysis. Efforts to relocate these bats up to distances of about 20 km from the study colony were unsuccessful. Long distance nomadic movement is common among members of the family *Pteropodidae* (Tidemann & Nelson, 2004; Richter & Cumming, 2008; Breed *et al.*, 2010; Roberts *et al.*, 2012). Hayman *et al.* (2012a) observed colony switching in *E. helvum* between colonies that were up to 300 km apart during a CMR study in Ghana. Future studies should consider colony connectivity with extra efforts to search and track for tagged bats over large areas.

In comparison with the estimates by Hayman *et al.* (2012a) (and the only other estimate for a pteropodidae), the monthly adult survival of 0.87 (95% CI: 0.78-0.92) estimated for *E. gambianus* in this study is lower than the estimated 0.96 (95% CI: 0.89-0.99) monthly adult survival for *E. helvum* in Ghana. While there is considerable reason that possible emigration could have led to an underestimation of survival for *E. gambianus* in this study, the difference in life history traits between the two species could also account for the differences in the survival estimates. For instance, Lentini *et al.* (2015) found that bats that produce fewer young each year had higher survival estimates, because of the energetic costs involved in pregnancy and the large size of bats at birth and weaning. On the basis of these differences in species-traits, would be expected that *E. gambianus* would have a lower survival rate because of its polyoestrous reproduction compared to *E. helvum* which reproduces once a year.

Due to restrictions on tag weights and size, juveniles could not be included in the CMR study. Based on Nichols *et al.* (2000) and Schmidt *et al.* (2005), population growth rate can be estimated simply as the sum of survival and recruitment. Assuming a stationary population growth rate of one (1) implies that recruitment of 0.91 per year is needed to ensure a stable population growth rate. However, with an estimated annual birth rate approaching two offspring per female, this would suggest that juvenile survival rates are very low for *E. gambianus*. Several authors [e.g. Eberhardt (2002); O'Shea *et al.* (2011); Papadatou *et al.* (2011)] suggest that adult survival is a more important demographic parameter than juvenile survival in the population growth of animals with high survival rates such as bats.

Several long term bat CMR studies [e.g. Sendor and Simon (2003); Papadatou *et al.* (2009); Schorcht *et al.* (2009); Humphrey and Oli (2015)] have shown varying survival over time. Factors such as environmental stochasticity has the ability to alter several vital population parameters and affect the dynamics of populations (Gaillard *et al.*, 2000; Papadatou *et al.*, 2009). Hence, additional research that focuses on long term monitoring of marked individuals is vital in order to gain a complete understanding of the demography and life history of bats (O'Shea *et al.*, 2011). Alternatively, successful aging of a cross section of the population, using methods such as tooth cementum annuli counts (Hayman *et al.*, 2012a) can help to determine age frequencies for fitting life table models to identify age specific survival and other demographics parameters.

#### **7.4.2 Population size changes in fruit bats**

Population size is an important variable that is often used to inform the implementation of management strategies for species conservation (Yoccoz *et al.*, 2001; Pollock *et al.*,

2002); and provides information for other ecological and biological aspects of wildlife populations, such as disease dynamics (Lloyd-Smith *et al.*, 2005). Estimates of population size and long term monitoring data are often lacking for several species (Wood *et al.*, 2012). In this study, a colony of *E. gambianus* and *M. pusillus* (at Ve-Golokuati) was monitored for population size changes over a three year period, the first for any colony of these species in Ghana.

It is uncertain what caused the decrease in *E. gambianus* numbers from the first year to the third year. Hunting of fruit bats is common, particularly in southern Ghana (Kamins *et al.*, 2011; Leach *et al.*, 2017; Ohemeng *et al.*, 2017) and can be implicated in bat population declines. During the study period however, very low levels of hunting (shooting of single individuals by children with catapults) were observed and this is unlikely to have caused the decline. Elsewhere (in Northern Ghana) significant hunting of this species occurs. The permanent loss of roosting trees and temporal displacement of bats due to pruning of trees however, were increasingly common within the study area. A combined effect of hunting and roost loss could have caused the observed reduction in the population at this colony or caused the migration of bats away from this colony, which would result in a reduction in the population. Several local bat populations are in decline following habitat loss, hunting and loss of roosting sites (Mickleburgh *et al.*, 1992;2002). The predictions are that increasing loss of suitable roosting sites as a result of habitat degradation and urbanization, together with substantial levels of hunting, could be causing declines in population sizes of *E. gambianus* across its range.

The colony studied could be part of a much larger network of *E. gambianus* colonies in Ghana, considering the numerous colonies identified across the country during the bat roost search. A clearer picture of the population trends of this species will require further



studies based on monitoring of a wider network of colonies. The use of genetic analysis could also provide important knowledge about the extent of interaction between colonies. Similarly, GPS monitoring of few bats to explore their movement could also help to inform this. In the absence of monitoring schemes over several colonies, estimates for single colonies (as done in this study) are still vital in understanding factors that affect population dynamics and could be useful in disease surveillance.

*Eidolon helvum* colony sizes showed typical notable variation in numbers in a year, as reported in several other studies (Sørensen & Halberg, 2001; Richter & Cumming, 2006; Hayman *et al.*, 2012a; Webala *et al.*, 2014). Numbers decreased drastically during the rainy season and increased during the dry season every year across all monitored sites and this is consistent with the rainfall-driven seasonal migration proposed by other studies such as in Thomas (1983). The occurrence of several of these *E. helvum* colonies of varying population sizes lends support to Hayman *et al.* (2012a)'s suggestion of a large network of *E. helvum* population in Ghana. The absence of bats at some colonies with corresponding increase in other larger colonies suggests that some colonies are only transient colonies that feed into much larger populations especially during peak population periods.

Hayman *et al.* (2012a) estimated the Accra colony to contain up to 1 million bats in the 2007/2008 dry season which subsequently decreased to about 300,000 bats during the 2009/2010 dry season. During this study, the Accra colony was estimated at about 124,000 during the 2012/2013 dry season and approximately 100,000 during the 2013/2014 dry season, indicating a further reduction in the colony size. It is unclear what is causing the reduction in the Accra colony size. Recent infrastructural developments in and around the area of this colony has led to the loss of some of the roosting trees within

the colony and this could have implications on population size. Hayman *et al.* (2012a) suggested the mass movement of bats from this colony to other nearby colonies as a possible reason for the decline. This reason could be plausible considering the many *E. helvum* colonies located across the country and the long distance movement capability of this species. Further research using telemetry techniques is however needed to confirm the possibility of mass movement and the connectivity of *E. helvum* colonies in Ghana. This would further enhance our understanding of bat movements and its implications for ecosystem services and infection dynamics.

Across its range of occurrence (including Ghana), *E. helvum* is subjected to intensive hunting and several local populations are reported to be in decline. During an earlier visit to the Tanoboase colony prior to this study, in late 2012, about 2 million bats were estimated to occur at this colony personally. Hayman *et al.* (2012a) had also reported this colony to hold about 3 million bats in 2008. During the dry season of 2013/2014, only 50,000 bats were estimated to be present at this colony and there were no bats in this colony for most periods in a year. This drastic decline in numbers at this colony is mostly likely to be as a consequence of the intensive hunting that occurs at this colony. Discussions with residents around the Sunyani colony (ca. 63 km away) indicated recent significant increase in the population at this colony, which appeared to coincide with the absence of bats at the Tanoboase colony. This suggests possible mass emigration of bats from the Tanoboase colony to the Sunyani colony as a result of persistent hunting pressure at the former roost site. Such mass movements following disturbance can alter population structure and may cause bats to move to less preferred roosting sites, which may decrease their fitness.

#### 7.4.3 Birth rates and reproductive chronology in fruit bats in Ghana

This study estimates that 56% to 100% of all adult *E. gambianus* females within the colony give birth during each reproductive season. These estimates translate to an annual birth rate of about 1.1 to 2 offspring per female per year (assuming each female successfully gives birth to one young during each reproductive season). These estimates are similar to the twice a year breeding reported for *E. gambianus* in other studies carried out in West Africa. (Thomas & Marshall, 1984; Boulay & Robbins, 1989). An estimated 8% of parous *M. pusillus* females failed to give birth or did not become pregnant during each reproductive season for this study, which meant an estimated birth rate of 0.92 young per female per reproductive season. Similarly, Thomas and Marshall (1984), detected reproductive failures in 7.9% of parous *M. pusillus* females.

In *E. gambianus*, there was an indication of increased mortality in neonate/juveniles during the second reproductive period of the first year, which likely resulted in the low proportion of females that were detected to be lactating. This observation suggests that using pregnancy rates alone as a proxy for birth rates should be done with caution. This is because birth rates can be overestimated since the assumption that observed pregnancies lead to successful births can be violated without detection.

Each birth season was followed by post partum oestrus with immediate embryonic development resulting in a period of simultaneous pregnancy and lactation in *E. gambianus* and *M. pusillus*. This confirms the reported reproductive chronology of both species as continuous bimodal polyoestry with post partum oestrus. The gestation period for *E. gambianus* lasted 5-6 months with a lactation period of 3-4 months (9-16weeks), while gestation in *M. pusillus* lasted about 5 months with a relatively shorter lactation

period of about 2-3 months; both of which are similar to the duration reported in other studies (Thomas & Marshall, 1984; Nowak, 1999; Happold & Happold, 2013).

Bimodal polyoestry is a very common reproductive pattern in African Pteropodidae that occurs around the equator. At least eight species are known to exhibit this chronology (Cumming & Bernard, 1997). In five of the other species examined in this study, parturition occurred twice in a year, with first births occurring around March/April and second births around September/October. In *R. aegyptiacus*, this second birth period appears to occur slightly later in November/December. The occurrence of simultaneous pregnancy and lactation, which is indicative of post-partum oestrus (Happold & Happold, 1990), confirmed polyoestry in four other species studied: *E. franqueti*, *E. buettikoferi*, *L. angolensis* and *R. aegyptiacus* in Ghana exhibited continuous bimodal polyoestry with post partum oestrus. Although post partum oestrus was not observed in *H. monstrosus* in this study, it has been reported in other studies within similar habitats (Happold & Happold, 1990; Langevin & Barclay, 1990). Data for *N. veldkampii* and *M. woermanni* were inconclusive.

In West Africa, *E. helvum* has been reported to exhibit restricted seasonal monoestry with delayed implantation and females give birth to a single young each year (Mutere, 1967a; Fayenuwo & Halstead, 1974; Happold & Happold, 1990). The timing of pregnancy and proportions of adult females that were detected to be pregnant in this study are comparable to previous estimates for *E. helvum* in Ghana (Hayman *et al.*, 2012a). However, records of lactating females in May at both Accra and Tanoboase roost suggests that at least some females give birth in Ghana during the migration period, contrary to suggestions made by Hayman *et al.* (2012a) that females migrate elsewhere to give birth. The detection of large foetus by palpation but no lactating females in

March, together with the presence of lactating females (some with suckling neonates) in May imply parturition in April or in May. This means parturition in *E. helvum* in Ghana occurs about a month or two later than reports from Uganda (Mutere, 1967a) and Nigeria (Fayenuwo & Halstead, 1974) although in all cases, the parturition appears to be in synchrony with the onset of the major rainy season.

In this study, majority of *E. gambianus* and *M. pusillus* births occurred around March and September each year and these periods coincided with the onset of the two rainy seasons for the Ve-Golokuati study area where the study colony was located. Yeboah (2008), reported breeding periods of *E. gambianus* as July/August and March/April at the Abirem District of the Eastern Region in Ghana. Marshall and McWilliam (1982) also suggested births of *E. gambianus* at the beginning of the rains in Mole and reported lactating females caught in early March; they also reported *M. pusillus* births to occur in late April and September. Elsewhere in West Africa, *E. gambianus* births have been reported to occur in April-May and October-November (Boulay & Robbins, 1989; Nowak, 1999; Happold & Happold, 2013). *M. pusillus* births were observed to occur around March and September in Cote d'Ivoire (Thomas & Marshall, 1984). Although several of these reported birth periods of *E. gambianus* and *M. pusillus* in West Africa are not specific, births appear to be synchronized with the bimodal rainy seasons which predict the timing of food abundance. Parturition was highly synchronised between most species with almost all the species in this study giving birth around March-April and in September-October which coincided with rainfall seasons in the study areas.

The synchronization of parturition with food abundance (and rainfall) is commonly reported and well illustrated among Pteropodidae in Africa (Happold & Happold, 1990; Cumming & Bernard, 1997). In this study for instance, lactation in *E. gambianus* lasted



till June (for births in March) and January (for births in September) each year. Considering only fruit availability, lactation appears to be timed so as to coincide with peaks in fruiting abundance as suggested by Marshall and McWilliam (1982). Flower resources (as shown in Chapter five) appear a major source of food for *E. gambianus* (and other fruit bats in this study area) especially during the lean fruiting seasons. The post weaning period coinciding with peaks in flowering abundance (particularly during the dry season) would imply that food may still be available to support bats during this period although not as abundant as in the rainy season. Hence, both lactating females and newly weaned young are supported throughout the year.

However, because fruits are relatively more abundant in the rainy season than in the dry season, and also because the peaks in flower resources lasts for relatively short periods (as reported in Chapter 5), bats born in the different seasons could grow under different nutritional conditions arising from possible differences in nutrition provided by a mainly fruit diet and that of a flower diet. Thomas and Marshall (1984) made a similar suggestion, and added that the growth rates of fruit bats may be dependent on the quality of their diets. However, they found no significant difference in growth rates of different cohorts of juvenile *Epomops buettikoferi* and *Micropteropus pusillus* that grew through wet and dry seasons. Contrary to their findings, in this study, the sizes of juvenile *E. gambianus* that grew under the different seasons were significantly different. This finding supports the earlier statement that food quality can affect growth of fruit bats. Thomas and Marshall (1984) also suggested that the difference in food quantity and quality may also affect reproductive success of females and cause increased reproductive failures during the dry season. This could be a contributing factor to the relatively low reproductive rate that was observed during the dry season of the first year of this study, although other factors (e.g. drier weather conditions) may have compounded this effect.



Future studies could explore further the effects of differential diet quantity and quality on growth rates and survival of bats as this may have consequences on their fitness.

The reproduction states of female bats that were trapped in the Northern Region of Ghana in this study suggest that the timing of reproduction in *E. gambianus* can vary across different locations. In late September/early October when births had occurred at Ve-Golokuati, most females that were caught in the northern part of Ghana (90% of 49 adult females) were found to be in their mid pregnancies, which suggest that births would occur around November/December for individuals trapped in the northern part of Ghana. Reproductive flexibility has been described in some African bats, particularly in species that are widely distributed (Happold & Happold, 1990). The possibility of *E. gambianus* exhibiting this flexibility, however, requires further assessment.

#### **7.4.4 Sex ratios, sexual size dimorphism and bimaturism in *E. gambianus*.**

Sexual size selection in bats usually produces females as the larger sex because of the need to carry the extra weight of young ones in flight (Welbergen, 2010). In a few exceptions, particularly among the family *Pteropodidae* (*E. gambianus* included), this is reversed, with males rather being the larger size. In such species where females are the smaller size, it would be expected that carrying young ones in flight imposes severe energetic constraints on females. In *E. gambianus*, neonates reached about 45% of the average body mass of adults after about a month of birth and at weaning age were up to 57% of adult body mass. Similar weights have been reported in *M. pusillus*, *E. buettikoferi* (Thomas & Marshall, 1984) and in *Pteropus poliocephalus* (Welbergen, 2010). These relative weights at volancy are known to be very low compared to those in microchiroptera that attain flight only when juveniles reach about 80% of adult body

mass and 95% of adult wing dimensions (Kunz & Robson, 1995; Kunz & Stern, 1995). Thus, young bats appear to be weaned at a relatively lower body mass and size in *E. gambianus* and other frugivorous bats.

In addition, juvenile bats joined the volant population just about a month after birth and this reduces constraints of females having to carry young bats in flight for prolonged periods. According to Welbergen (2010) females still have to carry substantial weights of non-volant juveniles, suggesting that they are not entirely freed from carrying extra weights. In *P. poliocephalus*, Welbergen (2010) established that females had longer forearms relative to their body weight and other skeletal dimensions compared to males, and this enabled females to carry extra weight. A similar observation was made in this study for *E. gambianus* where female adults had forearm to body weight ratio of 0.82 compared to 0.69 in Adult males.

This study provides evidence of bimaturism in *E. gambianus*. Bimaturism has been reported in some fruit bat species including *Hypsignathus monstrosus* (Bradbury, 1977), *P. poliocephalus* (Welbergen, 2010), *M. pusillus* and *E. franqueti* (Thomas & Marshall, 1984). Thomas and Marshall (1984) observed that *M. pusillus* and *E. buettikoferi* females became sexually matured at six months, while males of both species reached puberty only after seven months and eleven months respectively. Similarly, in this study *E. gambianus* females were observed to be sexually mature at the age of about six months while males did not become sexually mature until they were about 12 months old.

The difference in timing of maturity in *E. gambianus* could explain the differences in size between males and females at maturity (Sexual size dimorphism). In polygynous species (like *E. gambianus*) where males compete for breeding females, marked sexual size dimorphism often occurs (Welbergen, 2010) as sexual selection is likely to favour

the evolution of larger size in males as an adaptation to increase success in male to male competition for females (Andersson, 1994).

Estimates of sex ratio is an important demographic parameter that is key to understanding the health and persistence of populations (Skalski *et al.*, 2005). For several African pteropodids, this parameter is mostly unavailable. This study has revealed that while overall sex ratio for the entire colony of *E. gambianus* was significantly male dominated, variations in this overall sex ratio existed among the different age classes, with annual variations in age-specific sex ratios. In several mammalian species, sex ratios vary from unity (Barclay, 2012) and in bats, it is often skewed towards males (Perry *et al.*, 2010). Juvenile and sexually immature adult sex ratios in this study were both male biased with ratios of the latter being highly skewed towards males.

According to Barclay (2012), ratio of the sexes at birth depends on the value and the fitness benefits gained by producing a particular sex. Drawing on arguments by Trivers and Willard (1973) that females should invest more into the sex that is likely to benefit most from an added investment, Barclay (2012) suggests that polygynous species would invest more in male offspring since males are more likely to influence reproductive success. The biased juvenile sex ratios in *E. gambianus* could be attributed to similar reasons.

Bimaturism in *E. gambianus* is a possible justification for the strongly male biased sex ratio in sexually immature adults. Because females mature twice as fast as males, one would expect more males to remain in this sexually immature adult "transition period" compared to females, even if the initial sex ratio was 1:1. Hence, the highly skewed male sex ratio in the sexually immature adult age-class in *E. gambianus* is the result of the delay in male maturation that ensures more males than females occur in this age-class, in

addition to an already male biased juvenile sex ratio. The difference in the timing of maturation also causes the female biased sex ratio in adults. Temporal variations in sex ratios may however arise due to differential emigration or immigration of different sexes (Lovich & Gibbons, 1990) or as a result of spatio-temporal differences in patterns of abundance in sexes (Perry *et al.*, 2010). The substantial change in adult sex ratio observed during the second year of this study could be as a result of large movement of adult males from the study area. Typically, polygynous males, in an attempt to find suitable females, may emigrate to other colonies. The findings of the use of relatively larger roosting areas in radio-tagged males (Chapter six) provide support for this claim.

Additionally, the CMR analysis found recapture probabilities in males to be lower than females, which may be an indication of higher emigration in males. Although in CMR analysis, possible emigration is confounded by death, it is unlikely that the mass deaths of adult males caused this significant change.

#### **7.4.5 Sex ratios in *M. pusillus* and other fruit bats encountered**

Sex ratios were female dominated for *M. pusillus*, *E. buettikoferi* and *H. monstrosus* but significantly male dominated for *E. helvum* and *R. aegyptiacus*, but. The sex ratios for the other species did not differ from unity. Sex ratio estimates for *M. pusillus*, *E. helvum* and *R. aegyptiacus* were based on captures made within identified colonies and may reflect actual population demographic profiles of the respective colonies. For the other species where it could not be confirmed that they were captured within their colonies or roost sites, the estimates of the sex ratios may be prone to the influence of sex-differences in night-time movement or behaviour.

Captures made away from roosts or colonies may only indicate feeding sites, and in species where sex differences in foraging behaviour exists, sex ratios are likely to be biased. In *H. monstrosus*, males and females are known to forage differentially; females utilise same areas and flight paths for foraging, while males can fly long distances in search of food (Langevin & Barclay, 1990). Thus females may be more likely to be encountered within an area than males. Also aggregations of males, typical of species that exhibit lek mating behaviour (e.g. *H. monstrosus* and *E. buettikoferi*) can cause sex ratios to be largely skewed. Sex ratios may also be largely influenced by differences in spatial and temporal patterns of occurrence between males and females (Perry *et al.*, 2010).

In *E. helvum*, there is evidence to suggest that females are more likely to migrate than males (Hayman *et al.*, 2012a). Although the reason for this is not well described, this female-biased migration in this species can create highly skewed male sex ratios in non migratory sedentary populations. In species where males form and defend territories and compete for females, adult sex ratios could be largely female biased as unsuccessful males may be excluded from roosting sites. In such cases, sex ratios will be a reflection of the mode of social organization in the species rather than a true reflection of demographic profile of the entire population (Storz *et al.*, 2000). In the interpretation and application of sex ratios, careful consideration should be given to possible sex related differences in various aspects of ecology and behaviour that are likely to influence sex ratios. Sex ratios may be artefacts of differential sex-behaviour rather than true reflections of the demographic profile of the entire population.

Estimates of demographic parameters are vital to understanding the current condition and predicting future viability of populations under different environmental conditions. For

species like *E. gambianus* where population trends are unknown, but based on the assumption that their distribution and population is large enough to withstand declines under local threats, studies like this could be vital in providing the true states of populations. Considering the zoonotic importance of fruit bats, these estimates are also essential to the future analysis of infection dynamics in fruit bats in Ghana.





## CHAPTER EIGHT

### 8.0 EVIDENCE OF HENIPAVIRUSES IN FRUIT BATS AND THE RISK OF ZOO NOTIC DISEASE SPILLOVER IN GHANA

#### 8.1 Introduction

Throughout the history of human health, infections from zoonotic origins have caused some of the most devastating outbreaks such as the Black Death, Spanish influenza, and HIV/AIDS (Morens *et al.*, 2004; Lloyd-Smith *et al.*, 2009). Over the past few decades, there has been a significant rise in the incidence of diseases of zoonotic origins, particularly from wildlife (Jones *et al.*, 2008; Wang & Crameri, 2014). It is estimated that over 70% of all Emerging Infectious Diseases (EID) in humans are of wildlife origin (Morens *et al.*, 2004; Wolfe *et al.*, 2007; Jones *et al.*, 2008). Current trends indicate a rise in the incidents of EID's and this is expected to continue, with predictions that future pandemics are likely to be zoonotic and of wildlife origin (Morse, 1995; Aluwong & Bello, 2010; Wang & Crameri, 2014).

Globally, infectious diseases present a significant threat to ecosystem and public health and remain the leading cause of mortality in the world (Daszak *et al.*, 2001; Morens *et al.*, 2004; Jones *et al.*, 2008). The cost of emerging zoonotic diseases (including those from wildlife) on human mortality and morbidity can be substantial. The economic impacts of these diseases are also very huge, usually running into millions of dollars (Morens *et al.*, 2004; Hayman, 2011).

Bats have been implicated in the outbreak of several zoonotic diseases that are becoming increasingly common and usually with devastating effects on human and domestic animal populations. Flying foxes (*Pteropus* sp.) are recognized as the main natural host

for henipaviruses (Plowright *et al.*, 2011; Clayton *et al.*, 2013; Plowright *et al.*, 2015). Flying foxes do not occur in mainland Africa so these viruses were thought to be restricted to the range of occurrence of flying foxes. However, recent studies (Hayman *et al.*, 2008b; Drexler *et al.*, 2009; Baker, 2012; Peel *et al.*, 2012) have identified Henipa or henipa-like viruses to be circulating in non pteropid fruit bat species that are widely circulated in Africa. In Ghana, several of these species of fruit bats occur and some are known to form very large roosts in rural and urban centres. Spillover of bat borne viruses to some domestic animals have been identified (Hayman *et al.*, 2011) and this enhances the risk of an outbreak of zoonotic disease from bats.

The genus henipavirus contains viruses that are known to be very pathogenic to both humans and domestic animals; notably, Hendra virus (HeV) and Nipah virus (NiV) (Smith *et al.*, 2011; Clayton *et al.*, 2013). Both viruses are known to cause severe encephalitis in humans with very high fatality rates. Since its discovery in Australia in 1994, Hendra virus has caused the deaths of many horses with successful transmissions which have been fatal to humans (Murray *et al.*, 1995; Clayton *et al.*, 2013). NiV emerged in Malaysia in 1998 and caused an almost collapse of the Malaysian pig industry with the deaths of over one million pigs and the deaths of 100 humans. Other NiV outbreaks have occurred in India and Singapore with very high human fatality rates (Drexler *et al.*, 2009; Clayton *et al.*, 2013). A third member of the henipaviruses, Cedar virus (CedV), was recently identified in Pteropus bats in Australia. However, unlike HeV and NiV, CedV infected subjects showed no clinical signs of disease in experimental infection studies (Marsh *et al.*, 2012).

Identifying the pathways through which humans and domestic animals are exposed to bats may well be key to understanding the source of outbreak of bat-borne viruses and

help to prevent future outbreaks (Drexler *et al.*, 2009). This chapter provides additional serological evidence for the presence of henipaviruses in fruit bats in Ghana and identifies human bat-interaction pathways through which zoonotic disease spillover and/or transmission can occur to augment the pathways reported by recent studies in Ghana (Anti *et al.*, 2015; Lawson *et al.*, 2016; Leach *et al.*, 2017; Ohemeng *et al.*, 2017).

## 8.2 Methodology

Bat trapping and blood sampling procedure followed the methods as described in Chapter three (Sections 3.5 and 3.6 respectively). Blood samples were taken from five species of fruit bats that were trapped from four locations. Blood samples collected were screened for antibodies against soluble glycoproteins of selected paramyxoviruses; Hendra (HeV-G, HeV-F) Nipah (NiV-G and NiV-F) and Cedar (CedVG) viruses using the Luminex multiplexed binding assays (Baker, 2012) (see Chapter three, section 3.7 for methodology). The results of the binding assays are given as MFI values  $\geq 100$  microspheres for each type of virus.

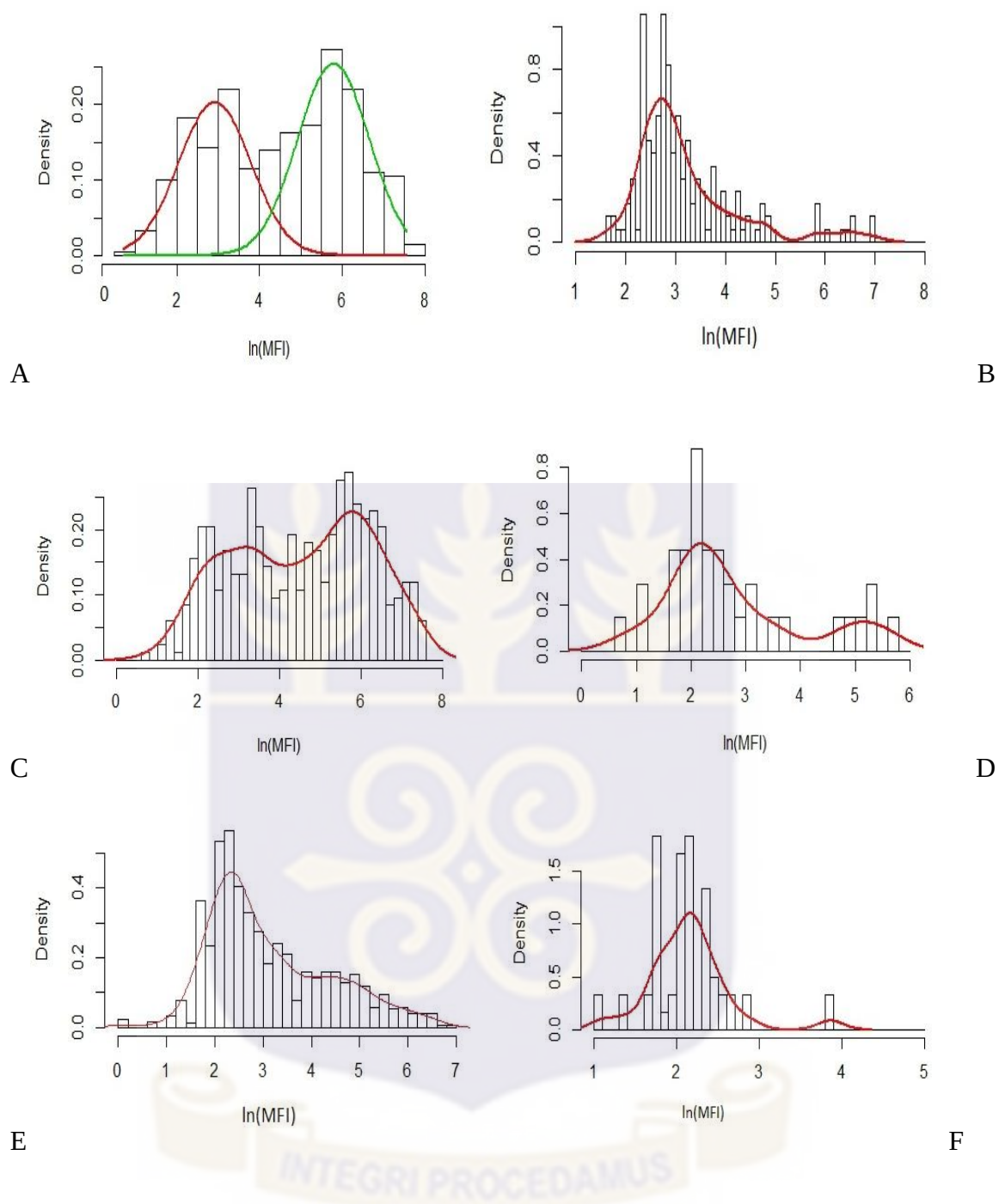
MFI values reported were negatively skewed so all values were log transformed ( $\ln$ ) before further analyses were performed. It was assumed that bats sampled from different sites were from single metapopulations. Hence, MFI values for each species was pooled across all sites but separate analysis was carried out for each soluble glycoprotein of each virus type.

### 8.2.1 Frequency distributions for $\ln(\text{MFI})$ values

Separate frequency distributions were plotted for  $\ln(\text{MFI})$  values for each species-glycoprotein-virus type combination in an effort to differentiate between "seropositive" and "seronegative" individuals. The assumption was that if there are only seronegative individuals in the population sampled, then the distribution of  $\ln(\text{MFI})$  values would be normally distributed around an unknown mean. In such a case, a normal distribution should describe the data very well.

However, if both seronegative and seropositive individuals are present in the population, then a bimodal frequency distribution of  $\ln(\text{MFI})$  values should be observed with peaks indicating seronegative and seropositive individuals. To examine whether  $\ln(\text{MFI})$  frequency distributions were unimodal or bimodal, a normal distribution model and a 4 parameter mixture model was fitted to each frequency distribution to assess which model best described the frequency distributions. Figure 8.1 shows the output of density plots for  $\ln(\text{MFI})$  distributions indicating bimodal distributions.

The best fit model was assessed using Akaike Information Criterion (AIC). The models are statistically significantly different if  $\text{AIC}_1 - \text{AIC}_2 > 2$ ; in which case the model with the lowest AIC value was selected as the best model. However, a difference of  $< 2$  implied all MFI values in that distribution was from seronegative individuals. If the models were significantly different and the normal distribution was the best fit model, then all MFI values were seronegative. However, if the mixture model was the best fit model, then the MFI frequency distribution contained both seronegative and seropositive individuals.



**Figure 8.1 Illustrations of frequency distributions of  $\ln(\text{MFI})$  values for virus binding assays.**

**A-** HeV-F for *E. helvum* showing bimodal peaks for seronegative individuals (red) and seropositive individuals (green). **B-** NiV-G for *R. aegyptiacus*. **C-** HeV-F for *E. helvum*. **D-** NiV-F for *L. angolensis*. **E-** HeV-G for *E. helvum*. **F-** CedV for *M. pusillus*.

### 8.2.2 Determination of appropriate cut-off for MFI values

For  $\ln(\text{MFI})$  distributions that were identified to be bimodal, peaks in  $\ln(\text{MFI})$  distributions were assumed to represent mixed distributions of seronegative bats (with peaks on the left) and seropositive bats (with peaks on the right) (see Figure 8.1). Appropriate cut-offs were chosen by determining a  $\ln(\text{MFI})$  value above which values were unlikely to be seronegative to differentiate between seronegative and seropositive individuals. This was calculated from the mean and standard deviations of the mixture models. The mixture model has two mean and standard deviation values (one for each of the observed distributions). The lowest of these means (and its standard deviation) belongs to the seronegative distribution. Since 99% of values in a normal distribution are within the mean  $\pm 3$  standard deviations, it implies that any value found above the “mean + 3sd” threshold for the seronegative distribution, has less than 1% chance of being negative, which suggests that it's most likely positive.

For each distribution, this value was calculated and used as a cut-off value to assign individuals as seropositive or seronegative. Prevalence with appropriate 95% confidence intervals was calculated where applicable. The association of gender and age factors on seropositivity was examined using chi square tests of associations or Fisher's exact tests. Model mixture fitting, model selection and estimation of cut-off values were done in R (R Core Team, 2014). The model mixture fitting was done using the package "mixtools" (Benaglia *et al.*, 2009).

### 8.2.3 Human Bat interactions

To explore the extent to which bats occur in close proximity to humans, bat roosts that were identified during roost searches (Chapter four) was related to human population



density in Ghana. The distance between identified roosts and nearest buildings and homesteads or to the nearest human activity point was also estimated. During visits to roost sites, direct observations were made to identify ways through which humans interacted with bats at roost sites. Any human action or human behaviour that was likely to bring humans in direct or indirect contact with bats or bat body fluids (saliva, blood, and faecal material) was recorded. During the questionnaire interviews that was conducted with residents around roost sites (Chapter four), respondents were also asked about the incidence and frequency of bat hunting at roost sites. This information, in addition to direct observation was used to assess bat hunting at roosts. Because domestic animals may also serve as intermediate hosts or amplifier hosts for some zoonotic diseases, ways in which domestic animals interacted with bats (direct or indirect ways) were also noted but in an unstructured way.

### **8.3 Results**

#### **8.3.1 Seroprevalence of henipaviruses in fruit bats**

A total of 1,047 individual fruit bats belonging to nine species were sampled from four locations for serology. Samples from *E. gambianus* and *E. helvum* were the most numerous, together comprising 82% of all samples tested. Samples from *H. monstrosus* and *N. veldkampii* were the least with 8 samples from each species. Table 8.1 gives details of the individual bats that were sampled.

With the exception of samples from *N. veldkampii* which showed no seroprevalence to any of the viruses, all other species were seropositive for at least one of the viruses tested. A total of 355 out of 1,047 individuals were seropositive to at least one of the three viruses (Nipah, Hendra and Cedar viruses). Of the individuals that were tested for

NiV (total of 1,047), 328 of these individuals were seropositive; 210 of 1,047 tested for HeV were seropositive and 13 individuals out of a total of 590 that were tested for CedV were seropositive.

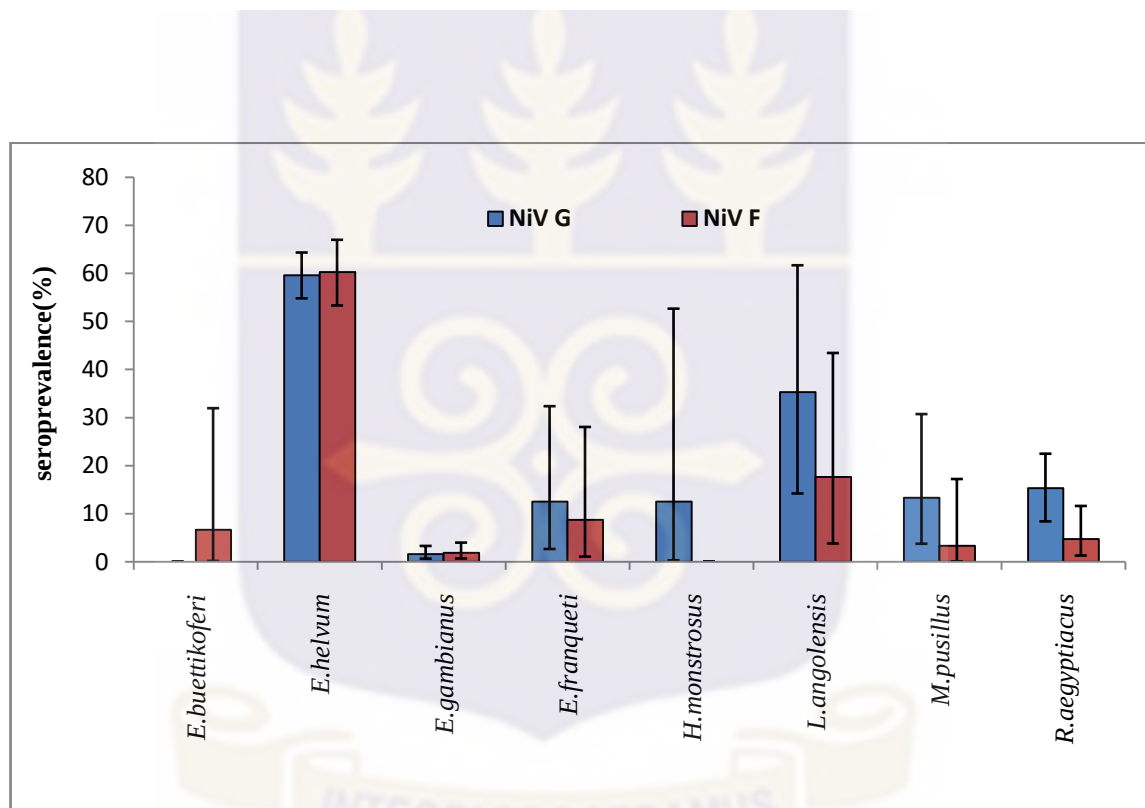
**Table 8.1 Summary of fruit bat species sampled.**

*Ad-Adult, SI-Sexually immature adult, Juv-Juvenile*

| SPECIES                | Female     |            |           | Male       |            |           | Total       | *un-classified | Grand Total |
|------------------------|------------|------------|-----------|------------|------------|-----------|-------------|----------------|-------------|
|                        | Ad         | SI         | Juv       | Ad         | SI         | Juv       |             |                |             |
| <i>E. buettikoferi</i> | 9          | 2          | 2         | 2          |            |           | 15          |                | 15          |
| <i>E. franqueti</i>    | 5          | 4          | 4         | 2          | 4          | 4         | 23          | 1              | 24          |
| <i>E. gambianus</i>    | 90         | 63         | 43        | 63         | 99         | 68        | 426         | 8              | 434         |
| <i>E. helvum</i>       | 73         | 45         | 9         | 230        | 52         | 17        | 426         |                | 426         |
| <i>H. monstrosus</i>   | 5          | 1          | 1         |            |            | 1         | 8           |                | 8           |
| <i>L. angolensis</i>   | 5          | 1          |           | 8          | 3          |           | 17          |                | 17          |
| <i>M. pusillus</i>     | 6          | 8          | 4         | 3          | 7          | 1         | 29          | 1              | 30          |
| <i>N. veldkampii</i>   | 1          |            |           | 6          | 1          |           | 8           |                | 8           |
| <i>R. aegyptiacus</i>  | 23         | 10         | 3         | 31         | 11         | 6         | 84          | 1              | 85          |
| <b>TOTAL</b>           | <b>217</b> | <b>134</b> | <b>66</b> | <b>345</b> | <b>177</b> | <b>97</b> | <b>1036</b> | <b>11</b>      | <b>1047</b> |

*\*individuals whose age or gender were not determined.*

Fifty-eight percent of all *E. helvum* samples were seropositive for at least one of the viruses tested. Possible infection with Nipah virus (NiV-G, F) was very high in *E. helvum* which showed seroprevalence of 59% and 60% to NiV-G and NiV-F respectively (Figure 8.2). *E. buettikoferi* showed reactivity to NiV-F (6.67%) while a single *H. monstrosus* showed reactivity only to NiV-G. In the other species, individuals sampled were reactive to both Nipah soluble proteins but seroprevalence was higher in NiV-G than NiV-F. Less than 2% of *E. gambianus* sampled showed seropositivity to both NiV-G and NiV-F (Figure 8.2).

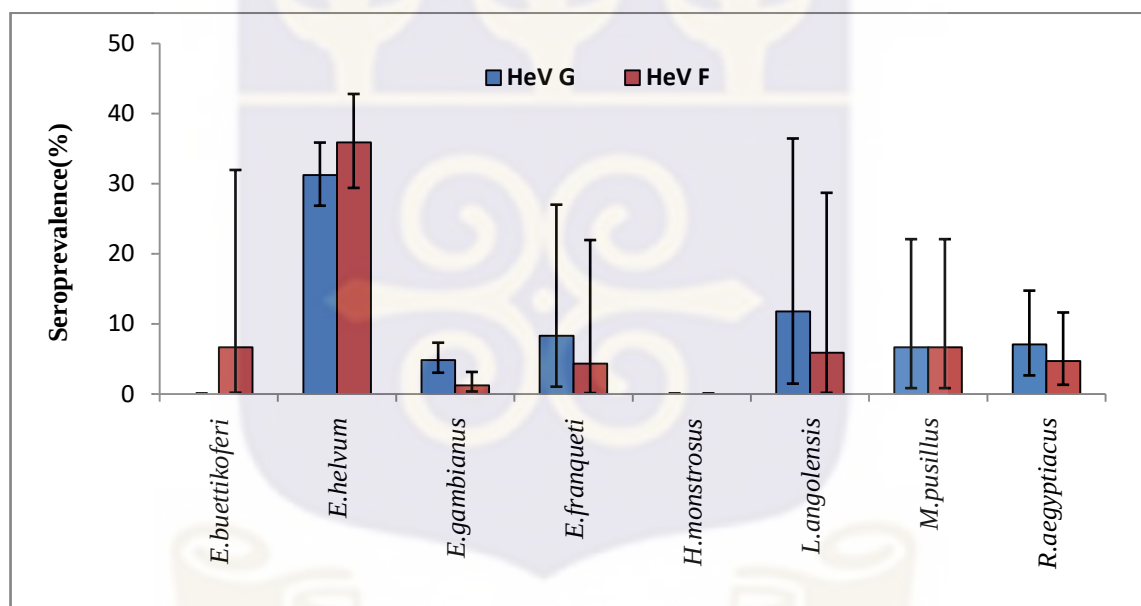


**Figure 8.2 Bat species and their respective seroprevalence rates for Nipah virus.**

Vertical lines are 95% confidence intervals.

Figure 8.3 shows seroprevalence and 95% confidence intervals of the various fruit bats for Hendra virus (HeV-G, F). None of the *H. monstrosus* was seropositive for Hendra virus. A single *E. buettikoferi* individual which was seropositive for NiV-G was also

seropositive for HeV-G. Again, evidence for infection with HeV virus in *E. helvum* was very common; 31% (95% CI: 27-36%) seropositive to HeV-G and 36% (95% CI: 29-43%) of individuals seropositive for HeV-F. A single *L. angolensis* showed reactivity to HeV-F and two individuals showed reactivity to HeV-G. In *M. pusillus* two individuals showed reactivity to both Hendra G and F proteins. Seroprevalence in *E. gambianus* was 4.8% (95% CI: 3.0-7.3%) for HeV-G and 1.2% (95% CI: 0.3-3.1%) for HeV-F. For all the other species except *E. helvum* and *E. buettikoferi*, reactivity to HeV-G was more common than HeV-F.

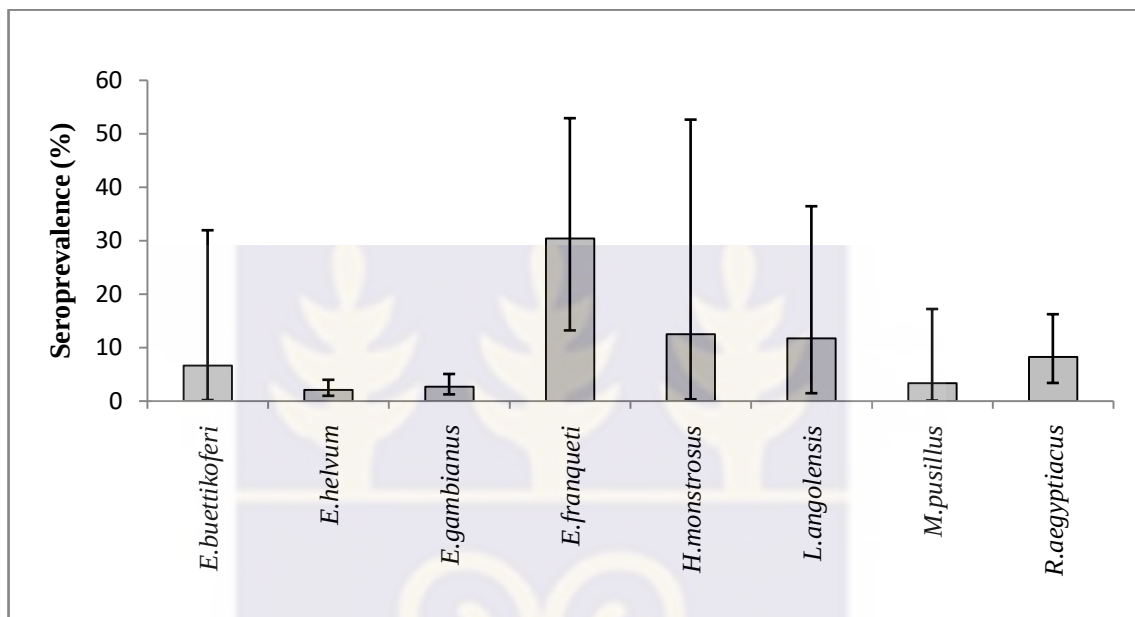


**Figure 8.3 Bat species and their respective seroprevalence rates for Hendra virus.**

Vertical lines are 95% confidence intervals.

Seropositivity to Cedar virus (CedV) was highest in *E. franqueti* with 30% (95% CI: 13-53%) of individuals showing reactivity to this virus (Figure 8.4). In *E. gambianus* and *E. helvum* seropositivity to CedV was observed in less than 3% of individuals sampled for each species. Single individuals of *E. buettikoferi*, *M. pusillus* and *H. monstrosus* were

also seropositive to CedV. In *L. angolensis*, two individuals (out of 17 sampled) showed reactivity to CedV whiles in *R. aegyptiacus*, seven individuals out of 85 showed reactivity to the virus.



**Figure 8.4 Bat species and their respective seroprevalence rates for Cedar virus.**

*Vertical lines are 95% confidence intervals*

In all the species except *E. helvum*, there was no significant association between gender and seropositivity to specific viruses. In *E. helvum* significant association between gender and seropositivity was observed for Nipah virus (NiV-G and F) only. For NiV-G, *E. helvum* males were significantly more likely to be seropositive than females (191 of 299 males were seropositive compared with 63 of 127 females;  $\chi^2=7.54$ ,  $p = 0.006$ ). Similarly, for NiV-F, *E. helvum* males were significantly more likely to be seropositive than females (94 of 142 males were seropositive compared with 32 of 67 females; Fishers exact test,  $p=0.015$ ). Table 8.2 shows gender specific seroprevalence results for the different species of fruit bats.

**Table 8.2 Sex-specific serological results for fruit bats sampled.**

♀- female, ♂-male. Figures shown in bold indicate significant sex differences in seroprevalence. +/N indicates number of seropositive samples / total number of samples tested.

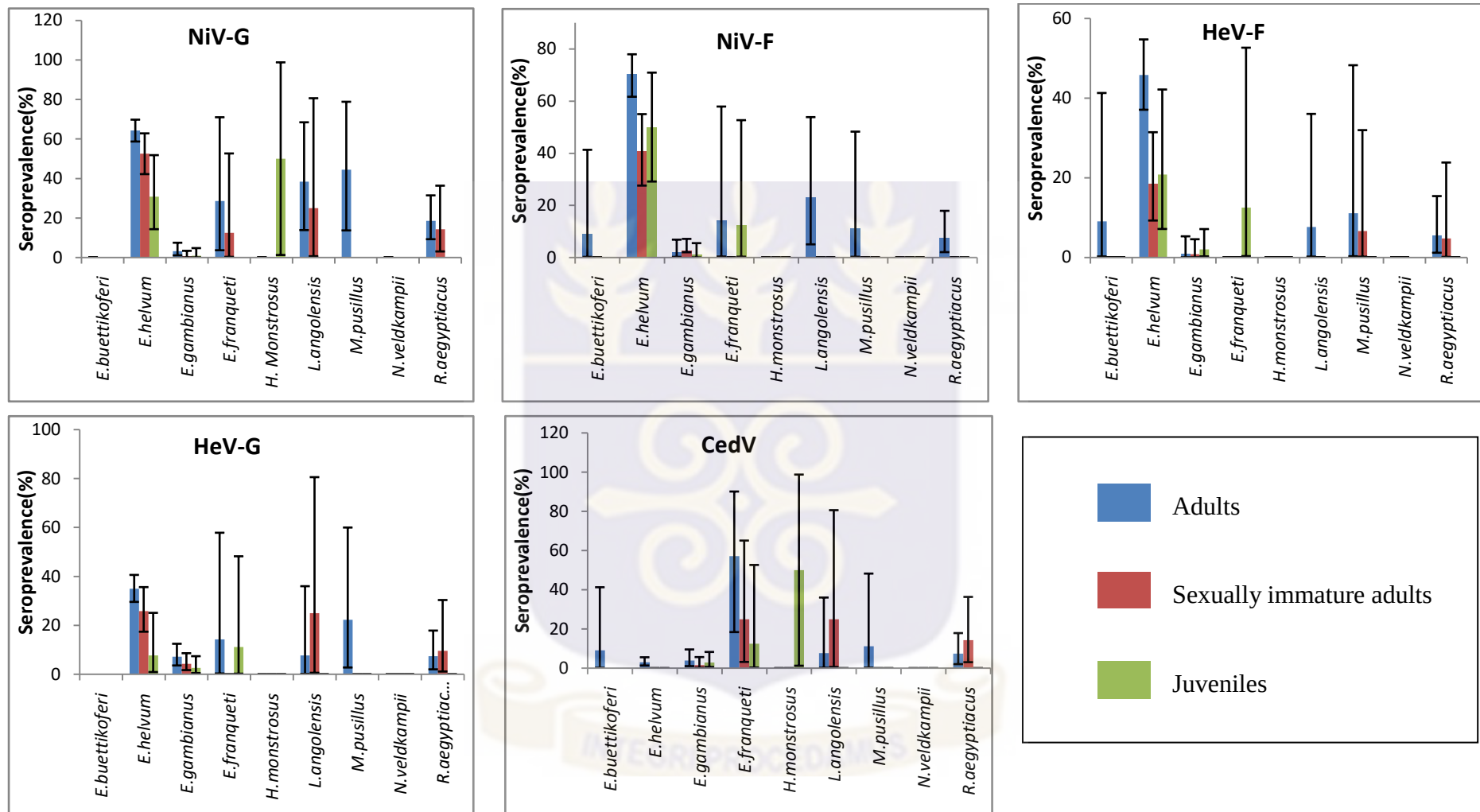
| SPECIES                | SEX | NiV-G   | NiV-F  | HeV-F  | HeV-G   | CedV  |
|------------------------|-----|---------|--------|--------|---------|-------|
|                        |     | (+/N)   | (+/N)  | (+/N)  | (+/N)   | (+/N) |
| <i>E. buettikoferi</i> | ♀   | 0/13    | 0/13   | 0/13   | 0/13    | 0/13  |
|                        | ♂   | 0/2     | 1/2    | 1/2    | 0/2     | 1/2   |
| <i>E. franqueti</i>    | ♀   | 1/13    | 0/13   | 0/13   | 0/13    | 5/13  |
|                        | ♂   | 2/10    | 2/10   | 1/10   | 2/10    | 2/10  |
| <i>E. gambianus</i>    | ♀   | 4/196   | 4/134  | 1/134  | 7/196   | 2/137 |
|                        | ♂   | 3/230   | 2/188  | 3/188  | 14/230  | 7/195 |
| <i>E. helvum</i>       | ♀   | 63/127  | 32/67  | 20/67  | 33/127  | 3/127 |
|                        | ♂   | 191/299 | 94/142 | 55/142 | 100/299 | 6/299 |
| <i>H. monstrosus</i>   | ♀   | 1/7     | 0/7    | 0/7    | 0/7     | 1/7   |
|                        | ♂   | 0/1     | 0/1    | 0/1    | 0/1     | 0/1   |
| <i>L. angolensis</i>   | ♀   | 3/6     | 1/6    | 1/6    | 1/6     | 0/6   |
|                        | ♂   | 3/11    | 2/11   | 0/11   | 1/11    | 2/11  |
| <i>M. pusillus</i>     | ♀   | 3/18    | 1/18   | 1/18   | 1/18    | 1/18  |
|                        | ♂   | 1/11    | 0/11   | 1/11   | 1/11    | 0/11  |
| <i>N. veldkampii</i>   | ♀   | 0/1     | 0/1    | 0/1    | 0/1     | 0/1   |
|                        | ♂   | 0/7     | 0/7    | 0/7    | 0/7     | 0/7   |
| <i>R. aegyptiacus</i>  | ♀   | 6/36    | 2/36   | 2/36   | 5/36    | 5/36  |
|                        | ♂   | 7/48    | 2/48   | 2/48   | 1/48    | 2/48  |



There was an association between age and seropositivity but this was observed only in *E. helvum*. Significant association between age and seropositivity in *E. helvum* was observed for Nipah and Hendra viruses. Adult *E. helvum*, were more likely to be seropositive than sub-adults and juveniles for NiV-G ( $\chi^2=14$ ,  $p=0.001$ ) and NiV-F ( $\chi^2=15$ ,  $p=0.001$ ). Similarly, for Hendra virus, adults were more likely to be seropositive than juveniles and sub-adults for both HeV-G ( $\chi^2=9.4$ ,  $p=0.009$ ) and HeV-F ( $\chi^2=15$ ,  $p=0.001$ ). Figure 8.5 shows the seroprevalence and 95% CI for the age groups for each species.

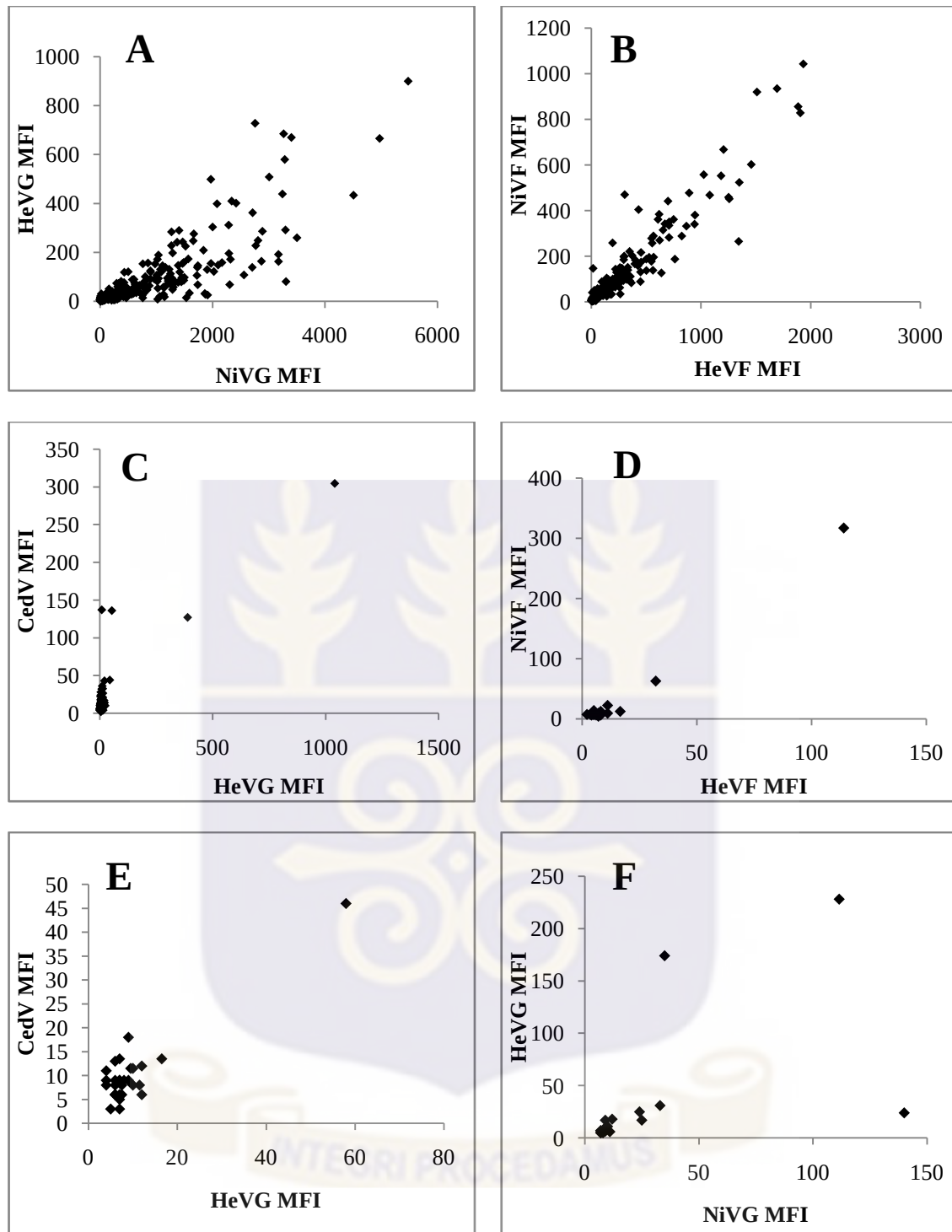
There was evidence for possible cross-reactivity to viruses in the sera analysed. Figure 8.6 illustrates cross reactivity to different viruses in sera from different fruit bat species. NiV cross-reactivity to HeV was common in several species but particularly evident in *E. helvum*. Cross-reactivity of CedV to HeV-G was also common in several species and appeared more evident than CedV cross-reactivity to NiV-G.

Co-infection with multiple viruses was very common. Over 52% of all seropositive individuals showed reactivity to at least two of the three viruses. 2.5% of all seropositive individuals were also reactive to all the three viruses (Figure 8.7). Of the individuals that were seropositive to NiV, 56.4% were also seropositive to HeV, with 3.4% also seropositive to CedV. A total of 88.1% of HeV seropositive individuals were also seropositive to NiV, and 9 of the 13 individuals that were seropositive for CedV were also seropositive to both NiV and HeV.



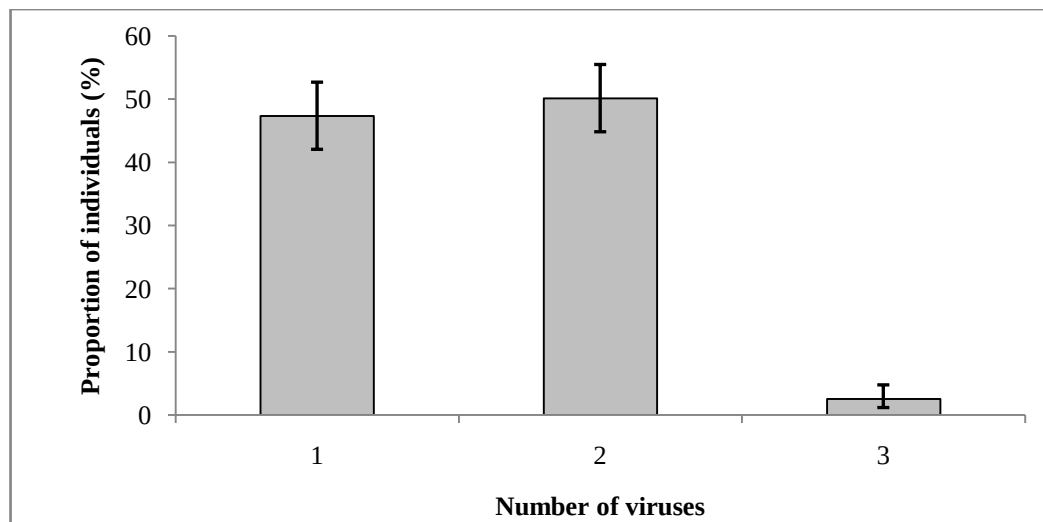
**Figure 8.5 Seroprevalence to viruses across age categories for fruit bats sampled.**

Vertical lines are 95% confidence intervals.



**Figure 8.6 Serological cross-reactivity between viruses in fruit bats.**

**A, B-** *E. helvum*; **C-** *E. gambianus*; **D-** *E. franqueti*; **E-** *M. pusillus*; **F-** *L. angolensis*



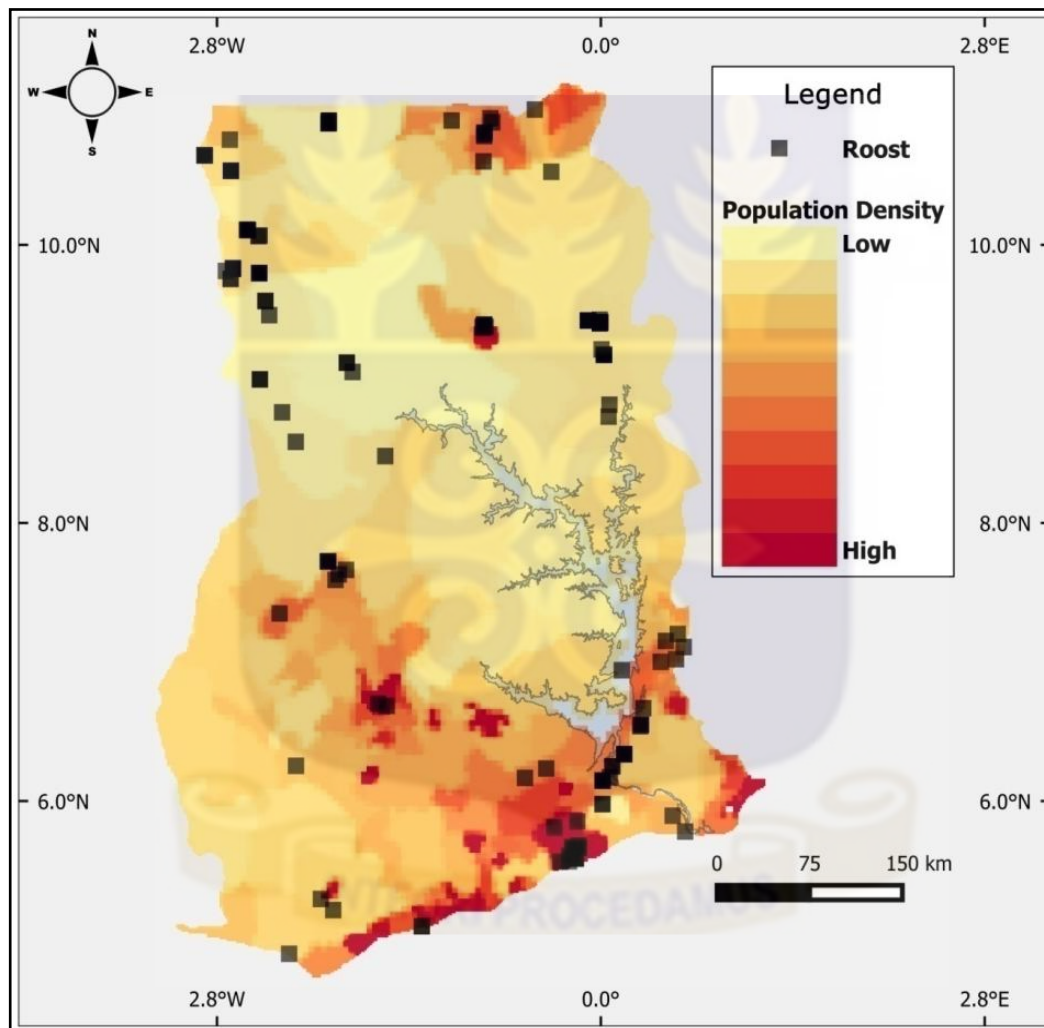
**Figure 8.7 Co-infection of viruses in fruit bats sampled.**

### **8.3.2 Human-bat interactions and potential disease spillover routes**

Fruit bat roosts that were identified from the citizen science roost reports and the nationwide roost search (see Chapter four), commonly occurred in densely populated places in both rural and urban areas (Figure 8.8). All detected roosts occurred within at least 100 m of some human activity, with a majority of these occurring within 50 m of buildings and homesteads, including animal pens.

From the interviews with respondents at roost sites, hunting was a common occurrence at most roost sites and one of the major source of human-bat interactions. Hunting of *E. gambianus* often occurred at small scales mostly by children using catapults while the much larger *E. helvum* was hunted by men at a more commercial and larger scale using shotguns or nets. A bat hunter in Sandema in northern Ghana however described the hunting of *E. gambianus* on a much larger scale using nets that was set between roosting trees to catch large numbers of this species. The bats trapped were killed, roasted and

eaten or smoked and sold for between GHC 0.5-1.0\*<sup>1</sup> within the town or transported to southern Ghana for sale. Most hunters handled bats with bare hands and came into direct contact with fresh bat blood and other bat body fluids. A hunter recounted being bitten by a bat when he picked it up with his bare hands because he wrongfully presumed it to be dead after he had shot it to the ground.



**Figure 8.8 Fruit bat roost distribution in relation to human population density of Ghana.**

\*<sup>1</sup> 1USD = 4 GHC

According to respondents, contact with bat faeces and urine was common at roost sites. Several activities including the sale of food, relaxation, keeping of domestic animals and cooking occurred under roosting trees and exposed both humans and domestic animals to regular contact with bat urine and faecal droppings. Contact between domestic animals and bats was also very common. A domestic cat was observed eating a bat (identified to be *E. gambianus*) in a bat roost tree after the cat had climbed up the tree and caught the bat. A respondent also described seeing pigs consume a bat just after it fell from a roosting tree. In some locations especially rural areas, domestic animals were also observed to be kept in open pens under bat roosts. The feed for such animals were placed on the bare ground under bat roosts where they could easily be contaminated with bat ejecta pellets, faeces and urine.

The collection and consumption of fruits partly eaten, or dropped by foraging fruit bats was another route for potential disease spillover. Local people were seen picking fruits (e.g. black plum *Vitex doniana*, shea fruits *Vittellaria paradoxia*, and mango *Mangifera indica*) that had fallen under trees for consumption; thus could pose risks of disease transmission. Plate 8.1 shows different scenarios that result in interactions between bats and humans/domestic animals.





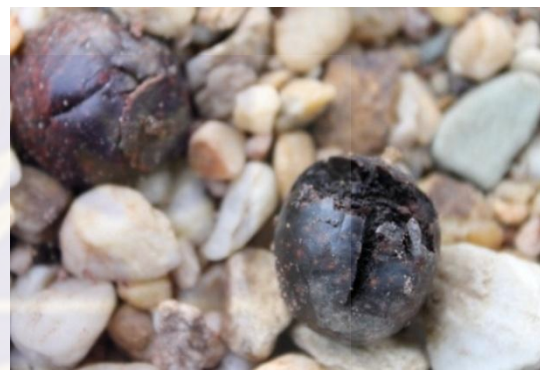
A hunter handling freshly killed *E. helvum*



Bat droppings on vegetables sold under a roost



A guava fruit partly eaten by bats



Partly eaten *Vitex doniana* fruits dropped by foraging bats



Bat faecal and ejecta pellets under roosts



Free ranging pigs feeding under bat roost

**Plate 8.1 Identified potential disease spillover routes between bats and humans/domestic animals.**

## 8.4 Discussion

### 8.4.1 Henipavirus infection in fruit bats in Ghana

Results from this study add extra evidence to the presence of zoonotic viruses, particularly henipaviruses, in fruit bats that occur in Ghana. Hayman *et al.* (2008a) used Virus Neutralizing tests and provided the first evidence of henipavirus infection in *E. helvum*, *E. gambianus* and *H. monstrosus* in Ghana. Other studies have confirmed henipa-like virus RNA in fruit bats in Ghana (Drexler *et al.*, 2009). Unlike HeV and NiV, there is very little known about the infection and circulation of Cedar virus in fruit bats in Ghana. This is likely because of a surveillance bias due to its rather more recent discovery (Marsh *et al.*, 2012).

Similar to the study by Hayman *et al.* (2008a), seropositivity to HeV and NiV was highest in *E. helvum* compared to other fruit bats sampled. *E. helvum* has been found to be genetically more related to flying foxes (Pteropus) (Alvarez *et al.*, 1999) which are known as the reservoir hosts for henipaviruses (Rahman, 2010; Plowright *et al.*, 2011; Clayton *et al.*, 2013; Plowright *et al.*, 2015). This may explain the high seropositivity of *E. helvum* to HeV and NiV compared to the other species. Other species may rather be spillover hosts for these viruses from *E. helvum*. Nevertheless, once successful spillover to other species from *E. helvum* occurs, these other fruit bat species may successfully sustain infections within their populations.

Host ecology can also influence pathogen infection dynamics within species (Hayman *et al.*, 2013). The difference in ecological strategies exhibited by the different fruit bat species may reflect the differences in their susceptibility to these viruses and their ability to maintain infections. This may provide an alternative explanation to the differences in seroprevalence observed in the different species. For instance, Hayman *et al.* (2008a)

suggested that the clustering and formation of large colonies in *E. helvum* may aid the spread and maintenance of henipavirus infection within this species compared to other species that form loose colonies of a few individuals.

There was an observed gender effect on seropositivity to NiV in *E. helvum* where males were more likely to be seropositive than females in this work. Hayman *et al.* (2008a) detected a slight interaction between gender and serostatus of *E. helvum* to HeV, where females were only marginally ( $p=0.09$ ) more likely to be seropositive than males. This is suggestive of gender as a risk factor in henipavirus infection in fruit bats particularly in *E. helvum*. In other studies (Plowright *et al.*, 2008; Breed *et al.*, 2011; Rahman *et al.*, 2013; Baker *et al.*, 2014) there was no gender influence on henipavirus serostatus but rather, other factors such as reproductive condition (pregnancy, lactation), were identified as risk factors for henipavirus infection.

Although the effect of reproductive condition on seroprevalence was not assessed in this study (due to low sample sizes across the different categories), there were some findings that suggested that these factors could increase the risk of henipavirus infection. For instance, in *E. gambianus*, and *R. aegyptiacus* all the adult females that were seropositive to HeV were either pregnant or lactating. This suggests an increased susceptibility to henipavirus infection during these energetically costly periods. Plowright *et al.* (2008) describes a similar observation for Hendra infection in the Little red flying foxes (*Pteropus scapulatus*). Some studies found no such effect of these factors on henipavirus infection in other *Pteropus* species (Epstein *et al.*, 2008; Halpin *et al.*, 2011).

The post neonate seropositivity to henipaviruses within bat populations has been shown to increase with age; the findings from this study were consistent with this observation. In *E. helvum*, adult bats were significantly more likely to be seropositive to HeV and



NiV than juveniles and sub-adults. Several studies [e.g. Plowright *et al.* (2008); Peel *et al.* (2013); Baker *et al.* (2014)] show that seroprevalence to henipaviruses is initially high among neonates and very young juveniles (due to transferred maternal antibodies). This decreases with increasing age (as maternal antibodies wane) until sub adult age after which susceptibility to natural infection (and seroprevalence) increases with increasing age.

Cross-reactivity between different henipaviruses is commonly reported in serology studies. In this study HeV showed cross reactivity to NiV. Cross-reactivity of Cedv to HeV and NiV has also been demonstrated (Marsh *et al.*, 2012); similar observations were made in this study. The very low MFI readings for CedV suggest that infections in the species of fruit bats sampled are more likely to be HeV or NiV. Nevertheless, for a few individuals, who were seropositive to HeV and NiV, relatively higher MFI readings for CedV were also recorded. This suggests the possibility of CedV infection and co-infection of multiple henipaviruses in some of these fruit bats. Marsh *et al.* (2012) describe CedV infection and co-infection with HeV in Australian bat populations. This study, like other serological studies does not provide proof of bats that are shedding viruses (Epstein *et al.*, 2008). Thus, additional research is still needed to fully understand henipavirus infection dynamics in fruit bats.

#### **8.4.2 Human bat interactions and implications for disease spillover.**

The increasing incidences of zoonotic disease emergence including those from bats have been primarily linked with anthropogenic causes and the increasing human population (Morse, 1995; Daszak *et al.*, 2000; Aluwong & Bello, 2010; Hayman, 2011). Several HeV and NiV outbreaks are known to occur in areas undergoing rapid expansion and

areas with high human population densities (Plowright *et al.*, 2011; Hahn *et al.*, 2014; Plowright *et al.*, 2015).

Most roosts identified occurred in close proximity to human habitations. It must be noted that the bat roosts identified in this study will not be the only bat roosts in Ghana and that there may be other roosts in remote and forested areas that are yet to be located. Intensive roost searching efforts and the use of high resolution GPS loggers to track bats may be required to locate such bat colonies and roosts.

Nevertheless, globally, there is an increasing human population with resulting demand for land which is causing increasing encroachment into natural habitat of wild animals (Daszak *et al.*, 2001; Wolfe *et al.*, 2005; Wang & Crameri, 2014). This has led to increasing proximity and contact between humans and wild animals, including bats, and could explain the occurrence of several roosts close to human habitation. Considering the current trends in the loss of forests, habitat degradation and human population growth rates, it is predicted that new bat roosts are likely to be formed close to humans.

This study's findings of several fruit bat roosts in areas with high human population densities raise serious concerns about the potential spillover of viruses from bats in Ghana. The proximity of bats to areas with high human population increases the potential for contact between bats and humans and with domesticated animals (Plowright *et al.*, 2011).

The likely pathways for zoonotic spillover from bats in Ghana would include contact with faeces and urine under bat roosts, direct contact with bats through hunting, consumption of partly eaten or bat contaminated fruits and through domestic animals acting as spillover host or as amplifier hosts. These routes have led to successful transmission of bat-borne diseases elsewhere although it required the bats to be shedding

the viruses. Studies have confirmed bats to be shedding viruses through urine which has successfully led to outbreaks of He-V in Australia (Plowright *et al.*, 2015) and Ni-V in Bangladesh (Hahn *et al.*, 2014). In Malaysia, NiV transmission from bats to pigs was reported to have occurred via the consumption of saliva-contaminated fruit pulp discarded by foraging bats or through faecal or urine contamination of pig sties (Pulliam *et al.*, 2012). In Ghana, RNA of henipaviruses have been identified in fruit bat faecal droppings collected under day roosts (Drexler *et al.*, 2009) and likely to occur also in bat urine (Chua *et al.*, 2002; Plowright *et al.*, 2008; Halpin *et al.*, 2011). A lot of humans and domestic animals in Ghana are in continuous contact and exposure to bat body fluids through these identified routes and this implies a high risk and probability of infection of zoonotic diseases from bats in Ghana.

Fruit bats are hunted across most of their range especially in Africa and Asia (Mickleburgh *et al.*, 2002; Mickleburgh *et al.*, 2009; Mildenstein *et al.*, 2016). Globally, bats are hunted for a variety of reasons, but in Ghana, they are hunted mainly for their meat (Kamins *et al.*, 2015; Mildenstein *et al.*, 2016). Kamins *et al.* (2015) suggest that bat meat is a preferred meat among several Ghanaians, highlighting the extent of exploitation of *E. helvum* in Ghana. Hunting was found to occur in several previously unreported roosts of this species during this study. This suggests that hunting levels may far exceed rates previously projected by Kamins *et al.* (2015). Other species like *E. gambianus* are also hunted to some extent in Ghana and form a significant part of bat bushmeat, particularly in northern Ghana.

Hunting is recognised as a high risk activity in the transmission of diseases from wildlife to humans (Wolfe *et al.*, 2005; Subramanian, 2012). Bat hunters come into direct contact with blood and other body fluids, receive bites and scratches from bats as their activities



are carried out without any protection (Kamins *et al.*, 2015) and can easily be infected with zoonotic pathogens. For instance, the direct contact and handling of bats during hunting was suggested as the cause of the Ebola outbreak in 2007 in Luebo, Congo (Leroy *et al.*, 2009). The high incidence of bat hunting recorded at roosts in Ghana is of great concern as this may imply higher risk of disease spillover through bat hunting in Ghana.

The occurrence of bat roosts near humans does not necessarily imply successful zoonotic transmission. For successful transmission of these viruses from bats to occur, this requires a series of enabling conditions to be met (Plowright *et al.*, 2015) and most often, human practices play a vital role in the events leading to successful zoonotic transmission from bats (Hahn *et al.*, 2014). For instance, in case of Nipah outbreaks in Bangladesh, it was the practice of collecting palm sap in bowls left uncovered which provided easy access for bats to lap the juice and thereby contaminating the collected palm sap. Hence, changes in human behaviour and practices such as avoiding partly eaten or contaminated fruits, wearing of protective gear when handling bats and keeping of domestic animals in covered pens away from roost trees, could reduce exposure levels and the risks of zoonotic spillover from bats in Ghana.

## CHAPTER NINE

### 9.0 GENERAL DISCUSSION

Bats are an ecologically important group of mammals. The ecological strategies in bats are often unique and diversified, thus giving them the ability to play key roles in ecosystem service provisioning and in zoonotic disease transmission. In tropical environments such as Africa, the outcome of the ecological strategies in fruit bats (family pteropodidae) includes vital processes such as the regeneration and maintenance of tropical forest and also the outbreak of zoonotic diseases. Knowledge of the ecological strategies of fruit bats is important and helps in identifying how they impact our ecosystems, what drives or affects their ecological decisions or how they influence disease transmission. Although such outcomes of fruit bat ecological strategies often involve an intricate mix of factors that may not be easily inferred, our ability to make any progress is hindered by the lack of knowledge of the ecology of several species.

This study investigated the ecology of fruit bats, with particular focus on *Epomophorus gambianus* and the role fruit bats play in the transmission of zoonotic diseases. The findings of this study are presented in five chapters namely;

- distribution of fruit bats and people's perceptions of bats in Ghana;
- demography of fruit bats in Ghana;
- seasonal variation in food availability and relative use of dietary items in *Epomophorus gambianus*;
- roost site selection and roosting behaviour of *Epomophorus gambianus*;
- evidence of henipaviruses in fruit bats and risk of zoonotic disease spillover in Ghana.

The set of results obtained are discussed under each chapter. This section of the thesis therefore draws out the key observations and discusses these in relation to the findings reported from other studies in the subject area. It also illustrates how different ecological aspects of bats are interrelated and how other factors influence bat ecology. The role of bat ecology and human impacts in determining zoonotic disease risks in Ghana and the implications for bat conservation in Ghana are also discussed.

### **9.1 Life history of bats: an interaction of multiple ecological strategies**

Bats are atypical mammals in several ways; from ecology, locomotion, biology, evolution and taxonomy. Within the chiroptera, although life histories are relatively similar, there is significant variation in the ecology and biology of different species (Barclay *et al.*, 2003); the different aspects of the ecology and biology of a species are interconnected, with each playing a role in shaping the life history of the species. Although the linkages between the various life traits of a species may be difficult to establish, our ability to understand life history traits of this unique group of animals is hindered by the lack of studies, which is in part driven by the difficulty in studying bats. Recent interests in bat research appear to have been triggered by their links to zoonotic diseases of public health importance (Calisher *et al.*, 2006; Wang *et al.*, 2011; Smith & Wang, 2013; Wang & Cramer, 2014) while very little emphasis is placed on their ecological strategies (which ultimately influences their ability to host and transmit diseases).

Survival for instance, is an important demographic feature of a species' population, and often determines the persistence of the population. In conservation management, this parameter is vital for setting up management strategies for species (for purposes of

conserving the species or regulating their populations) while in disease dynamics it may give an indication of the fitness of a population and susceptibility to diseases. The survival of a species depends on the ecological strategies such as reproductive strategies, foraging, and population dynamics. This study provides for the first time, estimates of the survival rates of *E. gambianus* and *Micropteropus pusillus*. Monthly adult survival rate of 0.87 (95% CI: 0.78-0.92) for *E. gambianus* was similar to 0.89 (95% CI: 0.67-0.96) for *M. pusillus*, but both were different from 0.96 (95% CI: 0.89-0.99) estimated for *Eidolon helvum* (Hayman *et al.*, 2012a); the differences in life ecological strategies and life history traits could account for the differences in monthly survival rates.

#### **9.1.1 Drivers of reproductive strategy in bats and its implications on population growth and survival.**

The reproductive strategy employed by bats has significant implications on the population size of species: successful reproduction increases the chances of population to successfully replace itself, or cause population growth and ultimately, influence the species' survival. The lifetime reproductive output of individuals in a population is a major determinant for the growth or decline of that population (Racey & Entwistle, 2000) and varies from species to species. It may appear that species that produce more offspring at birth (polyoestrous species and polytochous species) may be more successful and numerous than those that produce fewer offspring per female per year. Several factors however predict the success of a species far beyond the number of offspring produced. For example, the reproductive success of a species is known to depend on the prevailing environmental conditions, food availability, species survival and longevity (Racey & Entwistle, 2000). Other factors such as stress as a result of disturbance at

roosts, pesticides, loss of foraging habitats (Stebbing, 1988) can also influence reproductive success and output. Because reproduction is a very energy demanding process, fluctuations in food availability can have significant implications on reproductive success of species and even determine the reproductive chronology (when to give birth and how many offspring to produce) in bats (Happold & Happold, 1990; Cumming & Bernard, 1997). In this study, bimodal peaks in *E. gambianus* and *M. pusillus* parturition showed strong relation with bimodal peaks in fruit abundance with parturition occurring in March and September when fruits are most abundant.

The need to meet energy demands for reproduction and lactation by females can drive sex related differences in foraging behaviour and roosting behaviour; females may forage for longer periods in order to meet energy demands associated with pregnancy and lactation (Barclay & Jacobs, 2011). When there is insufficient food to support pregnancy, this could lead to post-implantation re-absorption of embryos or even the abortion of late pregnancies in bats (Heideman, 2000). During periods of insufficient food, there is usually a trade-off between aborting or abandoning an offspring and maternal survival to ensure potential future reproduction (Wasser & Barash, 1983; Heideman, 2000). In bats because the growth and persistence of populations is often dependent on adult survival rather than juvenile survival, juveniles and foetuses are likely to be sacrificed to increase overall lifetime reproductive output of females.

Lifetime reproductive output is also dependent on the reproductive output per year and reproductive lifespan of the species (Racey & Entwistle, 2000). Because reproductive lifespan is determined by time of sexual maturity and longevity, species that have relatively shorter lifespan or low survival rates (especially in females) may mature early and exhibit repeated reproduction events to increase their overall reproductive output. In

*Tadarida pumifa*, for instance Mcwilliam (1987) suggested that the success of this species is enhanced by the early sexual maturation in the species which enables females to produce enough offspring within their 5-year lifespan. The early sexual maturity observed in female *E. gambianus* in the current study, may imply that a similar adaptation is employed by this species to increase its overall reproductive output. This adaptation in *E. gambianus* could also be driven by the relatively low survival rates in females compared to males as shown by CMR analysis in this study, although this requires confirmation through further research.

In highly seasonal environments where bimodal reproduction occurs under two distinct conditions (one wet season and one very dry season) in a year, the differences in food quality (and quantity) has a significant effect on reproductive success of bats (Thomas & Marshall, 1984). In Microchiropterans, Happold and Happold (1990) showed that such differences can cause significant selective pressure leading to intraspecific reproductive flexibility at different latitudes and climatic environments. However, they proposed that differences in fruit abundance between seasons may not be that large enough to cause reproductive flexibilities in most African fruit bat species. Even though some amount of fruits may occur during both rainy and dry seasons, the quantity, nutritional value and water content of fruits are likely to vary. Plant phenology studies in this work indicated an abundance of fruits during the rainy season while in the dry season flowers were rather abundant with very few available fruiting species. This difference in food quantity and/or quality can lead to lower reproductive success (higher rates of abortion), increased mortality or lower fitness of young ones that are born and grow through the periods of low food quantity or quality (Thomas & Marshall, 1984). In the current study, different cohorts of juvenile *E. gambianus* that were born and grew through the different seasons of different fruit availability, showed significant size differences with juveniles born in



the rainy season showing larger size and heavier weights than those that were born in the dry season.

It is however uncertain from the current results how this difference in food availability influences mortality rates and fitness in the different cohorts of *E. gambianus* juveniles. This discrepancy in food quantity/quality may be particularly noticeable in savannah environments where rainfall is fused into a single wet season with a relatively long dry season. The rainfall pattern can result also in a greater discrepancy in food availability between the two seasons. The difference in food availability (as a consequence high seasonality in rainfall) could cause bats to modify slightly their reproductive periods to coincide with favourable conditions.

#### **9.1.2 Roosting ecology in fruit bats as shaped by other ecological and abiotic factors.**

Bats spend a significant amount of their life time at roosts, which makes roosts an important component of the life of bats. Roosts are an avenue for social interactions, information sharing, raising young ones and provide protection against adverse climatic conditions and predation. The conditions that enhance survivorship in bats are closely linked to roost characteristics (Kunz, 1982). The different strategies and decisions bats make with regards to roosting behaviour and roost site selection have significant consequences on the fitness of species and involves a complex interaction of the physiological, behavioural and morphological adaptations and demographic response which varies for different species *E. helvum* for instance forms large colonies of up to several million individuals and hence require areas with dense old growth and large trees to contain and support their large colonies (DeFrees & Wilson, 1988; Webala *et al.*, 2014). Similarly, colonies of *E. helvum* identified in this study ranged from 1,500 to over

110,000 individuals with roosts that occurred in old and large trees of species such as Mahogany, Neem and Silk cotton. This bat species may in turn gain an increased protection from roosting in very large numbers through predator dilution effect and may also benefit from social interactions.

In contrast, *E. gambianus* forms colonies, but of relatively smaller sizes and hence, may require trees that provide sufficient foliage cover to make them less conspicuous to predators. *E. gambianus* colonies identified ranged from single individuals up to maximum of nearly 6,000 bats. This species roosted only in well foliated trees but avoided or abandoned trees that became defoliated. Due to the relatively smaller *E. gambianus* numbers at roost sites, few scattered trees can sustain colonies and this is supported by the observation that roosts were more likely to be selected in plots that had fewer trees per hectare in this study. The frequent switching of roost as shown by the radio-tagged bats and the observed changes in numbers of bats at roost is suggestive of a fission–fusion roosting system in *E. gambianus*. In this system, the entire colony is divided into smaller groups that occupy different roosts, but ensures frequent mixing of individuals within the same colony (Willis & Brigham, 2004; McCracken *et al.*, 2006; Kerth *et al.*, 2011). This fission–fusion roosting system together with the frequent roost switching within a colony could also provide a means of avoiding predators by making roost sites unpredictable.

In temperate environments, the physical and thermal attributes of the roost sites have been shown to affect the fitness and survival of bats, especially during hibernation and periods of reproduction. In tropical bats however, thermal attributes of roosts may be of little influence during roost selection. In tropical African species such as *E. gambianus*,

roost selection may rather require a balance between structural suitability of roost trees and other factors such as food availability and predator avoidance.

Foraging ecology also influences roosting behaviour (Campbell *et al.*, 2006) and this relationship has been described in bats of the family Pteropodidae. The influence of food availability on roosting ecology in fruit bats has been used to explain the increase in fruit bats roosting near human habitations; the pursuit of food by bats has caused bats to roost nearer to human habitations so as to utilise fruits and flowers in gardens (Hahn *et al.*, 2014; Plowright *et al.*, 2015). Fruit bat colonies that were identified in this study typically occurred very close to human habitation with majority of roosts identified occurring within 50 m of houses. Additionally, in *E. gambianus*, majority of the plants that were identified as food sources for this species could be found within the immediate locality of the roost sites, suggesting a link between roosting ecology and proximity to food.

Access to food sources however, should not compromise on the quality of roosts. Hence, roost selection may involve a careful balance between energetic costs involved in commuting from roost to foraging areas and the quality of roosts available near these food resources. Different species may have different ranges within which this trade-off can be tolerated without significantly affecting their survival. Thus, the difference in tolerance levels may influence the distribution of bat species; species that have wider compromise levels between roost quality and access to food may be widely distributed and in different habitats than those that cannot compromise on roost quality.

It is worth noting that even in species that are tolerant to a wider range of roost-selection factors, the selection and utilisation of roosts depend mainly on the availability of preferred roosts (Lewis, 1995; Kunz *et al.*, 2003). In habitats where preferred roosts are

in abundance, species are less likely to show roost fidelity to particular roosts but may show fidelity to a larger area because resources are usually patchy and non uniform across landscapes. Because roosting ecology and behaviour is influenced by availability of resources, it is expected that current trends in habitat loss and modification may have caused changes in availability of roosting habitat leading to the modification in roosting ecology, even for widespread species like *E. gambianus*. Current observations of roosting behaviour in fruit bats may be a reflection of human-mediated modification of natural habitats available for species. Modification of bat roosting ecology and behaviour as a result of anthropogenic factors have been suggested (Meyer *et al.*, 2016); and this may be occurring in Ghana. For instance, in this study, Neem (*Azadirachta indica*) which is an introduced and invasive tree species, and the Indian mast tree (*Polyalthia longifolia*) also an introduced tree species in Ghana, were among the tree species preferred for roosting by *E. gambianus*, while other native tree species were avoided. This suggests that the introduction of these tree species have potentially led to a change in the roosting behaviour of *E. gambianus* to utilise these species instead of native tree species in Ghana.

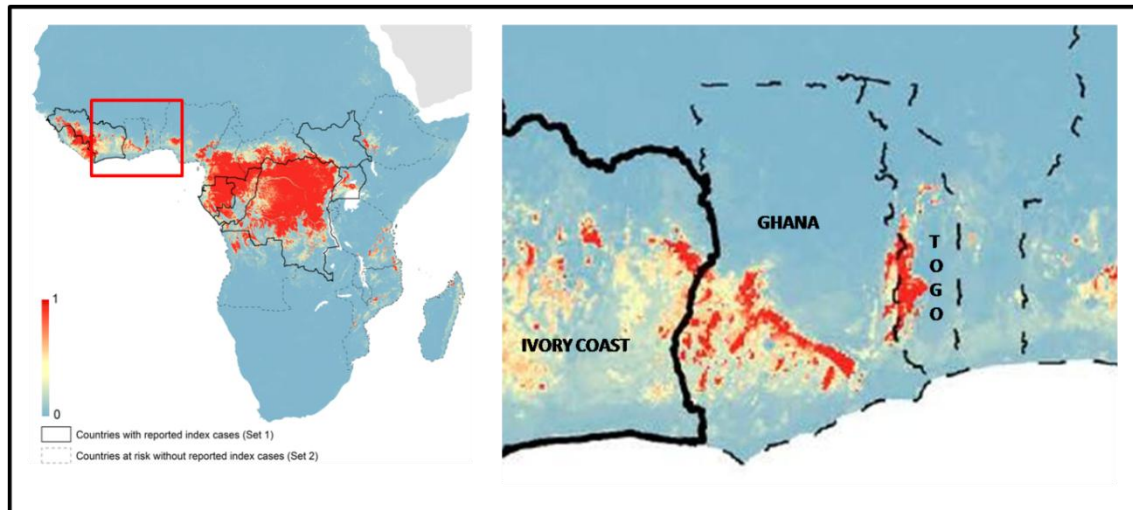
Even though the introduction of these species may be providing roosting (and feeding) opportunities to fruit bats, their use may have negative consequences such as increasing the proximity of bat roost to humans as most of these tree species are commonly planted as ornamental plants near homes. If roosting behaviour and roost selection in fruit bats have, and/are being modified as a consequence of anthropogenic change, then predictions are that current trends in habitat loss/change is likely to continue altering bat roosting ecology and ultimately influence population dynamics, diet composition and foraging behaviour, and increase human bat interactions with disease spillover implications. Bat species that have specialised roosting habits and cannot adapt to these

changes are likely to be affected the most and likely to be driven into population declines.

## **9.2 Zoonotic disease transmission risks in Ghana: the effect of fruit bat ecology and human impact**

The ecology of zoonotic disease infections and spillover events often involves complex processes (Lloyd-Smith *et al.*, 2009) and the understanding of how and where disease spillover and emergence is likely to occur depends on an understanding and knowledge of the ecology of the hosts of the disease pathogens (Hayman *et al.*, 2013). In trying to identify high risk areas for disease transmission from bats, the distribution of potential reservoir hosts of specific diseases can help make accurate predictions of which areas are at risk. Also, since different diseases may have different reservoir hosts, knowing which bat species are reservoir hosts for specific disease pathogens can define the risk areas for specific diseases. In this study, antibodies to Hendra virus, Nipah virus and Cedar virus were detected in blood samples from eight species of fruit bats (*E. helvum*, *E. gambianus*, *Rousettus aegyptiacus*, *M. pusillus*, *Lissonycteris angolensis*, *Epomops franqueti*, *Epomops buettikoferi* and *Hypsignathus monstrosus*), with seroprevalence of henipaviruses being highest in *E. helvum*. Risk maps for Ebola Virus Disease transmission based on species distribution modelling of fruit bat species such as *Hypsignathus monstrosus*, *Myonycteris torquata* and *Epomops franqueti*, which are the likely hosts of the virus, shows that forested areas are at a higher risk because these bat species occur mostly in forested areas (Pigott *et al.*, 2014). Thus in Ghana for instance, the high risk populations are those that occur in the moist evergreen and moist semi deciduous forest regions around the Western Region, Brong-Ahafo region, Eastern region and parts of the Volta region (Figure 9.1).





**Figure 9.1 Predicted geographical distribution of the zoonotic niche for Ebola virus showing risk areas for Ghana.**

*Source: Pigott et al. (2014).*

*E. helvum* is the likely host for henipaviruses among the fruit bats in Ghana (Hayman *et al.*, 2008b; Drexler *et al.*, 2009). Hence distribution patterns of *E. helvum* colonies may define areas at risk of henipa spillover in Ghana, which according to findings of this study, appears to be nationwide. Similarly, *R. aegyptiacus* is the likely reservoir for Marburg virus (Towner *et al.*, 2007; Pourrut *et al.*, 2009). Hence, areas where *R. aegyptiacus* roosting caves are located such as Buoyem and its surrounding villages will have a higher risk of Marburg emergence. Such species distribution modelling approaches can help to identify the areas at risk of disease emergence from bats specifically for Ghana. The relevance and robustness of the output of such modelling approaches will depend primarily on the availability of accurate data, including extensive species distribution and occurrence records for target species which is currently unavailable or obsolete. Studies such as this one which provides distribution of species



and identifies colonies of different bat species are important in providing the data required to improve our predictions of disease emergence and populations at risk.

The co-occurrence of multiple species within the same locality presents the possibilities for inter-species interactions and cross-species transmissions of pathogens and diseases. In this study, fruit bat communities at the four major trapping sites were made up of two to nine different fruit bat species. Typically, fruit bat species that constitute a community interact at foraging and roosting sites. Although species that are sympatric at roost sites may not mix at roosts (due to spatial segregation at roosts) indirect interactions can still occur through contact with faeces or urine at roosts. For instance, at the *E. helvum* colony in Accra, *E. gambianus* was observed to roost on lower branches below large numbers of *E. helvum* in the same roost trees. This implies that *E. gambianus* is in continuous contact with faeces and urine from *E. helvum* at the shared roosts. Scenarios such as this can cause the spillover of pathogens and diseases from actual hosts to accidental hosts and broaden the host range for the pathogens, thereby increasing the chances of spillover to humans and other animals.

In tropical landscapes, fruit and flower resources for bats are often patchy and show seasonal fluctuations in abundance which often lasts short periods (Dumont *et al.*, 2003). This can cause aggregations of several fruit bat species at ephemeral food sources and create the opportunity for interactions between sympatric species at foraging sites. For instance, during the flowering period of the Silk cotton tree, several species of fruit bats were observed flocking at these trees to feed. Inter-specific competition for food resources can result in aggressive behaviour through which individuals can sustain bites and scratches leading to the possible transfer of pathogens or diseases. Because a high species richness of wildlife host increases the emergence of diseases (Jones *et al.*, 2008),

places with the higher richness and diversity of fruit bat species are likely to have an increased risk of bat-related disease transmission to humans. Thus, bat studies conducted at the community level rather than single species level may provide better insight into how behaviour and ecological strategies can be influenced by other sympatric species at roost and foraging sites, which will have implications for the spread and transmission of diseases.

In wildlife disease dynamics, population size is an important parameter since a critical population size is usually needed to maintain a disease in the population (Lloyd-Smith *et al.*, 2005). Bat species with large population densities or those that form large roosts (such as *E. helvum*) have a higher chance of transmission of viral infections. The formation of large colonies facilitates contact between individuals through social interactions such as mutual grooming, scratching and biting at roosts which makes it easy for spread and maintenance of diseases among members of a colony. Sites with large fruit bat densities may have an elevated risk of disease spillover since the chances of contact with bat urine and faeces and the rate of encounter of humans and domestic animals with bats is high.

Although the distribution, roosting ecology, and aspects of the biology of fruit bats may determine where human populations are at risk of disease and transmission from bats, other anthropogenic factors may influence or increase the risk levels. Anthropogenic change associated with rapid human population growth and urbanization is causing humans to encroach into wildlife habitats and these increase contact rates with reservoirs of zoonotic diseases (Morse, 1995; Daszak *et al.*, 2000). Agricultural intensification and other related land use changes is depleting natural foraging habitats, causing fruit bats to feed in fruit orchards and backyard gardens. Intensification of animal husbandry and

practices such as keeping domestic animals on free range, in uncovered pens or feeding them on bare ground under roost trees, increase contact rates between domestic animals and bat fluids through saliva-contaminated, partly eaten fruits, ejecta pellets or direct contact with faecal material and urine. Other practices which are sometimes linked with livelihoods and poverty such as the collection of wild fruits, bat hunting and butchering, cooking in the open under roosts and rainwater harvesting, can increase risk levels of disease transmission in places where human population occurs within the niche of fruit bats. In several of the locations where bat roosts were identified in this study, these practices listed above were frequently observed and may further increase the risk of zoonotic disease transmission in Ghana.

Clearly, fruit bat distribution defines areas where human populations are at the most risk. Nonetheless, other ecological strategies pertaining to the roosting and foraging ecology, demography and inter-species interactions could influence risk levels. However, human activities that lead to increasing contact with bats potentially accelerate the risk levels of disease transmission, and this necessitates targeted awareness campaigns with well crafted messages on human-bat interactions.

### **9.3 Implications of findings for bat conservation in Ghana.**

Currently, all bat species that occur in Ghana are listed under Series C of the Third Schedule of the Wildlife Conservation Regulations [L.I. 1284-Wildlife Conservation (Amendment) Regulations, 1983] which means that their hunting is prohibited between 1<sup>st</sup> August and 1<sup>st</sup> December each year. However, the hunting of fruit bats was observed to occur within this prohibited period during this study implying that this wildlife law is clearly not adhered to and bats do not receive the necessary protection required by law.

For six of the fruit bat species observed in this study births occurred in March/April and September/October each year. This implies that the September/October birth period for these species adequately falls within the period when their hunting is prohibited by law. However for a species like *E. helvum* which reproduces once a year and the births occur around May, the species receives no protection during its birth and lactating periods. Changing the status of bats from the current Third Schedule to the Second Schedule (where the hunting of their young or adult accompanied by young ones is prohibited and their hunting is not allowed between 1<sup>st</sup> August and 1<sup>st</sup> December each year) seems to be a more appropriate way of protecting these ecologically important species.

In Ghana, the best protection for wildlife species occurs in Wildlife Protected Areas (PA). The proportion of bat population that occurs and receives protection in Ghana's Wildlife PAs however, is unknown because species assessments and population estimates often focus on only "charismatic" species and large mammals. Considering that about only 16% of Ghana's total land surface is in Wildlife PAs, a significant proportion of bat populations in Ghana occur outside these Wildlife PAs in areas such as rural and urban centres where they receive little or no conservation attention. Although most of the Forest Reserves in Ghana are good habitats for bats, populations occurring in Forest Reserves may not receive adequate protection as they would in Wildlife PAs. The occurrence of bats in large colonies in urban and rural centres makes them easy targets for hunters. Also, the fact that most of these fruit bat species exhibit high roost fidelity to roosting areas makes them very predictable. For instance, majority of colonies identified in this study had been used continuously or intermittently for 10 or more years, making them well known among local communities that hunt bats. Some colonies may receive some level of protection due to their occurrence in restricted areas including sacred groves or because of some cultural significance attached to them. For instance, the large

*E. helvum* roost which occurred at the premises of the 37 Military Hospital in Accra received protection from large scale hunters because of the military presence, although limited hunting with catapults still occur.

Hunting appears to be the biggest direct threat to fruit bat populations in Ghana, particularly for larger species such as *E. helvum* and *E. gambianus*. In the current study, fruit bat hunting at roost sites was very common at most of the bat colonies identified. Hunting levels have already been estimated to be unsustainable (Kamins *et al.*, 2011) and is one of the major factors for the decline of *E. helvum* numbers at some colonies. Other species like *R. aegyptiacus* and *E. gambianus* may also be affected in a similar way, but the lack of statistics on numbers harvested makes it difficult to assess the effects of hunting on the populations of these species. The persistence of *E. helvum* and *E. gambianus* in modified landscapes near human habitation with little or no forest cover creates the impression that these species are relatively resistant to the effects of deforestation, and habitat modification and that their populations may not be under intensive pressures. The formation of very large colonies by *E. helvum* and the annual return to colony sites with marked increase in numbers creates the common notion that the species can withstand intensive hunting pressures or their population is expanding. Such erroneous conclusions have the potential of masking the apparent decline of bat numbers especially for widespread and common species. True assessments of population declines lies only in proper and consistent (possibly, nationwide) monitoring schemes for different bat species. Only with long term population monitoring spanning over 15 years can population trends be accurately determined (Meyer *et al.*, 2010) hence, the need for continuous monitoring schemes.

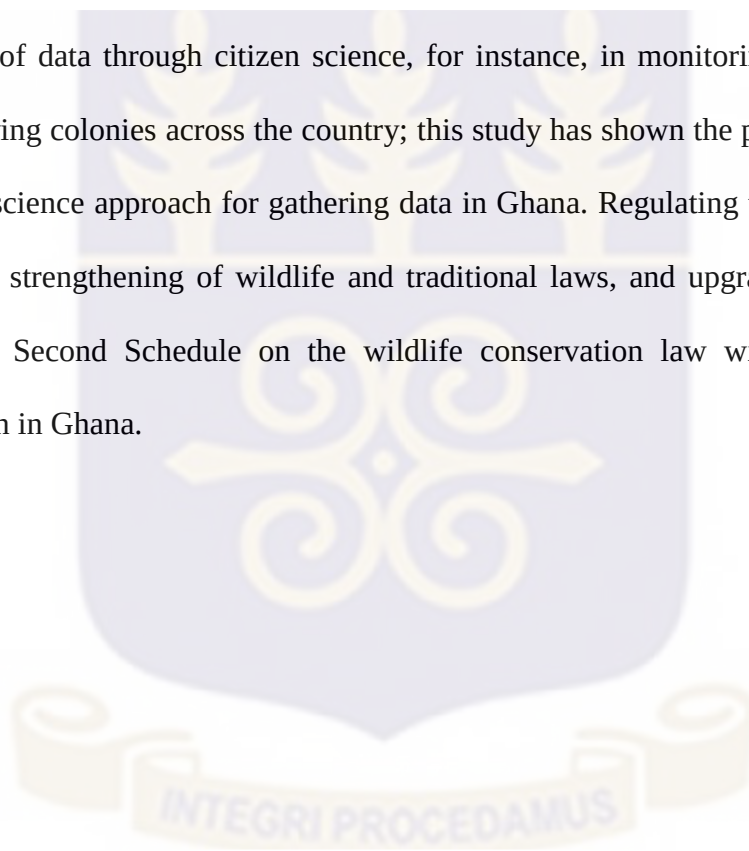
The increasing association of bats with zoonotic diseases with bats makes them unwelcomed occupants near people's homes for fear of contracting diseases from bats. The 2014 Ebola outbreak, for instance, triggered the fear of bats among people and this led to the persecution of bats, destruction of bat roosts and other cruel interventions aimed at killing bats that roosted near homes. In addition, large colonies near humans are seen as a nuisance as bat droppings create unpleasant smell and dirty people's compounds with concerns of health risks (Webala *et al.*, 2014). Similar complaints and concerns were raised by respondents living near bat roosts in this study. There were also concerns of large fruit bat aggregations destroying trees that have economic value (e.g. coconut trees) or aesthetic values and complaints of fruit bats destroying fruits planted on commercial and non-commercial scales. Such roosting and foraging behaviour is making bats increasingly unpopular among residents and farmers and creates the urge for people to get rid of bats when they occur very close to human habitation.

The challenge for successful bat conservation in Ghana appears to be how to balance the ecological importance and benefits obtained from bats, with the role bats play in zoonotic disease transmission, while ensuring that people's perceptions about bats are positively influenced so humans and bats can coexist without risks of diseases. Education is a fundamental part of the solution process, but should be based on accurate scientific information rather than perceptions. Education should highlight how bats are important to ecosystems and how people in both rural and urban areas depend (either directly or indirectly) on the ecological health and ecosystem services provided by bats (Pigott *et al.*, 2014).

Human behaviour is a key driver in the global wildlife loss (Vitousek *et al.*, 1997; Sala *et al.*, 2000); activities such as habitat modification, land use change, hunting and



deforestation, are primary threats to the loss and decline of wildlife populations, including bats. The success of bat conservation in Ghana will ultimately depend on the people. By taking responsible land-use decisions and reducing activities that lead to the loss of natural bat roosting and feeding habitats, people can provide conservation solutions through behavioural changes. Multidisciplinary research, focused on crosscutting themes in bat ecology, conservation, public health and social sciences are required to provide knowledge and evidence for establishing conservation interventions that ensure safe coexistence of humans and bats. Non-scientists can also help in the acquisition of data through citizen science, for instance, in monitoring bat populations and identifying colonies across the country; this study has shown the potential success of the citizen science approach for gathering data in Ghana. Regulating the hunting of bats through the strengthening of wildlife and traditional laws, and upgrading the status of bats to the Second Schedule on the wildlife conservation law will be vital to bat conservation in Ghana.



## CHAPTER TEN

### 10.0 CONCLUSIONS AND RECOMMENDATIONS

#### 10.1 Conclusions

The overall aim of this study was to describe the ecology of fruit bats in Ghana with particular reference to the widespread and important (ecological and public health) species *Epomophorus gambianus*, and the role fruit bats play in possible emergence and transmission of zoonotic diseases. The specific objectives of this study were to;

1. document the distribution and estimate the population of fruit bats in Ghana;
2. to determine the diet of *E. gambianus* and describe seasonal variations in food availability;
3. to investigate the roosting behaviour and site selection of *E. gambianus*;
4. to determine the demographic parameters of fruit bats in Ghana
5. to provide further serological evidence for prevalence of zoonotic viruses in fruit bats in Ghana and identify human bat interactions that can serve as potential routes for zoonotic disease transmission.

Ten species of fruit bats were recorded in this study; these were *Epomophorus gambianus*, *Eidolon helvum*, *Nanonycteris veldkampii*, *Epomops franqueti*, *Epomops buettikoferi*, *Hypsignathus monstrosus*, *Lissonycteris angolensis*, *Megaloglossus woermanni*, *Rousettus aegyptiacus* and *Micropteropus pusillus*.

This study identified 82 bat colonies in 74 different locations across Ghana and 73 of these colonies are reported for the first time. Several fruit bat roosts occurred in densely populated areas and in close proximity to humans. Majority of these roosts were occupied by *Epomophorus gambianus* and *Eidolon helvum* and these two species were

also the commonest fruit bat species among the 6,132 individuals captured from 11 sites across Ghana. A total *E. gambianus* population of 28,538 was estimated to occur at roost sites across the country while *E. helvum* population was estimated at over 3 million. Bats were generally perceived in a negative sense, and very few people appreciated the ecological importance fruit bats.

This study is the first to quantify the relative use of dietary items and describe the seasonal variations in food availability for *E. gambianus*. The dietary studies showed that *E. gambianus* utilised at least 35 species of plants as food resources and the use of the different plant species and plant parts was based on their seasonal availability. Figs were a relatively important food item in the diet of *E. gambianus* and constituted over 40% of all dietary samples. Plant phenology studies showed strong seasonal correlations between fruiting, flowering and rainfall patterns, where flowering occurred mostly in the dry periods of the year (November to February) and fruiting occurred during the rainy periods of the year. Flower abundance preceded fruiting abundance by one month. Flowers were found to be an important food source to *E. gambianus* particularly, during the dry seasons when fruit abundance was relatively low.

This is the first study to describe the roosting ecology and roost site selection in *E. gambianus* at a multi scale. Investigations on the roosting behaviour and site selection revealed that *E. gambianus* roosts were more likely to be found in bigger and taller trees that occurred in less dense tree plots and were closer to buildings. *E. gambianus* mainly selected mango (*Mangifera indica*), Neem (*Azadirachta indica*), Figs (*Ficus* sp.), Indian mast tree (*Polyalthia longifolia*), and the African tulip tree (*Spathodea campanulata*) within the study area for roosting, but avoided palm trees. Female *E. gambianus* utilised smaller roosting areas compared to males ( $p=0.016$ ) while maternal roosts of *E.*

*E. gambianus* were closer to each other ( $p < 0.0001$ ), more frequently occupied ( $p = 0.001$ ) and had relatively more bats ( $p < 0.0001$ ) compared to non maternal roosts.

The overall sex ratio for *E. gambianus* was male biased (0.69; 95% CI: 0.64-0.75) with varying sex ratios within each age class (female: male sex ratio for juveniles = 0.72; sexually immature adults = 0.28; Adults = 1.63); these varied across the 3 year study period. The overall sex ratio for *M. pusillus* was however significantly female biased (1.3; 95% CI: 1.1-1.5) with an adult sex ratio of (1.6; 95% CI: 1.3-2.0). The reproductive rate for *E. gambianus* was estimated to vary between 0.56 to 1 offspring per female per reproductive season while reproductive rates for *M. pusillus* were estimated to vary between 0.8-1.0 offspring per female per reproductive season.

The findings show bimaturism in *E. gambianus*, with females attaining sexual maturity at an earlier age (6 months) than males (ca. 12 months). The sizes (weight and forearm length) of cohorts of *E. gambianus* juveniles that were born and grew through the wet season where fruits were relatively more abundant were significantly larger than those that were born and grew through the dry season.

Monthly survival rates for *E. gambianus* were estimated at 0.91 (95% CI: 0.75-0.97) for adult males, 0.82 (95% CI: 0.67-0.91) for adult females and 0.74 (95% CI: 0.62-0.84) for sexually immature males. Monthly survival rates for *M. pusillus* were estimated at 0.9 (95% CI: 0.6-1.0) for males and 0.8 (95% CI: 0.6-0.9) for females. This is the first study to estimate survival rates for a colony of *E. gambianus* and *M. pusillus*.

Serological evidence showed Hendra virus, Nipah virus and Cedar virus infections in fruit bats in Ghana with an indication of age and gender effect on seropositivity. The interactions with bats that were identified and could serve as potential routes for zoonotic disease transmission were contact with faeces and urine under bat roosts, bat hunting and

the consumption of fruits partly eaten or mouthed by bats (either by humans or domestic animals).

## 10.2 Recommendations

The findings from this study raise further questions that are vital to our knowledge about the ecology of fruit bats and to our understanding of their role in transmission of emerging zoonotic diseases. Key questions include:

1. Are there other bat roosts across Ghana that is still unreported?
2. How does the ecology and demography of other fruit bat species differ/compare with that of *E. gambianus*?
3. How do the ecological strategies, population dynamics and life histories of different bat species shape their ability to transmit diseases and cause spillover to humans and domestic animal populations?
4. Does roost selection and habitat utilisation in *E. gambianus* vary across different landscapes and or vegetation types?
5. To what extent do bat species interact with other species and also with conspecifics at other roosts across the country?
6. Which factors (biotic and abiotic) affect the behaviour, ecological strategies, population structure and demography of different species?
7. Does the quantity and quality of differential diets have any implications on the survival and fitness of bats?
8. Is spillover of bat borne zoonotic pathogens to humans occurring in Ghana and which groups of people are more at risk?

Future studies aimed at addressing these questions should use an interdisciplinary approach, integrating several approaches/disciplines such as experimental studies, social studies, mathematical modelling, ecological studies and serological/virological studies, in order to improve our understanding of the complex linkages between bats and emerging zoonotic diseases.

As a result of time and financial constraints, this study was able to trap only a few bats that were tracked over a period of only 10 months. A much long term population monitoring is required in order to detect and estimate changes in colony size and population trends. Also, the long term monitoring of marked individuals is vital in order to gain a complete understanding of the demography and life history of bats.

Further research should quantify (in calorimetric contents) the relative use of flowers by fruit bats and the extent of pollen use as a dietary item in fruit bats as this would increase understanding on the role and extent of fruit bats in pollination of plants. Additional research should also focus on quantifying the extent and patterns of seed dispersal and pollination performed by *E. gambianus* and other fruit bats within different habitat types, particularly for economically and ecologically important plants that form part of the diet of bats.

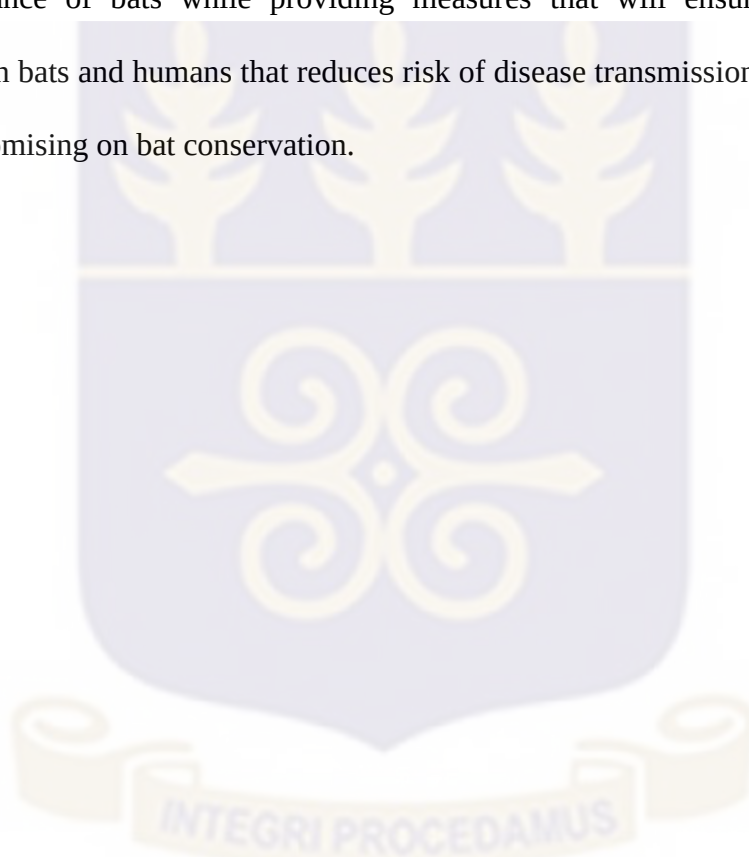
In order to minimize human-bat interactions and reduce the risk of spillover of zoonotic diseases from bats, the following recommendations are also made:

- Avoiding the consumption of partly eaten fruits or fruits that bear claw or bite marks;
- Wearing of protective gear when handling dead or live bats;
- Keeping of domestic animals in roofed pens away from roost trees or fruiting trees;
- Activities such as selling of food, rainwater harvesting and cooking under bat roosts should also be avoided to reduce chances of contamination with bat faeces and/ or



urine. In circumstances where exposure to bats at roosts sites is unavoidable, measures such as constructing roofed sheds under bat roosts can reduce contact with bat excreta and urine under roosts.

- There is an urgent need for increased surveillance and improved diagnosis for bat borne zoonotic diseases in the country, particularly in areas where bat roosts are very common and humans are likely to interact frequently with bats.
- Educational campaigns that stress on both the ecological value and the zoonotic importance of bats while providing measures that will ensure the coexistence between bats and humans that reduces risk of disease transmission from bats without compromising on bat conservation.



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## APPENDICES

**Appendix 1 Plant families and genera known to be utilised as food by fruit bats that occur in West Africa.***Source: Marshall (1985)*

| Food Type | Plant Family     | Plant genera                                   |
|-----------|------------------|------------------------------------------------|
| Flowers   | Anacardiaceae    | Mangifera                                      |
|           | Bignoniaceae     | Heterophragma, Kigelia, Oroxylum, Radermachera |
|           | Bignoniaceae     | Kigelia, Markhamia, Spathodea                  |
|           | Bombacaceae      | Adansonia, Bombax, Ceiba, Ochroma              |
|           | Chrysobalanaceae | Maranthes                                      |
|           | Lecythidaceae    | Careya                                         |
|           | Leguminosae      | Daniellia, Parkia                              |
|           | Meliaceae        | Azadirachta                                    |
|           | Moraceae         | Chlorophora                                    |
|           | Musaceae         | Musa                                           |
|           | Myrtaceae        | Eucalyptus, Eugenia, Psidium                   |
|           | Proteaceae       | Protea                                         |
|           | Sapotaceae       | Bassia, Mimosa                                 |
|           | Sonneratiaceae   | Sonneratia                                     |
| Fruits    |                  | Anacardium, Mangifera, Harpephyllum,           |
|           | Anacardiaceae    | Pseudospondias, Spondias                       |
|           | Annonaceae       | Annona                                         |
|           | Apocynaceae      | Acokanthera                                    |
|           | Bombacaceae      | Bombax                                         |
|           | Burseraceae      | Dacryodes                                      |
|           | Caricaceae       | Carica                                         |
|           | Celastraceae     | Cassine                                        |
|           | Chrysobalanaceae | Parinari                                       |
|           | Ebenaceae        | Diospyros                                      |
|           | Ehretiaceae      | Cordia                                         |
|           | Euphorbiaceae    | Bridelia, Sapium                               |
|           | Irvingiaceae     | Irvingia                                       |
|           | Lauraceae        | Persea                                         |
|           | Leguminosae      | Ceratonia                                      |
|           | Loganiaceae      | Anthocleista                                   |
|           | Loranthaceae     | Viscum                                         |
|           | Meliaceae        | Azadirachta, Ekebergia                         |
|           | Moraceae         | Antiaris, Artocarpus, Chlorophora, Ficus       |
|           | Musaceae         | Musa                                           |
|           | Myrtaceae        | Eugenia, Psidium, Syzygium,                    |
|           | Oleaceae         | Olea                                           |
|           | Palmae           | Borassus, Elaeis, Phoenix                      |

| Food Type | Plant Family   | Plant genera                     |
|-----------|----------------|----------------------------------|
|           | Passifloraceae | Adenia, Passiflora, Smeathmannia |
|           | Rhamnaceae     | Maesopsis                        |
|           | Rosaceae       | Eriobotrya, Prunus               |
|           | Rubiaceae      | Nauclea                          |
|           | Rutaceae       | Citrus                           |
|           | Sapindaceae    | Litchi                           |
|           | Sapotaceae     | Achras, Mimusops, Butyrospermum  |
|           | Solanaceae     | Solanum                          |
|           | Sterculiaceae  | Cola                             |
|           | Ulmaceae       | Celtis                           |
|           | Urticaceae     | Musanga                          |
|           | Verbenaceae    | Vitex                            |
| Leaves    | Leguminosae    | Albizia, Erythrina               |
|           | Moraceae       | Chlorophora, Ficus               |
|           | Sterculiaceae  | Theobroma                        |
|           | Zygophyllaceae | Balanites                        |

## Appendix 2 Locations of bat trapping sites

| Trapping site               | Region        | Coordinates |             |
|-----------------------------|---------------|-------------|-------------|
|                             |               | x           | y           |
| 37 Military Hospital, Accra | Greater Accra | -0.18346251 | 5.5886673   |
| Bolgatanga                  | Upper East    | -0.85219757 | 10.79384065 |
| Buoyem                      | Brong Ahafo   | -1.99239481 | 7.723741718 |
| Charia                      | Upper West    | -2.57236912 | 10.1056279  |
| Damongo                     | Northern      | -1.81150949 | 9.086043723 |
| Jirapa                      | Upper West    | -2.69939058 | 10.53256977 |
| Tamale                      | Northern      | -0.85620739 | 9.420923889 |
| Tano sacred grove           | Brong Ahafo   | -1.859041   | 7.662814166 |
| Tumu                        | Upper West    | -1.98415297 | 10.87745877 |
| Ve-golokuati                | Volta         | 0.438118    | 6.995945    |
| Yendi                       | Northern      | -0.00852381 | 9.461901253 |

**Appendix 3 Questionnaire used for interviewing key respondents at roost sites****Study of the Ecology of Fruit Bats in Ghana**

This study seeks to find out the distribution of the different species of bats in Ghana and people's perceptions of the socio-cultural and ecological value of bats. The study forms part of a PhD study by Mr. Kofi Amponsah-Mensah of the Dept. of Animal Biology and Cons. Science, University of Ghana. We would appreciate any assistance you can give to Mr. Amponsah-Mensah to enable him to complete this study. Any further questions on this study may be addressed to Prof. Yaa Ntiamoah-Baidu (0244769081)

|                     |                                                                                    |      |
|---------------------|------------------------------------------------------------------------------------|------|
| Questionnaire No.   | Locality                                                                           | Date |
| Name of Interviewer |                                                                                    |      |
| Name of Respondent  | Pls. sign here to indicate your voluntary agreement to participate in this survey. |      |

Exploration of knowledge of bats of people living around bats roosts (focus on elderly people)

1. Sex of respondent [ ] 0=Female 1=Male
2. Age of respondent [ ]
3. How long have you been staying in this community? [ ]
4. Are you aware of any bat roost/colonies in your area? [ ] 1=yes 2= no.
5. If yes name and describe the different types of bats you have seen in this area

| Name | Description |
|------|-------------|
|      |             |
|      |             |
|      |             |
|      |             |

6. What time of the year do you see bats in this area [pls give an indication of months, season etc].....
7. What time of day are bats at this place [ ] 1=all the time; 2= morning; 3=evening; 4= night
8. Have these bats been here all the time, i.e. [ ] [1=ever since you can remember] or [2= they only recently colonised this place].
9. If only recently, for how long have you been seeing them here? [ ]
10. What do you see as the value of bats [ ] [1=food, 2=source of income; 3=seed dispersal; 4=cultural value; 5=others (.....)]
11. Do you perceive any problem(s) that can be caused by bats [ ] [1=yes] [2=No]
12. If Yes, list the problem(s).....



**Appendix 4 Locations of bat colonies and the estimated population numbers.**

| Town/ Location               | Coordinates |        | Species               | Estimated number | Number of roosts | Source of information |
|------------------------------|-------------|--------|-----------------------|------------------|------------------|-----------------------|
|                              | x           | y      |                       |                  |                  |                       |
| Abekim                       | -1.306      | 5.0999 | <i>E. helvum</i>      | 8000             | 100              | a                     |
| Aburi                        | -0.172      | 5.8531 | <i>H. monstrosus</i>  | 11               | 1                | a                     |
| Accra (37 Military hospital) | -0.183      | 5.5887 | <i>E. gambianus</i>   | 113              | 6                | a                     |
|                              | -0.183      | 5.5887 | <i>E. helvum</i>      | 123966           | 404              | a,b,c                 |
| Ada Junction                 |             |        | <i>E. helvum</i>      | 4000             |                  | a                     |
| Ada Totime-Kope              | 0.6145      | 5.7805 | <i>E. helvum</i>      | 5000             | 5                | a                     |
| Agbasiagba                   | 0.152       | 6.9408 | <i>E. helvum</i>      | 50000            | 200              | a,b                   |
| Agu Meda                     | 0.011       | 5.9779 | <i>E. gambianus</i>   | 279              | 2                | a                     |
| Agumanya                     | 0.0117      | 6.1474 | <i>E. gambianus</i>   | 185              | 4                | a                     |
| Akosombo                     | 0.0563      | 6.2922 | <i>E. helvum</i>      | 1500             | 20               | a                     |
| Akwamuman                    | 0.0832      | 6.2501 | <i>H. monstrosus</i>  | 6                | 1                | a                     |
|                              | 0.0832      | 6.2501 | <i>E. gambianus</i>   | 1                | 1                | a                     |
| Ankobra                      | -2.282      | 4.9215 | <i>E. helvum</i>      | 2000             |                  | a                     |
| Anyinam                      | -0.557      | 6.3816 | <i>E. helvum</i>      | 8000             | 150              | a                     |
| Bakpaba                      | 0.0216      | 9.2098 | <i>E. gambianus</i>   | 810              | 7                | a                     |
| Bimbila                      | 0.0619      | 8.8501 | <i>E. gambianus</i>   | 20               | 1                | a                     |
| Binda                        | 0.0558      | 8.765  | <i>E. gambianus</i>   | 25               | 1                | a                     |
| Bole                         | -2.488      | 9.0327 | <i>E. gambianus</i>   | 46               | 2                | a                     |
| Bolgatanga                   | -0.851      | 10.808 | <i>E. gambianus</i>   | 161              | 4                | a,c                   |
| Buoyem                       | -1.988      | 7.7236 | <i>R. aegyptiacus</i> |                  | 2                | a,b                   |
|                              | -1.992      | 7.7237 | <i>M. pusillus</i>    | 20               | 1                | a                     |
| Charia                       | -2.572      | 10.106 | <i>E. gambianus</i>   | 759              | 7                | a,c                   |
| Damongo                      | -1.853      | 9.1532 | <i>E. gambianus</i>   | 500              | 3                | a                     |
| <sup>1</sup> Dua Apuwongo    | -0.792      | 10.882 | <i>E. helvum</i>      | 1000000          |                  | c                     |
| Frankadua                    | 0.1699      | 6.3364 | <i>M. pusillus</i>    | 5                | 1                | a                     |
|                              | 0.1697      | 6.3371 | <i>E. gambianus</i>   | 370              | 2                | a                     |
| Fumbisi                      | -1.309      | 10.452 | <i>E. gambianus</i>   | 70               | 2                | a                     |
| Ga                           | -2.493      | 9.797  | <i>E. gambianus</i>   | 2801             | 8                | a                     |
| Gbefi                        | 0.3807      | 7.0017 | <i>E. gambianus</i>   | 200              | 3                | a                     |
| Gbledze kpogame              | 0.5602      | 7.2014 | <i>M. pusillus</i>    | 23               | 1                | a                     |
| Ginginabani                  | 0.0041      | 9.2483 | <i>E. gambianus</i>   | 170              | 1                | a                     |
| Gulumpe                      | -1.573      | 8.4808 | <i>E. gambianus</i>   | 30               | 1                | a                     |
| Haatso                       | -0.21       | 5.6672 | <i>E. gambianus</i>   | 7                | 2                | a                     |
| Hohoe                        | 0.4733      | 7.1513 | <i>E. gambianus</i>   | 50               | 1                | a                     |
| Jasikan                      | 0.4588      | 7.4043 | <i>E. gambianus</i>   | 100              | 1                | a                     |
| Jirapa                       | -2.699      | 10.533 | <i>E. gambianus</i>   | 717              | 6                | a                     |
| <sup>1</sup> Kaneshie        | -0.232      | 5.5633 | <i>E. gambianus</i>   | 100              | 1                | c                     |
| KNUST                        | -1.563      | 6.6856 | <i>E. helvum</i>      | 5000             | 150              | a,b                   |
| <sup>1</sup> Koforidua       | -0.399      | 6.2326 | <i>E. helvum</i>      | 180000           |                  | c                     |
| Kpalime                      | 0.3089      | 6.6684 | <i>E. helvum</i>      | 2500             | 2                | a,c                   |
| Kpalsonado                   | -0.095      | 9.456  | <i>E. gambianus</i>   | 2500             | 4                | a                     |
| Kpong                        | 0.0639      | 6.17   | <i>E. helvum</i>      | 17224            | 31               | a                     |



| Town/ Location                                                                                                                             | Coordinates |        | Species             | Estimated number | Number of roosts | Source of information |
|--------------------------------------------------------------------------------------------------------------------------------------------|-------------|--------|---------------------|------------------|------------------|-----------------------|
|                                                                                                                                            | x           | y      |                     |                  |                  |                       |
| Kpongli                                                                                                                                    | -2.447      | 9.5962 | <i>E. gambianus</i> | 200              | 1                | a                     |
| Kumasi Zoo                                                                                                                                 | -1.625      | 6.6999 | <i>E. helvum</i>    | 80000            | 150              | a,b,c                 |
| Kyebi                                                                                                                                      | -0.553      | 6.1581 | <i>E. helvum</i>    | 2000             | 9                | a,b                   |
| Latiegbere                                                                                                                                 | -2.325      | 8.7956 | <i>E. gambianus</i> | 40               | 1                | a                     |
| Lawra                                                                                                                                      | -2.892      | 10.644 | <i>E. gambianus</i> | 455              | 4                | a                     |
| Legon                                                                                                                                      | -0.187      | 5.6459 | <i>E. gambianus</i> | 242              | 3                | a                     |
| Liate Wote                                                                                                                                 | 0.5476      | 7.0204 | <i>E. gambianus</i> | 40               | 1                | a                     |
| Madina                                                                                                                                     | -0.164      | 5.6787 | <i>E. gambianus</i> | 25               | 4                | a                     |
| <sup>1</sup> McCarthy Hill                                                                                                                 | -0.298      | 5.5637 | <i>E. gambianus</i> | 100              |                  | c                     |
| Nalerugu                                                                                                                                   | -0.362      | 10.526 | <i>E. gambianus</i> | 40               | 1                | a                     |
| <sup>1</sup> Nandon Toupuari                                                                                                               | -2.763      | 10.851 | <i>E. gambianus</i> | 800              |                  | a                     |
| Navrongo                                                                                                                                   | -1.089      | 10.894 | <i>E. gambianus</i> | 200              | 1                | a                     |
| <sup>1</sup> Nsawam                                                                                                                        | -0.337      | 5.8105 | <i>E. gambianus</i> | 600              | 3                | c                     |
| <sup>1</sup> Pwalugu                                                                                                                       | -0.852      | 10.597 | <i>E. gambianus</i> | 500              | 1                | c                     |
| Sakasaka                                                                                                                                   | -0.841      | 9.411  | <i>E. gambianus</i> | 50               | 1                | a                     |
| Sandema                                                                                                                                    | -1.286      | 10.733 | <i>E. gambianus</i> | 5842             | 87               | a                     |
| <sup>1</sup> Sefwi Asawinso                                                                                                                | -2.325      | 6.1935 | <i>E. helvum</i>    | 1000             |                  | c                     |
| Tamale                                                                                                                                     | -0.854      | 9.405  | <i>E. helvum</i>    | 110000           | 300              | a,c                   |
|                                                                                                                                            | -0.851      | 9.4264 | <i>E. gambianus</i> | 40               | 3                | a                     |
| Tano Sacred Grove                                                                                                                          | -1.859      | 7.6628 | <i>E. helvum</i>    | 1000000          | 500              | a,b                   |
| Tarkwa                                                                                                                                     | -1.973      | 5.2746 | <i>E. helvum</i>    | 50000            |                  | a,c                   |
| Techiman                                                                                                                                   | -1.936      | 7.5906 | <i>E. gambianus</i> | 50               | 3                | a                     |
| Tesano                                                                                                                                     | -0.232      | 5.6056 | <i>E. gambianus</i> | 6                | 1                | a                     |
| <sup>1</sup> Teshie                                                                                                                        | -0.482      | 10.973 | <i>E. gambianus</i> |                  | 1                | c                     |
| Tinga                                                                                                                                      | -2.226      | 8.5834 | <i>E. gambianus</i> | 100              | 1                | a                     |
| Tokale                                                                                                                                     | -2.701      | 9.7554 | <i>E. gambianus</i> | 1000             | 2                | a                     |
| Tsito                                                                                                                                      | 0.2922      | 6.5484 | <i>E. gambianus</i> | 220              | 3                | a                     |
| Tumu                                                                                                                                       | -1.984      | 10.877 | <i>E. gambianus</i> | 778              | 11               | a                     |
| Tuna                                                                                                                                       | -2.42       | 9.4943 | <i>E. gambianus</i> | 350              | 1                | a                     |
| Tuobodom                                                                                                                                   | -1.912      | 7.6306 | <i>E. gambianus</i> | 50               | 2                | a                     |
| UENR, Sunyani                                                                                                                              | -2.344      | 7.3493 | <i>E. helvum</i>    | 139253           | 200              | a                     |
| Ve-Golokuati                                                                                                                               | 0.436       | 7.0011 | <i>E. gambianus</i> | 5113             | 178              | a                     |
|                                                                                                                                            | 0.436       | 7.0011 | <i>M. pusillus</i>  | 174              | 27               | a                     |
| Wa                                                                                                                                         | -2.49       | 10.067 | <i>E. gambianus</i> | 30               | 2                | a                     |
| <sup>1</sup> Wassa Nsuta-Esuoso                                                                                                            | -1.953      | 5.2159 | <i>E. helvum</i>    |                  |                  | c                     |
| Weuchiau                                                                                                                                   | -2.736      | 9.8123 | <i>E. helvum</i>    | 5000             | 3                | a                     |
|                                                                                                                                            | -2.684      | 9.8279 | <i>E. gambianus</i> | 231              | 5                | a                     |
| Wli                                                                                                                                        | 0.6037      | 7.108  | <i>E. helvum</i>    | 70000            |                  | a,b,c                 |
| Yendi                                                                                                                                      | -0.008      | 9.4364 | <i>E. helvum</i>    | 164000           | 300              | a                     |
|                                                                                                                                            | -0.003      | 9.4433 | <i>E. gambianus</i> | 1422             | 7                | a                     |
| <b>N =74</b>                                                                                                                               |             |        | <b>S=5</b>          | <b>3057220</b>   | <b>2956</b>      |                       |
| a= personal observation , b=literature record, c= citizen science report. <sup>1</sup> = sites reported by citizen science but not visited |             |        |                     |                  |                  |                       |

**Appendix 5 Tree species identified within the study area but not used as roosts by bats.**

| <b>Tree species</b>                 | <b>Plant family</b> | <b>Proportion of all trees</b> |
|-------------------------------------|---------------------|--------------------------------|
| <i>Albizia lebeck</i>               | Leguminosea         | 0.001                          |
| <i>Alstonia boonei</i>              | Apocynaceae         | 0.001                          |
| <i>Anacardium occidentale</i>       | Anacardiaceae       | 0.003                          |
| <i>Annona muricata</i>              | Annonaceae          | 0.027                          |
| <i>Anthocleista vogelii</i>         | Gentianaceae        | 0.001                          |
| <i>Bambusa vulgaris var vittata</i> | Poaceae             | 0.001                          |
| <i>Bauhinia</i> sp.                 | Fabaceae            | 0.003                          |
| <i>Bombax buonopozense</i>          | Bombacaceae         | 0.001                          |
| <i>Borassus aethiopum</i>           | Arecaceae           | 0.001                          |
| <i>Cananga odorata</i>              | Annonaceae          | 0.003                          |
| <i>Carica papaya</i>                | Caricaceae          | 0.008                          |
| <i>Cascabela thevetia</i>           | Apocynaceae         | 0.001                          |
| <i>Cassia fistula</i>               | Fabaceae            | 0.001                          |
| <i>Citrus</i> sp.                   | Rutaceae            | 0.009                          |
| <i>Cocos nucifera</i>               | Arecaceae           | 0.049                          |
| <i>Corymbia</i> sp.                 | Myrtaceae           | 0.001                          |
| <i>Crescentia cujete</i> L.         | Bignoniaceae        | 0.003                          |
| <i>Daniellia oliveri</i>            | Fabaceae            | 0.039                          |
| <i>Dracaena fragrans</i>            | Asparagaceae        | 0.002                          |
| <i>Eucalyptus</i> sp.               | Myrtaceae           | 0.012                          |
| <i>Holarrhena floribunda</i>        | Apocynaceae         | 0.002                          |
| <i>Jatropha</i> sp.                 | Euphorbiaceae       | 0.001                          |
| <i>Khaya</i> sp.                    | Meliaceae           | 0.003                          |
| <i>Lagerstroemia speciosa</i>       | Lythraceae          | 0.001                          |
| <i>leucaena leucocephala</i>        | Fabaceae            | 0.001                          |
| <i>Moringa oleifera</i>             | Moringaceae         | 0.004                          |
| <i>Parkia biglobosa</i>             | Fabaceae            | 0.001                          |
| <i>Peltophorum pterocarpum</i>      | Fabaceae            | 0.002                          |
| <i>Persia americana</i>             | Lauraceae           | 0.004                          |
| <i>Pithecellobium dulce</i>         | Fabaceae            | 0.004                          |
| <i>Plumeria rubria</i>              | Apocynaceae         | 0.001                          |
| <i>Psidium guajava</i>              | Myrtaceae           | 0.012                          |
| <i>Roystonea regia</i>              | Arecaceae           | 0.002                          |
| <i>Samanea saman</i>                | Fabaceae            | 0.001                          |
| <i>Terminalia catappa</i>           | Combretaceae        | 0.001                          |
| <i>Theobroma cacao</i>              | Malvaceae           | 0.001                          |
| <i>Vitellaria paradoxa</i>          | Sapotaceae          | 0.001                          |
| <i>Unknown species</i>              |                     | 0.022                          |

**Appendix 6 Capture-mark-recapture monthly encounter history results from 60 radio- tagged *E. gambianus*.**

*Data shown are monthly capture-recapture data with 1 representing detection in a particular month; 0 representing no detection that month. The bat identification number is shown (/x\*/) preceding the recapture history; the last four digits represent the age-sex class of the bat (whether male, female, adult, sexually immature adult)*

```

/* 1 */ 10000000 1 0 0 1;
/* 2 */ 10000000 1 0 0 1;
/* 3 */ 11111111 1 0 1 0;
/* 4 */ 11111010 1 0 0 1;
/* 5 */ 11111010 1 0 0 1;
/* 6 */ 11000000 1 0 0 1;
/* 7 */ 11111010 1 0 1 0;
/* 8 */ 11111111 1 0 1 0;
/* 9 */ 11110000 1 0 0 1;
/* 10 */ 10000000 1 0 0 1;
/* 11 */ 11111111 0 1 1 0;
/* 12 */ 10000000 0 1 1 0;
/* 13 */ 11110111 0 1 1 0;
/* 14 */ 10000000 0 1 1 0;
/* 15 */ 11101111 0 1 1 0;
/* 16 */ 10000000 1 0 0 1;
/* 17 */ 11110000 1 0 0 1;
/* 18 */ 11010000 1 0 0 1;
/* 19 */ 11111101 1 0 1 0;
/* 20 */ 10000100 1 0 1 0;
/* 21 */ 00001010 1 0 0 1;
/* 22 */ 00001000 0 1 0 1;
/* 23 */ 00001000 0 1 1 0;
/* 24 */ 00001000 0 1 1 0;
/* 25 */ 00001000 1 0 0 1;
/* 26 */ 00001111 0 1 1 0;
/* 27 */ 00001110 0 1 1 0;
/* 28 */ 00001111 0 1 1 0;
/* 29 */ 00001111 1 0 0 1;
/* 30 */ 00001000 0 1 1 0;

```

```

/* 31 */ 00001110 1 0 0 1;
/* 32 */ 00001000 0 1 1 0;
/* 33 */ 00001101 0 1 1 0;
/* 34 */ 00001000 1 0 0 1;
/* 35 */ 00001110 1 0 0 1;
/* 36 */ 00001111 1 0 0 1;
/* 37 */ 00001000 1 0 0 1;
/* 38 */ 00001100 0 1 1 0;
/* 39 */ 00001000 1 0 0 1;
/* 40 */ 00001111 1 0 0 1;
/* 41 */ 00001100 1 0 0 1;
/* 42 */ 00001000 0 1 1 0;
/* 43 */ 00001000 1 0 1 0;
/* 44 */ 00001100 1 0 0 1;
/* 45 */ 00001000 1 0 0 1;
/* 46 */ 00001111 1 0 1 0;
/* 47 */ 00001110 0 1 1 0;
/* 48 */ 00001000 1 0 1 0;
/* 49 */ 00001111 1 0 0 1;
/* 50 */ 00001111 1 0 1 0;
/* 51 */ 00001111 1 0 0 1;
/* 52 */ 00001110 1 0 1 0;
/* 53 */ 00001000 1 0 0 1;
/* 54 */ 00001010 1 0 1 0;
/* 55 */ 00001101 1 0 0 1;
/* 56 */ 00001100 1 0 1 0;
/* 57 */ 00001111 1 0 1 0;
/* 58 */ 00001000 0 1 0 1;
/* 59 */ 00001110 1 0 0 1;
/* 60 */ 00001000 1 0 1 0;

```

**Appendix 7 Capture-mark-recapture monthly encounter history results from 287*****M. pusillus* fruit bats marked with RFID PIT tags.**

|                                                   |                                                   |
|---------------------------------------------------|---------------------------------------------------|
| /* 1 */ 00100000000000000000000000000000 1 0 0 0; | /* 145 */ 000010000000000000000000000000 0 1 0 0; |
| /* 2 */ 00100000000000000000000000000000 0 0 0 1; | /* 146 */ 000100000000000000000000000000 0 1 0 0; |
| /* 3 */ 00100000000000000000000000000000 0 1 0 0; | /* 147 */ 000010000000000000000000000000 0 0 1 0; |
| /* 4 */ 00100000000000000000000000000000 1 0 0 0; | /* 148 */ 000100000000000000000000000000 0 1 0 0; |
| /* 5 */ 00100000000000000000000000000000 0 0 1 0; | /* 149 */ 000000001000000000000000000000 0 0 0 1; |
| /* 6 */ 00100000000000000000000000000000 0 1 0 0; | /* 150 */ 000000001000000000000000000000 0 0 0 1; |
| /* 7 */ 00100000000000000000000000000000 0 1 0 0; | /* 151 */ 000000001000000000000000000000 0 0 1 0; |
| /* 8 */ 00100000000000000000000000000000 0 1 0 0; | /* 152 */ 0000000010000010000000000000 0 0 1 0;   |
| /* 9 */ 00100000000000000000000000000000 0 1 0 0; | /* 153 */ 000010000000000000000000000000 1 0 0 0; |
| /* 10 */ 000000000100000000000000000000 1 0 0 0;  | /* 154 */ 000001000000000000000000000000 0 0 0 1; |
| /* 11 */ 000000000100000000000000000000 0 0 1 0;  | /* 155 */ 000010000000000000000000000000 0 1 0 0; |
| /* 12 */ 000000000100000000000000000000 0 0 0 1;  | /* 156 */ 000000001000000000000000000000 0 0 0 1; |
| /* 13 */ 000000000100000000000000000000 1 0 0 0;  | /* 157 */ 000010000000000000000000000000 0 1 0 0; |
| /* 14 */ 000000000100000000000000000000 0 0 0 1;  | /* 158 */ 000001000000000000000000000000 0 1 0 0; |
| /* 15 */ 000000000100000000000000000000 0 0 1 0;  | /* 159 */ 000001001000000000000000000000 0 0 0 1; |
| /* 16 */ 000000000100000000000000000000 0 0 0 1;  | /* 160 */ 000100000000000000000000000000 0 0 1 0; |
| /* 17 */ 000000000100000000000000000000 0 0 1 0;  | /* 161 */ 0000000010000000001000000 0 0 1 0;      |
| /* 18 */ 000000000100000000000000000000 0 1 0 0;  | /* 162 */ 000010000000000000000000000000 0 1 0 0; |
| /* 19 */ 000010000000000000000000000000 0 0 0 1;  | /* 163 */ 00000000100000100000000000 0 0 0 1;     |
| /* 20 */ 000000000010000000000000000000 0 1 0 0;  | /* 164 */ 000000100000000000000000000000 1 0 0 0; |
| /* 21 */ 110000000000000000000000000000 0 0 0 1;  | /* 165 */ 000000001000000000000000000000 0 0 1 0; |
| /* 22 */ 00000000000000100000000000 0 0 1 0;      | /* 166 */ 000000001000000000000000000000 0 0 0 1; |
| /* 23 */ 0000000000100000000000000000 0 0 1 0;    | /* 167 */ 000001000000000000000000000000 0 0 0 1; |
| /* 24 */ 0000000010000000000000000000 0 1 0 0;    | /* 168 */ 000010000000000000000000000000 0 1 0 0; |
| /* 25 */ 0000001000000000000000000000 0 1 0 0;    | /* 169 */ 000001000000000000000000000000 1 0 0 0; |
| /* 26 */ 0000000000100010000100000 0 1 0 0;       | /* 170 */ 000001000000000000000000000000 0 0 1 0; |
| /* 27 */ 0000000000100000000000000000 1 0 0 0;    | /* 171 */ 000000001000000000000000000000 0 1 0 0; |
| /* 28 */ 0000100000000000000000000000 0 0 1 0;    | /* 172 */ 0000000101000000000000000000 0 0 0 1;   |

|                                              |                                               |
|----------------------------------------------|-----------------------------------------------|
| /* 29 */ 00001000000000000000000000 0 1 0 0; | /* 173 */ 00001000000000000000000000 1 0 0 0; |
| /* 30 */ 10000000000000000000000000 1 0 0 0; | /* 174 */ 00000001000000000000000000 0 0 0 1; |
| /* 31 */ 10000000000000000000000000 0 0 1 0; | /* 175 */ 00000001000000000000000000 1 0 0 0; |
| /* 32 */ 00010000000000000000000000 1 0 0 0; | /* 176 */ 00010000000000000000000000 0 0 0 1; |
| /* 33 */ 00000001000000000000000000 0 0 1 0; | /* 177 */ 00000010000000000000000000 0 1 0 0; |
| /* 34 */ 00001000000000000000000000 1 0 0 0; | /* 178 */ 00000000100000000000000000 0 1 0 0; |
| /* 35 */ 00000000000000100000000000 1 0 0 0; | /* 179 */ 00000000100000000000000000 0 0 0 1; |
| /* 36 */ 00000000000000100000000000 1 0 0 0; | /* 180 */ 00000000100000000000000000 1 0 0 0; |
| /* 37 */ 10000000000000000000000000 0 0 1 0; | /* 181 */ 00000010000000000000000000 0 1 0 0; |
| /* 38 */ 10000000000000000000000000 0 1 0 0; | /* 182 */ 00001000000000000000000000 0 0 1 0; |
| /* 39 */ 10100000000000000000000000 0 0 0 1; | /* 183 */ 00000001000000000000000000 0 0 1 0; |
| /* 40 */ 00000000000000100000000000 0 1 0 0; | /* 184 */ 00000000010000000000000000 0 0 1 0; |
| /* 41 */ 00000000001000000000000000 0 0 0 1; | /* 185 */ 00001000000000000000000000 1 0 0 0; |
| /* 42 */ 10000000000000000000000000 0 1 0 0; | /* 186 */ 00001000000000000000000000 0 0 0 1; |
| /* 43 */ 10000000000000000000000000 0 0 0 1; | /* 187 */ 00000001000000000000000000 0 0 1 0; |
| /* 44 */ 00000001000000000000000000 0 1 0 0; | /* 188 */ 00010000000000000000000000 0 0 0 1; |
| /* 45 */ 00000000000000100000000000 0 0 1 0; | /* 189 */ 00000000100000000000000000 1 0 0 0; |
| /* 46 */ 10000000000000000000000000 0 0 1 0; | /* 190 */ 00000001000000000000000000 0 0 1 0; |
| /* 47 */ 00000000000000100000000000 0 0 1 0; | /* 191 */ 00001000000000000000000000 0 0 0 1; |
| /* 48 */ 00000000000000100000000000 0 0 0 1; | /* 192 */ 00000000001000000000000000 0 0 0 1; |
| /* 49 */ 00001000000000010000000000 0 0 0 1; | /* 193 */ 00010000000000000000000000 0 0 1 0; |
| /* 50 */ 00000000000000100000000000 0 0 1 0; | /* 194 */ 00001000000000000000000000 0 0 1 0; |
| /* 51 */ 00001000000000000000000000 0 0 0 1; | /* 195 */ 00000010000000000000000000 0 1 0 0; |
| /* 52 */ 00000010000000000000000000 0 1 0 0; | /* 196 */ 00000010000000000000000000 0 0 0 1; |
| /* 53 */ 00000000000000100000000000 1 0 0 0; | /* 197 */ 00000001000000000000000000 0 0 0 1; |
| /* 54 */ 00000000000000100000000000 0 1 0 0; | /* 198 */ 00000001000000000000000000 0 0 1 0; |
| /* 55 */ 00000000000000100000000000 0 0 0 1; | /* 199 */ 00000000100000000000000000 0 0 1 0; |
| /* 56 */ 00000000000000100000000000 1 0 0 0; | /* 200 */ 00000000100000000000000000 1 0 0 0; |
| /* 57 */ 10010000000000000000000000 0 0 1 0; | /* 201 */ 00000100000000000000000000 1 0 0 0; |
| /* 58 */ 00000010000000000000000000 0 0 1 0; | /* 202 */ 00010000000000000000000000 1 0 0 0; |



|                                              |                                              |
|----------------------------------------------|----------------------------------------------|
| /* 59 */ 000000000000010000000000 1 0 0 0;   | /* 203 */ 000000001000000000000000 0 0 1 0;  |
| /* 60 */ 000000000000010000000000 0 1 0 0;   | /* 204 */ 000000010000000000000000 0 0 1 0;  |
| /* 61 */ 000000000000010000000000 0 0 0 1;   | /* 205 */ 000010000000000000000000 1 0 0 0;  |
| /* 62 */ 100000000000000000000000 0 0 0 1;   | /* 206 */ 000010000000000000000000 1 0 0 0;  |
| /* 63 */ 000010000000000000000000 1 0 0 1 0; | /* 207 */ 000000001000000000000000 0 0 0 1;  |
| /* 64 */ 000000001000000000000000 0 0 0 1;   | /* 208 */ 000010000000000000000000 0 0 1 0;  |
| /* 65 */ 000000000000010000000000 0 0 0 1;   | /* 209 */ 000000011000000000000000 0 0 1 0;  |
| /* 66 */ 000000000000010000000000 0 1 0 0;   | /* 210 */ 000000001001000000000000 0 0 1 0;  |
| /* 67 */ 000000000000010000000000 0 0 0 1;   | /* 211 */ 000100000000000000000000 0 0 1 0;  |
| /* 68 */ 000000001000000000000000 0 0 0 1;   | /* 212 */ 000000100000000000000000 0 1 0 0;  |
| /* 69 */ 000000000000010000000001 1 0 0 0;   | /* 213 */ 000000100000000000000000 0 1 0 0;  |
| /* 70 */ 000000000000010000000000 0 1 0 0;   | /* 214 */ 0000000000000000000100000 1 0 0 0; |
| /* 71 */ 000010000000000000000000 0 1 0 0;   | /* 215 */ 0000000000000000000100000 1 0 0 0; |
| /* 72 */ 000000000000010000000000 0 0 0 1;   | /* 216 */ 0000000000000000000100000 1 0 0 0; |
| /* 73 */ 000000000000010000000000 0 0 1 0;   | /* 217 */ 0000000000000000000100000 0 0 1 0; |
| /* 74 */ 000000000000010001000000 0 0 1 0;   | /* 218 */ 000000000000010000000000 0 0 1 0;  |
| /* 75 */ 000000000000010000000000 0 0 1 0;   | /* 219 */ 000000000000010000000000 0 0 1 0;  |
| /* 76 */ 100000000000000000000000 0 0 1 0;   | /* 220 */ 000000000000010000000000 0 0 1 0;  |
| /* 77 */ 000000000000010000000000 0 0 0 1;   | /* 221 */ 000000000000010000000000 0 0 1 0;  |
| /* 78 */ 000000000000010000000000 0 0 0 1;   | /* 222 */ 000000000000010000000000 0 0 1 0;  |
| /* 79 */ 100000000000000000000000 0 0 0 1;   | /* 223 */ 000000000000010000000000 0 1 0 0;  |
| /* 80 */ 000000000000010000000000 0 0 1 0;   | /* 224 */ 000000000000010000000000 0 0 0 1;  |
| /* 81 */ 000000000000010000000000 0 1 0 0;   | /* 225 */ 000000000000010000000000 0 0 0 1;  |
| /* 82 */ 000000000000010000000000 0 0 1 0;   | /* 226 */ 000000000000010000000000 0 1 0 0;  |
| /* 83 */ 000000000000010000000000 0 0 1 0;   | /* 227 */ 000000000000010000000000 0 0 0 1;  |
| /* 84 */ 000000000000010000000000 0 0 1 0;   | /* 228 */ 000000000000010000000000 0 1 0 0;  |
| /* 85 */ 000000000000010000000000 0 0 0 1;   | /* 229 */ 000000000000010000000000 0 0 1 0;  |
| /* 86 */ 000000000000010000000000 1 0 0 0;   | /* 230 */ 000000000000010000000000 0 0 1 0;  |
| /* 87 */ 000000000001000000000000 0 0 0 1;   | /* 231 */ 000000000000011000000000 0 1 0 0;  |
| /* 88 */ 000000000000010000000000 0 1 0 0;   | /* 232 */ 000000000000010000000000 0 1 0 0;  |



[illegible]

|                                              |                                               |
|----------------------------------------------|-----------------------------------------------|
| /* 119 */ 0000001010010010011000000 0 0 0 1; | /* 263 */ 0000000000010000000000000 1 0 0 0;  |
| /* 120 */ 0000000100000000000000000 0 0 0 1; | /* 264 */ 0000000000010000000000000 0 0 1 0;  |
| /* 121 */ 0000010000000000000000000 0 0 0 1; | /* 265 */ 0000000000010000000000000 1 0 0 0;  |
| /* 122 */ 0000000100000000000000000 0 0 0 1; | /* 266 */ 00000000000000000001000000 0 0 0 1; |
| /* 123 */ 0001000000000000000000000 1 0 0 0; | /* 267 */ 00000000000000000001000000 0 0 0 1; |
| /* 124 */ 0000100000000000000000000 0 0 0 1; | /* 268 */ 0000000000010000000000000 0 0 1 0;  |
| /* 125 */ 0000000010000000000000000 0 0 0 1; | /* 269 */ 0000000000001000000000000 0 0 0 1;  |
| /* 126 */ 0000100000000000000000000 0 0 0 1; | /* 270 */ 0000000000001000000000000 0 1 0 0;  |
| /* 127 */ 0000000100000000000000000 0 1 0 0; | /* 271 */ 00000000000000000001000001 0 0 1 0; |
| /* 128 */ 0000000100000000000000000 1 0 0 0; | /* 272 */ 0000000000010010000000000 0 0 0 1;  |
| /* 129 */ 0001000000000000000000000 0 1 0 0; | /* 273 */ 0000000000010000000000000 0 0 0 1;  |
| /* 130 */ 0000000010000000000000000 0 0 1 0; | /* 274 */ 00000000000000000001000000 0 0 0 1; |
| /* 131 */ 0001000000010000000000000 0 1 0 0; | /* 275 */ 00000000000000000001000000 0 1 0 0; |
| /* 132 */ 0000000010000000000000000 0 0 0 1; | /* 276 */ 0000000000001000000000000 0 1 0 0;  |
| /* 133 */ 0000000100000000000000000 0 1 0 0; | /* 277 */ 0000000000010000000000000 0 0 1 0;  |
| /* 134 */ 0000010000000000000000000 0 0 1 0; | /* 278 */ 0000000000010010010000000 0 0 0 1;  |
| /* 135 */ 0001000000000000000000000 1 0 0 0; | /* 279 */ 00000000000000000100000000 0 0 1 0; |
| /* 136 */ 0000001000000000000000000 1 0 0 0; | /* 280 */ 0000000000010000000000000 1 0 0 0;  |
| /* 137 */ 0000000100000000000000000 0 1 0 0; | /* 281 */ 0000001000000000000000000 1 0 0 0;  |
| /* 138 */ 0000010000000000000000000 1 0 0 0; | /* 282 */ 0000000000010000000000000 0 0 1 0;  |
| /* 139 */ 0000000100000000000000000 0 1 0 0; | /* 283 */ 00000000000000000100000000 0 0 0 1; |
| /* 140 */ 0000100000000000000000000 0 1 0 0; | /* 284 */ 00000000000000000100000000 1 0 0 0; |
| /* 141 */ 0000100000000000000000000 0 0 1 0; | /* 285 */ 00000000000000000100000000 0 1 0 0; |
| /* 142 */ 0001000000000000000000000 0 0 1 0; | /* 286 */ 00000000000000000100000000 0 0 0 1; |
| /* 143 */ 0000000010000000000000000 0 0 0 1; | /* 287 */ 00000000000000000100000000 1 0 0 0; |
| /* 144 */ 0000001000000000000000000 1 0 0 0; |                                               |