

Bats in an Afrotropical agricultural landscape: foraging ecology and implications for insect pest control services

A thesis submitted for the degree of Doctor of Philosophy

School of Natural Sciences

Biological and Environmental Sciences

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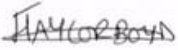
September 2024



Declaration

I hereby declare that this thesis has been composed by myself and that it embodies the results of my own research.

Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.



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Helen Taylor-Boyd

Summary abstract

Overwhelming evidence of detrimental impacts of anthropogenic activity on the environments in which we live, has instigated global efforts to curb the biodiversity and climate change crises. One such activity is agriculture, which serves to illustrate the clash between meeting the needs of growing human populations, and addressing these crises. The role that biodiversity plays in the provision of ecosystem services in agriculture, needs to be considered for production to be sustainable in the long term. As such, we need to understand the ecological functions and requirements of species assemblages in agricultural landscapes, to design and implement conservation management strategies. Insectivorous bats have been shown to suppress insect populations, including crop pests, to an extent that can constitute an insect pest regulation service. However, such research has lagged behind in the Afrotropical region, with only a handful of studies investigating the pest regulating contributions made by bats as natural predators. This PhD project set out to build on the understanding of species assemblages, habitat use and insect predation by bats in the agroecological context in an Afrotropical commercial agricultural landscape. Firstly it addresses one limitation to the use of bioacoustics methodology to study bats in the region, by presenting the first acoustic call library of its scale for Zambia, an Afrotropical country in the ecological transition zone between southern and central African habitats, where many bat species ranges cross country borders. Secondly, bioacoustic methods were used to study the foraging activity of functional groups of bats utilising commercial agricultural landscapes in Zambia, and to explore local and landscape scale factors that may influence this. Functional groups recorded acoustically in these agricultural landscapes, responded differently to woodland cover within the local habitat and across the landscape. Thirdly, molecular methods were employed to explore diet to build understanding of the relationships between bat predators and their insect prey in these agricultural habitats. Consumption of insect pests was confirmed and results demonstrate the importance of maintaining populations of multiple functional groups in species assemblages, which aids in the regulation of the range of insect orders and suppress crop pests present. Finally, potential prey abundance in different crops was determined. Bat foraging activity did not differ between maize, soya and tobacco crops, and this was supported by the finding that potential prey taxon abundance was similar in these crops. The combined results of this thesis lay the foundations for research into the role that bats

play in commercial agricultural landscapes in this Afrotropical context. In addition to considering functional groups, future studies should conduct species-specific research, and should go into further detail exploring the ecology and behaviour of bats in these agricultural landscapes by taking advantage of advances in bioacoustic, genetic and telemetry technology. By gaining a better general understanding of this understudied group of mammals, on the understudied African continent will be of great benefit to both bats and people.

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“If farm ecology and economics go wrong, nothing else will go right in agriculture.”

Prof. M.S. Swaminathan (1925-2023)

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Chapter 1. General Introduction

1.1 Biodiversity crisis

1.1.1 *Loss of biodiversity*

Over the last 500 years, anthropogenic change has been dramatically altering the face of the planet and resulting in drastic declines in biodiversity at an accelerated rate; this is described as the ‘sixth mass extinction’ (Brook et al., 2008; Ceballos et al., 2010, 2017; Dirzo et al., 2014; Cowie et al., 2022; Díaz and Malhi, 2022). Estimates of species extinctions are likely to be far lower than the true value, due to the limited information available for many Taxa, and discoveries of previously undocumented species present added complications (Ceballos et al., 2010). Global assessments of conservation status can be a useful starting point for prioritisation of species at higher levels of risk, however they do have limitations, primarily due to assumptions often being based on limited data available for a species across its range (Mace et al., 2008; Hayward, 2009; Martín-López et al., 2011). Levels of threat presented in global assessments can also be more subjective and may overemphasise localised threats (Hayward, 2009). As such, assessments made over larger geographic areas often have higher levels of uncertainty, yet they are over-relied on for conservation prioritisation (Ladle, 2009). Caution should be taken for example, when applying global assessments to prioritising localised conservation action (Mace et al., 2008).

Currently, the two main direct drivers of population declines and extinctions globally, across taxa and regions, are land/sea use change and exploitation of wild organisms, followed by pollution and climate change (Díaz and Malhi, 2022). When considering extinction drivers such as habitat loss, over-exploitation, invasive species, chains of extinction and climate change, drivers are often considered in isolation and synergistic effects are ignored, which may result in inadequate conservation action (Brook et al., 2008; Díaz and Malhi, 2022). In addition to using a species’ current distribution, population trend and threats, to determine conservation status, a consideration of life history and ecological traits is essential, but often overlooked (Isaac, 2009).

1.1.2 Functional traits

Adjustments in a species' behavioural, morphological and life history traits in response to a threat can result in negative or positive impacts on fitness, and so influence the species assemblages that are able to persist in human dominated landscapes (Isaac, 2009). . In particular, understanding of key functional traits such as 'response traits' (influencing how a species responds to a specific threat), and 'effect traits' (determining ecological functions, which influence ecosystem function), can help to monitor biodiversity changes (Hevia et al., 2017). Drastic declines in population size and range of species with effect traits are of imminent concern, as they can have significant negative impacts on ecosystem function (Ceballos et al., 2017). Therefore, understanding correlations between functional traits and extinction risk is important in making predictions about species likely to be most at risk, as well as the impacts of extinctions on ecosystem functioning (Gross and Cardinale, 2005).

Although species diversity on the whole is known to be important in forming resilient ecosystems, there is growing evidence that that species do not necessarily contribute equally to ecological processes required to maintain ecosystem function and also that some species play similar ecological roles (Petchey and Gaston, 2002). This has led to the development of the concept of 'functional diversity', which encompasses the abundance, kind and range of traits in species assemblages (Petchey and Gaston, 2002; Díaz et al., 2007).

Functional diversity can be described and measured in terms of richness, evenness and divergence, in a similar way to species diversity (Mason et al., 2005; Schleuter et al., 2010). These measures can be useful in determining anthropogenic impacts on ecosystem function, however using these for conservation prioritisation should be done with caution, as they are very context specific and information should be collected through studies on local species assemblages, taking into account rarity (Petchey and Gaston, 2006). The choice of functional traits to include in analyses can also highly influence functional diversity analyses (Petchey and Gaston, 2006). Species with identical or similar ecological functions can be categorised into 'functional groups', however, these can be subjective and functional group diversity is greatly dependent on the number of species in a group and the

number of groups considered (Petchey and Gaston, 2002; Petchey et al., 2004; Díaz et al., 2007). The use of the continuous measures of functional diversity, when more comprehensive trait data is available, can result in more accurate estimates (Petchey et al., 2004). Despite its limitations, categorisation by functional groups, is still widely used by ecologists to represent functional diversity, due to the relatively low level of trait information needed to separate species into groups; this approach can be more appropriate for species assemblages which are not well studied and for which trait data is limited (Schleuter et al., 2010).

1.1.3 Ecosystem services

Species with effect traits provide ecologically valuable functions, particularly those seen as beneficial to humans (Braat and de Groot, 2012). The concept of ‘ecosystem services’ as ecological functions useful to humans, has developed as a way of engaging people in nature conservation by assigning an extrinsic value to it, and which can be incorporated into daily lives and by institutions (Braat and de Groot, 2012). The concept has been widely publicised following the United Nations Environment Policy (UNEP) Millenium Ecosystem Assessment (MA) (www.millenniumassessment.org), broadly categorising ecosystem services as provisioning, regulating, cultural and supporting services, which have now been incorporated into both local and global policies, such as through the Sustainable Development Goals (SDGs) (<https://sdgs.un.org/>) and the global assessment report on biodiversity and ecosystem services (IPBES, 2019). Sustainable development is frequently seen to involve trade-offs with nature conservation which can be dependent on stakeholder opinion, however, in this case, ecosystem services often demonstrate a synergy between the two, as seen in the implementation of the SDGs (Gómez Martín et al., 2020; Yang et al., 2020). Regulating services in particular have shown a significant decline since the 1960’s, which warns of decreases in other ecosystem services, such as provisioning services (Carpenter et al., 2009). Impacts of policies on ecosystem services need rigorous testing so that evidence-based action by stakeholders can be taken to maintain these in the long term, however baseline reference data collected prior to environmental change is often not available for accurate assessments (Carpenter et al., 2009).

Species contributing unequally to ecological functions has led to the controversial concept of ‘functional redundancy’ (Naeem, 1998). In theory, functional diversity could be maintained despite relatively high extinction rates due to selection against functionally redundant species, as indicated by the Caribbean mollusc fossil record (Pimiento et al., 2020). From a wider perspective however, there is evidence of a much more complex association between biodiversity and ecosystem services; with biodiversity being pivotal in delivering ecosystem services, and in turn the maintenance of ecosystem services sustains biodiversity (Mace et al., 2012). This complexity can introduce confusion for conservation decision makers with regard to the value of native biodiversity, as opposed to functional diversity (Thompson and Starzomski, 2007; Díaz and Malhi, 2022). Linking the two concepts is a way of linking biological community and ecosystem ecology in an applied manner (Loreau, 2010). This can be demonstrated when species playing supportive roles to those providing the ecosystem services are shown to be critical to robust ecosystems (Keyes et al., 2021). There is also evidence that ecological stability and resilience are positively associated with the level of functional redundancy, although more empirical studies are needed to assert this (Biggs et al., 2020). Higher biodiversity can be seen to insure against species loss (insurance hypothesis) by increasing the likelihood that other species will be able to maintain functionality (Yachi and Loreau, 1999). There is therefore a need to consider the complex ecological relationships between species, the cascading effects of extinction and the increased resilience provided by biodiversity, which also facilitates habitat regeneration and renewal (Peterson et al., 1998). Landscapes with temporal and spatial changes in anthropogenic pressure levels, such as agricultural landscapes, can allow ecological relationships to be explored at differing levels of disturbance.

1.2 Agricultural ecosystems

1.2.1 Expansion and intensification

The threat of agricultural activity as a driver of biodiversity loss dates back thousands of years (Díaz and Malhi, 2022). Yet due to ever-rising demand, crop production is anticipated to increase by 100-110% from 2005 to 2050 with significant implications for land use change (Tilman et al., 2011). Decisions around the most sustainable options for

meeting food demand are complex and there is ongoing debate over the ‘land-sharing’ (low intensity farming over larger areas, enabling biodiversity to be sustained on farmland) versus ‘land-sparing’ (intensive farming using smaller areas and allowing for land to be left as natural habitat) continuum (Kremen, 2015; Luskin et al., 2018; Phalan, 2018; Ramankutty et al., 2018; Baudron et al., 2021). Intensive farming relies on high external inputs such as water, fertilizers, agrochemicals, seed and mechanisation, but is usually not labour intensive and so this often results in negative environmental impacts and sometimes even social impacts (Kremen, 2015). Agricultural expansion rates globally have slowed and intensification primarily seems to be achieving production increases needed to keep up with demand (Ramankutty et al., 2018). Intensification of agriculture in itself however, creates barriers to arable production, such as significantly impacting ecosystem services in the longer term (Barros-Rodríguez et al., 2021). Shifting the focus to developing existing under-yielding croplands with moderate intensification, is predicted to have much lower global impacts than the current intensification and extensification trends (Tilman et al., 2011).

With intensification, crop pests in particular pose a challenge for farmers, causing significant crop losses; overall global crop loss to animal pests is around 18% (Oerke, 2006). The majority (57%) of costs associated with invasive animal species across Africa from 1970 to 2019 (USD 11.6 billion) are attributed to three Lepidopteran crop pests: spotted stem borer (*Chilo partellus*), fall armyworm (*Spodoptera frugiperda*) and tomato leafminer (*Tuta absoluta*) (Diagne et al., 2021). Insect pest impacts are projected to increase significantly by about 10-25% for every degree increase in mean global surface temperature rise due to climate change (Deutsch et al., 2018). To combat this ever growing threat to production, there has been increased indiscriminate use of chemical pesticides, which can have detrimental effects on human health, biodiversity and even crop production in the long term, by disrupting natural pest control services and promoting pesticide resistance (Pimentel, 2005). Reducing and rationalising pesticide use is of imminent concern to both conservationists and farmers (Dudley et al., 2017). Despite clear increased pesticide use globally, there has been little evidence of significantly reduced crop losses since the 1960s, although pesticides have allowed for productivity to exceed economically acceptable crop loss thresholds (Oerke, 2006). With the reducing efficacy of many pesticides and future climate change scenarios likely to favour crop pest populations due to

their high dispersal and colonising abilities, as well as resilience in changing conditions, adaptive Integrated Pest Management (IPM) strategies, which incorporate monitoring and prediction tools, are vital (Ehler, 2006; Gregory et al., 2009; Skendžić et al., 2021). It is particularly important to gain a better understanding of how ecological relationships between predators and their prey may be affected (Guiden et al., 2019) and subsequent implications for pest suppression service provision by natural predators of crop pests in agroecosystems.

1.2.2 Agroecology

Action to promote biodiversity conservation on farmland is more important than ever, given the globally significant agricultural impacts on the environment are likely to be exacerbated by climate change, for example, resulting in favourable conditions for pests whilst reducing populations of natural predators. More work needs to be done collaboratively, by researchers and practitioners from agricultural, ecological and conservation sectors, to identify and implement more sustainable farming practices that maintain ecosystem services (Mamabolo et al., 2020). A broader understanding of market and political influences should also be taken into consideration (Méndez et al., 2013). ‘Green growth’ in the agricultural sector, indicated by a combination of economic and environmental factors in countries across the globe, has demonstrated that there is still much progress to be made in the agricultural industry to improve sustainability (Habib et al., 2023).

The discipline of ‘agroecology’ spans from taking a primarily ecological perspective in an agricultural setting, to more of a transdisciplinary approach to combining ecological and agronomy principles with social science, to tackle agro-food system issues (Méndez et al., 2013; Gómez-Echeverri et al., 2016).

Some agroecological farming methods are becoming well integrated in practice, whilst others are still to be widely adopted (Wezel et al., 2014; Prost et al., 2023). Diversified farming in particular, can have multiple ecological benefits at the farm level, including promoting ecosystem services and climate resilience (Altieri et al., 2015; Rosa-Schleich et al., 2019; Jaworski et al., 2023). Crop diversification for example, can increase natural

enemy populations and reduce pests, to an extent that is comparable to non-crop measures (Jaworski et al., 2023). It also can have positive impacts on food security and nutrition (Bezner Kerr et al., 2021). These benefits may be insufficient in the short term to outweigh economic outlays, e.g. higher labour costs associated with polyculture (Huss et al., 2022), however in the longer term, diversified farming systems have the potential to increase and stabilise both yield and profitability (Rosa-Schleich et al., 2019; Jaworski et al., 2023). A consensus on the concept of ‘regenerative agriculture’ is still to be reached and can constitute a range of conservation farming techniques and outcomes that aim to reduce environmental impacts (Newton et al., 2020).

Natural and semi-natural habitats within agricultural landscapes are also essential in maintaining biodiversity and it has been proposed that at least 20% per km² should be allocated to semi-natural vegetation, providing native species assemblages with a range of habitats (García-Vega et al., 2024). Nevertheless, to identify and implement the most appropriate strategies to promote biodiversity and ecosystem services in farming landscapes, we need to understand influences of different spatial and temporal scales (Jeanneret et al., 2021).

In highly disturbed agricultural habitats, interactions with landscape features, can influence recolonising abilities of both crop pests and natural predators (Tscharntke et al., 2005). Consequently, ecosystem service provision in these landscapes may be driven by species with higher dispersal ability and higher tolerance to anthropogenic change (Tscharntke et al., 2005). Landscape composition is an important predictor of pest suppression, however responses by pests and natural enemies seem to be very context specific, hindering the development of generalizable IPM strategies (Karp et al., 2018). Heterogeneity in the landscape for example can result in higher diversity levels (Tscharntke et al., 2005) and predation rates by natural predators (Tortosa et al., 2023). However, larger proportions of non-crop area does not always increase biological control (Karp et al., 2018). In addition, increases in diversity and abundance of pests and predators, may not always translate to increased pest regulation or higher yields (Mitchell et al., 2014). It is therefore important to consider the dynamics between specific crop, pest and predator when developing integrative pest control strategies (Bonato et al., 2023).

1.3 Bats

1.3.1 A diverse order

Pest suppression services provided by bats have received increased attention in recent years (Tuneu-Corral et al., 2023). Approximately 20% of mammal diversity is made up of the bat (Chiroptera) order (Wilson and Reeder, 2005). The number of Chiropteran species is currently recognized to be over 1400 (Simmons and Cirranello, 2024) and there has been a clear difference in speciation rates between the 18 families, with highest species richness found in the Vespertilionidae (Hutson et al., 2001; Shi and Rabosky, 2015). By being highly mobile and making use of the aerosphere, bats have high dispersal abilities compared to other mammals, however significant geographic and environmental barriers have allowed for differences in phylogenetic diversity between biogeographic regions (Peixoto et al., 2014). It is predicted that many more species in this mammal order are yet to be described (Parsons et al., 2022). The majority (58%) of bat species assessed by the IUCN (n=1327) have been categorised as Least Concern (IUCN, 2025) (Figure 1.1.1). Nevertheless, bats make up an important part of described species diversity for most ecoregions of the world and approximately 80% of assessed bat species require conservation or research attention due to significant threats or limited data available on their conservation status and population trends (Frick et al., 2020). There also is a need to increase the geographical scope for studies on responses to anthropogenic change (Park, 2015; Russo et al., 2021).

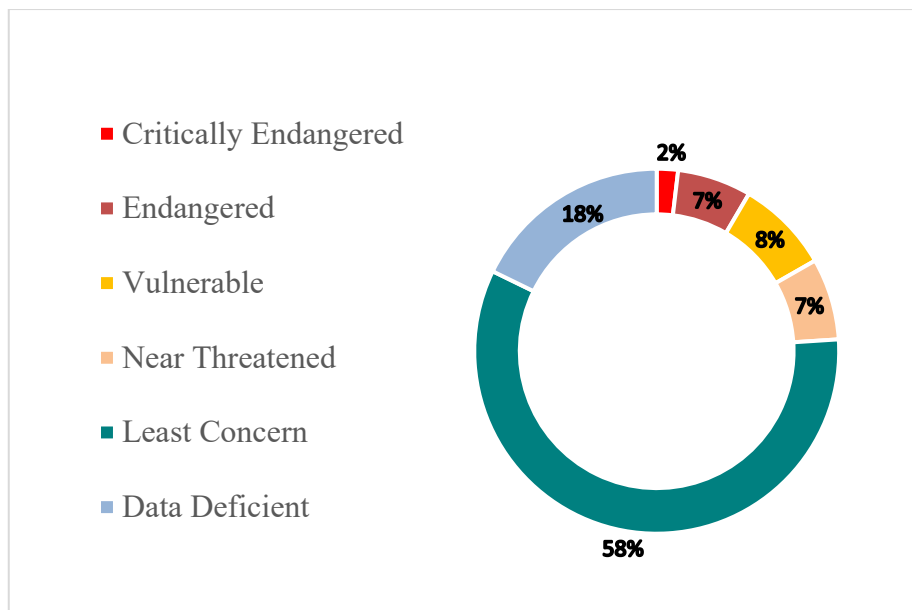


Figure 1.1: IUCN Red List categories for 1327 assessed bat species across the globe (IUCN, 2025)

Across the globe, the primary threat to bat populations is habitat loss or modification (particularly of forests which provide critical foraging and roosting habitat for bat species), with deforestation caused by logging and agricultural land clearance being the two main drivers (Mickleburgh et al., 2002; Frick et al., 2020). Habitat loss and modification through more intensive agriculture in particular can have impacts on foraging and roosting requirements for over 50% of bat species, though low intensity agriculture can actually benefits some (Frick et al., 2020). Fear-based, indiscriminate mass culling of bats is known to occur following outbreaks of zoonotic diseases due to their roles as wildlife reservoirs of various pathogens, despite evidence that it is not an effective way to control spread and compromising conservation efforts (Guyton and Brook, 2015; Olival, 2016; Fenton et al., 2020). Direct persecution by humans was previously the most significant cause of multiple bat mortality until the early 2000s, since then however, the outbreak of white nose syndrome and increases in wind turbine developments have been reported to be the main causes of multiple mortalities, which can be linked to population declines (O'Shea et al., 2016). Climate change is also likely to affect bat species ranges, populations and behaviour, but much of the literature on the subject is based on species distribution models (SDMs) and to provide better predictions of impacts, more empirical study is needed on which to base the models (Festa et al., 2023). Extinction risk is estimated to be highest in

species with smaller geographic ranges and low wing aspect ratios i.e. shorter, broader wings usually associated with manoeuvring in cluttered environments, such as forests or woodland (Jones et al., 2003; Moir et al., 2021). These species are particularly difficult to study, as cryptic roosts are often hard to find and capture rates can be very low, making it difficult to assess populations (Frick et al., 2020).

1.3.2 Monitoring

Ecological monitoring of wildlife populations to inform and prioritise conservation action requires relatively high research inputs and collaborative expertise to collect, analyse and utilise appropriate, question-driven information over long periods (Lindenmayer and Likens, 2010). Technological advances in the field are moving towards automated monitoring to reduce field survey effort whilst increasing the quantity and quality of data collected, however this requires considerable collaboration between specialists in ecology, electronic engineering and artificial intelligence (Besson et al., 2022). Remote sensing in particular can provide spatial contexts to ecological monitoring and can detect variation in vegetation, soil and water properties across landscapes and habitats, as well as changes over time (Kerr and Ostrovsky, 2003; Stephenson, 2020; Jiao, 2024). It can even provide 3-dimensional habitat information (D'Urban Jackson et al., 2020). Remote sensing also has applications in monitoring specific anthropogenic impacts, such as observing treeline shifts (Garbarino et al., 2023), desertification (Yussupov and Suleimenova, 2023) and fire (Kerr and Ostrovsky, 2003; Szpakowski and Jensen, 2019), as well as evaluating conservation action, such as restoration schemes (Camarretta et al., 2020). In addition, it has even been possible to monitor some species distributions and populations using remote sensing (Stephenson, 2020). Imagery provided by cameras e.g. drone cameras and camera traps, as well as sound recordings provided by passive acoustic devices allow for more localised, non-invasive monitoring of species assemblages, behaviour and populations (Stephenson, 2020). Ecological modelling can combine remote sensing and localised monitoring data collected by ecologists such as species presence data, to evolve a more predictive approach to ecological monitoring, for example utilising information on current species distributions combined with landscape and habitat characteristics to predict distributions under alternative scenarios (He et al., 2015; Randin et al., 2020). Species distribution modelling (SDM) approaches have the potential to predict future anthropogenic impacts and climate

scenarios (Randin et al., 2020). Occurrence data used to inform SDMs can however be spatially biased and predictor variables may not be spatially explicit so habitat characteristics may not be fully captured and outputs should be interpreted with caution (He et al., 2015). As monitoring devices, such as camera traps and acoustic detectors, become even more affordable and available to ecologists and the general public, there is an increased capacity, such as through citizen or community science projects, and with the aid of Artificial Intelligence (AI) systems this has the potential to increase the capacity for ecological monitoring and to improve the spatial extent, quantity and quality of occurrence data collected (McClure et al., 2020).

A consensus for reliable survey methodology, taking into account animal detectability, is essential for ensuring that monitoring is comparable (Stahlschmidt and Brühl, 2012). Due to the volant and nocturnal habits of bats in particular, they can be very difficult to study and monitoring methods need to take into account differences in detectability between species and in different habitats (Meyer et al., 2011; Voigt et al., 2021). Sampling methodology can greatly influence the detectability of rarer species so a range of methods may be needed to detect all species present, sufficient replication also reduces biases in species richness and presence estimates (Meyer et al., 2011; Gibb et al., 2019; Dekker et al., 2022). For acoustic surveys, a correction factor can be calculated from detection distances to improve accuracy in activity comparisons between bat species (Monadjem et al., 2017).

Monitoring of bats has required invasive and often lethal techniques involving capturing and handling bats which can be challenging given their nocturnal habits and ability to evade capture using echolocation, and also puts both handler and bat at risk of injury or even transfer of pathogens, however less invasive methods are being more widely employed to study them (Kunz and Parsons, 2009). For example molecular identification of species through faeces to confirm presence is being increasingly used, either by collecting droppings from captured bats without having to take lethal specimens, or alternatively from roosts without the need for handling individuals at all (Walker et al., 2016, 2019). Also, as vocalising species, the development of ultrasound detector technology has enabled non invasive Passive Acoustic Monitoring (PAM) of echolocating bat species using vocalisations investigate species assemblages and activity levels, with

calls being visualised and analysed using readily available software (Parsons et al., 2000; Gibb et al., 2019). We have come a long way in the relatively short time since the 1930s when ultrasound detectors were invented and 1970s when sonorous clicks were first used to identify species, through to utilising a variety of ways to hear, record and analyse bat calls, and we are now developing the use of AI in this field in an attempt to automate the analysis of the large amount of data generated in a more efficient way (Zamora-Gutierrez et al., 2021).

The morphometrics of flight, such as wing loading, can be a reflection of the behavioural ecology of a species, and echolocation call structure is closely related to this (Norberg and Rayner, 1987). Species with high wing loading (longer pointed wings) tend to fly higher faster in more open environments and so tend to have lower frequency calls that travel further, whilst those with low wing loading usually have short, broad wings to allow manoeuvrability in more cluttered vegetation and so tend to have higher frequency calls to allow detailed echoes across shorter distances (Norberg and Rayner, 1987; Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). Echolocating bats have been shown to emit echolocation pulses which can be categorised into sonotypes based on characteristic acoustic measures or parameters (Sherwin et al., 2000; Schnitzler et al., 2003; Denzinger and Schnitzler, 2013). Further identification into lower taxonomic levels, including species, has been shown to be possible for many assemblages (Jones et al., 2000; Furey et al., 2009). However parameters can overlap between species and even functional groups, making more precise and accurate acoustic identification difficult (Jones et al., 2000; Blumstein et al., 2011). There are also differences in detectability, due to the properties of the sound emitted as well as characteristic behaviour, which need to be accounted for when undertaking PAM surveys (Braun de Torrez et al., 2017; Monadjem et al., 2017). Species calling at higher frequencies for example, can have shorter detection distances (Figure 1.2) due to atmospheric attenuation (Adams et al., 2012).

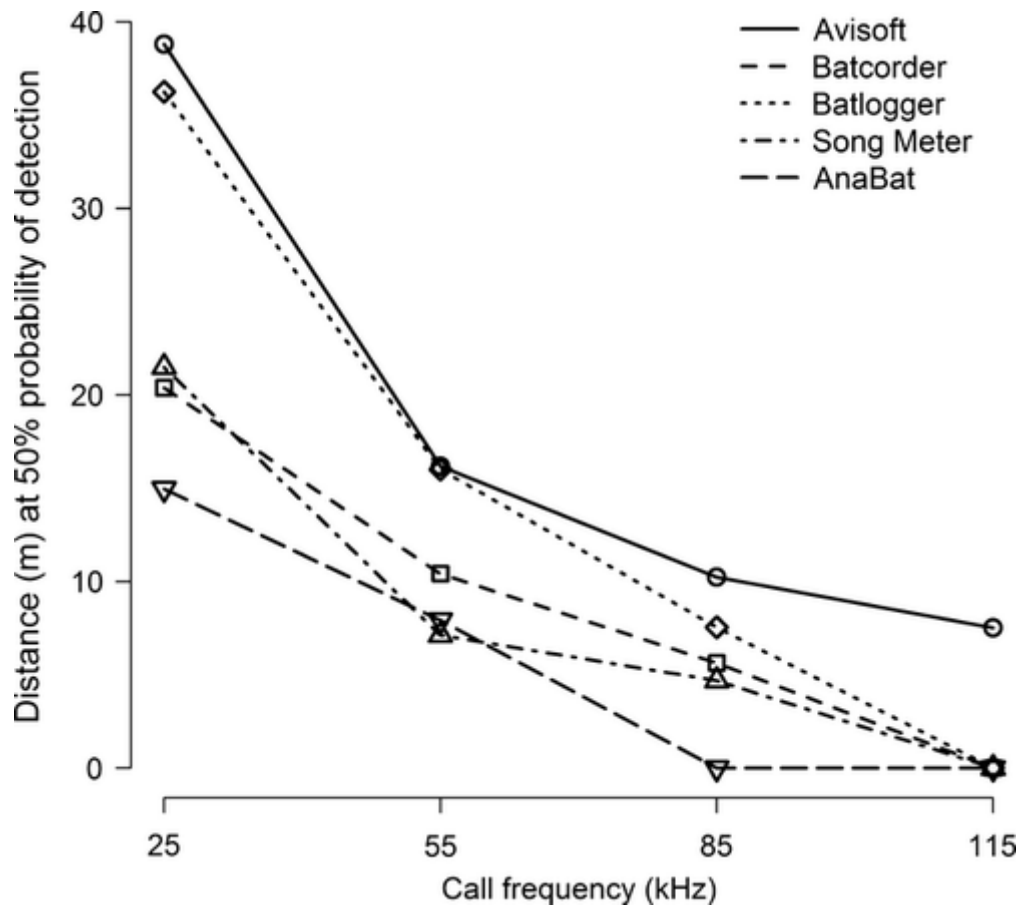


Figure 1.2: Detection distances calculated using playback calls using different detector models all show attenuation at higher frequencies (taken from (Adams et al., 2012)).

PAM sampling strategies can be context specific and based on cost-benefit analysis, reliant on a compromise between available resources and the detectability of target taxon in specific habitats and across timescales (Froidevaux et al., 2014; Pieretti et al., 2015). Also, because of the range of ultrasound detector equipment and acoustic analysis software now available, there are considerations in terms of functionality and comparability (Fenton, 2000; Adams et al., 2012; Britzke et al., 2013; Perea and Tena, 2020). Wider scale monitoring can result in large amounts of data which can be analysed more efficiently using filtering software and auto-identifications (Nocera et al., 2019). Machine learning has even been applied to semi-automate call identifications (Miller, 2001; Tabak et al., 2022). Nevertheless, misidentifications can be highly dependent on the software and training datasets used, and can become a significant issue, especially for datasets containing species with similar call parameters, or where reference calls for the full species

assemblage are unavailable and exclude rarer species (Clement et al., 2014; Barré et al., 2019; Nocera et al., 2019).

Understanding the traits of bat species can help to monitor ecological responses and tailor management strategies in anthropogenic landscapes (Jung and Threlfall, 2018). In agricultural landscapes for example, bat species assemblages are generally known to benefit from low intensity farming practices, such as organic farming or agroforestry, however there is still limited information on the mechanisms behind this (Park, 2015).

In addition to species richness and diversity indices often used to monitor species assemblages, activity levels have been traditionally used to quantify temporal changes and spatial comparisons relating to bat species.. Measures of activity are usually based on a measure of ‘number of passes’ per unit time, although they can differ in what metric constitutes a ‘pass’ and the unit of time used (Kerbiriou et al., 2019). To better assess responses to long-term environmental changes, more recent measures have been proposed which incorporate habitat and climatic parameters (Tuneu-Corral et al., 2020). An in-depth understanding of how functional groups and species utilise the aerosphere is needed to accurately assess the relative importance of habitat compared to landscape scale features (Williams-Guillén et al., 2016).

Due to resource limitations, the monitoring of species that have pivotal roles to play in ecosystems is often prioritised and these used as surrogates to represent trends across broader species assemblages (Tälle et al., 2023). Surrogate species have been most effective when they are species groups or higher taxon, such as birds and mammals, those that have close ecological similarities with the species they are intended to represent, or when they are used at larger spatial scales of more than 1000km² (Tälle et al., 2023). Indicator or bioindicator species for example, are increasingly being used to signify ecosystem health (Burger, 2006; Siddig et al., 2016). Unfortunately, there is a growing use in the literature of a single species indicator with often little or no justification provided for the selection (Siddig et al., 2016). This can mean that the indicator species chosen does not necessarily accurately represent the complexity present in ecological systems or the range of responses exhibited by different taxa (Lindenmayer and Likens, 2011). Bat species are known to be responsive to both rapid and gradual environmental change; for carnivorous

or insectivorous bats, this is due to their higher trophic level, and for fruit eating bats, it is their close association with plants (Jones et al., 2009; Russo and Jones, 2015). This makes them a useful target taxon to monitor the effects of anthropogenic change (Jones et al., 2009; Sherwin et al., 2013; Russo et al., 2021). Yet there are limitations to using bats as bioindicators in terms of survey methods, taxonomic resolutions and complex ecological relationships, which can make associations with stressors more difficult to identify and often context specific (Russo et al., 2021). For example, in comparison to other taxa such as insects, quantifying richness using capture methods can require higher sampling effort for bats, but obtain similar results (Syaripuddin et al., 2015). However, the increase in non-invasive survey techniques, such as bioacoustics and genetic analysis of roost droppings is helping to increase the efficiency of monitoring bats as bioindicator species (Ware et al., 2020; Russo et al., 2021). Dietary analysis has even been used to monitor insect prey species, such as the brown marmorated stink bug pest (*Halyomorpha halys*) consumed by big brown bats (*Eptesicus fuscus*) in the USA (Maslo et al., 2017).

1.3.3. Insect pest suppression

Bats occupy a wide range of niches and have an array of ecosystem functions such as seed dispersal, pollination and insect predation (Williams-Guillén et al., 2016). The vast majority of bat species worldwide (over 60%) are insectivorous (Hutson et al., 2001).

Although many insectivorous bat species show more specific prey preferences, they are often seen as generalist predators, able to take advantages of fluctuations in prey availability (Clare and Oelbaum, 2023). That being said, differences in sensory perceptions may result in differing target prey taxon, even between very similar, co-existing species of bat (Siemers and Swift, 2006). There may also be dietary niche separation between males and females, possibly due to different energy requirements (Mata et al., 2016). Predator-prey interactions between bats and insects are complex and have even resulted in some extreme insect morphological and behavioural adaptations, such as in some moth auditory systems (Waters, 2003).

Bat activity can be influenced by food availability, with higher activity sometimes found where there is higher abundance of specific insect taxon (Wickramasinghe et al., 2004).

Dietary components consumed by an individual species can vary across landscapes (Aizpurua et al., 2018) and seasonally in response to prey availability (Ramos Pereira et al., 2002). Species can even spend more time foraging at different aerosphere heights to target specific prey e.g. Molossid species foraging at heights of 400-500m above ground level, which migratory insects are known to utilise to disperse (McCracken et al., 2007). Prey availability often depends on intact habitat required for multiple ontogenetic stages of prey species, such as insect larvae, which may differ from bat foraging habitat (Arrizabalaga-Escudero et al., 2015). Bats with more specialist diets especially may not be able to persist when their preferred diet is removed by land use change (Alberdi et al., 2020).

Understanding bat diet and ecological networks can indicate bat species that are important for pest control in order to prioritise conservation efforts (Mata et al., 2021a). Molecular methods of studying bat droppings in particular have given important insights into ecology, such as target prey taxon (Burland and Wilmer, 2001). Genetic evidence for the presence of insect pests in bat diet has been found across a range of agricultural and surrounding natural mosaic landscapes (Tuneu-Corral et al., 2023). Bat activity has been shown to increase during pest irruptions over some crops (Baroja et al., 2021). Some studies have even demonstrated evidence for raised pest presence in bat diet during pest irruptions (Baroja et al., 2021).

Quantifying the effects on yield of pest predation by bats as a regulating ecosystem service that translates to a monetary value can be complicated, nevertheless, some attempts have been made (Tuneu-Corral et al., 2023). Two main approaches have been taken. Firstly, field-based exclusion experiments can demonstrate crop damage and yield reductions caused by pests when nocturnal predators (predominantly bats) are excluded, using netting enclosures over crop study plots at night. Some bat exclusion studies have successfully demonstrated suppression of some pests, mainly in agroforestry systems (Cassano et al., 2016; Maas et al., 2016; Librán-Embid et al., 2017; Linden et al., 2019; Ancillotto et al., 2024) but also in rice cultivation (Bhalla et al., 2023; Sottomayor et al., 2024; Tuneu-Corral et al., 2024). Other studies however, have indicated no effect of bats presence on yield such as in cacao (Gras et al., 2016). Secondly, models quantifying cost avoidance can be used to quantify pest control by bats, which take into account both direct reduction of

pest damage, and the indirect savings made by reduced pesticide costs. For example, research from the United States, showed that pest control services by bats amounts to approximately 2-29% of the annual yield value, using data from cotton growing areas of Texas (Cleveland et al., 2006), which at the time of the study gave a mid-range value of 22.9 billion USD per year (Boyles et al., 2011). In South Africa, it has been estimated that control by bats of stink bug pests is worth 0.53–1.29% of annual yields to the macadamia nut industry (Taylor et al., 2018), and in Thailand, 0.008% of annual yields for the rice industry was estimated for *Tadarida plicata* predation on the planthopper pest *Sogatella furcifera* (Wanger et al., 2014).

Despite the mounting evidence of pest control services by bats in a range of crops and agricultural landscapes, there are very few studies identifying direct links between particular agricultural management practices and impacts on bat populations (Tuneu-Corral et al., 2023). Nonetheless, existing studies do indicate that heterogenous and low intensity agricultural landscapes can be of benefit to bats (Park, 2015; Tuneu-Corral et al., 2023). If agricultural intensification is to increase to meet food demands, it is likely that bat populations of many species, and associated pest control services, may drastically decline, leading to concerns for food security and human well-being (Williams-Guillén et al., 2016).

1.4 Afrotropical context

1.4.1 Biodiversity and agricultural expansion

Developing better links between scientists and decision makers is critical in maintaining the flow of biodiversity information that is available for African countries and in building on these datasets in a targeted manner to improve environmental decisions (Stephenson et al., 2017). However, there is still limited capacity in the tropics to take advantage of technological advances in biodiversity monitoring and so comprehensive information is often lacking (Stephenson, 2020). Africa is particularly rich in biodiversity but accelerated rates of development and human population growth puts sustainable development at risk if the environment is not prioritised (Archer et al., 2021). Despite rates slowing globally, habitat loss driven by deforestation continues at relatively high rates across the African

continent; with the highest annual net loss (3.9 million ha) in the years 2010-2020 compared to other global regions (FAO, 2020). However, agriculturally driven deforestation in African dry forest or woodland ecosystems is still poorly quantified; this is partly due to limited study and data collection capacity, but also due to the dynamic, heterogenous landscapes with many indistinguishable habitat characteristics, making satellite imagery analysis and interpretation difficult (Pendrill et al., 2022). The most extensive dry forest or woodland ecosystem on the continent is miombo woodland (Frost, 1996). It is distinguished from other African vegetation types by the dominance of Fabaceae tree species such as *Brachystegia*, *Julbernardia* and *Isoberlinia* species (Frost, 1996). This ecosystem is particularly important in Zambia, where it is the most widespread woodland type (Syampungani, 2008) and also holds the highest tree species diversity and relatively high levels of endemism compared to other countries where it is found (Frost, 1996). There is a climatic and soil composition change from north to south of the country, resulting in a transition from ‘wet’ to ‘dry’ miombo and also four ecological zones applicable to agricultural production, termed ‘agro-ecological zones’ (Figure 1.3) (Mukosha and Siampale, 2009).

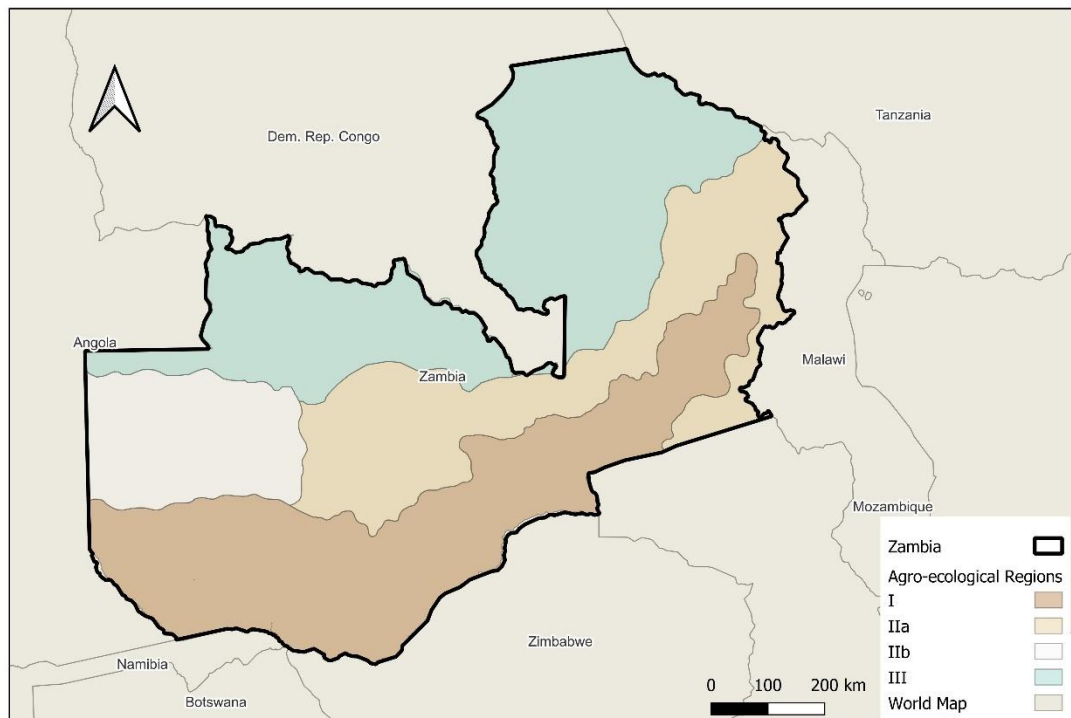


Figure 1.3: Agro-ecological zones present across Zambia. (I = Luangwa and ambezi Rift Valley Zone - semi-arid low rainfall (< 800mm), low altitude (400-900m); IIa = Central, Eastern and Southern plateau - medium rainfall (800-1000mm), altitude 900-1300m; IIb = Kalahari (Barotse) sand plateau and the Zambezi flood - medium rainfall (800-1000mm), altitude 900-1200m; III = North, North-Western Zone - high rainfall (>1000mm), altitude (1100-1500m) (adapted from Mukosha and Siampale, 2009))

Higher deforestation rates in countries in sub-Saharan Africa have been found to correlate with higher agricultural production (Goulart et al., 2023). Following global patterns, agricultural expansion has seen an increase since the 1980s in Zambia causing significant land clearance and impacts on miombo woodland, which has now reached a plateau since around 2012 (Figure 1.4).

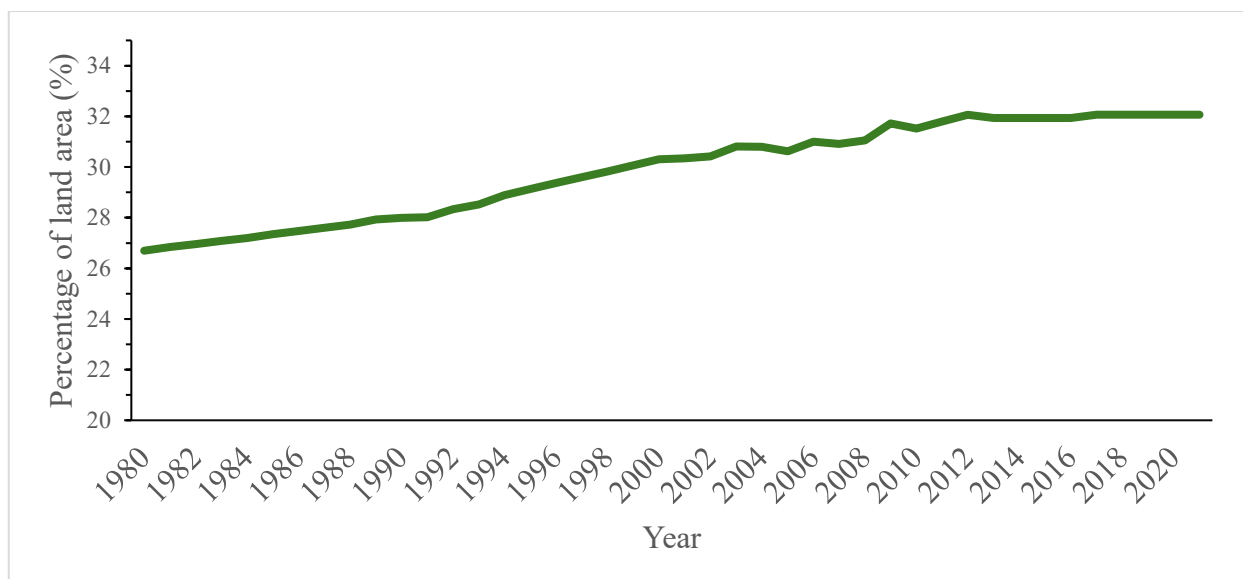


Figure 1.4: The percentage of land area allocated to agricultural use in Zambia since the 1960s (source: World Bank)

These woodlands have traditionally provided valuable provisioning services to poorer local communities and have supplied resources in times of hardship (Mukosha and Siampale, 2009; Campbell et al., 2013; Kalaba et al., 2013). Drivers of agricultural expansion across the region include loss of soil fertility and changing climatic conditions, proximity to services (expanding in areas where there is better access to markets, schools, health care etc.) and meeting increased product demands (Jellason et al., 2021). Nevertheless, the vast majority of farms in sub-Saharan Africa, remain smaller than 2ha (Lowder et al., 2016), indicating the dominance of subsistence or small-scale farming which has traditionally involved extensive, shifting, ‘slash and burn’ agriculture, contributing significantly to deforestation (Rudel, 2013). Although regeneration of miombo woodland is possible to some extent after traditional ‘slash and burn’ practices, there are long term effects on woodland structure of this more extensive farming approach, as demonstrated in Mozambique, where there was higher tree density in regenerated woodland after 30-35years in comparison to mature woodland and also differing tree species compositions (Montfort et al., 2021). There is also evidence that in comparison with intensive agricultural, these extensive agricultural approaches in the Miombo region will contribute a higher net effect on climate forcing or drivers overall, when taking into account the larger areas required for the same rate of production (Wilson and Scholes, 2020). Furthermore,

larger scale land acquisitions for intensive commercial agriculture in Africa seem to target areas which have already undergone some degree of land clearance (Davis et al., 2023).

Given that agricultural intensification is likely to rise to meet the growing demands across Africa, it is essential for agricultural sustainability that studies exploring the balance between productivity and maintaining ecosystem functionality in Miombo woodland agro-ecosystems are carried out. There has been limited progress in the application of conservation farming practices on a small scale (Bouwman et al., 2021). However, it has been shown that increased agricultural production by mechanisation in sub-Saharan Africa can still allow for conservation agricultural techniques, such as ripping tillage and direct sowing, which don't incur significant additional cost in the short term but do benefit profitability in the longer term (Omulo et al., 2022). There are also growing opportunities for engaging women in agriculture, which may introduce a more holistic approach (Glazebrook and Opoku, 2020). Although education and regulation in sub-Saharan Africa on appropriate pesticide applications has lagged behind the rest of the world (Oerke, 2006; Isgren and Andersson, 2021), there has been some progress in pest monitoring, and forecasting models have been developed so that country-specific alerts can now be communicated with national agencies, which will aid implementation of integrative pest management strategies (Day et al., 2024).

1.4.2 African bats

The Eocene period, around 30-50 million years ago, saw the greatest bat species diversification (Gunnell and Simmons, 2005; Jones et al., 2005; Simmons, 2005) with the modern families originating somewhere in the southern hemisphere, likely within Africa (Eick et al., 2005). Despite holding relatively high diversity, there has been far less research effort focussed on African bats in comparison to other regions (Hutson et al., 2001; Meyer et al., 2015) and Africa has been 'largely a void, so far as bat conservation is concerned' (Racey, 2013). The increased efforts by both the scientific community and community science projects, such as bat groups, has been invaluable in increasing capacity for the study of African bats (Taylor, 1999). However, taxonomic resolution has still not been reached for many species complexes and with a combination of morphometric, acoustic and genetic evidence, many species are still undergoing taxonomic revision and

description across the continent (Morales et al., 1991; Cakenberghe, Van and Vree, De, 1998; Volleth et al., 2001; Hutson et al., 2001; Kearney et al., 2002; Happold, 2005; Ammerman et al., 2012; Goodman et al., 2017; Monadjem et al., 2020a, 2021; Benda et al., 2022). Increased research on African bats has also revealed range extensions of some species (Shapiro and Monadjem, 2016). SDMs have been useful in identifying areas of high species endemism and richness, which often do not intersect, so this has implications for prioritisation of research and conservation efforts (Schoeman et al., 2013; Cooper-Bohannon et al., 2016; Herkt et al., 2016).

Much of the African bat diversity is also outside of protected areas and is likely to be highly impacted by both land use and climate change (Smith et al., 2016). On the whole, species richness does seem to increase towards the equator (Herkt et al., 2016) and the area between Zambia and Zimbabwe has been highlighted as an area of relatively high species richness (Hutson et al., 2001). Previous records of numbers of species confirmed for Zambia for example, have increased in the last 20 years or so, from 65 (Hutson et al., 2001) to 74 species (Monadjem et al., 2020b) to 76 (Benda et al., 2022). The phenology of bats in this area is closely related to rainfall patterns and peaks in insect abundance with seasonal patterns of parturition before wet seasons (Cumming and Bernard, 1997; Cotterill and Fergusson, 1999). There have been some studies looking at agricultural landscape use and pest consumption by bats in the southern African region, although these have focussed on more southerly locations in South Africa (Weier et al., 2018, 2019, 2021; Mphethe et al., 2023) and Eswatini (Noer et al., 2012) where climate and habitats are different from more northerly locations.

With limited information on many African bats, current conservation status and extinction risk is very difficult to assess for most species (Hutson et al., 2001; Frick et al., 2020). The IUCN lists 63 (22%) of the 289 assessed sub-Saharan African bats as ‘Data Deficient’ (IUCN, 2025). Habitat and roost loss, agricultural expansion and persecution of bats have been identified as key threats to bats across the region (Hutson et al., 2001; Frick et al., 2020). So in particular, more studies on Afrotropical bats in relation to anthropogenic change, including agricultural expansion and intensification are needed (Williams-Guillén et al., 2016; Festa et al., 2023; Xavier et al., 2023).

1.5 Thesis Aims & Outline

There is a clear need to increase the study of bats in agricultural landscapes, due to their biodiversity and ecosystem service value. In particular African bats have been highlighted as priority subjects for efforts in this research area and this thesis adds to the growing knowledge of bats in rapidly changing Afrotropical landscapes. With Zambia being largely dominated by miombo woodland and a growing focus on both agricultural expansion and intensification, the country presents a useful study location to build an understanding of impacts on bat species assemblages and the role they may play in these changing environments.

Firstly however, robust monitoring methods are required for ecological assessment and to track changes in populations and species assemblages. Passive Acoustic Monitoring (PAM) has been demonstrated to be a useful tool for monitoring bats, but the application of PAM in Africa has been hindered in part by lack of availability of reference acoustic data. This study builds and utilises an acoustic dataset of bat calls, collected collaboratively, which can be used by future researchers, ecologists and amateur naturalists.

Secondly, despite being recognised as being one of the greatest threats to biodiversity, agricultural expansion and intensification also present an opportunity to manage large areas of agroecological land, with ecosystem service provision being a motivation for promoting conservation action in these landscapes. Commercial agriculture (production for sale or profit) in this Afrotropical context is characterised by farmland of over 100ha, utilising mechanisation and usually with irrigation systems in place, such as centre pivot irrigation (CIAT and World Bank, 2017). Commercial farms in the study region the on the most part retain some areas of natural vegetation, either left in its natural state or utilised for low intensity grazing and harvesting of resources such as firewood. These areas consist of either Miombo woodland or Dambo wetland in the study areas. Pest control is a significant issue for commercial agricultural production and because of the negative impacts associated with chemical pesticides, farmers are increasingly turning to nature-based solutions. Understanding habitat use by natural predators such as bats, as well as interactions with crop pest prey, is pivotal in designing management strategies for promoting natural pest control services.

This PhD project set out to build on the understanding of species assemblages, habitat use and insect predation by bats in the agroecological context across an Afrotropical commercial agricultural landscape in Zambia. To do this it aims to:

- i. Collate the first bat acoustic library for Zambia which can be used to study bats across species ranges ([Chapter 2](#)). No echolocation call recording has been taken within Zambia for most species known to occur in the country, whilst for some species there has been no echolocation call documented anywhere.
- ii. Assess the relative importance of insect prey availability, local habitat and landscape characteristics in influencing bat activity across commercial agricultural landscapes ([Chapter 3](#)). Although there is some literature on this subject globally, there has been limited work presented for the southern African region, with notable gaps for habitats in more northern areas of the region such as Zambia.
- iii. Determine the dietary composition of bats utilising the commercial agricultural landscape for foraging and confirm their consumption of insect crop pests in this Afrotropical context ([Chapter 4](#)). This is a growing area of research in the African context, again with some limited work presented but focussed on southerly locations such as South Africa.
- iv. Investigate the abundance of insect prey taxa across different crops to better understand prey availability to bats in arable habitats ([Chapter 5](#)). Despite being essential to the development of IPM strategies, there are very few studies globally looking at insect assemblages in different crops which urgently needs to be addressed.

1.6. Ethical Standards

All of the work conducted in this study was approved by the University of Stirling's Animal Welfare and Ethical Review Body (Ref: AWERB 2023 15052 10438).

Chapter 2. Acoustic parameters of bat echolocation calls in Zambia: a collaborative effort to develop a call library for non-invasive research and monitoring

An adapted version of this Chapter has been submitted with the following authors and has now been published by the journal ‘Acta Chiropterologica’:

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Hugo Rebelo^{7,8}, A – Conceptualization (supporting), Methodology (supporting), Investigation (supporting), Writing - review & editing (supporting)

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2.1. Abstract

Passive acoustic monitoring (PAM) of bats enables non-invasive research that improves monitoring efficiency, and can be used for species identification, documenting occurrence and measuring activity levels, making PAM valuable for applied research on this diverse and enigmatic taxon. However, equipment costs and a dearth of experienced personnel, as well as a lack of local open access reference datasets (call libraries), have limited the study of African bat communities using PAM. This study compiles and uses recordings from the first publicly available call library of this scale from Zambia. Echolocation calls were recorded upon release of captured bats during various projects from 2015 to 2023, using full spectrum ultrasound detectors. Acoustic calls from 238 individuals of 22 species were collated. I aimed to determine whether Zambian bat species could be accurately distinguished using acoustic measures (parameters). I hypothesised that, given the species richness known to occur in the region, some species (or species groups) would be readily identifiable, but that there would be substantial similarities between some species, which would hinder identification. After taking into account multicollinearity, I selected five acoustic parameters for further analysis of recordings. Principal Component Analysis (PCA) was conducted to identify parameters that were best able to separate the calls of different functional groups (identified by sonotype) or species. Discriminant Function Analysis (DFA) was then used to determine the accuracy with which the parameters may be used to acoustically distinguish species or sonotypes. The parameters ‘Start Slope’ and ‘Frequency of Maximum Power’ were the most useful for separating the species considered. It was possible to separate some sonotypes and species with over 95% accuracy. Many species however, could not be identified with certainty, underscoring the importance of other identification techniques for these cases, such as morphological measures or genetic sampling.

Key words: Chiroptera, bat survey, ultrasonic acoustic detector, South-Central Africa, passive acoustic monitoring

2.2. Introduction

During this time of accelerated anthropogenic change, impacts on biodiversity are of urgent concern. Monitoring species distributions and populations remains a priority for researchers and conservationists, as they aim to build baseline data with which to record and track ecological changes over time. For enigmatic species the task becomes particularly difficult, however improvements in technology have allowed for data to be collected non-invasively and remotely (such as visually using cameras and acoustic recorders) and vastly increasing our understanding of the behaviour and ecology of many species across taxon (Stephenson, 2020). Passive acoustic monitoring (PAM) using acoustic recorders promises to be a particularly useful tool for studying vocalising species (Britzke et al., 2013; Gibb et al., 2019; Stephenson, 2020).

One such enigmatic group of vocalising species are bats (Chiroptera), which represent the second largest order of mammals and a large component of biodiversity in most ecoregions. Their vocalisations can serve navigational, as well as communicative purposes, as most species emit ultrasonic echolocation calls in order to avoid obstacles and catch prey more efficiently in darkness. These echolocation calls are emitted as relatively short pulses of sound with an interval between each to allow the bat to listen for echoes. Bats occupy diverse niches and perform important ecosystem functions, such as suppression of pests in agroecosystems (Cleveland et al., 2006; Boyles et al., 2011; Riccucci and Lanza, 2014; Taylor et al., 2018), plant pollination, and seed dispersal (Seltzer et al., 2013; Aziz et al., 2021). Furthermore, bats are good bioindicators in a variety of landscapes and as a result, they are an important target taxon for conservation monitoring (Jones et al., 2009; Park, 2015; Russo and Jones, 2015). Some forms of infrastructure developments, such as wind farms (O'Shea et al., 2016) and mining (Theobald et al., 2020), can have a direct negative impact on bat populations and reduce the ecosystem services that they provide (Scholz and Voigt, 2022). In contrast, there are species that can adapt relatively well to various anthropogenic landscapes (Schoeman, 2016; Jung and Threlfall, 2018).

The nocturnal and volant habits of bats has meant that research on them has required specialist biologists, often working with invasive techniques and expensive equipment (Kunz and Parsons, 2009). This is an area where PAM can be applied to collect large amounts of behavioural and monitoring data (Gibb et al., 2019). A significant contribution

to improved research on bats has been the development of ultrasound detectors, which enables identification of many echolocating species without capture (Britzke et al., 2013; Gibb et al., 2019). Technological advances have led to greatly reduced size and cost of ultrasonic detectors, which facilitates non-invasive and remote monitoring of bat occurrence and activity over larger spatial scales (Gibb et al., 2019).

The specific characteristics of bat echolocation calls are a reflection of its morphology and the niche it occupies; acoustic parameters such as frequency attributes, bandwidth, duration, inter-pulse interval and amplitude, can determine how the bat navigates different aerosphere habitats and targets specific prey (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987; Denny, 2004; Kalko et al., 2007). Hence there is a close association between the call parameters of a species and its functional group (Schnitzler and Kalko, 2001; Jones and Teeling, 2006; Jones and Holderied, 2007).

It should be noted that there are distinct limitations of using PAM. Many bat species do not emit laryngeal ultrasonic calls (e.g. Pteropodid fruit bats) and there are also differences in detection distances for many echolocating species, which will favour the recording of some over others by bat detectors (Monadjem et al., 2017; Dekker et al., 2022). Additionally, identification of bat calls is complicated by plasticity (Odendaal et al., 2014; Russo et al., 2018; Montauban et al., 2021) and regional variation (Aspetsberger et al., 2003). In the tropics, higher species diversity also increases the chance of overlapping call parameters for co-existing species (Ferrara and Leberg, 2005; Gibb et al., 2019). This difficulty in distinguishing some co-existing bat species on echolocation calls alone can limit our ability to use bat detectors as effective monitoring tools (Russo et al., 2018). In addition to specialist knowledge and equipment, familiarity with local species assemblages and accurate reference call recordings, are required for the analysis of acoustic data (Kunz and Parsons, 2009; Stephenson, 2020). There are also other considerations when using ultrasound detectors, such the choice of detector model, microphones and analysis software to ensure comparability (Adams et al., 2012; Gibb et al., 2019). Calls were primarily recorded in frequency division zero-crossing files from the 1980s, which only presents the loudest part of calls, and it was only in the mid-2000s when detectors recording in full spectrum with built in storage became available, recording in real time and retaining call detail (Zamora-Gutierrez et al., 2021). Although the increased use of bat detector technology has contributed to improving the study of bats, the limitations of PAM in terms

of accurate species identifications are often not fully appreciated and so this, in addition to inadequate reference material and insufficient surveyor skills and experience, may result in species assemblages and activity levels being mis-represented; meaning that assessments of anthropogenic impacts may also be inaccurate (Clement et al., 2014; Russo et al., 2018).

Reference acoustic datasets (call libraries) for confirmed species, collected across their distribution ranges, are essential to improve the accuracy of species identifications from acoustic data. Efforts are needed to collate sufficient samples with which to obtain parameter ranges, explore regional variation and to better determine the parameter combinations for separating species with similar echolocation calls (Karine and Kalko, 2001; Clement et al., 2014; Görföl et al., 2022). In some parts of the world, collections of acoustic data are managed in open access databases, e.g. the Asian Bat Call Database (ABCD), ChiroVox (Görföl et al., 2022) and The Sonozotz project (Zamora-Gutierrez et al., 2020). However, research on African bats has lagged behind (Racey, 2013; Monadjem et al., 2020b) creating obstacles to their effective study. Despite a surge in interest in bat ecology across the continent in the past ten years (Racey, 2013; Cooper-Bohannon et al., 2016; Monadjem et al., 2020b), access to acoustic technology remains a challenge for African researchers. As a result, few acoustic studies have been conducted in tropical Africa, with call libraries published only for a handful of countries and a small proportion of species across the continent (Monadjem, 2005; Monadjem et al., 2007, 2010, 2017, 2020b; Taylor et al., 2012, 2013a).

This paper compiles and utilises the first large-scale collection of bat acoustic data for Zambia, a country situated at an ecological transition zone between southern and central Africa and representing a diverse bat fauna of approximately two-thirds of the 125 bat species known to occur in the southern African region (Monadjem et al., 2020b; Benda et al., 2022). The calls collated are held in a call library managed by Bats without Borders (www.batswithoutborders.org); for access or to make contributions to it, an email request can be sent to info@batswithoutborders.org.

In this study I set out to determine whether Zambian bat species could be accurately distinguished acoustically. Our aims are to:

- i) Provide reference bat call data with which academics, professional ecologists and amateur naturalists can compare acoustic recordings.

- ii) Explore detector equipment variation as a potential issue when combining data from multiple sources as I have done here. I test for systematic differences in the call parameters from the different full spectrum detectors used to record echolocation calls.
- iii) Investigate the potential for distinguishing Zambian bat species from acoustic recordings by identifying call parameters contributing the most to call variation and then testing the use of these parameters to distinguish between functional groups and species acoustically.

I hypothesise that separation by functional group is possible due to distinct sonotype characteristics (Schnitzler and Kalko, 2001) but that accurate identification to species level may not always be possible, given the diversity of bats known to occur in Zambia.

2.3. Materials and Methods

2.3.1. Field Surveys

Zambia is located in south-central Africa, and comprises a highly diverse landscape, encompassing nine ecoregions (Dinerstein et al., 2017). Bats were captured with the use of mist nets, mostly during the rainy season (November to April), between 2015 and 2023. Mist netting was carried out in predominantly Miombo woodland dominated landscapes at multiple locations in 16 study sites (Figure 2.1). Nets were checked at maximum intervals of 15 min and after processing, bats were released the same night at the site of capture.



Figure 2.1: Locations of the 16 study sites across Zambia. Bat mist-netting was conducted at multiple locations within these sites.

2.3.2. Taxonomy and Identification

Species identifications were based on morphological features, following reference field guides for the region (Monadjem et al., 2010, 2020b). Morphometric length measurements were taken using dialMax Vernier Dial Callipers (error $\pm 0.1\text{mm}$) and mass calculated using Pesola Spring Scales (accuracy $\pm 0.3\%$).

In addition, species identification was confirmed for some individuals of cryptic species via genetic analysis of faecal or non-lethal wing tissue samples, following lab procedures outlined in Mata et al. (2021). Polymerase chain reactions were done using the SFF primer set (Walker et al., 2016) to amplify a 202 bp region of the mitochondrial Cytochrome Oxidase I gene (COI), or primers LGL 765F and LGL 766R (Bickham et al., 1995, 2004) to amplify the full mitochondrial cytochrome b gene. Sequencing was done on a MiSeq platform (Illumina, USA) and with a 3730xl DNA Analyzer (ThermoFisher, USA). Sequences were compared to BOLD (Ratnasingham and Hebert, 2007) and NCBI GenBank databases (Benson et al., 2013) for species identification.

Scientific names follow Monadjem *et al.* (2020), with the exception of the pipistrelle-like vespers, where I follow the recent revision of these (Monadjem *et al.*, 2021). *Laephotis botswanae* has recently been shown to be genetically and morphologically identical to *Laephotis angolensis* (Taylor *et al.*, 2022) and the two are now considered conspecific as *L. angolensis* (Taylor *et al.*, 2024). The *Miniopterus* complex remains unresolved in the region (Monadjem *et al.*, 2013) and hence I refer to our specimens as *Miniopterus* sp. The single *Nycteris* captured is referred to as *Nycteris* sp. due to inconclusive genetic results.

I categorised species into one of five functional groups based on habitat type and foraging mode: open aerial, edge aerial, edge trawling, narrow flutter and narrow passive (Schnitzler and Kalko, 2001).

2.3.3. Echolocation Calls

I used full spectrum bat detectors to take acoustic recordings of the echolocation calls of bats during their release (*sensu* Monadjem *et al.*, 2017) with recording starting as the bat flew from the hand and continuing as it was being followed for as long as possible whilst it was in sight. These calls were collated in a library held by Bats without Borders (www.batswithoutborders.org). The following detector models were used across multiple expeditions, depending on availability at the time: BatBox Baton XD (Batbox Ltd, UK) with R05 recorder (Roland Europe Group Ltd, UK), Batlogger M (Elekon AG, Switzerland), Petterson D240x (Pettersson Elektronik AB, Sweden), Anabat Walkabout (Titley Scientific, UK), Echo Meter Touch 2 (Wildlife Acoustics, USA), and Echo Meter Touch 2 Pro (Wildlife Acoustics, USA). SonoBat software (version 30 Universal) was used to measure call parameters for individual pulses, and to rate their quality (a synthesized measure ‘based on the total points of the sonogram above a threshold value’). Only calls with quality ratings over 0.8 were included in the dataset. To reduce deviation from search phase call parameters, only sequences with 10 or more pulses (up to a maximum of 32) were included in further statistical analysis. Parameters for sequences with <10 pulses are also reported but were not included in analyses.



Figure 2.2: *Macronycteris vittatus* being released from the hand for a call recording (photo courtesy of Jane Sedgeley-Strachan)

2.3.4. *Statistical Analysis*

I calculated the mean of each call parameter extracted by SonoBat software for a sequence from each bat. Of the 102 parameters given by the software, measurements based on amplitude (which can show significant variation with distance from the microphone) were removed, as well as those derived by additional computation (e.g. ratio or percentage calculations), reducing the number of parameters down to 20. Statistical analyses were performed using R 4.2.2 (R Core Team, 2023) through RStudio 2023.06.1+524 (Posit team, 2023). Multi-collinearity between the remaining parameters was assessed by using the ‘vifcor’ function of the ‘usdm’ package Version 1.1-18 which combines the use of variance inflation factor (VIF) and correlation coefficients (Naimi et al., 2014). The most correlated pair of variables is selected and the one with the highest VIF is removed; this process is repeated until reaching the correlation threshold and allowing for selection of variables for further analysis. I applied a correlation threshold of 0.5, which resulted in the selection of five uncorrelated variables for further analysis (Table 2.1). Given the sample sizes of calls available in the call library, this number of variables allows for the use of the selected statistical tests.

Table 2.1: Definitions of five echolocation call parameters selected based on VIF analysis and used in further analysis (www.sonobat.com)

Parameter	Definition
‘FreqMaxPwr’	Frequency of Maximum Power (kHz) - The frequency of the maximum amplitude of the call.
‘CallsPerSec’	Calls Per Second - Mean calls per second of the recording or section of recording displayed.
‘StartSlope’	Start Slope (kHz/ms) - Slope at the start of the call, calculated from the first 5% of the call duration.
‘EndSlope’	End Slope (kHz/ms) - Slope at the end of the call, calculated from the final 5% of the call duration.
‘LedgeDuration’	Ledge Duration (ms) - Duration of the ledge, i.e., the most extended flattest slope section of the body of the call preceding the characteristic frequency.

Descriptive statistics for all 20 parameters are given for the call library calls as a reference in Appendix A, Appendix B, Appendix C and Appendix D, including for species not used for further analysis due to small sample sizes.

To assess the likelihood of erroneous morphological identifications, comparisons between call sequences of individuals with and without genetic identifications were made using a t-test, where sample sizes allowed. The selected call parameters did not differ significantly - with the exception of Start Slope for *Laephotis capensis* ($t(15.965) = 3.40$, $p = 0.004$) and *Scotophilus dinganii* ($t(13.234) = 2.97$, $p = 0.01$) and End Slope for *Scotophilus dinganii* ($t(13.943) = 3.02$, $p = 0.009$). Given that there is no indication of differences in the other parameters, and that distributions of these slope parameters overlap, it is likely that these differences are due to factors not considered in this study, such as release environment.

The influence of different detectors on parameter variation was investigated using an ANOVA, randomised blocked by species, followed by Tukey multiple comparison tests, using the ‘aov’ and ‘TukeyHSD’ functions of the ‘stats’ package Version 3.6.2 (R Core Team, 2023).

To investigate the relative contribution of each acoustic parameter to the variation in bat calls among functional groups and species, a Principal Component Analysis (PCA) was carried out using scaled parameter variables for species with a sample size greater than the

number of variables using the ‘prcomp’ function of the ‘stats’ package Version 3.6.2 (R Core Team, 2023).

To assess how well bat echolocation calls could be assigned to functional groups using the selected acoustic parameters, Discriminant Function Analyses (DFA) were carried out for 19 species with a minimum sample size to variable ratio of 3:1 (Williams and Titus, 1988). Firstly I used Quadratic Discriminant Function Analysis (QDA) as the assumption of common covariance was not true for some of the parameters, as indicated by the ‘leveneTest’ function of the ‘car’ package Version 3.1-2 (Fox and Weisberg, 2019). However, Linear Discriminant Function Analysis (LDA) has been shown to be robust for bat echolocation data, so is additionally reported here as this method generates discriminant function coefficients, which highlight the most important parameters for group assignment (Papadatou et al., 2008). The data were split into a training (70%) and testing dataset (30%) randomly within groups using the ‘caret’ package Version 6.0.94 (Kuhn, 2008) ‘createDataPartition’ function and then normalized using ‘preProcess’ and ‘predict’ functions. DFA were carried out using the ‘MASS’ package Version 7.8-53.1 (Venables and Ripley, 2002). DFA was then repeated to assess how well bat echolocation calls can be assigned to species using the parameters with the highest LDA coefficients separating functional groups.

2.4. Results

A total of 238 individual bats of 22 species (Table 2.2), captured at 16, widely distributed sites across Zambia (Figure 2.1), contributed to this acoustic dataset, representing around a quarter of the bat species currently recognised to occur in Zambia.

Table 2.3 presents the five bat call parameters for the 22 species investigated in this study. The full dataset for all 20 parameters is included in Appendix A, Appendix B, Appendix C and Appendix D.

Table 2.2: The number of individuals of each species with release calls used in the analyses and the functional group that they are allocated to based on functional groups described by Schnitzler and Kalko (2001)

Functional group	Family	Species	Total number of bats	Genetically identified bats	PCA	DFA – by functional group	DFA – by species
Open aerial	Molossidae	<i>Mops nigeriae</i>	9	2	9	9	9
	Molossidae	<i>Mops pumilus</i>	6	4	6	6	6
Edge aerial	Miniopteridae	<i>Miniopterus</i> sp.	12	0	12	12	12
	Vespertilionidae	<i>Afronycteris nana</i>	12	0	12	12	12
	Vespertilionidae	<i>Glauconycteris variegata</i>	8	0	8	8	8
	Vespertilionidae	<i>Laephotis angolensis</i>	11	7	11	11	11
	Vespertilionidae	<i>Laephotis capensis</i>	46	36	46	46	46
	Vespertilionidae	<i>Neoromicia anchietae</i>	16	16	16	16	16
	Vespertilionidae	<i>Nycticeinops schlieffeni</i>	8	1	8	8	8
	Vespertilionidae	<i>Neoromicia zuluensis</i>	12	11	12	12	12
	Vespertilionidae	<i>Pipistrellus rusticus</i>	18	11	18	18	18
	Vespertilionidae	<i>Scotophilus dinganii</i>	16	9	16	16	16
	Vespertilionidae	<i>Scotophilus viridis</i>	10	9	10	10	10
	Vespertilionidae	<i>Vansonia rueppellii</i>	8		8	8	9
Edge trawl	Vespertilionidae	<i>Myotis bocagii</i>	3	2	0	0	0
	Vespertilionidae	<i>Myotis welwitschii</i>	9	0	9	0	9
Narrow flutter	Hipposideridae	<i>Hipposideros caffer</i>	1	0	0	1	0
	Hipposideridae	<i>Hipposideros ruber</i>	1	0	0	1	0
	Hipposideridae	<i>Macronycteris vittatus</i>	19	0	19	19	19
	Rhinolophidae	<i>Rhinolophus mossambicus</i>	2	0	0	2	0
	Rhinolophidae	<i>Rhinolophus simulator</i>	9	0	9	9	9
Narrow passive	Nycteridae	<i>Nycteris</i> sp.	1	0	0	0	0

Table 2.3: Mean, standard deviation (SD), minimum (Min) and maximum (Max) measures of the five parameters explored in this study for all 22 species regardless of sample size. Lines separate species of the same family.

Species	Calls per second			Frequency of Max Energy (kHz)			Start Slope (kHz/ms)			End Slope (kHz/ms)			Ledge Duration (ms)		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
<i>M. nigeriae</i> (N = 9)	12.9 (13.8)	10.6	8.3	24.6 (3.6)	20.7	30.3	-4.0 (1.8)	-1.7	-6.5	-2.7 (1.9)	0	-5.7	0.4 (0.0)	0.4	0.5
<i>M. pumilus</i> (N = 6)	8.3 (4.1)	10.7	6.7	25.7 (4.0)	23	33.6	-3.1 (1.3)	-2.1	-5.5	-3.8 (1.3)	-2.1	-5.3	0.4 (0.1)	0.3	0.5
<i>Miniopterus</i> sp. (N = 12)	15.5 (10.5)	10.8	6.7	59.5 (2.3)	54.1	63	-24.0 (5.8)	-13.1	-38.2	-8.8 (4.0)	-10.1	-5.6	0.5 (0.1)	0.3	0.7
<i>A. nana</i> (N = 12)	8.6 (4.0)	10.8	8.3	70.1 (3.1)	65.7	76.9	-27.7 (5.1)	-19.1	-37.5	-8.2 (4.0)	-11.6	-8.4	0.6 (0.1)	0.4	0.8
<i>G. variegata</i> (N = 8)	9.2 (3.5)	11	9.7	37.6 (2.7)	34.6	42.6	-17.7 (7.3)	-12.1	-5.9	-6.4 (4.6)	-0.1	-4.7	0.6 (0.1)	0.4	0.8
<i>L. angolensis</i> (N = 11)	10.8 (3.6)	10.8	9	40.8 (3.4)	36.9	46.4	-16.0 (3.3)	-11	-21.6	-7.9 (2.6)	-11	-9.3	0.4 (0.1)	0.3	0.6
<i>L. capensis</i> (N = 46)	11.0 (8.1)	10.7	9.9	46.0 (4.3)	41.1	58.7	-23.0 (3.9)	-15.4	-31.5	-8.2 (3.3)	-1.4	-9.9	0.4 (0.1)	0.3	0.6
<i>M. bocagii</i> (N = 3)	9.1 (4.8)	14.5	7.3	47.6 (3.4)	44.9	51.4	-14.2 (2.9)	-10.8	-16	-20.2 (6.6)	-13.3	-26.4	0.3 (0.0)	0.3	0.3
<i>M. welwitschii</i> (N = 9)	16.4 (12.4)	12.4	9.7	39.7 (5.0)	34.7	49.9	-19.2 (3.7)	-14.1	-24.8	-18.8 (4.5)	-13.6	-25.9	0.4 (0.1)	0.3	0.6
<i>N. anchietae</i> (N = 16)	7.6 (3.9)	10	9.6	48.8 (3.1)	44.6	56.2	-22.6 (3.3)	-16.3	-27.6	-5.7 (2.3)	-0.9	-9.5	0.5 (0.1)	0.4	0.6
<i>N. schlieffeni</i> (N = 8)	9.0 (4.3)	10.8	8.7	48.5 (4.5)	43.4	57.2	-29.1 (9.8)	-24.1	-7.7	-5.7 (3.4)	-1.1	-7.1	0.5 (0.1)	0.3	0.6
<i>N. zuluensis</i> (N = 12)	10.1 (4.0)	10.8	9.6	52.8 (4.0)	45.3	57.9	-29.1 (12.7)	-18	-8.2	-2.7 (2.3)	-0.6	0.9	0.5 (0.1)	0.3	0.8
<i>P. rusticus</i> (N = 18)	8.6 (3.7)	10.2	8.9	61.5 (4.5)	57.3	72.1	-23.9 (4.3)	-12	-29.3	-7.2 (3.8)	-1.7	-9.8	0.5 (0.1)	0.3	0.6
<i>S. dinganii</i> (N = 16)	11.3 (3.6)	10.4	9.3	37.7 (2.6)	32.2	43.3	-15.1 (2.8)	-10.4	-21	-6.7 (3.2)	-10.5	-9.8	0.4 (0.1)	0.3	0.5
<i>S. viridis</i> (N = 10)	12.1 (3.2)	10.2	9.6	48.3 (4.8)	42.2	58.3	-16.7 (6.7)	-13.5	-9.7	-6.4 (3.0)	-1.2	-9.6	0.4 (0.0)	0.4	0.5
<i>V. rueppellii</i> (N = 8)	12.0 (5.1)	10.2	8.6	49.9 (2.2)	46.5	53.7	-23.1 (4.0)	-19	-28.2	-7.4 (5.1)	-10.7	0.4	0.5 (0.1)	0.4	0.5
<i>H. caffer</i> (N = 1)	15.1 (NA)	15.1	15.1	148.1 (NA)	148.1	148.1	-0.1 (NA)	-0.1	-0.1	-36.9 (NA)	-36.9	-36.9	0.4 (NA)	0.4	0.4
<i>H. ruber</i> (N = 1)	23.6 (NA)	23.6	23.6	133.4 (NA)	133.4	133.4	-0.1 (NA)	-0.1	-0.1	-12.7 (NA)	-12.7	-12.7	0.4 (NA)	0.4	0.4
<i>M. vittatus</i> (N = 19)	16.5 (5.7)	11.3	9.7	64.4 (1.9)	60.5	66.8	-0.1 (0.0)	-0.1	-0.2	-1.7 (1.1)	-0.6	-4.7	1.3 (0.9)	0.3	3.3
<i>R. mossambicus</i> (N = 2)	16.0 (1.9)	14.7	17.3	38.5 (2.1)	37	40	-0.1 (0.0)	-0.1	-0.1	-3.0 (1.3)	-2	-3.9	0.4 (0.0)	0.3	0.4
<i>R. simulator</i> (N = 9)	13.6 (5.2)	14.7	9.5	77.9 (1.6)	75.7	79.9	-0.1 (0.0)	-0.1	-0.2	-2.4 (1.2)	-1.1	-4.5	0.7 (0.9)	0.3	3.1
<i>Nycteris</i> sp. (N = 1)	1.8 (NA)	1.8	1.8	71.3 (NA)	71.3	71.3	-17.7 (NA)	-17.7	-17.7	-16.5 (NA)	-16.5	-16.5	0.5 (NA)	0.5	0.5

2.4.1. Detector variation

For the 18 species with release calls from multiple detectors, of all five call parameters, only End Slope indicated a significant difference between detectors ($F(4, 211) = 5.78$, $p < 0.001$); differences were found between the Echo Meter Touch 2 and both the Batbox Baton ($p = 0.004$) and the Anabat Walkabout ($p = 0.046$). These differences between detectors, were not consistently higher or lower across species.

2.4.2. Principal Component Analyses (PCA)

To identify the parameters contributing most to the variation in call parameters, a PCA was conducted for 17 species in four functional groups (Table 2.2). The first two PCs, combined explain 57.5% of the variation, rising to 76% with PC3, demonstrating that there is relatively good separation into functional groups (Figure 2.3). In PC1, loadings are highest on a combination of slope and duration measures, whilst for PC2, Frequency of Maximum Power is emphasised most and for PC3 it is Calls per Second (Table 2.4).

Table 2.4: PCA loadings for each of the principal components with most positive or negative values indicating greatest contribution to the component.

Parameter	PC1 (36%)	PC2 (22%)	PC3 (18%)	PC4 (14%)	PC5 (10%)
Calls Per Second	0.3081	-0.3075	0.8688	-0.2246	-0.0722
Frequency of Maximum Power	0.2720	0.8204	0.11092331	-0.1734437	-0.4588
Start Slope	0.5153	-0.4054	-0.29232219	0.3279931	-0.6141
End Slope	0.5072	-0.1034	-0.37586406	-0.7104516	0.2934
Ledge Duration	0.5553	0.2394	0.07827028	0.5541417	0.5667

Narrow flutter species tend to have calls with a longer Ledge Duration and higher End Slope, whilst those of open aerial species have a lower Frequency of Maximum Power. Calls of edge trawling species tend to have lower values of all parameters compared to other species, but seem to be separated best by lower Ledge Duration.

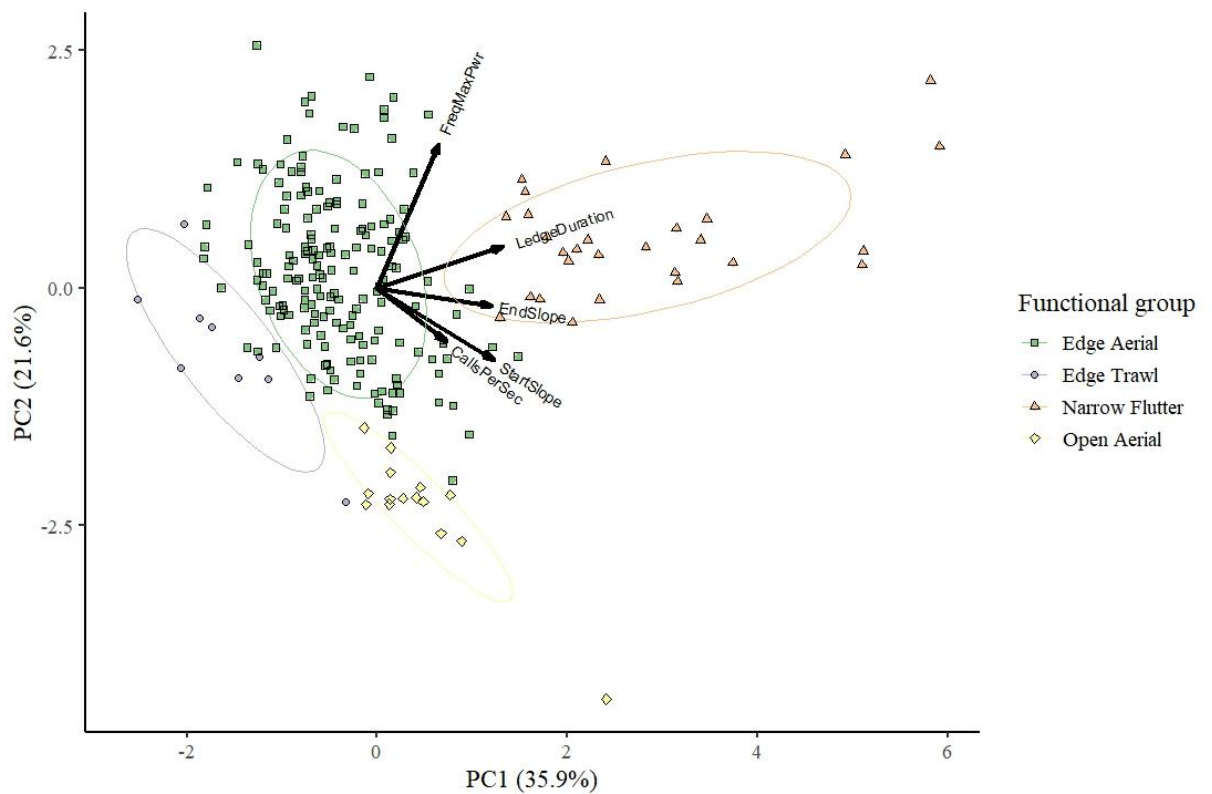


Figure 2.3: Plot of Principal Components 1 (PC1) and 2 (PC2), which combined explain 57.5% of the variation. Each point is an individual bat call sequence with shape and colour indicating functional group. Confidence intervals of 68% are represented by ellipses. Arrows indicate the direction and strength of the correlation of a parameter with the principal components.

Species within functional groups, however, show considerable overlap based on the first principal components (Figure 2.4).

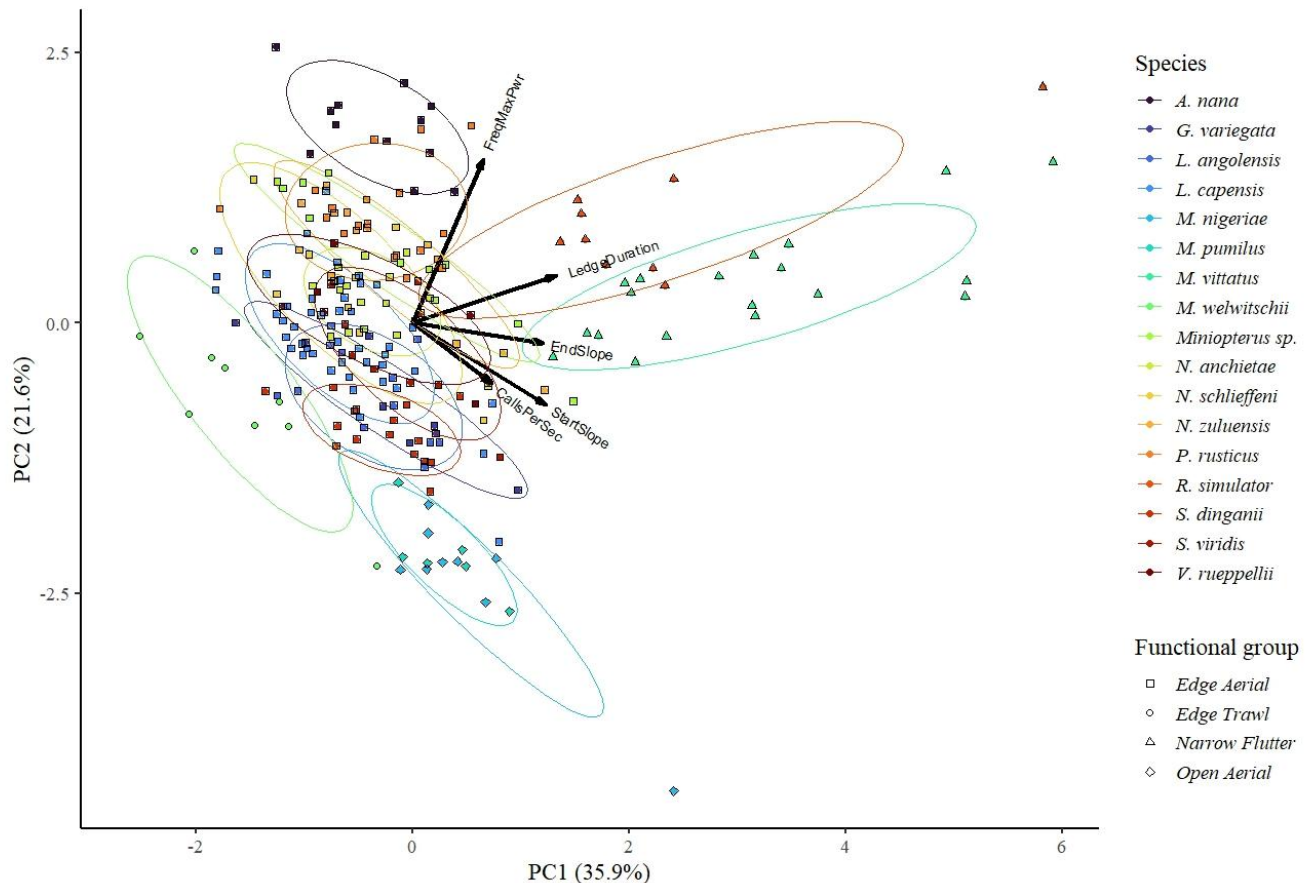


Figure 2.4: Plot of Principal Components 1 (PC1) and 2 (PC2), which combined explain 57.6% of the variation. Each point is an individual bat call sequence with shape indicating functional group and colour indicating species. Confidence intervals of 68% are represented by ellipses. Arrows indicate the direction and strength of the correlation of a parameter with the principal components.

2.4.3. Discriminant Function Analyses (DFAs)

To explore the extent to which functional groups can be separated using the five echolocation call parameters, DFA were carried out for 19 species belonging to three functional groups; open aerial, edge aerial and narrow flutter, with most being edge aerial species (Table 2.2). Both the QDA ($p < 0.001$) and LDA ($p = 0.001$) analysis resulted in a mean model accuracy of 98.5% for assigning calls to functional group level. LDA coefficients indicate that Frequency of Maximum Power and Start Slope contribute most to this separation (Table 2.5).

Table 2.5: Coefficients of linear discriminants for five call parameters; the most positive or negative values indicating greatest contribution to functional group separation in each discriminant function.

Parameter	LD1 (89%)	LD2 (11%)
Calls Per Second	0.0954	-0.0840
Frequency of Maximum Power	1.0492	-1.0040
Start Slope	1.7273	0.6848
End Slope	0.4033	-0.0478
Ledge Duration	0.3473	-0.2084

Species separation, using Frequency of Maximum Power and Start Slope, resulted in similar QDA and LDA accuracy rates of 53% ($p < 0.001$) and 56% ($p < 0.001$) respectively, with LD1 placing most emphasis on Frequency of Maximum Power (Table 2.6). Only three species of the 17 included were identified to an accuracy of over 95%, each of which are of different functional groups: *Macronycteris vittatus* (100%), *Mops nigeriae* (99.1%), *Afronycteris nana* (98.2%).

Table 2.6: Coefficients of linear discriminants for the two call parameters with most contribution to functional group separation (Table 2.5); the most positive or negative values indicating greatest contribution to species separation in each linear discriminant.

Parameter	LD1 (81%)	LD2 (19%)
Frequency of Maximum Power	-3.5455	-0.2274
Start Slope	-0.5493	1.8963

2.5. Discussion

With the increasing use of PAM techniques to study bats, the development of open access reference call libraries is vital (Kunz and Parsons, 2009). I present the first large scale bat call reference library and description of acoustic parameters collated for Zambia, providing an important resource for future acoustic research and monitoring of the 22 species presented here, which constitute a quarter of the bat species known to occur in the country (Monadjem

et al., 2020b). I show that calls collected using a variety of acoustic detector equipment are comparable for this dataset. Finally, I demonstrate that reliable separation of bat sonograms into functional groups is possible using only five parameters of full spectrum recordings, with Start Slope and Frequency of Maximum Power being the most suitable for this purpose. Functional group categories as described by Schnitzler and Kalko (2001) have been widely used in studies on bat echolocation. Despite subsequent arguments for the use of guilds (Denzinger and Schnitzler, 2013) to group bat species, functional groups remain the preferred approach in this field of study as they extend to include ecosystem functions. As hypothesised, despite a good level of accuracy for some species, such as *M. vittatus*, *M. nigeriae* and *A. nana*, identification to species level within functional groups using these parameters can be unreliable given the considerable overlap in call parameters for even this subset of Zambian functional groups and species. Additional parameters may be needed to aid in the identification of species where there is overlap, and further research is needed to explore more subtle acoustic differences in more detail. The study emphasizes the potential for PAM for research on Zambian bats.

There is a need to consider detector technology, as well as software used when presenting or using reference datasets from multiple sources, for example community science projects. For this study, calls recorded using different detector equipment were used but this did not result in substantive differences in most acoustic parameters. Although differences in End Slope were found between some detectors, this was not identified as one of the key parameters to assign bat calls to functional groups or species. My analyses suggested that data collected by different types of detectors can be combined for projects involving recordings from multiple sources e.g. community science projects, as long as subsequent call analysis is conducted using parameters known to be unaffected by this variability. Further studies, using multiple detectors for recording the same bat and considering larger sample sizes, are required to provide a better understanding of this potential issue. Despite the lack of detector variation in call parameters shown here, I still recommend caution when making direct comparisons between recordings using different detectors and also for comparison with call libraries and published parameters. The acoustic equipment used by data contributors should be recorded and explored as a potential variable.

The Frequency of Maximum Power values in this study differ somewhat compared with the equivalent Frequency of Maximum Energy values presented by Monadjem et al. (2020b), with higher mean values but overlapping distributions for most species. The difference may be due to the measurement methods; Sonobat computes measures for each call pulse, whilst BatSound used by Monadjem et al. (2020) requires a manual approach. Release calls are also known to be generally higher frequency than free flying calls and release habitat may also have been an influential factor. However, for some species there are larger differences which could indicate regional variation or the need for taxonomic clarification. *Vansonia rueppellii* for example is over 10kHz higher in this study than Monadjem et al. (2020), with no distribution overlap. This is also the case when compared to the Frequency of Maximum Energy measured manually for the species at a site in the Kafue National Park, Zambia (Kearney et al., 2010). For the other species with no overlap, the difference is less than 10kHz and there are small sample sizes in one or both of the datasets. The *Miniopterus* species Frequency of Maximum Power is closer to *M. mossambicus* than *M. natalensis*, however, further genetic analysis is needed especially since both species are now known to occur in Zambia (Benda et al., 2022).

In addition to presenting acoustic parameters for 22 African bat species recorded in Zambia, in this study I show that separation of echolocation calls into functional groups, based on sonotype categories, is highly accurate (98.5%), in agreement with suggestions that an automatic classifier by broader sonotype categories is possible (Roemer et al., 2021). Our study also highlights the need for caution when attempting species level identifications, in agreement with Russo et al. (2018). This difficulty in identifying to species level can influence our ability to accurately measure bat diversity and to monitor species assemblages, as grouping by sonotype can potentially exclude some species and risks overlooking rarer ones. Despite a large sampling effort and spatial coverage, this dataset includes only 25% of the species known to occur in Zambia and already shows overlaps in acoustic parameters between several species. More information on the distributions and ecological niches as well as comparisons with recordings of the full suite of co-occurring species in the country are required. Unresolved taxonomy can also present an issue, as was encountered here, when identifying cryptic species and those which are difficult to distinguish by morphology. In further studies, genetic material should be collected wherever possible and a better collection of barcoded specimens from the country is required to aid future non-lethal genetic

confirmation of individuals (e.g. Benda *et al.*, 2022). I also call on other bat researchers and ecologists working in Zambia and across species ranges to add species and increase sample sizes for this call library.

Chapter 3. Landscape use by bats in a commercial agroecosystem: Zambia as an Afrotropical case study with implications for ecosystem service provision

3.1. Abstract

There is a wealth of evidence that agriculture is one of the most significant drivers of habitat and biodiversity loss. However some species assemblages are able to persist, and even thrive, in these heavily modified landscapes. Insectivorous bats make up a large part of mammal diversity and can be bioindicators, as well as providers of insect pest control services, so it is important to understand the factors that influence their presence and abundance in agroecosystems. This study aims to examine how the activity of foraging bats is influenced by habitat and the surrounding landscape in an Afrotropical context. It focuses on commercial farms set in miombo woodland landscapes across Zambia. Each farm consists of a combination of irrigated arable fields, woodland and wetland, resulting in a mosaic of natural and anthropogenic habitats. Farms were surveyed using acoustic bat detectors at point locations and along driven transects, recording numbers of bat passes in different functional groups as a measure of activity. Simultaneously, light traps sampled insects in crop habitats as a measure of prey availability. Remote sensing was used to collect vegetation data and habitat was categorised using field observations. Bats within open and edge aerial functional groups were the most common in these landscapes, with edge trawling and narrow flutter bats recorded only occasionally. Prey availability and vegetation measures at a local scale did not seem to influence bat activity of either open or edge aerial bats foraging over arable fields. Although activity levels did overlap across habitats (both cropped and natural), activity of open aerial bats was significantly lower at woodland locations in comparison to all other habitats. The activity of open aerial bats is also negatively associated with the percentage of woodland at a larger scale along transects (50m buffer). However, this association is not exhibited when considering wider landscape effects (3km buffer). In contrast, activity of edge aerial bats was highest in woodland habitat with no landscape effects of vegetation measures. The findings suggest that local habitat is an important influence on both functional groups and that the influence of vegetation measures can differ between them as well as at different scales. Future research should make use of advances in monitoring technology, such as telemetry, to understand habitat and landscape use of all functional groups present in the landscape in more detail, including those with low activity detected. This will help to better identify the ecological requirements of these species to develop habitat management strategies to increase both functional diversity and abundance of bats in these ecosystems.

3.2. Introduction

Agriculture is a key driver in global forest loss (DeFries et al., 2010). The prevalence of intensive monoculture food production systems has reduced heterogeneity in agricultural landscapes, so as a result, there has been a decline in biodiversity, which needs to be addressed to allow associated ecosystem services to be maintained (Rosa-Schleich et al., 2019; Mamabolo et al., 2020) and for adaptation to climate change scenarios (Altieri et al., 2015). The rising food demand of a rapidly growing global human population, predicted to reach around 9.8 billion by 2050 (Kaneda et al., 2022), has resulted in a growing interest by governments, as well as the research and agricultural sectors to produce crops in a more environmentally sustainable way, utilizing ecosystem services provided by biodiversity through the integration of conservation into farming practice (Mamabolo et al., 2020). In this respect, farming landscapes provide significant opportunities to focus biodiversity conservation efforts across large areas of land outside of protected areas.

Bats represent a diverse mammal taxa, consisting of a range of functional groups with varying ecological roles, in both natural and anthropogenic landscapes (Voigt and Kingston, 2015). There has been increased interest in the ecology of bats in agricultural landscapes to understand the effects of land use change on species assemblages, but also to explore the provisioning services that they can potentially provide, such as insect pest control (Tuneu-Corral et al., 2023; Xavier et al., 2023).

Identifying habitat preferences at multiple scales can inform local management decisions and can also contribute to wider scale conservation measures in these anthropogenic environments (Maas et al., 2016; Razgour et al., 2016). In some landscapes there may be little effect of forest fragmentation on the number of bat species present (Estrada and Coates-Estrada, 2002; Lesiński et al., 2018). Species assemblages may even be unaffected, at least in the short term (Bernard and Fenton, 2007). Interestingly, moderately fragmented forest landscapes can contain higher bat species richness or diversity (Gorresen and Willig, 2004; Struebig et al., 2008; Klingbeil and Willig, 2009; Ethier and Fahrig, 2011; Cisneros et al., 2015; Alurralde and Díaz, 2021). However, in landscapes with smaller forest fragments, species assemblages may vary more drastically from intact forest (Struebig et al., 2008) and can have both lower species richness and higher dominance (Rocha et al., 2017). Hydric habitats, such as open wetlands may have higher bat activity levels than surrounding forest

(Fulton et al., 2014). Larger waterbodies present in a landscape may also attract foraging bats (Lisón and Calvo, 2011; Seibold et al., 2013; Hintze et al., 2016; Korine et al., 2016; Torrent et al., 2018; Ancillotto et al., 2019; Starbuck et al., 2020).

Within agricultural landscapes, bat activity above different crop types has shown some variability (Williams-Guillén et al., 2016). For example, bat activity was highest in fields next to forest, but also in orchards, cereals and vegetables when compared to vineyards in Germany (Stahlschmidt et al., 2017). In intensive agricultural landscapes dominated by soya and maize, bat activity and diversity declines with distance from forest edges (Louis et al., 2022). In contrast, over irrigated rice crops in Madagascar there were higher levels of bat activity than in forest habitats (Kemp et al., 2018).

Smaller and often more isolated patches of natural or manmade arboreal habitat in agricultural landscapes can still show relatively high levels of bat activity (Estrada et al., 2004; Frey-Ehrenbold et al., 2013; Fuentes-Montemayor et al., 2013), and so the nature of the localised 3-dimensional aerosphere can have greater influence on activity than wider landscape. Isolated or more scattered trees can also be particularly important for foraging bats (Lumsden and Bennett, 2005; Hackett et al., 2013). In agricultural landscapes where humans have dominated for longer periods of time, with relatively high levels of habitat modification, however, assemblages can include more generalist species and there may be very little response to more recent landscape modification (Kellner et al., 2019).

Habitat management practices can affect natural predator-prey interactions (Tscharntke et al., 2005). Conservation farming practices have been considered in relation to bat activity in temperate areas, sometimes with apparently conflicting results. For example, in Scotland, farms with field margins, hedgerows, species-rich grasslands and water margins did not seem to increase *Pipistrellus* species activity in comparison to conventional farms (Fuentes-Montemayor et al., 2011). In contrast, the incorporation of both hedgerows and flower fields do increase bat activity in comparison to open wheat fields in Germany (Krings et al., 2022). Responses may differ between bat species, such as at farms in England where field boundaries positively influenced activity for some bat species and not others (Pocock and Jennings, 2008)

Pest outbreaks are exacerbated in monoculture cropping and so damage by arthropod crop pests poses a major limitation on crop productivity, leading to over-reliance on chemical pesticides (Oerke, 2006). As part of integrative pest management strategies, promotion of natural predators in agroecosystems can help to decrease crop damage and reduce reliance on chemical pesticides (Crowder and Harwood, 2014; Rosa-Schleich et al., 2019). Nevertheless, the balance between productivity and maintaining natural pest control services is complex; it can depend on both landscape and local factors, as well as specific ecological interactions between crops, pests and natural predators (Bonato et al., 2023). Understanding functional groups with traits particularly suited to roles as natural enemies of crop pests is an important step towards conservation biological control (Straub et al., 2008). Specialist predators for example, may target particular crop pests resulting in high predation rates on those species, however generalist predators may be more resilient and maintain populations in times of reduced pest presence, due to alternative prey availability; so a combination of these traits may result in ideal biological control scenarios (Straub et al., 2008).

There is mounting evidence for the importance of insectivorous bats in providing regulating services through pest suppression (Clarkson et al., 2022). As such, it is essential to identify the impact of farming landscapes on species assemblages and actions that can be taken to maintain bat populations and diversity (Maas et al., 2016; Tuneu-Corral et al., 2023). There is still much to learn about the dietary niches of bats, however it is becoming clear that although there are specialists with morphological and behavioural adaptations to specific dietary items, across different bat species, there is also widespread dietary plasticity, allowing for more generalist and even opportunistic diets (Clare and Oelbaum, 2023). Opportunistic foragers in particular are able to exploit periodic or sporadic resources, such as when there are insect pest eruptions (McCracken et al., 2012). Quantifying the pest regulating services provided by insectivorous bats however is complex and relies on quantifying links between bats and the agricultural outputs, and also requires an integrative approach, combining the fields of agroecology, social sciences and economics (Kunz et al., 2011).

Prey availability may influence foraging activity more than habitat characteristics (de Oliveira et al., 2015). For some selective predators, prey preferences may actually depend on availability; for example, moth consumption by the Greater Horseshoe Bat (*Rhinolophus*

ferrumequinum) increased in line with availability, but this was not the case with other insect prey taxon (Jones, 1990). However, dietary composition and abundance of prey taxon in the diet can often differ from availability, such as indicated in Indian pygmy bat (*Pipistrellus mimus*) (Whitaker et al., 1999) and big brown bats (*Eptesicus fuscus*) (Menzel et al., 2000). Particular insect characteristics may influence bat activity, such as taxon (Weier et al., 2018; Straka et al., 2020; Chaperon et al., 2022; Metcalfe et al., 2023) or size (Lumsden and Bennett, 2005). Studies looking at specific crop pest abundance in relation to bat activity have also demonstrated contrasting results, from evidence of some influence of the abundance of pest Hemiptera (Weier et al., 2018) and highest bat activity found during pest outbreaks in grape crops (Baroja et al., 2021), to the absence of, or even negative, associations of pest species abundance with activity levels (Puig-Montserrat et al., 2021).

Although there has been a relatively recent increase in studies focussing on bat activity in relation to agricultural habitats and potential pest control services, Africa still remains largely understudied (Meyer et al., 2016; Williams-Guillén et al., 2016; Tuneu-Corral et al., 2023). The only studies conducted in southern Africa on this subject have focussed on sugar-cane crops in Eswatini, indicating selection of agricultural habitats for foraging by Molossid species (Noer et al., 2012) and macadamia crops in South Africa, providing evidence for pest consumption, as well as exploring habitat use (Taylor et al., 2013b, 2017, 2018; Linden et al., 2019; Weier et al., 2019; Swartz et al., 2022). Some bat species in the region are known to travel and average of around 5km from the roost to forage (Noer et al., 2012) whilst others have smaller ranges of an average of about 1km from the roost (Monadjem et al., 2009). Although home range studies which use telemetry techniques are valuable in providing insights into habitat use, the cost and survey effort required can be prohibitive and given the small size of these aerial species, the technology only allows for tracking over a relatively short time (Teague O'Mara et al., 2014). Acoustic measures of activity, such as recording the number of call sequences per unit time, is a widely used, non-invasive way of assessing habitat use (Zamora-Gutierrez et al., 2021).

Miombo woodlands represent the most extensive dry forest formation in Africa, covering an approximately 2.7 million km² (Frost, 1996). Despite land clearance for agriculture likely to have increasing environmental and climatic impacts in Miombo-agroecosystem mosaic

habitats, they have received relatively little research attention (Wilson and Scholes, 2020). By collecting data from commercial farms across agro-ecological regions, I investigate landscape-wide patterns in an Afrotropical country where Miombo woodland is the predominant vegetation type (Frost, 1996; Syampungani, 2008) and where agricultural expansion has been happening for decades (FAOSTAT, 2024). Commercial agriculture (production for sale or profit) in the Zambian context is characterised by farmland of over 100ha, utilising mechanisation and usually with irrigation systems in place, such as centre pivot irrigation (CIAT and World Bank, 2017). Commercial farms on the most part retain some areas of natural vegetation either left in its natural state or utilised for low intensity grazing and harvesting of resources such as firewood. These areas consist of either Miombo woodland or Dambo wetland in the study areas with the principle cash crops being maize, soya and tobacco. This study aims to evaluate how foraging bats are influenced by agricultural landscapes in Zambia, and the implications this could have for ecosystem provision in the context of insect pest suppression. This can be used to inform agricultural and land management practices, including integrative pest control strategies.

In particular the study aims to answer the following questions:

- i. Do insect prey availability and vegetation characteristics influence bat activity in arable crop fields?
In general, I expect locations with higher prey availability and higher vegetation density, or more woodland in the vicinity, to be associated with higher bat activity.
- ii. Does bat activity differ between crop types and semi-natural habitats found on commercial farms?
I expect there to be higher activity at locations in semi-natural habitats than in crops.
- iii. Do vegetation characteristics such as density and woodland presence influence bat activity in a commercial agricultural landscape?
Landscapes with higher vegetation density and more woodland were expected to have higher bat activity levels.

3.3. Materials & Methods

Three established commercial agricultural areas across two agro-ecological zones within Zambia were chosen for this study (Figure 3.1) which take into account rainfall and soil type (Mukosha and Siampale, 2009). A selection of 10 farms in each area (total $n = 30$ farms) was based on size and scale of production, including only those defined as mechanised farms, producing maize, soya or tobacco for commercial sale. Although field sizes were variable (6-78ha), most were 50ha centre pivot irrigated fields (approximately 800m in diameter) throughout the study. To ensure statistical independence, farms were separated by a minimum of 2km. The 30 farms were surveyed across the period of between 2016 and 2019, during cropping periods of November to March. Surveys were repeated within a few days of each other at each farm twice where possible, however some farm survey locations were not surveyed twice due to adverse weather conditions or equipment failure.

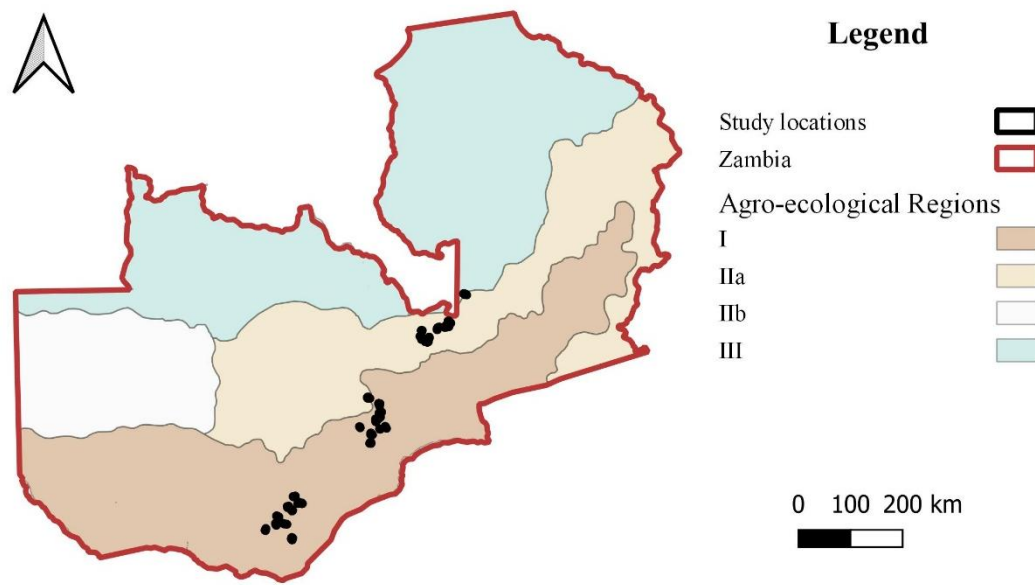


Figure 3.1: Study farm locations in three clusters, spanning agro-ecological zones I and IIa. (I = Luangwa and Zambezi Rift Valley Zone - semi-arid low rainfall (< 800mm), low altitude (400-900m); IIa = Central, Eastern and Southern plateau - medium rainfall (800-1000mm), altitude 900-1300m; IIb = Kalahari (Barotse) sand plateau and the Zambezi flood - medium rainfall (800-1000mm), altitude 900-1200m; III = North, North-Western Zone - high rainfall (>1000mm), altitude (1100-1500m) (Mukosha and Siampale, 2009))

3.3.1. *Acoustic recording*

To quantify bat activity, acoustic recording methods were employed. To measure local bat activity (to answer questions 1 and 2), Anabat SD detectors (Titley Scientific, UK) were placed in three arable fields planted with maize, soya or tobacco on each farm where possible (at least 10m from the edge) with the microphone at a height of 3m from the ground (hereafter referred to as static detectors). The microphone detection distances vary depending on environmental factors and the frequency of echolocating bats with some species only detected at less than 1m whilst others can be detected at 30m (Monadjem et al., 2017).

Comparisons were made with semi-natural habitats within the farm boundaries, with static detectors placed in Miombo woodland and Dambo wetland habitats. Acoustic recording was carried out for three hours at static detector locations, initiated 30 minutes post-sunset. Peak foraging time was targeted so as to avoid commuting bats or calls associated with other

behaviours. To measure activity levels across the farm landscape (to answer question 3), a driven transect was also conducted during this time within the boundary of the farm property being surveyed, using an Anabat Express (Titley Scientific, UK) detector, driving at approximately 15km per hour, combined with stationary points every kilometre for five minutes, with the vehicle and lights switched off. I repeated static and transect surveys within a few nights on each farm where possible; 29 static detector locations and 4 transects could not be repeated due to adverse weather or equipment failure. Data from a total of 239 static location surveys (402h of recording) across all habitats (

Figure 3.2: The number of static detector surveys conducted in each habitat type in each area (as indicated by colour).

) and 56 transects (covering a total distance of 538km) spanning the three cropping periods was collected.

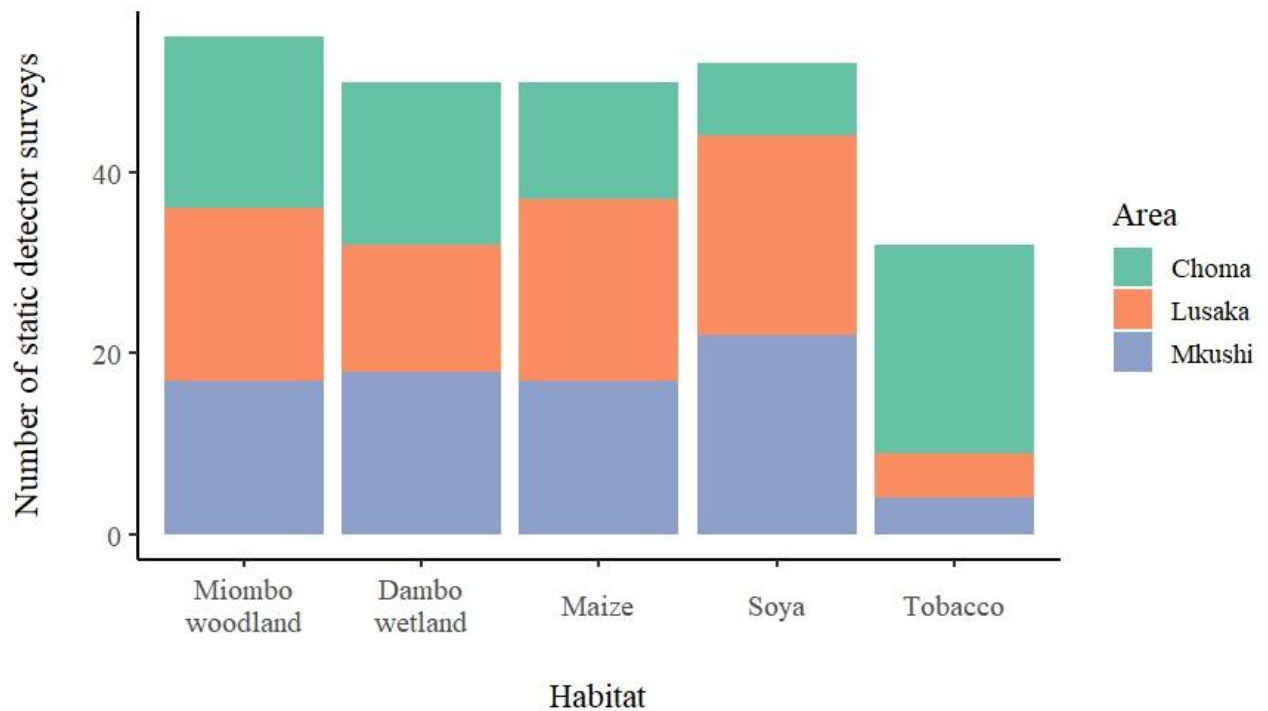


Figure 3.2: The number of static detector surveys conducted in each habitat type in each area (as indicated by colour).

3.3.2. Prey availability

Prey availability data was collected by capturing insects using heath light traps (6W actinic bulbs) mounted at a height of around 2.5m, which were paired with the static detectors in crop fields at a distance of approximately 50m away to reduce potential impacts on bat activity, such as attraction or avoidance, at the static detector locations (Froidevaux et al., 2018). The lights were timed to switch on at the same time and duration as static detector recording. Although this sampling technique captures only insects attracted to light it samples a wide range of orders consumed by bats such as Lepidoptera, Diptera and Coleoptera, and so gives comparative estimates of prey availability (Merckx and Slade, 2014; Froidevaux et al., 2018; Mata et al., 2021b). Following sampling, ethyl acetate was used to euthanize the insects and traps were kept closed overnight. Insects were then stored in ethanol and were counted and identified to order. The total number of insects was found to be correlated with the number of individuals of the Coleoptera (beetle) order and so the total number of insects was

used to indicate prey availability. Analysis considering the most abundant orders was also conducted. As there was the same sampling effort at each field location, these are directly comparable.

3.3.3. *Habitat variables*

To quantify habitat and vegetation variables (Table 3.1) that may influence bat activity, a combination of field observations and satellite imagery was used. At each static detector location, the primary habitat/crop type was recorded (semi-natural habitat: miombo woodland, dambo wetland or crop types: maize, soya, tobacco) (Figure 3.3).



Figure 3.3: Habitat variables at static detector locations: A = Miombo woodland; B = Dambo wetland, C = maize; D = soya; E = tobacco (photo courtesy of Jane Sedgely-Strachan). A and B are semi-natural habitats whilst C, D and E are cropped habitats

Google Earth Engine (GEE) (Gorelick et al., 2017) was used to source satellite imagery for woodland cover and Normalized Difference Vegetation Index (NDVI) data; remote sensing layers were imported into QGIS Desktop version 3.28.1 (QGIS.org) for further analysis. Global Forest Canopy Height layers (Potapov et al., 2021) were used to map mature woodland areas of over 0.5ha with trees of 5m and above in height, and to calculate the distance of woodland edge to static detectors and the proportion of woodland cover in transect buffers. Composite median NDVI maps were generated using GEE from Landsat-8 Level 2, Collection 2, Tier 1 image collection, courtesy of the U.S. Geological Survey, after masking cloud cover for each season running from November through to the end of March,

from 2016 to 2019. The mean of the composite NDVI was calculated for buffers of both static detector locations and transects.

A 50m buffer around static detector locations was used as a measure of local habitat (for questions 1 & 2) so as to consider the immediate habitat without encompassing other habitat types. Around the transects 50m buffers were also used to quantify local habitat in the landscape whilst 3km was used to represent the wider landscape (for question 3, see Figure 3.4). Larger buffers of up to 5km have been used in some studies reflecting the large home ranges of some bat species e.g. Molossids can travel on average of around 4-5km from the roost to forage (Noer et al., 2012). However, adopting such a large scale would have resulted in significant overlap between farms, so the 3km buffer allowed a compromise between potential flight distance and independence of bat activity, and is comparable to larger scales used in other studies (Fuentes-Montemayor et al., 2011).

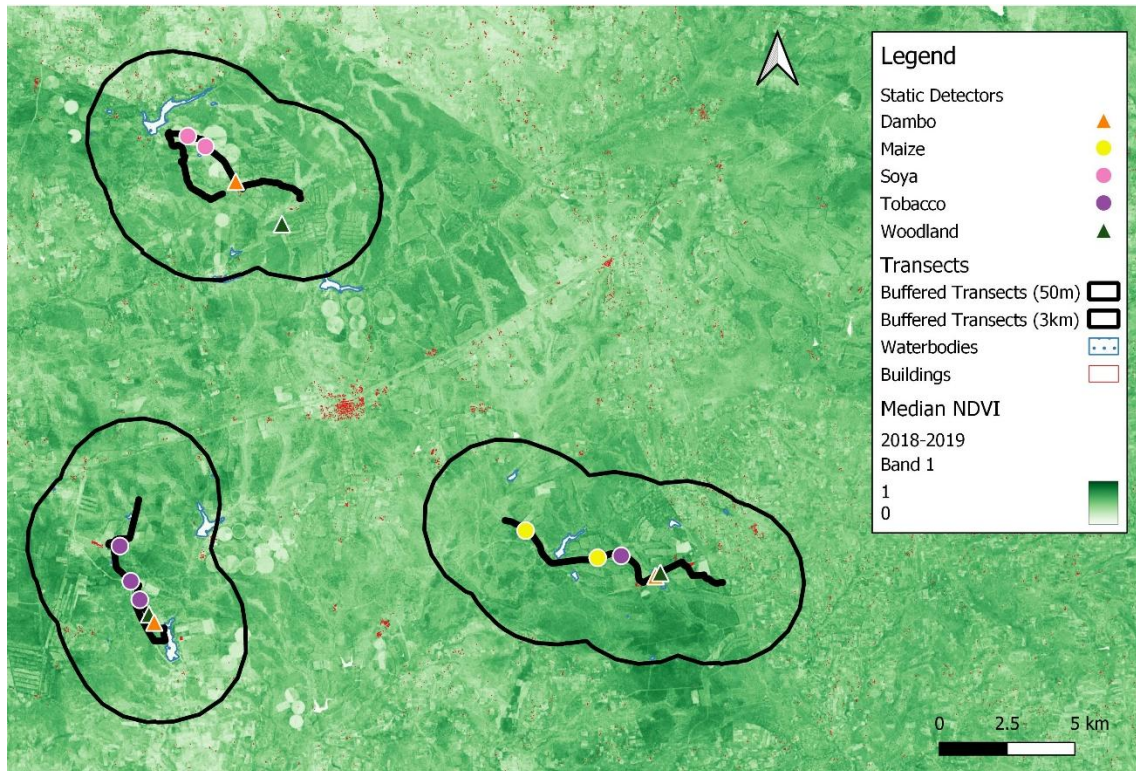


Figure 3.4: An example of the transect buffers and locations of static detectors and paired insect traps on three of the study farms

3.3.4. *Acoustic analysis*

Analook W Version 4.6e (Corben, 2021) was used to analyse the recordings. Due to the lack of a comprehensive call library, species identification by call parameters was not possible and so calls were categorised into sonotypes and assigned to a foraging functional group based on Schnitzler and Kalko (2001). Chapter 2 demonstrates that four functional groups of Zambian bats can be assigned to sonotypes based on their call parameters; open aerial, edge aerial, edge trawling and narrow flutter foragers. An additional functional group, narrow passive bats, occur in Zambia but cannot be easily recorded using the bat detectors available for this study, as they record the frequency of most energy at any one time using zero-crossing recording (Parsons et al., 2000). These are known to be particularly quiet bats and were not detected. The number of bat passes was used as a measure of foraging activity, with a bat pass defined as a sound file, of a maximum of 15 seconds (the set limit for the detectors), with two or more characteristic search-phase calls within a second of each other (sensu Fuentes-Montemayor et al., 2011). Files with more than one sonotype pass were considered as a pass for each. For static detectors the response variable was the number of bat passes

over the 3h survey duration whereas for transects the number of bat passes for the duration of the transect was used.

3.3.5. *Statistical analysis*

Multicollinearity of predictor variables was explored using the ‘vifcor’ function (correlation threshold of 0.7) of the ‘usdm’ package Version 1.1-18 (Naimi et al., 2014) which finds variable pairs with the maximum linear correlation greater than the threshold and removes the greater variance inflation factor (VIF), then repeats until all correlations are below the threshold. After scaling the selected numeric predictor variables to enable comparisons, I performed Generalised Linear Mixed Models (GLMMs), using the ‘glmmTMB’ function of the ‘glmmTMB’ package (Brooks et al., 2017) (assuming negative binomial error, accounting for zero inflation and applying quadratic functions where appropriate) to determine variables with significant effects on bat activity within each functional group.

A GLMM was performed with the activity of each functional group as the response variable. All variables of interest were included as predictor variables and no model selection was performed. Statistical analyses were performed using R 4.2.2 (R Core Team, 2023) through RStudio 2023.06.1+524 (Posit team, 2023). Due to the small number of passes recorded for other functional groups, only open and edge aerial foragers were included in analysis for this study. Where a variable consists of more than two categorical variables, the ‘relevel’ function (R Core Team, 2023) was used to change the reference category to obtain all comparative combinations.

For static detector locations (questions (i) & (ii)), repeat surveys and use of multiple detectors on each farm meant that the farm and location of the detector within the farm were applied as nested random effects in GLMMs. For transect data (question (iii)), the farm was applied as a random effect and transect length was included as an offset measure of survey effort.

Residual diagnostics were carried out using the ‘DHARMA’ package (Hartig, 2022) to verify model assumptions and no problems were detected with any of the models.

Table 3.1: Variables considered as potential predictors of bat activity and included as fixed effects in the models.

Fixed effects	Description
Insect abundance	Number of insects caught in each light trap as a measure of prey availability – this was categorised for the most abundant orders (Coleoptera, Lepidoptera, Hemiptera and Diptera)
Habitat	Natural (Miombo woodland, Dambo wetland) or crop (maize, soya, tobacco) habitat classifications at the static detector locations
Distance to Woodland	Distance (m) from the static detector to the edge of the closest mature woodland patch of over 0.5ha with trees of 5m and above in height
NDVI	Normalized Difference Vegetation Index mean of a 50m buffer around the static detector, and of 50m and 3km buffers around the transect
Woodland percentage	The percentage of transect buffer area covered by woodland within 50m and 3km around the transect
Latitude	Position of static detector (WGS 84 decimal degree co-ordinate system) as an indication of distance from the equator
Julian date	Date the survey was undertaken using the Julian calendar
Temperature	Temperature at the start of the survey - degrees Celsius (°C)

3.4.Results

The static bat detectors recorded 15,002 bat passes; 60% were edge aerial foragers (8989 passes), followed by 39% open aerial foragers (5889 passes), with the remaining 1% made up of 71 edge trawling and 53 narrow flutter forager passes.

A total of 4814 bat passes were recorded from the transects, an average of approximately 9 passes per km. Of these 56% were open aerial foraging bats (2717 passes), 43% were edge aerial (2074 passes) and the remaining 1% was made up of 2 flutter and 5 trawl forager passes.

A total of 351,084 insects were sampled in 117 insect traps (351h) paired with static detector locations, the majority of which were Coleoptera (71%), followed by Hemiptera (19%), Diptera (4%) and Lepidoptera (3%).

3.4.1. *Do insect prey availability and vegetation characteristics influence bat activity in arable crop fields?*

No significant association was found between bat activity and insect abundance, distance to woodland or NDVI at the static detector locations in the arable fields. This was the case for both open and edge aerial bats (

Table 3.2). For open aerial bat activity there was greater variability for farms as a random effect, with intercept variance of 0.79 (SD=0.89), than the nested random effect of location within the farm, with intercept variance of 0.05 (SD=0.22). This was the same for edge aerial bat activity, with farm intercept variance of 0.53 (SD=0.73), and location intercept variance of 0.12 (SD=0.34). Only date influenced bat activity for both groups, with activity increasing with each cropping period rather than within a season.

There was also no significant influence of the abundance of Coleoptera, Lepidoptera, Hemiptera or Diptera abundance on either open or edge aerial activity, when also considering date as a fixed effect without woodland, NDVI, latitude or temperature (Table 3.3). For open aerial bat activity there was greater variability for farms as a random effect, with intercept variance of 0.91 (SD=0.96), than the nested random effect of location within the farm, with intercept variance of 0.07 (SD=0.26). This was the same for edge aerial bat activity, with farm intercept variance of 0.55 (SD=0.74), and location intercept variance of 0.17 (SD=0.41).

Table 3.2: Results of GLMMs carried out for open and edge aerial bat activity at static detector locations as response variables with Farm and Location as random effects.

Significant p values ($p < 0.05$) given in bold.

Fixed effects	Open aerial			Edge aerial		
	exp(β)	SE [†]	p-value	exp(β)	SE [†]	p-value
Insect abundance	1.10	0.109	0.34	1.03	0.081	0.67
NDVI	0.88	0.105	0.27	0.95	0.098	0.60
Distance to Woodland (m)	0.97	0.162	0.85	0.76	0.114	0.069
Julian date	2.35	0.485	<0.001	1.62	0.273	0.004
Temperature (°C)	0.96	0.145	0.80	0.95	0.118	0.69
Latitude	1.32	0.298	0.22	0.84	0.159	0.34
Intercept	15.7	3.10	<0.001	21.8	3.55	<0.001

[†] SE = Standard Error

Table 3.3: Results of GLMMs carried out for open and edge aerial bat activity at static detector locations as response variables with Farm and Location as random effects and considering abundance of insects categorised by order as predictor variables. Significant p values ($p < 0.05$) given in bold.

Fixed effects	Open aerial			Edge aerial		
	exp(β)	SE [†]	p-value	exp(β)	SE [†]	p-value
Coleoptera abundance	1.09	0.131	0.48	0.94	0.089	0.51
Lepidoptera abundance	1.15	0.113	0.15	1.08	0.098	0.37
Hemiptera abundance	0.95	0.129	0.69	1.17	0.136	0.18
Diptera abundance	1.03	0.097	0.74	1.08	0.090	0.37
Julian date	2.23	0.452	<0.001	1.79	0.291	<0.001
Intercept	15.6	3.23	<0.001	21.6	3.60	<0.001

[†] SE = Standard Error

3.4.2. Does bat activity differ between crop types and semi-natural habitats found on commercial farms?

As expected, bat activity was significantly lower at Miombo woodland locations for open aerial foragers in comparison to all other habitats (Table 3.4). Despite this, there is much overlap in activity levels across habitat types (**Error! Reference source not found.**), even

between lowest activity levels seen in woodland with median (IQR) number of passes of 3.5 (12.2) and highest activity levels in soya with median (IQR) passes of 18 (38.8).

In contrast, for edge aerial foragers there was highest activity in Miombo woodland, but this was only significantly different to arable fields and not to Dambo wetland (Table 3.4).

Activity in maize is also significantly lower ($p < 0.05$) than in wetland (Table 3.4). Again, overlap in activity levels across all habitats is evident (**Error! Reference source not found.**), even between lowest activity levels seen in maize with median (IQR) number of passes of 13.5 (14) and highest activity levels in woodland with median (IQR) passes of 31 (42).

For open aerial bat activity there was greater variability for farms as a random effect, with intercept variance of 1.10 (SD=1.05), than the nested random effect of location within the farm, with intercept variance of 0.29 (SD=0.54). This was the opposite for edge aerial bat activity, with farm intercept variance slightly higher at 0.25 (SD=0.50), and location intercept variance of 0.34 (SD=0.58).

Bat activity was also influenced by date, showing an overall decline in activity over the three cropping periods surveyed, and for edge aerial foragers, there was also significantly higher bat activity at more southern locations (Table 3.4).

Table 3.4: Results of the GLMM carried out for each of open and edge aerial bat activity at static detector locations as response variables with Farm and Location within the farm as random effects. Significant p values ($p < 0.05$) are shown in bold. Lines between habitat comparisons indicate change of reference level.

Fixed effects	Open aerial			Edge aerial		
	exp(β)	SE [†]	p-value	exp(β)	SE [†]	p-value
Habitat comparisons						
<i>Woodland - Wetland</i>	1.68	0.408	0.032	0.89	0.180	0.55
<i>Woodland - Maize</i>	2.16	0.523	0.002	0.53	0.109	0.002
<i>Woodland - Soya</i>	2.61	0.633	<0.001	0.64	0.136	0.035
<i>Woodland - Tobacco</i>	2.75	0.782	<0.001	0.58	0.143	0.027
<i>Wetland - Maize</i>	1.28	0.311	0.31	0.60	0.126	0.014
<i>Wetland - Soya</i>	1.55	0.387	0.078	0.72	0.157	0.13
<i>Wetland - Tobacco</i>	1.64	0.470	0.088	0.65	0.165	0.093
<i>Maize - Soya</i>	1.21	0.305	0.45	1.21	0.267	0.38
<i>Maize - Tobacco</i>	1.28	0.366	0.40	1.10	0.279	0.72
<i>Soya - Tobacco</i>	1.05	0.326	0.87	0.90	0.247	0.71
Julian date	2.47	0.539	<0.001	1.53	0.184	<0.001
Temperature (°C)	0.91	0.092	0.33	1.00	0.075	0.99
Latitude	1.15	0.255	0.53	0.78	0.097	0.048
Intercept	0.02	0.016	<0.001	0.00	0.004	<0.001

[†] SE = Standard Error

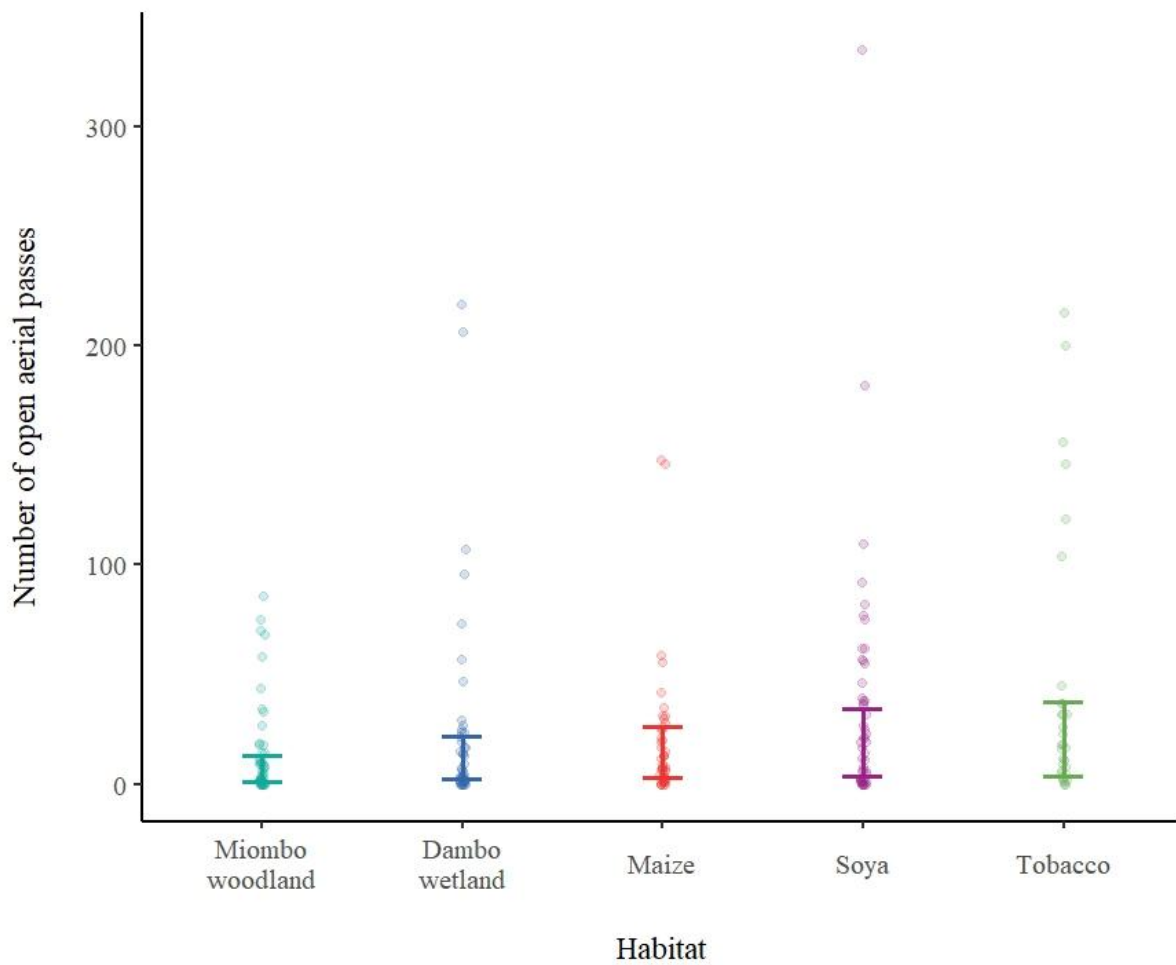


Figure 3.5: Open aerial activity (points) measured by the number of passes during each 3h survey in each habitat type category, with bars indicating GLMM estimates with 95% confidence intervals.

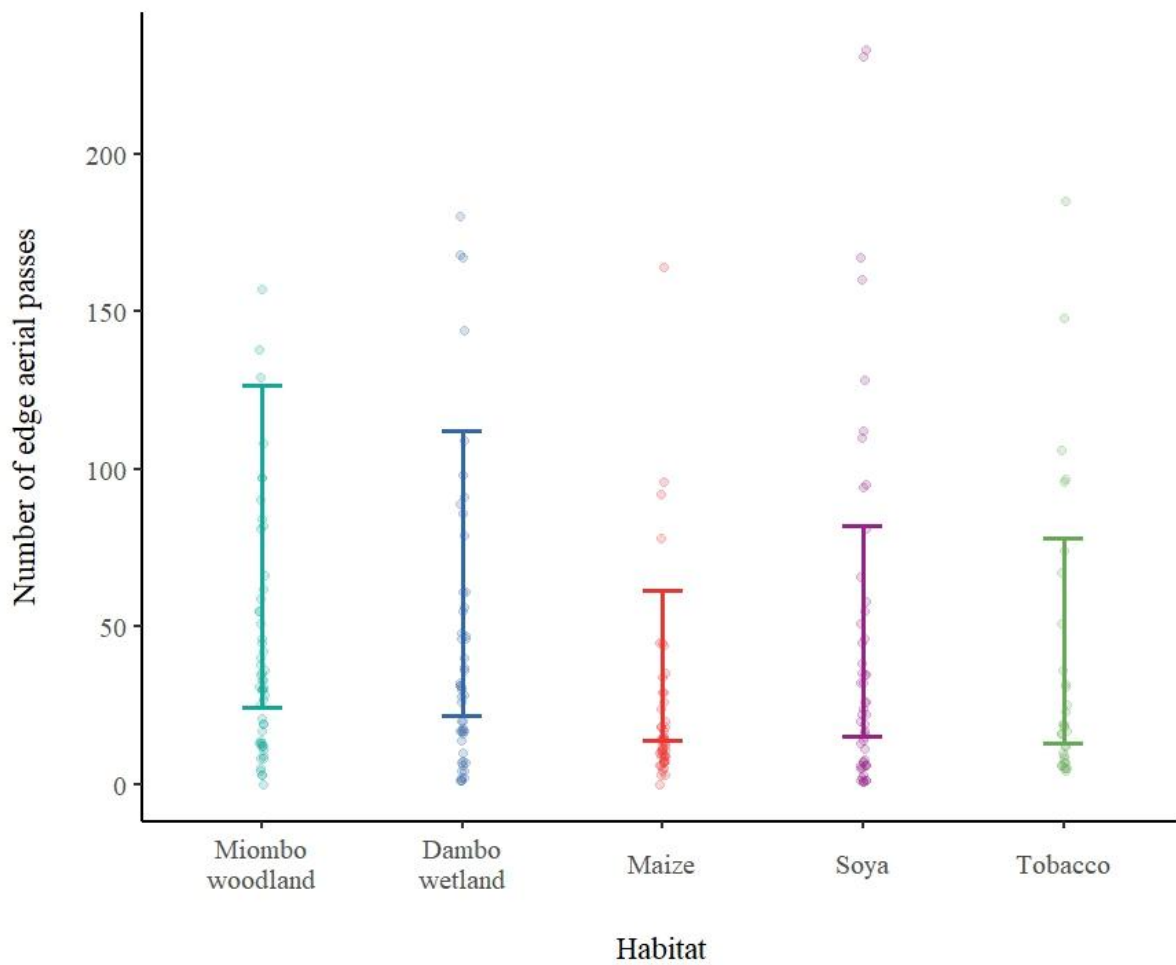


Figure 3.6: Edge aerial activity (points) measured by the number of passes during each 3h survey in each habitat type category, with bars indicating GLMM estimates with 95% confidence intervals.

The Julian date was a significant influence on activity of both functional groups at static detector locations and this is an effect of the different cropping seasons rather than within cropping season effects (**Error! Reference source not found.**).

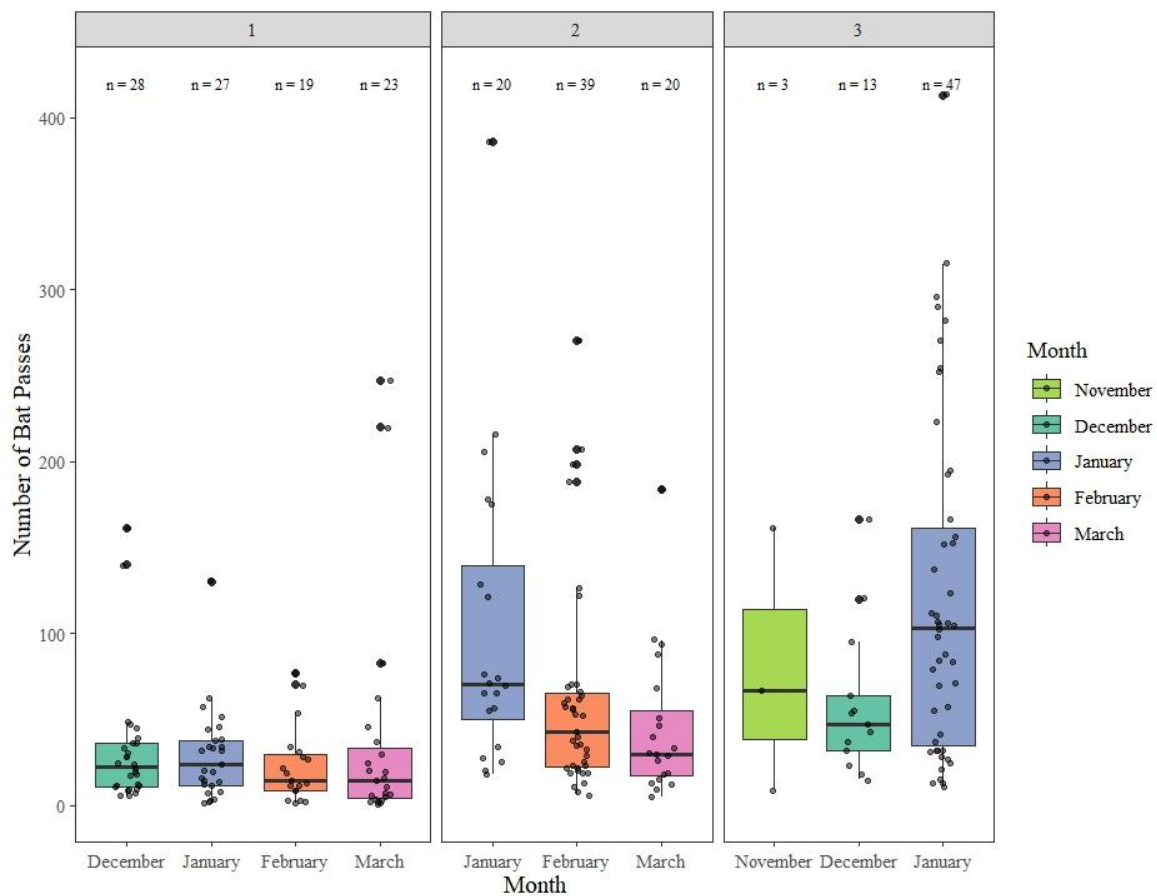


Figure 3.7: Variation in total bat activity at static detector locations between cropping periods (1 = 2016-17; 2 = 2017-18; 3 = 2018-19) and in monthly activity within each cropping period.

3.4.3. *Do wider vegetation characteristics influence bat activity in a commercial agricultural landscape?*

At the 50m buffer scale, the intercept variance of the farm random effect was 1.12 (SD=1.06) for open aerial bats compared to 0.32 (SD=0.57) for edge aerial bats. Activity levels of open aerial foragers were higher along transects with lower woodland cover (Table 3.5), whilst there was no significant effect of NDVI. Edge aerial foragers were not influenced by either woodland proportion or NDVI at this scale.

Table 3.5: Fixed effects of the transect 50m buffer modelled with transect distance as an offset and farm as a random effect. Significant p values ($p < 0.05$) given in bold.

Fixed effects	Open aerial			Edge aerial		
	exp(β)	SE [†]	p-value	exp(β)	SE [†]	p-value
NDVI of 50m buffer	1.18	0.199	0.31	1.00	0.107	0.98
Proportion of woodland in 50m buffer	0.61	0.104	0.004	0.85	0.091	0.13
Julian date	1.34	0.327	0.24	1.04	0.162	0.79
Temperature (°C)	0.94	0.172	0.75	1.08	0.140	0.56
Latitude	1.16	0.270	0.52	0.93	0.132	0.63
Intercept	0.00	0.000	<0.001	0.00	0.000	<0.001

[†] SE = Standard Error

At the 3km buffer scale, the intercept variance of the farm random effect was 1.04 (SD=1.02) for open aerial bats compared to 0.22 (SD=0.47) for edge aerial bats. At this scale, none of the vegetation characteristics influenced open or edge aerial bat activity (Table 3.6).

Table 3.6: Fixed effects of the transect 3km buffer modelled with transect distance as an offset and farm as a random effect. Significant p values ($p < 0.05$) given in bold.

Fixed effects	Open aerial			Edge aerial		
	exp(β)	SE [†]	p-value	exp(β)	SE [†]	p-value
NDVI of 3km buffer	0.78	0.146	0.18	0.85	0.095	0.15
Proportion of woodland in 3km buffer	0.99	0.234	0.96	0.98	0.151	0.91
Julian date	1.34	0.286	0.24	1.04	0.147	0.79
Temperature (°C)	0.94	0.191	0.75	1.08	0.147	0.56
Latitude	1.16	0.287	0.52	0.93	0.126	0.63
Intercept	0.00	0.000	<0.001	0.00	0.000	<0.001

[†] SE = Standard Error

3.5. Discussion

Open and edge aerial foragers are clearly able to take advantage of this anthropogenic landscape. On the other hand, the relatively low activity rates recorded in this study for trawl and flutter foraging functional groups (less than 1% of all calls) indicate that they are rarer across these landscapes. These largely gleaning species may be particularly important in pest suppression due to their ability to forage close to vegetation where insect pest species may be more active and may also be accessible in their larval stages (e.g. caterpillars). More research is needed to understand the ecological requirements for these species, such as those in the Hipposideridae, Rhinophidae and Nycteridae families, so as to understand how to enable them to persist agricultural landscapes.

Neither vegetation characteristics or insect prey availability (median = 1122 (IQR 3788)) influenced activity recorded by static detectors for either open or edge aerial functional groups. Consideration of the influence of the abundance of main orders of insects also does not change this finding. This is in contrast to other studies finding positive associations with these variables (Meyer et al., 2004; Hackett et al., 2013). However, there are other studies with similar results indicating that overall activity may not be affected by prey availability or vegetation structure (Helbig-Bonitz et al., 2015). The findings indicate that at local scales in

cropped habitat, bats of these functional groups are able to persist and maintain feeding activity in intensively farmed locations. .

Activity levels of both open and edge aerial bats at this local scale was similar across natural and cropped habitats with overlapping activity levels, demonstrating that all of the habitats provide foraging opportunities for these functional groups. However, the activity of open aerial bats was significantly lower in Miombo woodland habitats than in Dambo wetland or cropped areas. This is not surprising for this functional group, given that they are known to make use of more open aerosphere habitats for foraging and also fly high above vegetation with good high dispersal abilities, allowing them to forage further away from roosting sites primarily in trees or buildings (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). In contrast, activity of edge aerial bats was highest in woodland and wetland habitats, and lower in the three crop types, with lowest levels in maize. This indicates that semi-natural habitats may have greater availability of resources than cropped habitats. The apparent preference for woodland and wetland could also be associated with the commonly observed utilisation of vegetation edge lines for foraging behaviour by this functional group, with woodland and wetland vegetation creating lines of contrasting vegetation heights along which to forage (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). The crops may not provide this level of vegetation contrast with either woodland or grassland field margins. These findings suggest that agricultural management strategies aiming to boost pest suppression services by bats should focus on maintaining habitat heterogeneity to encourage multiple functional groups of bats. This is in line with recommendations in the literature (Tuneu-Corral et al., 2023).

For open aerial bats, transects with larger proportions of woodland in the 50m buffer had lower activity, but this effect was not seen using the wider landscape scale of the 3km buffer. In contrast, for edge aerial bats, landscape scale variables along transects had no effect on activity at either buffer size. This again indicates that bats of these functional groups are able to exploit these fragmented agricultural landscapes.

The influential variable consistent between the two functional groups at both static location and transect scales is the Julian date, which seems to be an indication of between rather than within cropping period fluctuations (**Error! Reference source not found.**). Highest levels of

bat activity are seen in the 2018/19 cropping period. This may be due to the latent effects of climatic variables on bat populations that were not considered in this study, such as rainfall patterns in previous years with a peak rainfall seen in 2017 (Figure 3.8).

Interestingly, more southern static locations, which are set in drier miombo woodland, seem to have higher edge aerial bat activity than those further north with wetter Miombo (towards the equator) as indicated by latitude, but this does not appear to be an influence at transect scales or for open aerial foragers. The factors influencing the activity of edge aerial foraging at a local scale at different latitudes in these agricultural landscapes should be explored further on a species-specific level and in relation to the agroecological zones, taking into account climatic as well as habitat variables.

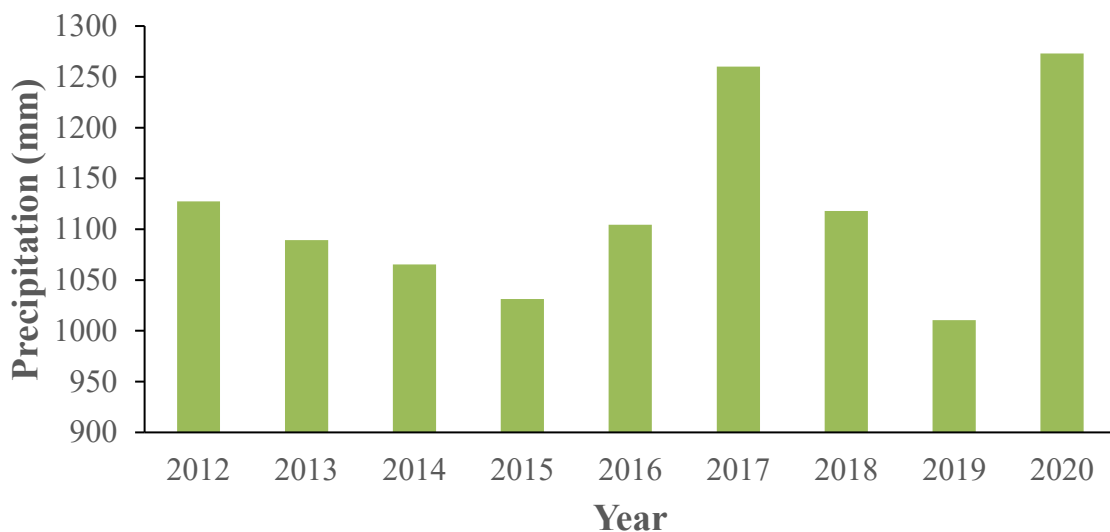


Figure 3.8: The trend in annual rainfall across Zambia covering the study period from 2016 to 2019 (Source: World Bank).

The number of species within each functional group is unknown, due to limitations in acoustic identification to species level, and may also influence activity levels. It is therefore essential for future studies to build on call libraries such as the one developed in Chapter 2, so as to improve on PAM research such as this.

The foraging requirements of bats considered by this study are not the only ecological factors to consider however, and future studies should consider roosting and breeding requirements, which for many species are still poorly understood. Most of the studies on fragmentation effects have considered only foraging behaviour, however, roosting opportunities are also a consideration when understanding landscape use by bats. Some species rely heavily on arboreal roost features (Boughey et al., 2011) and others are able to make use of anthropogenic structures, thus conferring in an adaptive advantage in anthropogenic landscapes (Bergeson et al., 2015). Some species will travel an average of 5km to foraging sites (Noer et al., 2012) whereas others will only travel an average of 1km (Monadjem et al., 2009).

Given the increased use of irrigation to extend the cropping periods, future studies during the dry season and at early stages of crop growth should be conducted. Future studies should also consider the movements of individual bats within the landscape, so as to highlight foraging requirements, as well as commuting and social behavioural patterns.

**Chapter 4. Arthropod consumption by bats in an
Afrotropical commercial agroecosystem: does
this indicate pest control services?**

4.1. Abstract

There is increasing evidence that bats can play a role in arthropod pest suppression and so there has been a recent increase in studies interested in the diets of bats, especially in relation to agricultural landscapes. Despite this, there have been few studies on the diets of Afrotropical bat species and even fewer undertaken to investigate their consumption of insect pests. To gain insights into the diets of bats in an Afrotropical farming landscape dominated by commercial agriculture, we collected bat droppings of 14 species from 2016 to 2019 at 23 sites across Zambia. Metabarcoding techniques were used to identify dietary components to 1) better understand functional group dietary resource partitioning, 2) identify crop pest species present in bat diets and to 3) explore the changes in diet of a species commonly found in Zambian agricultural landscapes, *Mops nigeriae*, from roost droppings collected monthly over six months. The analysis of a total of 335 droppings from three different bat functional groups resulted in the identification of 719 prey Molecular Operational Taxonomic Units (MOTUs). There was greater overlap between the diets from the more generalist edge and open aerial bats, whereas the more specialised diet of narrow passive bats showed much less overlap with both other functional groups. Across all samples, we identified 16 crop pest species in the diet, with some overlap in consumption between the functional groups, but some only consumed by a single functional group. The highest rate of pest consumption was seen for the Lepidopteran pest *Thysanoplusia orichalcea* found in 40.7% of narrow passive dropping samples. The diet of *Mops nigeriae* was dominated by Lepidoptera for most of the sampling period, however during December, Hymenoptera was most commonly consumed taxa. The presence of most of the identified crop pests in the diet was not influenced by the collection date, however Hemipteran pest *Nezara viridula* was only detected in the diet in April when 40% of the droppings collected contained this species. Overall, this study demonstrates differences between the diet of functional groups in this landscape and confirms the presence of crop pests in all functional group diets, indicating that these species may be playing important roles as insect predators in these landscapes. It also highlights the importance of monitoring species-specific diets over time to better understand dietary fluctuations.

4.2. Introduction

With the growing demand for agricultural productivity to feed a growing human population, the adoption of monocultural cropping has become more prevalent and as a consequence there has been an increase in pest species that are able to multiply rapidly in response to increased food resources, and persist in the environment between cropping periods (Oerke, 2006). Given the negative consequences of pesticide over-use, such as a build up of resistance and effects on non-target species, there is increasing interest in promoting natural predators in integrative pest management strategies (Crowder and Harwood, 2014; Rosa-Schleich et al., 2019).

Research on natural enemies of arthropod pests has often focussed on specialists, which can be used as biocontrol agents for target pest species, such as parasitic wasps. The role of generalist predators as pest suppressors has been under some debate given that they may consume beneficial arthropods as well as pests, however there is growing evidence that they can play a significant biocontrol role (Hsu et al., 2021).

Widespread anthropogenic change can expose species assemblages to ecological novelty, impacting on predator-prey interactions which can be difficult to predict and has implications for ecosystem function (Guiden et al., 2019). Three-dimensional habitat modifications, such as land clearance for agriculture, can impact species using the aerosphere, such as Chiroptera (bats) (Kalko et al., 2007). Given the diversity of insectivorous bat species, it is important to understand their prey consumption in anthropogenic landscapes, such as those modified for agriculture, to determine the top-down role they may play in arthropod suppression (Whitaker et al., 2009).

Insectivorous bats are predators of a wide range of arthropods. Bat species assemblages can be categorised into functional groups, determined by morphometric, acoustic and flight behaviour traits, which may influence access to prey types (Schnitzler et al., 2003; Denzinger and Schnitzler, 2013). Some species exhibit generalist or opportunistic foraging, however many generalist species or functional groups exhibit a degree of preference for prey of various taxonomic groups (Wray et al., 2021). Even species appearing to occupy similar

niches can show significant differences in diet composition, potentially to avoid competition, as was found in two relatively common bat species in Japan (*Murina ussuriensis* and *Myotis ikonnikovi*) utilising the same landscape (Heim et al., 2021). There is also evidence of resource partitioning between males and females in some species, such as female *Tadarida teniotis* found to be consuming larger and more migratory moths than males in Portugal (Mata et al., 2016).

There are few studies that make direct links between prey availability and measures of bat diet, so as to infer prey preference (Kunz and Parsons, 2009). Nevertheless, temporal differences in diet have been recorded for some species, dependent to some extent on seasonal prey availability (Tiede et al., 2020; Aihartza et al., 2023; Andreas et al., 2023). Differences in prey preference may also arise as a result of changes in local abundance of prey types across species ranges, allowing the species to take advantage of locally abundant prey types (Andreas et al., 2023).

Traditionally, bat diet has been characterised by analysing stomach contents or faecal pellets using microscopy. These methods allow for quantification of dietary items, but are time consuming, require specialist entomological skills and in most cases are unable to identify prey to species level, especially with regard to soft-bodied arthropods (Kunz and Parsons, 2009). However, advances in molecular methods have allowed for more precise identification of prey items and evidence for the consumption of crop pest species by bats, has been found through genetic analysis of bat faecal pellets (Brown et al., 2015; Puig-Montserrat et al., 2015; Taylor et al., 2017; Kemp et al., 2018; Weier et al., 2019; Mata et al., 2021a). However, quantifying pest consumption and the effects on yields to determine pest control service is challenging. Bat exclusion studies have demonstrated suppression of some pests through increased crop damage in the absence of bats, mainly in agroforestry systems (Cassano et al., 2016; Maas et al., 2016; Librán-Embid et al., 2017; Linden et al., 2019; Ancillotto et al., 2024) but also in rice cultivation (Bhalla et al., 2023; Sottomayor et al., 2024). Other studies however, have shown no effect of bat presence or activity on yield of crops (Gras et al., 2016). Attempts have been made to quantify the economic value of bats' pest control services over large landscapes. For example an estimate for the United States, amounts to about 2-29% of the annual yield value, using data from cotton growing areas of Texas (Cleveland et

al., 2006), which at the time of the study gave a mid-range value of 22.9 billion USD per year (Boyles et al., 2011). In South Africa, it has been estimated that control by bats of stink bug pests is worth 0.53–1.29% of annual yields to the macadamia nut industry (Taylor et al., 2018), and in Thailand, 0.008% of annual yields for the rice industry was estimated for *Tadarida plicata* predation on the planthopper pest *Sogatella furcifera* (Wanger et al., 2014).

. For some bat species it appears that specific insect crop pests form an integral part of their diet and they will even show increased foraging activity when there are larger populations of pest species, coinciding with higher detections of the pest in faeces, such as shown in a vineyard region of the Iberian Peninsula (Baroja et al., 2021). However studies into the diet of bat species in agro-ecosystems have notably lagged behind those in natural or semi-natural ecosystems and so more research is needed in this field (Taweesub et al., 2022)

Africa has a relatively high diversity of bats (over 200 species) but dietary studies on the continent are scarce (Taweesub et al., 2022). Most dietary studies have used morphological analyses of bat droppings using microscopes to identify arthropod fragments and to even quantify dietary items (Findley and Black, 1983; Seamark and Bogdanowicz, 2002; Aspetsberger et al., 2003; Andriafidison et al., 2007). However, in more recent years, molecular techniques have become a popular way to characterise the diets of some African bat species in agricultural landscapes. Studies in Macadamia orchards in South Africa for example, have demonstrated the presence of crop pests in the diet of several bat species (Taylor et al., 2017; Weier et al., 2019). A study conducted in Rwanda in agricultural areas growing rice, tomato, maize and bananas, characterised the diets of eight bat species, with the presence of 28 agricultural pest species confirmed (Nsengimana et al., 2023). Quantification using these molecular techniques however remains challenging (Deagle et al., 2019).

Zambia is a southern African country heavily reliant on its commercial agricultural industry, with intensification of cropping systems becoming more prevalent across the landscape. Commercial agriculture (production for sale or profit) in this Afrotropical context is characterised by farmland of over 100ha, utilising mechanisation and usually with irrigation systems in place, such as centre pivot irrigation (CIAT and World Bank, 2017). Commercial farms in the study region, on the most part, retain some areas of natural vegetation, either left

in its natural state or utilised for low intensity grazing and harvesting of resources such as firewood. For integrative pest management strategies to be implemented successfully, an evidence-based understanding of natural predators is essential. With little information available on the diet of most Afrotropical bats, this study aims to increase our understanding of the diets of species assemblages in the commercial agricultural context. Conducted across commercial agroecological landscapes in Zambia, this study addresses the following questions:

1. Is there dietary partitioning between functional groups of bats?
As functional groups exhibit different foraging behavioural strategies and habitat use, dietary partitioning is expected at the functional group level.
2. Is there predation of crop pests by bats in agricultural landscapes?
Given that studies conducted elsewhere in the region have found the presence of crop pests in bat diet, it is expected that crop pest will be found in the diet of bats in these landscapes.
3. Does dietary composition change over a time period of six months during the cropping period for an open aerial bat species, *Mops nigeriae* on a commercial farm?
Dietary composition is expected to change over time in line with seasonality and cropping periods, which may influence insect prey availability in these landscapes.

4.3. Materials & Methods

4.3.1. Field methods

This study was conducted across 23 study sites in three main commercial agricultural areas of Zambia. Bat droppings were collected from roosts and captured bats on commercial farmland from 2016 to 2019, with capture sites and roost locations spread across the three areas (Figure 4.1). Bat species identifications were based on molecular identifications where possible.

Where molecular identification was inconclusive due to inadequate bat DNA in the sample, morphometric features and molecular identifications of other individuals at the location were used. Species were categorised into three functional groups: edge aerial, open aerial and narrow passive (Schnitzler and Kalko, 2001).

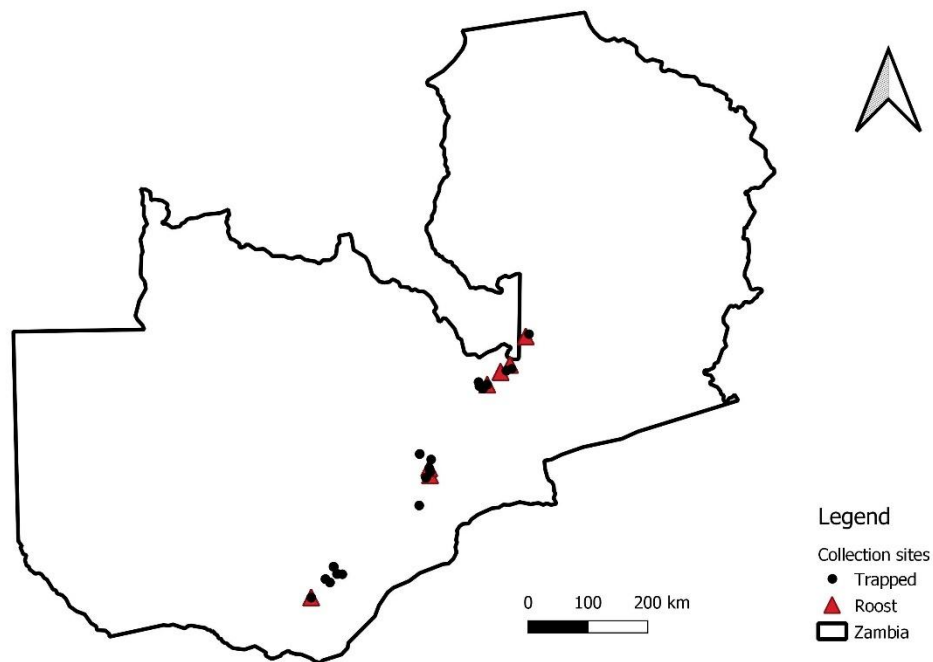


Figure 4.1: Locations of dropping collections indicating both roosts and trapping locations

Between 2016 and 2019, during cropping periods (November to March), bats were captured at a total of 18 farms using mist nets, whilst simultaneously collecting data on species distributions, acoustics, morphometrics and reproduction (see also Chapter 2). Captured bats were placed in bleached cotton bags for a maximum of 15 minutes and bats were released at the capture site as soon as possible after data collection. Droppings were collected from the bags where available, with any multiple pellets from the same individual bat analysed as a single dropping sample, to ensure they were independent. Droppings were analysed from a total of 84 trapped bats of eight species (to address questions 1 and 2); all categorised as edge aerial foragers (Table 4.1).

Roost sampling of droppings was also conducted between 2017 and 2019, during cropping periods (November to March) when crop pests are likely to be present in the landscape and feeding on crops. A bleached cloth was placed under roosting bats for a single night at each roost. The following morning individual pellets (5 to 20 pellets from each roost) were

collected from as far apart as possible from each other and not touching, with the assumption that each was from a different individual and so independent, meaning each could be analysed as a single dropping sample. Droppings collected from a total of 8 roosts (to address questions 1 and 2), consisted of droppings from two roosts of *Nycteris* (narrow passive) species (a total of 27 droppings), and open aerial bat droppings from six roosts of *Mops* species (a total of 105 droppings) (Table 4.1). Exact numbers of bats in each roost were unknown, however *Nycteris* roosts were smaller and estimated to have up to 10 bats, whereas *Mops* roost numbers were in the hundreds, with the exception of one smaller roost of *Mops pumilus* with approximately 20 individuals.

One roost of *Mops nigeriae* in a house on a farm in the Lusaka area, was subsequently monitored over six months (December 2018 to May 2019). At approximately the same date each month, 20 dropping pellets were collected in line with sample sizes used in most studies (20-50) for each study group as a compromise between prey detection and costs (Whitaker et al., 2009; Mata et al., 2019). This yielded a total of 119 pellets (one sample data missing), which were each analysed separately based on the assumption that they were likely to be from different individuals as recommended by Mata et al. 2019, to examine diet and detect pest consumption over time (addressing question 3).

Table 4.1: Sample sizes (n) of droppings collected for species of three functional groups. All droppings from edge aerial bats were from captured bats (n is equal to the number of individual bats), whilst droppings from open aerial and narrow passive bats were collected from roosts (n is the number of pellets from an unknown number of individuals but assumed to be different individuals).

Functional group	Species	Common name	n
Edge aerial	<i>Afronycteris nana</i>	Banana bat	5
	<i>Laephotis capensis</i>	Cape serotine	48
	<i>Neoromicia anchietae</i>	Anchieta's serotine	6
	<i>Neoromicia zuluensis</i>	Zulu serotine	2
	<i>Pipistrellus rusticus</i>	Rusty pipistrelle	12
	<i>Scotophilus dinganii</i>	Yellow-bellied house bat	7
	<i>Scotophilus viridis</i>	Green-bellied house bat	2
	<i>Vansonia ruepellii</i>	Rüppell's bat	2
Open aerial	<i>Mops condylurus</i>	Angolan free-tailed bat	40
	<i>Mops nigeriae</i>	Nigerian free-tailed bat	20
	<i>Mops pumilus</i>	Little free-tailed bat	25
	<i>Mops sp</i>	Free-tailed bat species	20
Narrow passive	<i>Nycteris thebaica</i>	Slit-faced bat species	17
	<i>Nycteris sp</i>	Slit-faced bat species	10

The droppings were desiccated using silica beads and stored in a chest freezer at -18°C until transportation to Portugal by courier for analysis by Dr Vanessa Mata at Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado (CIBIO).

4.3.2. DNA extraction and PCR amplification methods

DNA was extracted using the E.Z.N.A. tissue DNA kit (Omega Bio-Tek, Norcross, Georgia), following Gonçalves et al. (2024), and in batches of 23 samples plus one negative control without a faecal pellet. Extracted DNA was distributed into 96-well plates, leaving the last well empty for PCR negative control. DNA extracts were stored at -20 °C prior to amplification. Diet of bats was assessed using arthropod general COI primers (fwhF2-R2n; (Vamos et al., 2017)) modified with Illumina overhangs. Each PCR reaction (10 µL) included

5 µL of QUIAGEN Multiplex PCR Master Mix, 0.25 µL of forward primers, 0.25 µL of reverse primers, 2.5 µL of ultrapure water, and 2 µL of DNA extract. PCR cycling conditions included an initial denaturation at 95 °C for 15 minutes, 40 cycles of denaturation at 95 °C for 30 seconds, annealing at 52 °C for 30 seconds, extension at 72 °C for 30 seconds, and a final extension at 72 °C for 10 minutes. PCR success and quality were assessed by running 2% agarose gels stained with GelRed. PCR products were diluted 1:4 with water and then tagged for individual identification in a second amplification step using P5 and P7 Illumina adaptors with unique 7-bp barcodes. The PCR mix included 7 µL KAPA HiFi HotStart ReadyMix (Rocher, KAPA Biosystems, Basel, Switzerland), 2.8 µL ultrapure water, 0.7 µL of each P5 and P7 index, and 2.8 µL diluted PCR product. Indexing PCR cycling conditions included an initial denaturation at 95 °C for 3 minutes, followed by 9 cycles of 95 °C for 30 seconds, annealing at 55 °C for 30 seconds, extension at 72 °C for 30 seconds, and a final extension at 72 °C for 5 minutes. Indexed PCR products were cleaned with Agencourt AMPure XP beads (Beckman Coulter, Brea, California) at a 1:0.8 ratio, following the manufacturer's instructions. Libraries were quantified with an Epoch dsDNA quantification system and normalized to 25 nM in a 10 µL volume. Samples were pooled equimolarly and assessed on a TapeStation (Agilent, Santa Clara, California) using High Sensitivity D1000 ScreenTape to verify average amplicon length and exclude small nontarget amplicons or primer dimers. DNA concentration was validated by qPCR (KAPA Library Quant Kit qPCR Mix, Rocher) and diluted to 4 nM. Finally, libraries were sequenced on an Illumina MiSeq platform using a MiSeq Reagent Kit v3 (2 × 250 bp), targeting a depth of 30k reads per sample.

Raw sequencing data were processed with ObiTools (Boyer et al., 2016) and VSEARCH (Rognes et al., 2016). First, paired reads were merged with "illumina-paired-end", while primer sequences were removed with "ngsfilter". Reads were then dereplicated per sample using "obiuniq", and artifacts and sequences of unexpected lengths (202–208 bp) were removed using "—cluster_unoise". Chimeric sequences were removed with "--uchime3_denovo", followed by clustering at 99% similarity using "--cluster_size". Finally, initial reads were mapped back to retained OTUs using "--usearch_global" at 99% identity. Further filtering was performed with the R package LULU (Frøslev et al., 2017) to remove additional PCR and sequencing artifacts, as well as nuclear copies of the mitochondria. Taxonomic assignment of OTUs was done with BOLDigger (Buchner and Leese, 2020) using the

“digger_hit” method, followed by manual curation. OTUs assigned to the same higher taxon (e.g., family level) were attributed with different numbers, so that they could be differentiated in analyses. OTUs were classified as being diet if identified to the order level or below within the classes Insecta or Arachnida, excluding parasites like Trombidiformes, Mesostigmata, Ixodida, and Siphonaptera.

For OTUs with >98% similarity to species level, identifications were accepted after checking distribution likelihood. Those with $\geq 95\%$ similarity to Species or Genus were also checked for geographical distribution likelihood, and the BOLD phylogenetic tree (Kimura 2 Parameter Distance Model, marker COI-5P, 1st, 2nd, 3rd codon positions) was used to identify the next highest taxon containing those with identical or close similarity scores for several taxa.

4.3.3. *Statistical analysis*

For each sample, OTUs with <1% of the total reads were first removed from the dataset to reduce the likelihood of contaminants and rarer sequences from disproportionately affecting the results (Deagle et al., 2019). Statistical analyses were then performed using R 4.2.2 (R Core Team, 2023) through RStudio 2023.06.1+524 (Posit team, 2023).

For arthropods likely to be a food item for the bats only (for example, parasites were excluded), Percentage of Occurrence (POO) values were calculated using the sum of occurrences of each prey taxon, as a percentage of total occurrences of all prey taxa, within a bat functional group (Deagle et al., 2019). This gives a measure of the proportion of the combined diet of the functional group that is made up of a particular dietary component, in order to address question 1. To examine dietary differences between functional groups, niche breadth was calculated using Levin’s index (B) as a measure between 0 and 1, with higher values indicating more generalist diets. This index uses the proportion of each dietary item found in the diet across the group to calculate an overall measure of evenness. In addition, Pianka’s index (O) was used to calculate niche overlap as a value between 0 and 1, with higher values indicating greater overlap. These indices were calculated using the ‘spaa’ package Version 0.2.2 (Zhang, 2016).

A list of species known to be significant crop pests for Zambia was collated using Prinsloo & Vivienne (2015) with the addition of more recent accidental introductions, such as *Spodoptera frugiperda* (Fall armyworm) checked for pest status using Centre for Agriculture and Bioscience International datasheets (CABI, 2024). Frequency of Occurrence (FOO) was calculated as the percentage of droppings containing the dietary item (Deagle et al., 2019), which calculates the proportion of individuals of a functional group consuming a particular pest MOTU, to address question 2. The FOO measure quantifies whether multiple individuals are consuming a pest species, which is not shown by the measure of POO.

For the *Mops nigeriae* roost monitored over time, the FOO was also calculated, for each monthly roost dropping collection, to look at changes over time in dietary composition to order and for crop pest species, to address question 3. To investigate the influence of sampling date (as a fixed variable) on the occurrence of crop pests in the diet, Generalised Linear Models (GLMs) were used with the presence of consumed orders and pests as response variables, incorporating a binomial distribution. Residual diagnostics for all GLMs were carried out using the ‘DHARMA’ package (Hartig, 2022) to verify model assumptions and no problems were detected with any of the models.

4.4. Results

There were 719 prey Molecular Operational Taxonomic Units (MOTUs) with more than 1% Relative Read Abundance (RRA) of sample reads detected across all of the 335 samples analysed. Many of these were MOTUs which were not identified to order (29%) and only classified as Arthropoda (51) or Insecta (156). There were 155 Coleoptera MOTUs (22%), followed by 129 Lepidoptera (18%) and 76 Diptera (11%), with all other orders making up less than 10%.

4.4.1. Dietary niche separation

Dietary niche breadth at order level (Figure 4.2) was similar between edge ($B = 6.75$) and open aerial ($B = 6.98$) foragers, whilst narrow passive foragers had a lower niche breadth ($B = 4.97$). There is relatively high niche overlap (closer to 1.0), when considering orders, between edge and open aerial foragers ($O = 0.89$) whilst narrow passive foragers have lower

overlap with both edge ($O = 0.72$) and open aerial ($O = 0.71$) bats. At MOTU level, niche overlap again was highest between edge and open foragers ($O = 0.36$) and lower between narrow passive foragers and both edge aerial ($O = 0.14$) and open aerial bats ($O = 0.03$ only).

Coleoptera and Diptera were the most common prey items for edge aerial bat species (POO = 19 and 18% respectively). Blattodea made up the largest part of open aerial bat diets (POO = 20%), followed by Coleoptera (POO = 18%). Lepidoptera (POO = 36%) dominated narrow passive bat diet, followed by Coleoptera (POO = 19%) (Figure 4.2).

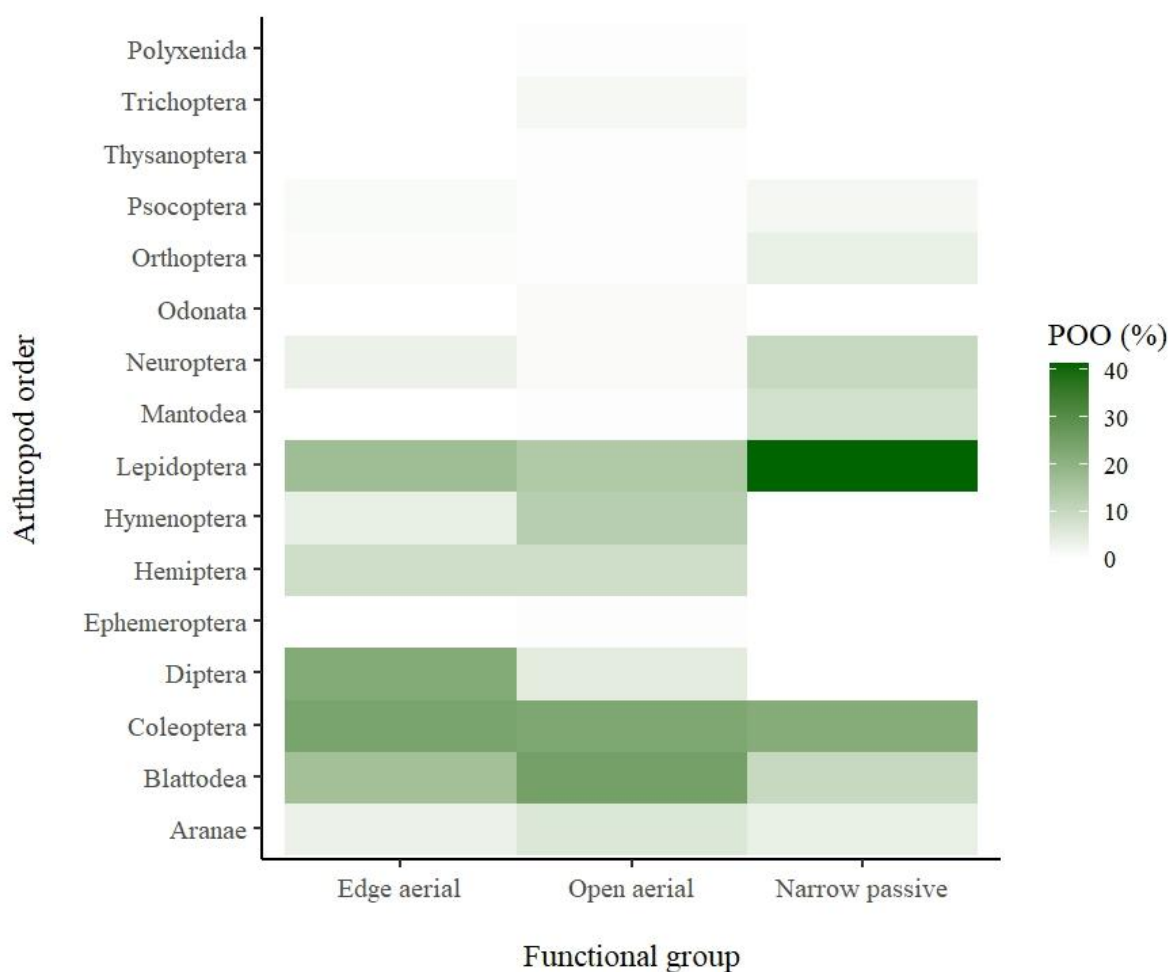


Figure 4.2: Percentage of Occurrence (POO) of arthropod Orders in bat droppings found in each functional group. Darker shading indicates higher POO values.

4.4.2. Do bats eat crop pests?

Across all 335 dropping samples, 16 crop pest species were detected with RRA of more than 1% (Table 4.2). The molecular identification of two beetle species were only possible to genus level but were treated as crop pests: *Anomala* (leaf chafer) and *Heteronychus* (Black beetle). Despite not being genetically matched to pests that have been barcoded within these taxa, they are likely to be pest species identified from light traps in these agricultural areas ([Chapter 5](#)). The lack of genetic identification to species level may be due to significant regional variation with no reference genetic material from the country, or they may be alternative pest species which are morphologically similar.

Most of the insect pest species are only present in the diet of a single functional group, with five of the 16 being consumed by more than one functional group (Table 4.2, Figure 4.3).

Thysanoplusia orichalcea (Lepidopteran pest) is however the only insect pest species consumed by all three functional groups, although it is most frequently consumed by narrow passive bats (FOO = 40.7%).

Table 4.2: Pest species present in all samples representing three bat functional groups as measured by Frequency of Occurrence (FOO) as a percentage (n= number of samples).

Order	Pest species	Common name	Bat functional group		
			Edge aerial (n=84)	Open aerial (n=224)	Narrow passive (n=27)
Coleoptera	<i>Anomala sp</i>	Leaf chafer species	4.8	8.9	0.0
	<i>Heteronychus sp</i>	Black beetle species	1.2	0.0	0.0
Hemiptera	<i>Bathycoelia</i>	Two-spotted stink bug	0.0	0.4	0.0
	<i>distincta</i>				
	<i>Empoasca</i>	Green leafhopper	1.2	0.0	0.0
	<i>decipiens</i>				
	<i>Nezara viridula</i>	Green vegetable bug	0.0	3.6	0.0
	<i>Rhopalosiphum padi</i>	Grain aphid	0.0	0.4	0.0
Lepidoptera	<i>Chrysodeixis</i>	Tunbridge wells	0.0	1.3	7.4
	<i>acuta</i>	gem			
	<i>Earias biplaga</i>	Spiny bollworm	0.0	0.4	0.0
	<i>Ectomyelois</i>	Carob moth	0.0	1.8	0.0
	<i>ceratoniae</i>				
	<i>Marasmia</i>	Lesser rice-leafroller	0.0	1.8	0.0
	<i>poeyalis</i>				
	<i>Marasmia</i>	Trapeze moth	2.4	1.3	0.0
	<i>trapezalis</i>				
	<i>Maruca vitrata</i>	Legume pod borer	0.0	1.8	0.0
	<i>Spoladea</i>	Beet webworm moth	0.0	1.3	0.0
	<i>recurvalis</i>				
	<i>Spodoptera</i>	Fall armyworm	0.0	0.0	11.1
	<i>frugiperda</i>				
	<i>Thaumatotibia</i>	False codling moth	1.2	0.0	0.0
	<i>leucotreta</i>				
Orthoptera	<i>Thysanoplusia</i>	Slender Burnished	6.0	4.9	40.7
	<i>orichalcea</i>	Brass			
	<i>Tuta absoluta</i>	Tomato leafminer	1.2	1.8	0.0
	<i>Gryllus</i>	Two-spotted cricket	0.0	0.9	0.0
	<i>bimaculatus</i>				

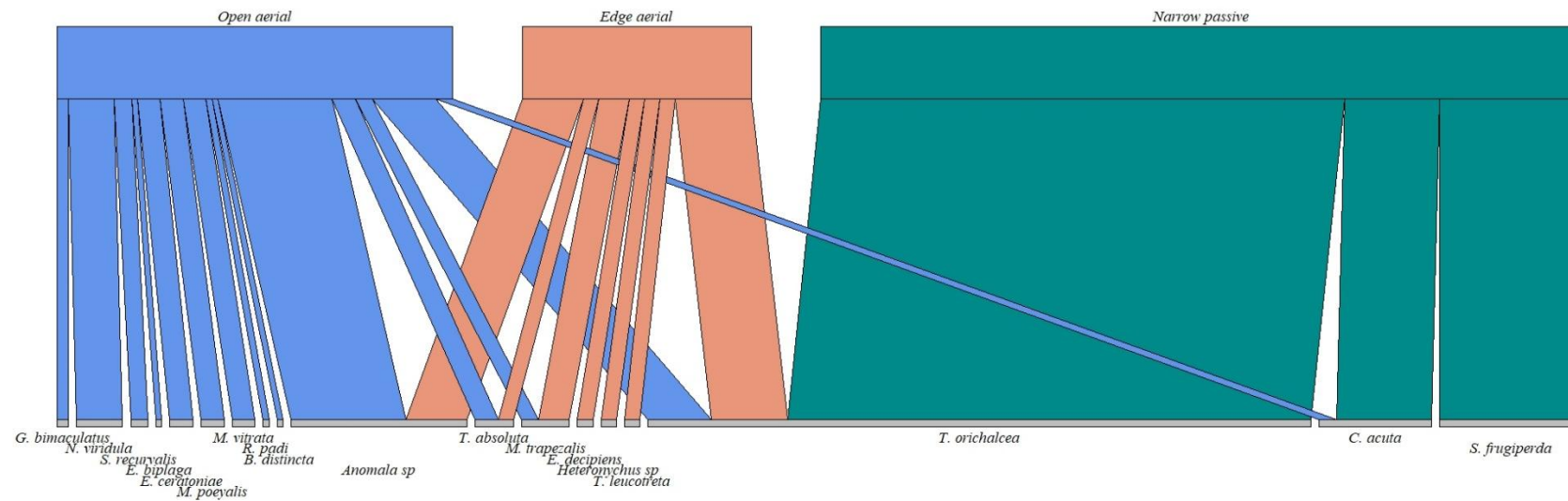


Figure 4.3: Frequency of Occurrence (FOO) of pest species (grey boxes at base) in the diets of different bat functional groups (as indicated by coloured links). The wider the links, the greater the FOO.

4.4.3. Dietary changes over time

For the *Mops nigeriae* roost monitored over time, the most commonly consumed order throughout the six months was Lepidoptera (Figure 4.4). This is especially evident during the time when the largest dietary similarities between months, by insect orders consumed, are seen from January to May ($O > 0.79$). Hymenoptera is the dominant order in December however (POO = 42%), when there is least overlap by order with all of the other months ($O < 0.70$) (Figure 4.4).

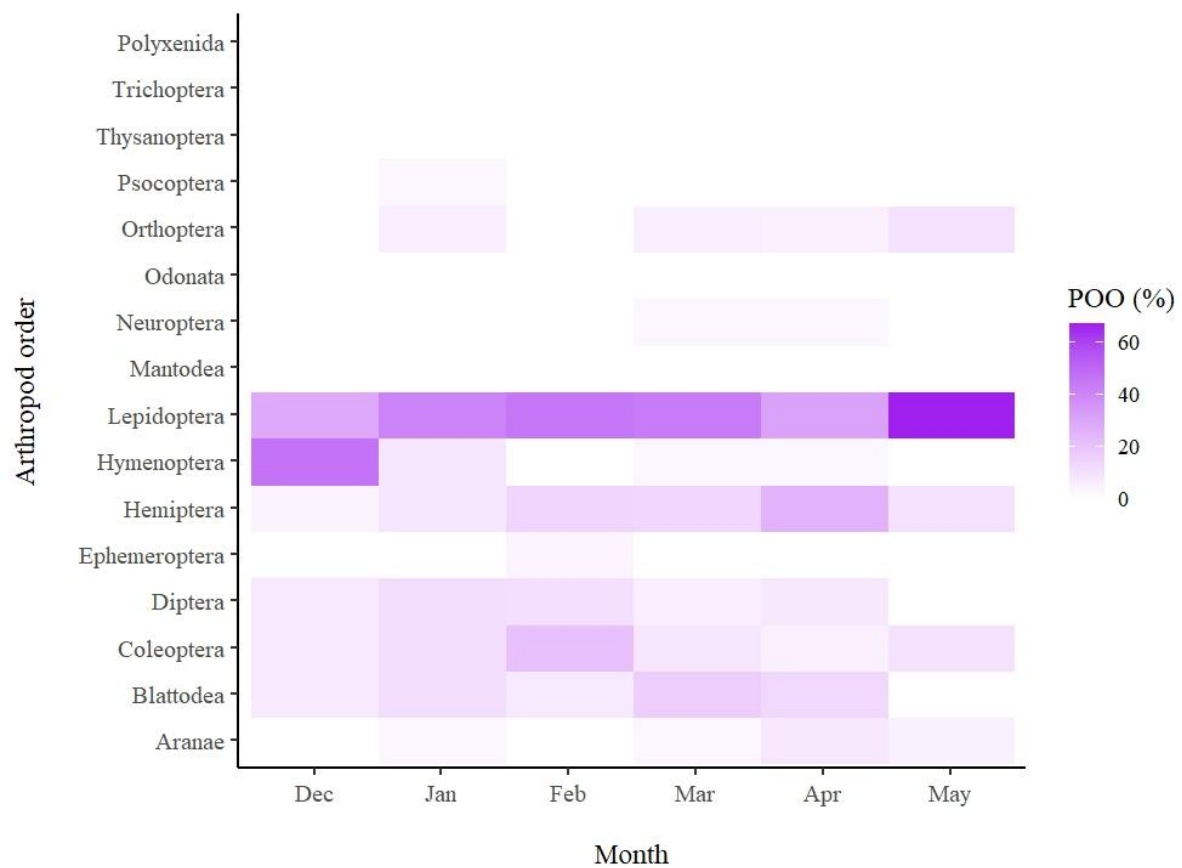


Figure 4.4: Dietary composition (Percentage of Occurrence) of *Mops nigeriae* between the months of December 2018 and May 2019

When considering all OTUs, there is variability in specific prey items throughout the year with niche overlap values (O) between 0.35 (January and March) and only 0.007 (December and May) but many prey items consumed across multiple months (Figure 4.5).

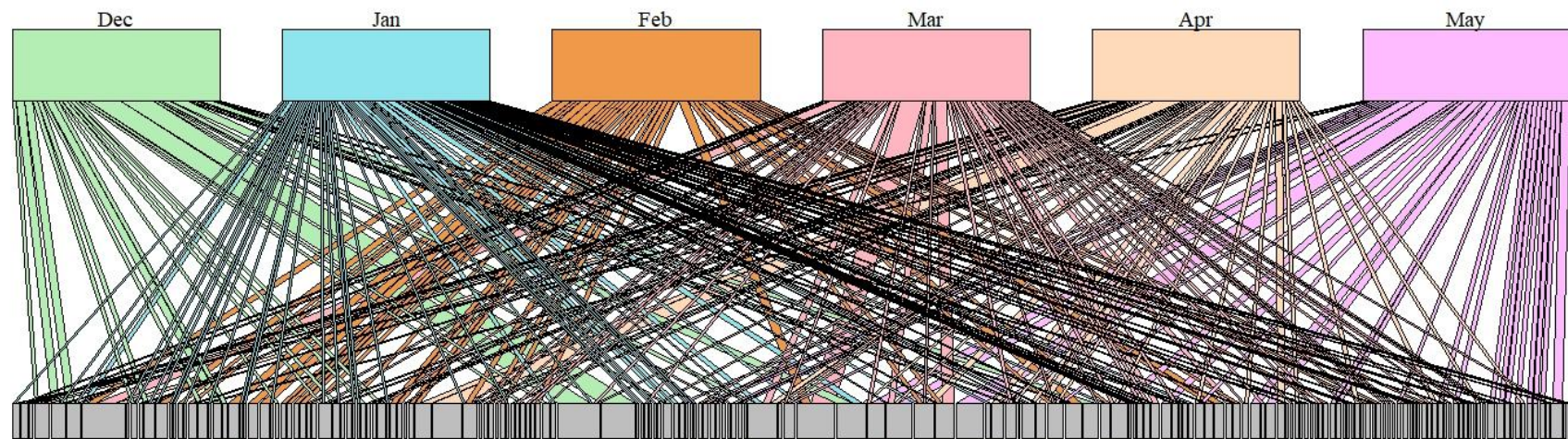


Figure 4.5: Bipartite network indicating prey Operational Taxonomic Unit (OTU) presence (grey boxes at the base indicate each OTU) in the diet of *Mops nigeriae* in the months December 2018 to May 2019 (shown by links colour coded by month).

From the droppings collected across the 6-month period from the *M. nigeriae* roost, 12 crop pest species of the 16 found across all species droppings, were identified (Figure 4.6). January had the highest number of pest species detected (6 species) and February the lowest (2 species).

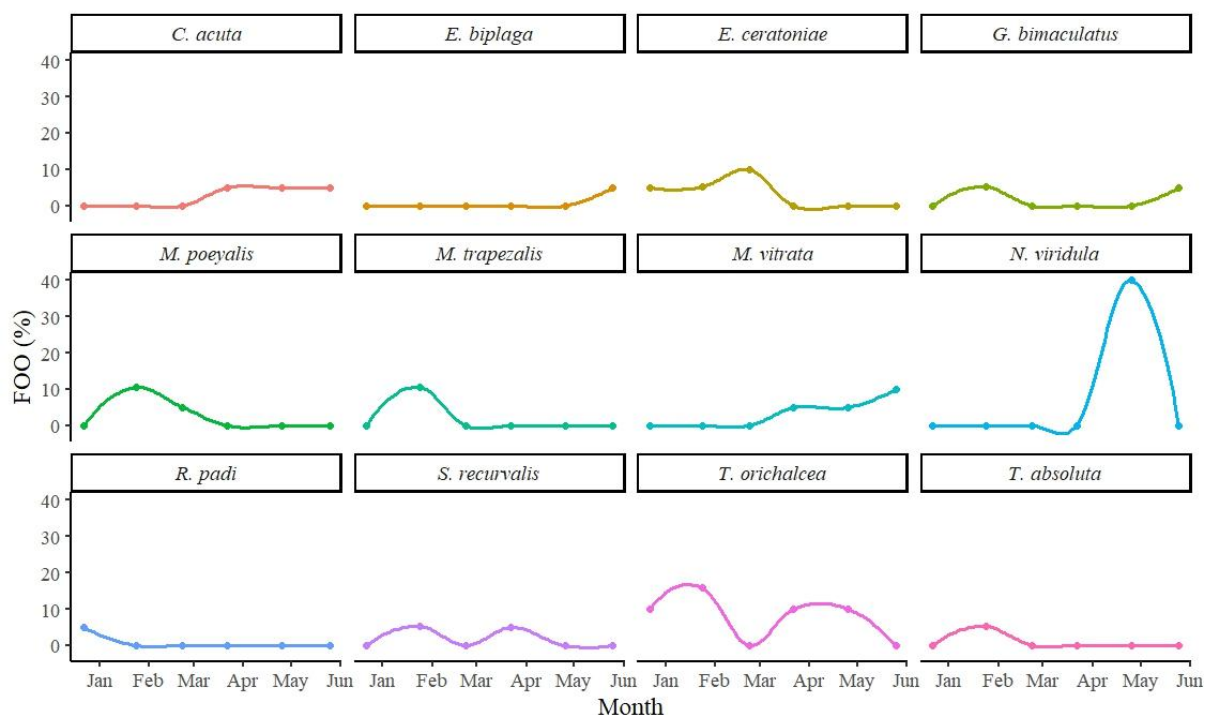


Figure 4.6: Frequency of Occurrence of crop pests in the diet of the *Mops nigeriae* roost sampled monthly over a six-month period from December 2019 to May 2018 (total n =119 droppings).

Although there are fluctuations in the presence of the pest species over the six months (Figure 4.6), sample collection date was not a significant predictor, with the exception of *Nezara viridula* (Green vegetable bug) presence, which is only detected in April (Table 4.3).

Table 4.3: Summarised results of each GLM investigating the influence of the fixed effect of sample date on the presence of each crop pest in the diet of *Mops nigeriae*.

Pest species	Estimate	SE	z value	p value
<i>C. acuta</i>	0.02056	0.01503	1.368	0.171
<i>E. biplaga</i>	0.06077	0.00179	0.003	0.997
<i>E. ceratoniae</i>	-0.01643	0.01179	-1.394	0.163
<i>M. poeyalis</i>	-0.01446	0.01304	-1.109	0.267
<i>M. trapezalis</i>	-0.01978	0.01788	-1.106	0.269
<i>M. vitrata</i>	0.02704	0.01536	1.761	0.078
<i>N. viridula</i>	0.00227	0.00975	2.324	0.020
<i>R. padi</i>	-0.55480	0.01737	-0.003	0.997
<i>S. recurvalis</i>	-0.00607	0.01403	-0.433	0.665
<i>T. orichalcea</i>	-0.00772	0.006924	-1.115	0.265
<i>T. absoluta</i>	-0.01958	0.02512	-0.779	0.436

4.5. Discussion

Functional groups of bats explored by this study show some overlaps in dietary niche with regard to arthropod prey, as measured using Pianka's index. Similarly to other studies, such as Brazilian bats (Kruszynski et al., 2022), open aerial bats in this study present the highest dietary niche breadth as measured by Levin's index, indicating a range of arthropod species being consumed. Nevertheless, in this study, open aerial niche breadth was very similar to edge aerial bats, indicating that both are generalist predator functional groups, also with less resource partitioning in terms of prey consumed. This is unexpected given that functional groups are categorised by differing utilisation of different foraging spaces which are likely to accommodate different arthropod assemblages, although they both use the aerial foraging mode (Schnitzler and Kalko, 2001; Denzinger and Schnitzler, 2013). Schoeman and Jacobs (2011) also demonstrated that dietary overlap in species assemblages in South Africa was relatively high, although it was usually higher within functional groups than within ensembles. Narrow passive bats have a lower dietary niche breadth than either open or edge aerial bats, indicating that they are more specialist predators. As there is less overlap in diet between narrow passive and both edge and open aerial bats, there is also clear partitioning in

terms of dietary niche as expected. It is important to note however that the number dropping samples and number of species studied within each functional group differed, ranging from only two species in the narrow passive group to eight in the edge aerial group, and this could have influenced the niche width and overlap values. This was unavoidable in this study given the unpredictability and bias introduced by mist net trapping surveys and roost detections, however future study on dietary partitioning between species within functional groups will give better insight into predator-prey interactions in agricultural landscapes.

The diets of open aerial species indicates overall dominance of Blattodea and Coleoptera. Blattodea was also dominant in the diets of *C. pumilus* in Tanzania using microscope analysis of droppings (Aspetsberger et al., 2003). In Eswatini however, Molossids in this functional group, studied by Bohmann et al. (2011) using molecular techniques, showed a dominance of Lepidopteran prey. Dietary analysis of the open aerial species *M. nigeriae* in this study however indicates that for January to May the species-specific diet is dominated by Lepidopteran prey. This coincides with the sample collection timing (April and May) of Bohmann et al. (2011) whereas the droppings used for the functional group analysis in the present study were collected from November to March.

Edge aerial functional group diet was found to be dominated by Coleoptera and Diptera in this study. In species-specific dietary analysis of edge aerial species in other studies, Lepidopteran prey have been more dominant in these species e.g. *P. hesperidus* (n=3) and *S. dinganii* (n=2) in South Africa (Taylor et al., 2017), *A. nana* (n=1) and *S. dinganii* (n=1) in Rwanda (Nsengimana et al., 2023) although sample sizes for these studies were relatively low.

In this study, the narrow passive diet is clearly dominated by Lepidoptera (POO = 36%) which has been found in narrow passive *Nycteris* species in agricultural landscapes South Africa using molecular methods (Taylor et al., 2017). In contrast, in Rwanda, a single dropping from a *Nycteris* captured from a cave in an agricultural landscape contained a single Orthoptera species (Nsengimana et al., 2023). However, seasonal fluctuations in dietary composition has been recorded using analysis of culled parts collected from a roost in a South African national park, with Lepidoptera, Orthoptera and Hemiptera dominating at different

times of year (Seamark and Bogdanowicz, 2002). An older study at a cave site in Zambia looking at the stomach contents of three *Nycteris* species indicates species specific dietary differences (Findley and Black, 1983).

These species-specific, spatial and temporal differences demonstrated within and between all functional groups of bats in African studies highlights the lack of consistency and so variables influencing species-specific diets across species ranges and seasonally requires further exploration.

This study has highlighted the presence of 16 important agricultural pests in the diet of bats in these Afrotropical agricultural landscapes. Although other studies have reported much higher numbers of pest species detected in bat diet elsewhere, such as 173 agricultural pest species recorded in the diet of just four bat species in China (Zhu et al., 2024), this study has sampled from landscapes where pesticides are routinely used and has focused on crop pests present at Relative Read Abundance (RRA) of more than 1%. It is likely therefore that there are many other crop pests present in smaller quantities which are not highlighted here, as was revealed in a study on the diet of *Plecotus auritus* which compared molecular dietary analyses methods (Andriollo et al., 2019). There is also the possibility of insect taxonomic bias and misidentifications due to the quality and coverage of the reference library as there has been little work done across Africa to assess consistency between morphological and barcoding identifications (Salis et al., 2024). In addition, there are many OTUs for which identifications were inconclusive which is likely due to the lack of barcoded specimens covering the Arthropod diversity of the region. This has been encountered by other African studies on bat diet (e.g. Bohmann et al., 2011). There are locally important pest species that have not been barcoded as yet, such as *Gonocephalum simplex* (Dusky surface beetle) and so many pest species have been potentially missed.

Whilst there is some overlap between crop pests eaten by open and edge functional groups, there is almost none between these groups and narrow passive bats. For example, *Spodoptera frugiperda* (Fall armyworm), an accidentally introduced pest to the region recently (Kenis et al., 2023), was only found in the diet of the *Nycteris* species in this study. The presence of *S. frugiperda* in bat diet has been investigated in China where FOO was also found to be higher

in some bat species than others (Liu et al., 2023). This highlights the importance of maintaining populations of a diverse range of bats species to allow maintenance of pest control services for a range of crop pests. Higher diversity in bats has also been shown to be associated with reduced presence of the pine processionary moth, with key predators of this pest being forest adapted specialists in Lepidopteran predation (Augusto et al., 2024). This scenario is mirrored in this study; *Nycteris* species are known to be well adapted to cluttered environments, and we found a dominance of Lepidoptera prey in the diet, with the moth pest *Thysanoplusia orichalcea* in particular being detected in 40.7% of droppings. The findings support the ‘insurance hypothesis’ that suggests that increasing biodiversity protects against losses in ecological functions incurred by species loss, by increasing the likelihood that they can be provided by other species in an assemblage (Yachi and Loreau, 1999). A previous morphological study investigating the diet of *Nycteris* species in Zambia have reported the presence of larval Lepidoptera, indicating the importance of this functional group as a gleaner, able to catch prey directly from the surface of vegetation (Findley and Black, 1983). The findings of [Chapter 3](#) of this thesis highlight that narrow passive bat species were not recorded in these agricultural landscapes despite their presence being confirmed by roosting and trapped bats [Chapter 2](#). This could be due to the acoustic sampling method, as these species are known to have particularly quiet echolocation calls which are difficult to detect using the zero-crossing bat detectors used (Monadjem et al., 2017) or could also be due to reduced populations of this species. Further study needs to clarify the population status of species in this functional group which clearly have a potential role to play in the predation of particular crop pest species.

There is a clear seasonal change in prey consumption by *Mops nigeriae* (Nigerian free-tailed bat) with regard to insect orders, which could follow prey availability as demonstrated here by increased Hymenoptera consumption during December in comparison to other months. This coincides with the timing of emergence of alates of ant species in response to the beginning of the rain season becoming more abundant and accessible prey as they fly. There is also a clear peak in the presence of the species *Nezara viridula* (Green vegetable bug) in the diet in April, which could be related to the pest’s phenology or disturbance by harvesting causing flight. However, despite some insect order and species trends are evident, seasonality is less clear with regard to the full suit of prey items indicated by OTUs. There is niche

overlap between some months in the study period, but the first (December) and last (May) months show most difference in dietary composition for this species. These findings emphasise the need to monitor diet over time and extending over the whole year to gather a wider understanding of a species' dietary niche and also potential pest consumption.

Mops nigeriae diet is clearly dominated by Lepidoptera for the majority of the six-month monitoring period, whereas the open aerial functional group indicates a dominance of Blattodea and Coleoptera. This could be as a result of sampling times for most species being around the time of emergence of alate termite species or hatching beetles, when these prey items may become more abundant and accessible. *M. nigeriae* roost dropping sampling continued after this time. Alternatively, it could be a result of resource partitioning between open aerial species. One study in Eswatini on the diets of *Mops condylurus* and *M. pumilus* indicated that these species do not show resource partitioning (Bohmann et al., 2011). However, the findings regarding the inconsistencies between the open aerial foraging group diet as a whole and that of member species *M. nigeriae*, highlight the importance of investigating these species-specific diets and not being reliant on functional group assumptions of dietary niche similarities.

Future studies should investigate dietary resource partitioning between species in Afrotropical landscapes, and also within species, such as partitioning between males and females who may have differing nutritional requirements and paired with studies on other aspects of ecology and behaviour, to allow for accurate conservation action and prioritisation (Clare and Oelbaum, 2023). Bat diet studies should also simultaneously collect data on prey availability to compare to quantifiable dietary measures (such as POO and FOO) so as to more clearly understand prey preference and temporal and spatial changes in diet within a bat species.

Chapter 5. Insect prey available to bats is similar across commercial arable habitats in an Afrotropical context

5.1. Abstract

The balance between agricultural production and conservation of biodiversity is a contemporary dilemma which cannot be solved without an understanding of agroecological processes. One growing threat to crop production is the impact of crop pests, which has driven an increase in pesticide use. This increase has had detrimental effects on biodiversity by indiscriminate use of broad spectrum and persistent agrochemical use. Integrative pest management (IPM) strategies involving natural predators of crop pests has received more attention in the search for ways to reduce the negative effects of agrochemicals on the environment and human health. However, the top-down role played by natural predators requires an understanding of the distributions and abundance of potential prey species. Bats are known to play a role in insect suppression in agricultural landscapes from studies conducted across the globe, however it is still unclear whether some crops may benefit more than others from these protection services within the same landscapes and so influence management strategies to maximise natural pest predation. Research on bats in commercial agricultural landscapes in Zambia, an Afrotropical country dominated by Miombo woodland, has shown that the activity of bats of the most commonly recorded functional groups over three main crops (maize, soya and tobacco) was similar and was not driven by overall insect abundance. Prey items were also identified through dietary analysis. To determine whether there is any association between potential prey and particular crop types, we used light traps to catch insects and explored the influence of crop type on the abundance of Lepidoptera, Coleoptera and Hemiptera. In addition, influences on the abundance of two more commonly caught crop pest species, *Anomala* sp (leaf chafer beetle) and *Thysanoplusia orichalcea* (slender burnished brass moth) were explored. There were no significant associations between either the abundance of the insect orders or the two crop pests with crop type, apart from slightly higher abundance of *T. orichalcea* in tobacco. Although impacts of these insect taxon on the individual crops may differ, this finding indicates that their suppression by bats is relevant across the farming landscape and reiterates a need for landscape scale conservation farming practices to encourage generalist foraging by bat species as part of integrative pest control strategies.

5.2. Introduction

It is well established that biodiversity is not only intrinsically important, but is also essential for maintaining healthy ecosystems (Ehrlich and Mooney, 1983). Although the value of nature has in the past been largely overlooked, ecosystem services to humans are now being increasingly acknowledged (Perrings et al., 2009; Farley and Voinov, 2016). Humans currently consume natural resources at an unsustainable level and having recognised this, organisations and governments have started to focus on finding more efficient and sustainable ways to feed the world's population, such as with the implementation of the 2015 International Development Goals and 2030 UN Agenda for Sustainable Development (*A Better World for All*, 2000; FAO et al., 2015; United Nations General Assembly, 2015).

Due to the complicated interactions in ecology and the need to take into account open access natural resources, there has been limited data with which to accurately assess ecological thresholds and provide economic valuations of ecosystem services that can be applied in practice (Farley and Voinov, 2016). Agricultural landscapes benefit from ecosystem services such as soil maintenance, nutrient cycling, water management, pollination and insect pest suppression. Agriculture however, is seen as one of the largest drivers of habitat loss and loss of biodiversity (Vorlaufer et al., 2017). The dilemma is how to maintain or increase agricultural productivity without jeopardizing the ecosystem services required for sustainability.

The expansion of monoculture agriculture, combined with favourable climatic conditions result in rapid population growth for insects that are well suited to feeding on particular crops (Andow, 1983; Prinsloo and Vivienne, 2015). Damage by arthropod pests is a particular issue for farmers and accounts for around 18% crop destruction worldwide (Oerke, 2006).

Agrochemicals are commonly used to combat these (Oerke, 2006; Sparks and Lorschbach, 2017). Despite the increased use of pesticides since the 1960s however, the proportion of crop loss have not decreased, which could be in part due to evolved resistance in pests and inefficient or mis-application of agrochemicals (Oerke, 2006). Pesticide use is also known to be a significant contributor to biodiversity loss, through use of broad spectrum and persistent

chemicals affecting non-target species, as well as bioaccumulation affecting species at higher trophic levels (Pimentel, 2005; Dudley et al., 2017).

There is also a growing threat of importing invasive pest species, for example 36% of plant imports into South Africa between 2015 and 2019 contained at least one arthropod (Saccaggi et al., 2022). There have been significant accidental introductions of crop pests throughout Africa recently such as: *Tuta absoluta* (Tomato leaf miner) in 2014, impacting tomato crops (Abass et al., 2019; Mwamba et al., 2022) and *Spodoptera frugiperda* (Fall Armyworm) in 2016, which feeds on a range of crops but has become particularly important in maize (Day et al., 2017; Kenis et al., 2023). Both serve to illustrate the potential impacts on yields of economically important crops.

The populations and impacts of crop pests may vary within a cropped area and could also depend upon the surrounding landscape. Damage in maize by *S. frugiperda* for example has been shown to be higher further from forest edges (Clarkson et al., 2022). Stink bug abundance in soya was shown to also increase with distance to woodland (González et al., 2017). In contrast, in another study, damage by soyabean herbivores was shown to be higher closest to forests, with higher numbers of aphids noted per plant, despite also having higher numbers of aphid predators (Mitchell et al., 2014). There is also evidence for example, that responses to cropped area size is highly variable, with many pest species being unaffected by field size (Rosenheim et al., 2022).

Insect species assemblages may also depend on the crop grown but can be highly context specific. For example, tobacco insect communities were dominated by Coleoptera and Hemiptera in Central Java (Wiranto and Sumarmi, 2022). Coleoptera also dominated maize crops in Mexico (del-Val et al., 2021) whereas, the dominant taxonomic groups of insects recorded in maize in Indonesia were Hymenoptera, Diptera and Hemiptera (Suliansyah et al., 2022). However, in maize crops in India, higher insect pest species richness was found for Lepidoptera pests, than for other pest orders (Mallesh et al., 2023). A study on maize crops showed that increased proportions of highly managed orchards in a Spanish agricultural landscape, were associated with a higher abundance of herbivorous homopterans and lower abundance of predators (Clemente-Orta et al., 2020). Farms with larger proportions of alfalfa

were associated with both higher aphid abundance, and also their predators (Clemente-Orta et al., 2020).

With crop pests being an ever increasing threat to crop production and harmful effects of pesticides becoming apparent, many insect pest control studies have turned to ecosystem services provided by natural predators as part of Integrated Pest Management (IPM) strategies to reduce pest eruptions (Clark and Yamaguchi, 2001; Dudley et al., 2017). Many have focussed on Arthropod natural predators (Bashir et al., 2023), however, there is a growing recognition of the insect pest suppression roles played by vertebrates such as birds and bats (Sivault et al., 2024). The relative contributions to pest control by birds and bats can vary depending on geographical location, season and management (Maas et al., 2016).

Bat species have been reported to consume a wide range of pest arthropods in agricultural landscapes (Maas et al., 2016; Tuneu-Corral et al., 2023). In particular, Lepidopteran pest species have been highlighted in bat diets (Riccucci and Lanza, 2014; Kemp et al., 2018; Weier et al., 2019; Zhu et al., 2024). Many studies also show relatively high levels of Coleopteran and Hemipteran pest species, such as in maize and soya dominated agricultural landscapes (Whitby et al., 2020). Seasonal increases in the presence of Coleopteran sugarcane pest *Anomala albopilosa* was noted in *Hipposideros turpis* in Japan (Fukui et al., 2009). Hemipteran pests in South Africa, such as the polyphagous stink bug *Nezara viridula*, have been shown to be present in bat diets in macadamia orchards, with ongoing and long term research in these landscapes providing evidence for economically important levels of suppression (Taylor et al., 2017, 2018; Kemp et al., 2018; Weier et al., 2019).

There is evidence that monitoring of the gregarious Lepidopteran pest *Spodoptera frugiperda* (Fall armyworm) in cereals through bat dropping analysis can result in earlier detection of this crop pest than other conventional pest surveillance methods (Liu et al., 2023). However, this ‘Chirosurveillance’ method has been shown to have limited application in insect pest control monitoring tool in a mixed agricultural landscape as it resulted in lower detectability of pests in comparison to conventional monitoring methods. (Maslo et al., 2022).

Commercial agriculture (production for sale or profit) in the Zambian context is characterised by farmland of over 100ha, utilising mechanisation and usually with irrigation systems in place, such as centre pivot irrigation (CIAT and World Bank, 2017). Zambia has experienced an overall trend of decreasing rainfall in recent decades and this is predicted to continue in future climate change scenarios (Hamududu and Ngoma, 2020; Chisanga et al., 2023). Areas of suitable habitat for some pest species within the country is predicted to increase in future climate scenarios e.g. *Spodoptera frugiperda* and *Maruca vitrata* (Nguru and Mwongera, 2023). Although irrigation may help to mitigate the effects of reduced rainfall on production for commercial farms it could exacerbate impacts of pest outbreaks by range expansion (Wang et al., 2023). Given the mounting evidence of pest consumption and suppression by bats globally, and the presence of crop pests in the diets of Zambian bats demonstrated in [Chapter 4](#), it is clear that the conservation of bats within agricultural landscapes in this context should be encouraged. It provides evidence for relatively high levels of consumption of insects in the orders Lepidoptera, Coleoptera, Diptera and Hemiptera by bats in the agricultural landscape in which this study is set. Lepidopteran, Coleopteran and Hemipteran pests are particularly economically important (Prinsloo and Vivienne, 2015).

Despite the need to develop integrative pest management strategies involving natural predators, it is unclear from the literature if the pest suppression benefits apply equally distributed to all crops.

For this study, I aimed to understand insect order assemblage and pest associations with three main crop types: maize, soya and tobacco. Firstly, at a broader level, I examined whether there is an association between crop and three insect orders commonly found in insectivorous bat diets, which also contain significant crop pest species (Lepidoptera, Coleoptera and Hemiptera). Then I explored the associations between crop type and crop pest species that are consumed by bats in these landscapes. As Chapter 3 indicates that bat activity is not influenced by crop type and is actually similar between semi-natural and cropped areas, this would imply that the crops have similar prey availability for the functional groups studied.

5.3. Materials & Methods

Three established commercial agricultural areas across two agro-ecological zones within Zambia were chosen for this study (**Error! Reference source not found.**) which take into account rainfall and soil type (Mukosha and Siampale, 2009). A selection of farms in the three agricultural areas (total n = 29 farms) was based on size and scale of production, including only those defined as mechanised farms, producing maize, soya or tobacco for commercial sale. To ensure statistical independence, farms were separated by a minimum of 2km. The data from these farms were also included in the study on bat activity in [Chapter 3](#) (see Figure 3.1 for the map of farms & Figure 3.4 for example farm survey locations), with one of the initially selected farms missing the insect collection data, due to human error, as samples were missing during fieldwork travel. Here the focus of the data analysis was the insect taxa variability across crop type.

Surveys were conducted at 69 field locations with the aim of surveying each of the different crops on each farm, however this was not always possible due to availability of fields which resulted in disproportionate numbers of fields of each crop type (Figure 5.1). Although field sizes were variable (6-78ha), most were 50ha centre pivot irrigated fields (approximately 800m in diameter) throughout the study. There were up to three crop field locations sampled at each farm. Surveys were conducted during three cropping seasons (November to March) between 2016 and 2019 and were repeated at each location within a few days of each other where possible, resulting in a total of 117 surveys (maize = 42, Soya = 47, Tobacco = 28) as 21 locations could not be repeated due to adverse weather conditions or equipment failure.

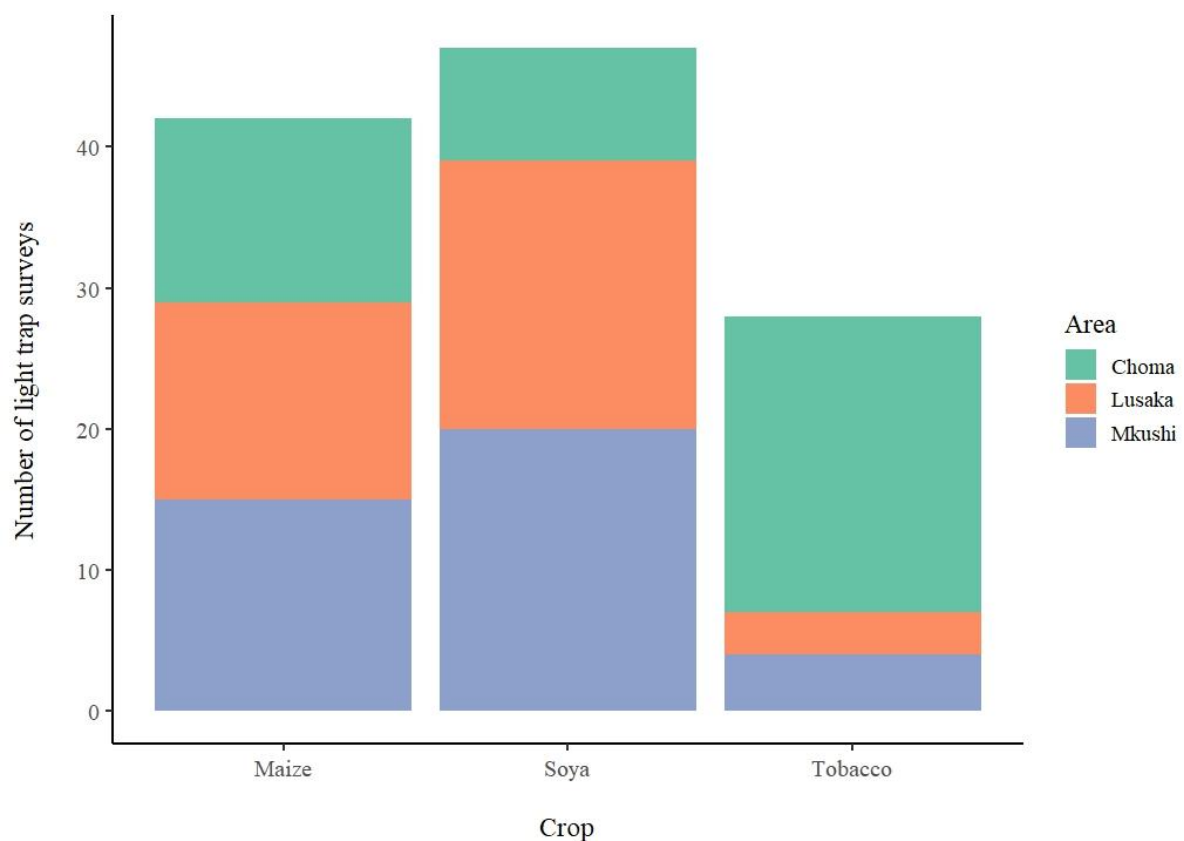


Figure 5.1: Numbers of light trap surveys conducted in different crop types across the three commercial farming areas (indicated by colour).

For each light trap location, the crop type was recorded. Google Earth Engine (GEE) (Gorelick et al., 2017) was used to source satellite imagery for woodland cover and Normalized Difference Vegetation Index (NDVI) data; remote sensing layers were imported into QGIS Desktop version 3.28.1 (QGIS.org) for further analysis. Global Forest Canopy Height layers (Potapov et al., 2021) were used to map mature woodland areas of over 0.5ha with trees of 5m and above in height, and to calculate the distance of woodland edge to trap locations and the proportion of woodland cover in transect buffers. Composite median NDVI maps were generated using GEE from Landsat-8 Level 2, Collection 2, Tier 1 image collection, courtesy of the U.S. Geological Survey, after masking cloud cover for each season running from November through to the end of March, from 2016 to 2019. The mean of the composite NDVI was calculated for a 50m buffer around trap locations and used as a local vegetation measure.

5.3.1. Arthropod sampling

Arthropods were captured using heath light traps (6W actinic bulbs) mounted at a height of around 2.5m to minimise light obstruction by the tallest crops (Figure 5.2). Crop type (maize, soya, tobacco) of the light traps were recorded during surveys. The lights were timed to switch on at each survey location from half an hour after sunset for three hours simultaneously. Following sampling, ethyl acetate was used to euthanize the insects and traps were kept closed overnight. Insects were then stored in ethanol and were counted and identified to order. As the main concern for this study is for agriculturally important insect pests with the potential of consumption by bats, Lepidoptera, Coleoptera and Hemiptera were chosen as focal taxa for this study.



Figure 5.2: Light traps were consistently erected at a height of approximately 2.5m so that the light was above the highest crop (photo courtesy of David Lee).

Crop pests were identified where possible using a list of species known to be significant crop pests for maize, soya and tobacco in Zambia collated using Prinsloo & Vivienne (2015) with the addition of possible more recent introductions, such as *Spodoptera frugiperda* (Fall

armyworm) checked for pest status using Centre for Agriculture and Bioscience International (CABI) datasheets (CABI, 2024).

5.3.2. Statistical analysis

I performed GLMMs, to determine whether the abundance of three insect orders (Lepidoptera, Coleoptera and Hemiptera) varies between crop type. GLMMs were also conducted for two known crop pests *Anomala* sp (Coleoptera) and *Thysanoplusia orichalcea* (Lepidoptera) caught in light traps that are also found to be consumed by bats ([Chapter 4](#)), to determine whether they were associated with crop type. Due to the repeat surveys at each location and multiple light traps on each farm, the farm and location of the trap within the farm were applied as nested random effects. Vegetation characteristics (NDVI and distance to the nearest woodland) were also included as predictors as well as latitude, Julian date and temperature. Statistical analyses were performed using R 4.2.2 (R Core Team, 2023) through RStudio 2023.06.1+524 (Posit team, 2023). After scaling the selected numeric predictor variables to enable comparisons, we used the ‘glmmTMB’ function of the ‘glmmTMB’ package (Brooks et al., 2017) (assuming negative binomial distribution with zero inflation where appropriate) to determine variables with significant effects. Residual diagnostics were carried out using the ‘DHARMA’ package (Hartig, 2022) to verify model assumptions and no problems were detected with any of the models.

5.4. Results

The total number of insects collected was 351 084, the majority of which were Coleoptera (71%), followed by Hemiptera (19%), Diptera (4%) and Lepidoptera (3%) (Figure 5.3).

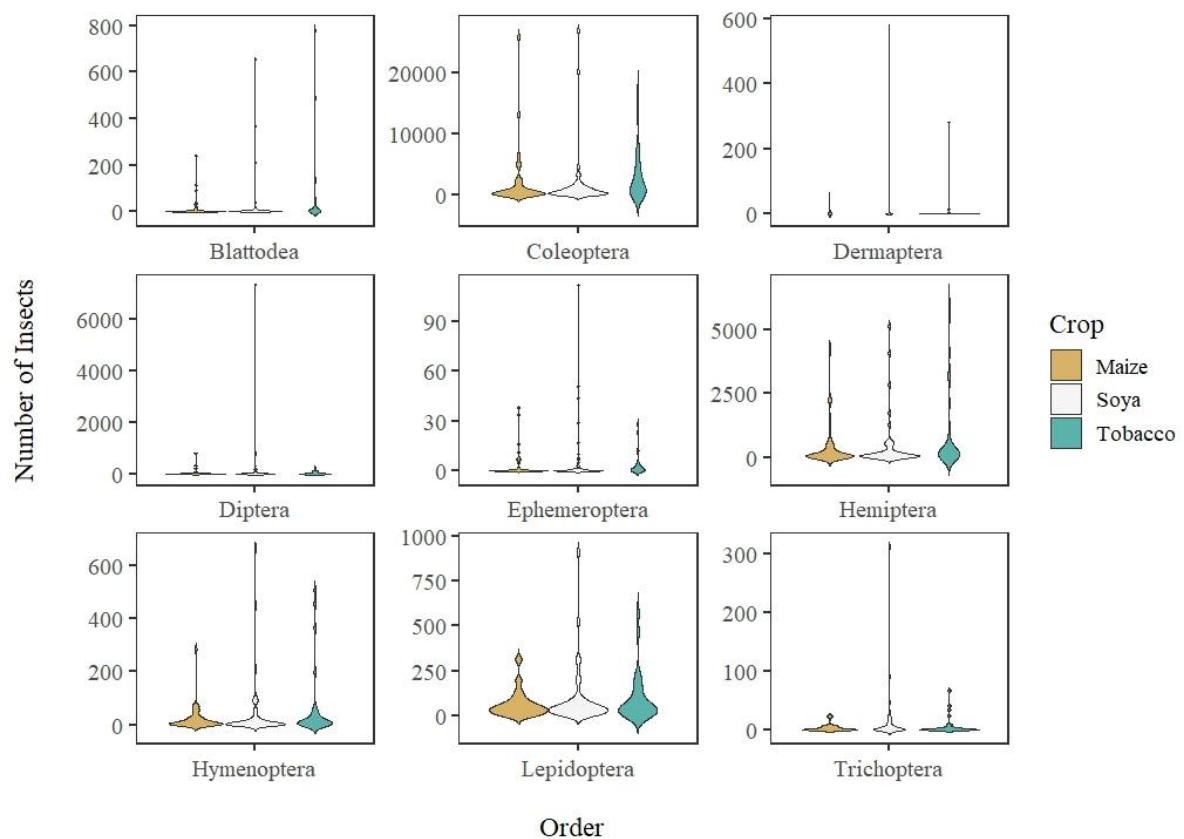


Figure 5.3: The abundance of insects of different orders in each trap shown as kernel probability density violin plots in different crops (indicated by colour)

The abundances of Coleoptera, Lepidoptera and Hemiptera were similar across crop types (Table 5.1). In addition, there is also no influence of NDVI or the distance to woodland for any of these orders (Table 5.1). There were higher abundances of Coleoptera and Hemiptera at the more southerly locations (lower latitudes), and Coleoptera numbers were higher during the last cropping period (2018-19) as indicated by Julian date (Table 5.1).

Table 5.1: Summarised results of GLMMs with the abundance of insect orders as response variables and with Farm and Location as random effects. Significant p values (p<0.05) are in bold.

Fixed effects	<u>Coleoptera</u>			<u>Lepidoptera</u>			<u>Hemiptera</u>		
	exp(Beta)	SE ^I	p-value	exp(Beta)	SE ^I	p-value	exp(Beta)	SE ^I	p-value
Crop comparisons									
<i>Maize - Soya</i>	1.32	0.412	0.38	1.13	0.325	0.67	1.36	0.489	0.40
<i>Maize - Tobacco</i>	1.63	0.594	0.18	1.79	0.590	0.08	1.66	0.658	0.20
<i>Soya - Tobacco</i>	1.23	0.485	0.59	1.58	0.58	0.21	1.22	0.519	0.64
NDVI	0.94	0.146	0.70	1.09	0.160	0.54	1.12	0.197	0.52
Woodland	1.13	0.216	0.53	1.11	0.225	0.60	1.21	0.264	0.39
Julian date	2.08	0.446	<0.001	1.09	0.186	0.49	0.93	0.216	0.76
Temperature	0.96	0.174	0.83	1.09	0.184	0.60	1.22	0.242	0.32
Latitude	0.51	0.121	0.005	0.95	0.227	0.84	0.38	0.098	<0.001
Intercept	6.56	0.26	<0.001	3.77	0.26	<0.001	5.57	0.30	<0.001

^I SE = Standard Error

The five most abundant pest species caught in the light traps (Figure 5.4) were three Coleoptera species (*Anomala* sp (n=665 in 46 traps (39%)), *Gonocephalum* sp.(n=2971 in 38 traps (32%)), *Heteronychus* sp.(n=135 in 28 traps (24%)) and two Lepidopteran species (*Omiodes indicate* (n=901 in 28 traps (24%)), *Thysanoplusia orichalcea* (n=91 in 30 traps (26%)).

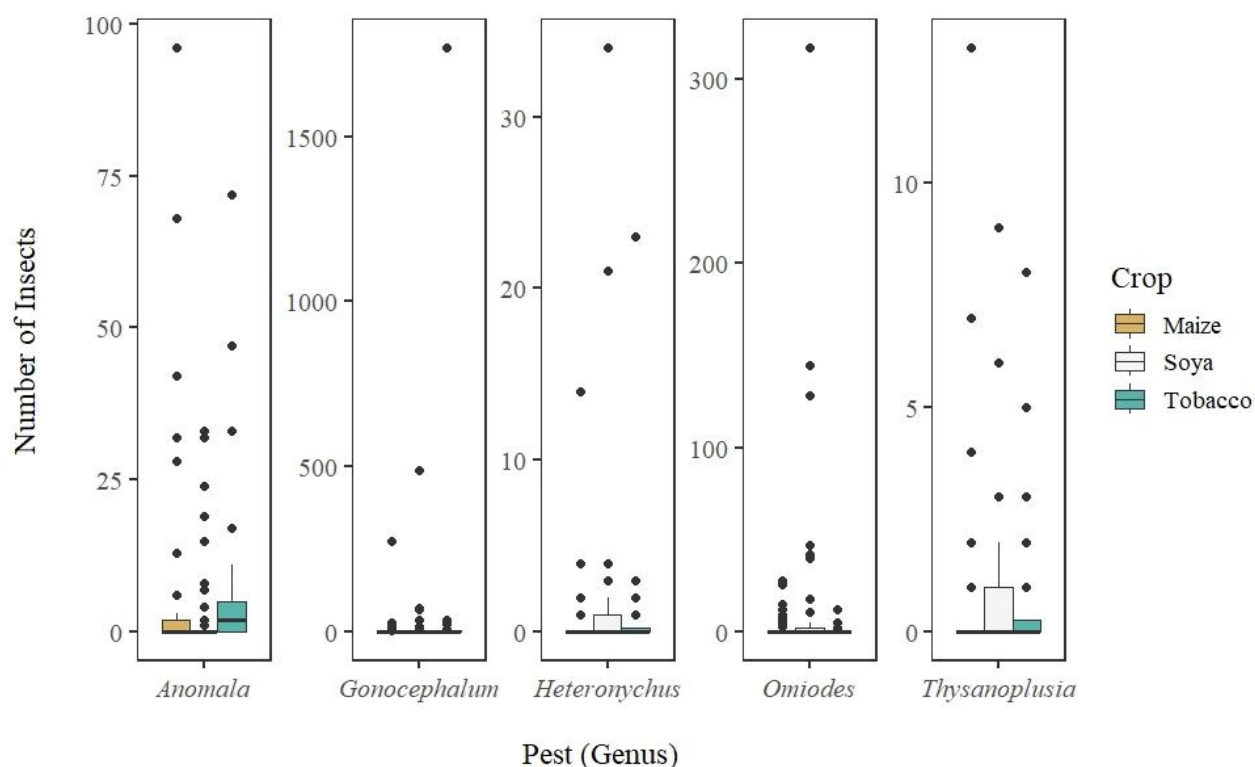


Figure 5.4: The abundance of five crop pests most commonly caught in each light trap (illustrated by boxplots with median line and interquartile range box (bottom line = 25% quartile (Q1); top line = 75% quartile (Q3))) in each crop type (indicated by colour). Whisker values are calculated as $Q1/Q3 \pm 1.5 \times \text{Inter Quartile Range (IQR)}$. Points represent outliers.

Anomala sp abundance was similar across crop types, but *T. orichalcea* was sampled in higher abundances in tobacco fields than in soya (Table 5.2, Figure 5.5).

Table 5.2: GLMM results summary for the two pest species caught in the light traps that are also consumed by bats (Ch4) with Farm and Location as random effects – *Anomala* is a chafer beetle and *Thysanoplusia* is a Noctuid moth – significant p values ($p < 0.05$) are in bold

Fixed effects	<i>Anomala</i>			<i>Thysanoplusia</i>		
	exp(Beta)	SE ¹	p-value	exp(Beta)	SE ¹	p-value
Crop comparisons						
<i>Maize - Soya</i>	0.96	0.528	0.95	0.73	0.426	0.59
<i>Maize - Tobacco</i>	0.58	0.359	0.38	3.24	2.56	0.14
<i>Soya - Tobacco</i>	0.61	0.429	0.48	4.47	1.81	<0.001
NDVI	0.34	0.103	<0.001	2.05	0.646	0.02
Woodland	0.85	0.290	0.64	2.13	0.615	0.01
Julian	1.73	0.901	0.29	0.73	0.242	0.34
Temperature	0.45	0.163	0.03	1.37	0.330	0.19
Latitude	0.15	0.086	<0.001	5.63	1.99	<0.001
Intercept	0.03	0.066	0.27	0.00	0.00	<0.001

¹ SE = Standard Error

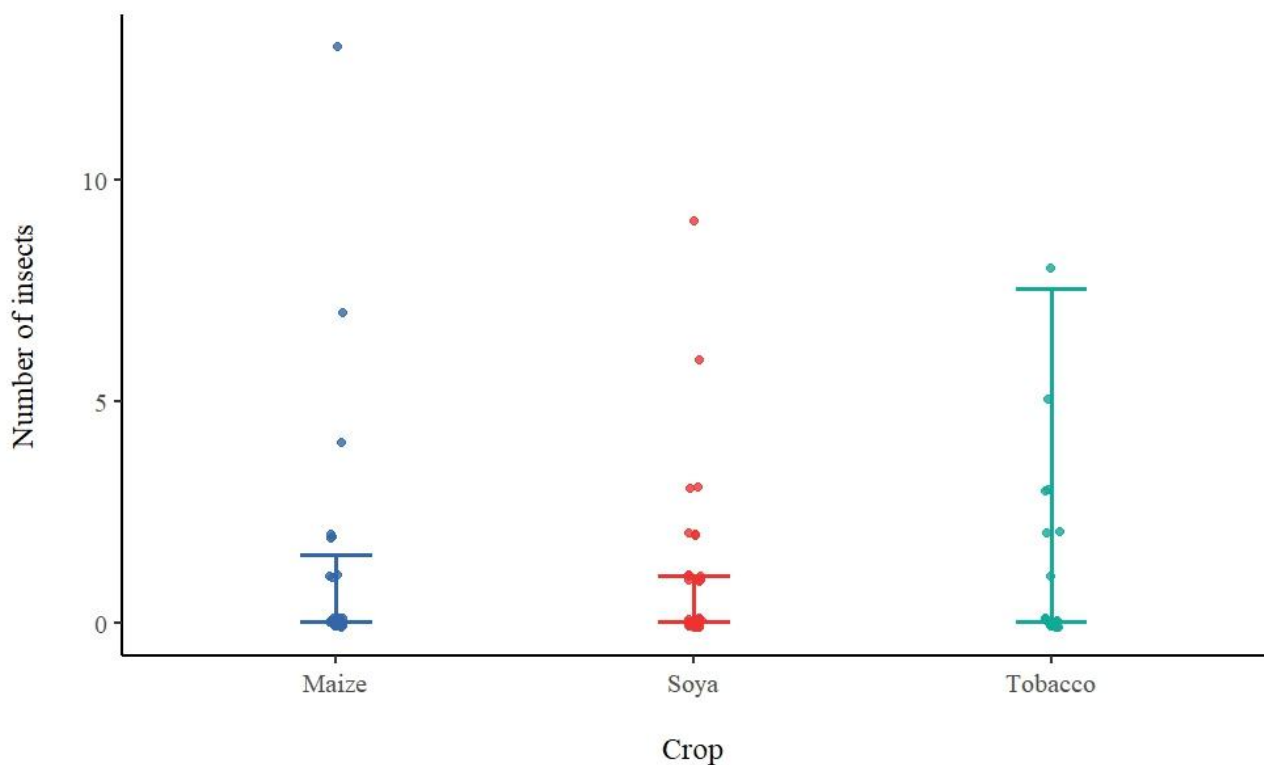


Figure 5.5: *Thysanoplusia orichalcia* abundance (points) in each light trap across the three crop types with bars indicating GLMM estimates with 95% confidence intervals.

5.5. Discussion

This study demonstrates that the abundance of insect orders Lepidoptera, Coleoptera and Hemiptera, consumed by bats in this landscape ([Chapter 4](#)), and also known to contain significant crop pests for the region (Prinsloo and Vivienne, 2015), are similar across maize, soya and tobacco crops. This indicates that although the impacts of these insect taxon may differ between crops and was not explored here, the approaches to management strategies to increase bat activity in these types of agricultural landscapes with the aim of encouraging natural predation of crop pests are relevant, regardless of which of these three crops is grown.

The leaf chafer beetle, *Anomala* sp. was similar in abundance across crop types. The species closest in morphological identification to the specimens collected is *A. ustulata*, which is known to be associated with maize root damage by their white grubs (Prinsloo and Vivienne, 2015). However, the sequences for *Anomala* in bat diet could only be confirmed to genus ([Chapter 4](#)), despite several

species having been genetically barcoded, including *A. ustulata* indicating a significant regional differences or a different morphologically similar species as yet to be barcoded. Further research should be conducted to confirm species identification and to barcode specimens. This would help with genetic approaches to the surveillance of this species. Higher numbers of *T. orichalcea* were found in tobacco, followed by maize and then soya crops. Although this species is consumed by three functional groups of bats, the highest consumption was by *Nycteris* (narrow passive functional group) ([Chapter 4](#)). Targeted management strategies to increase populations and activity of this functional group are therefore relevant across the three crops to encourage natural predation of this pest species.

This study used light trapping to target nocturnal insect taxon known to be consumed by bats, however, it is limited to trapping insects that are also attracted to light. Many species will not be active at night at all and will not have been sampled in the light traps. There is also evidence that different wavelengths of light may be more attractive than others for some insects, such as the Lepidopteran armyworm pest *S. frugiperda* being most attracted to blue light compared to UV or green (Yang et al., 2024). This introduces bias towards sampling of nocturnal insects and those attracted to the wavelengths of light used in the study. For example, one study conducted in Pakistan making comparisons between arthropod pest monitoring methods has noted the specificity of light traps compared to other methods (Murtaza et al., 2019). As such, it can be particularly useful when monitoring specific pests, such as the Brown planthopper (Bookeri et al., 2021). Interestingly, studies using light traps to understand broader insect assemblages, and even pests, in crops, could not be found in the peer-reviewed literature with which to make comparisons. The dominant insect orders in relation to crops in this agricultural landscape are difficult to compare directly with studies with similar objectives conducted elsewhere, as these use alternative methodology, such as direct observational counts, pitfall traps, yellow traps and modified vacuums. Nevertheless, there are similar findings to this study, for example, the most common insect order in tobacco in Central Java (Wiranto and Sumarmi, 2022) and on maize in Mexico (del-Val et al., 2021) is Coleoptera. Future studies could use multiple insect sampling methods to compare insect assemblages in this context.

The similarity of the abundances of insect orders and pests considered here may be due to the fact that fields of the different crops are often found on the same farm. With these relatively mobile

insect taxa able to move to alternative crop hosts or even in surrounding seminatural habitats, variability may not be as clear as if there were larger distances between the fields of different crop types. Although larger areas farmed for single crops may have yielded different results, the sites included in this study are representative of commercial production systems in Zambia.

As vegetation characteristics appear to have no influence on the insect orders or the two crop pests, manipulating habitat surrounding fields may not greatly affect the insects present. More detailed study may identify insect families or species that are more sensitive to surrounding vegetation. Southerly locations however, did yield higher numbers of Coleoptera, which is where there was also higher activity of edge aerial bats ([Chapter 3](#)). As the diet of this functional group is made up a relatively large proportion of Coleoptera ([Chapter 4](#)), the relationship between latitude, edge aerial bats and Coleoptera should be explored further to determine driving factors.

In conclusion, with little variation across the three crops in the abundance of Coleoptera, Lepidoptera and Hemiptera as well as the two crop pests studied, it is likely that management to encourage of bats as natural predators is equally beneficial to maize, soya and tobacco cultivation. The recommendations from Chapter 3 can therefore be incorporated into IPM strategies across commercial farms cultivating these crops in Zambia.

Chapter 6. General Discussion

During this time of anthropogenic change, it is essential that we understand the dynamic impacts human activities, both the direct and indirect drivers, have on biodiversity, so that we can co-exist in ways that are not detrimental to the natural world or to human survival, health and wellbeing (IPBES, 2019; Department of Economic and Social Affairs of United Nation, 2022). The balance between maintaining agricultural productivity, whilst maximising ecosystem service provision such as pest control, through biodiversity conservation, relies on an understanding of the ecological functions of species assemblages and their relationship with environmental and biotic factors in habitats and landscapes (Landis et al., 2000; Karp et al., 2013). The diversity of bats, their provision of ecosystem services and their differing responses to anthropogenic change, make them a model taxa to monitor in agricultural landscapes (Jones et al., 2009; Park, 2015; Russo and Jones, 2015; Russo et al., 2021).

The overall aim of this research project was to investigate the role that bats play in the agricultural context in a country with limited information to refer to. This PhD thesis presents a firm foundation for future research in this field and contributes to our growing knowledge base on African bats and their ecological relationship with agricultural insect pests. This research project required a multidisciplinary approach, using traditional trapping and morphometrics, combined with bioacoustics and molecular techniques, to study both bats and their insect prey. Through this project I was able to develop the basis for an acoustic call library of Zambian bats, and expand our knowledge on the landscape use and prey of functional groups of bats persisting in commercial agricultural landscapes in this Afrotropical context.

6.1. The potential of Passive Acoustic Monitoring (PAM) for Zambian bats

The development of the first acoustic call library of this scale for Zambia outlined by [Chapter 2](#), is a significant step towards encouraging the use of this non-invasive methodology for studying bats across the region. As equipment and training becomes more accessible, it is envisaged that PAM can be a useful tool for monitoring echolocating bats and so there is a need for publicly available acoustic reference datasets for improving accuracy and increasing participation in the field of bioacoustics (Britzke et al., 2013; Gibb et al., 2019; Stephenson, 2020). There are only a few acoustic libraries that have been published for countries in the southern African region, and none for Zambia (Monadjem, 2005; Monadjem et al., 2007, 2010, 2017, 2020b; Taylor et al., 2012, 2013a).

This study showed that although different equipment was used for recording echolocation calls, we can still make direct comparisons, as there were no significant differences in the parameters used. This indicates that projects reliant on acoustic data collected from multiple sources using different equipment, such as community science projects, can pool these data for further analysis. However, clarification of this through statistical comparisons between acoustic parameters, such as those carried out in this study, should always be conducted.

Unfortunately, using PAM for bats is still limited by the ability to accurately differentiate between calls with similar acoustic parameters within a species assemblage (Russo et al., 2018) and this was demonstrated here. Nevertheless, this study also highlighted that differentiation between sonotypes, reflecting functional groups, can be a helpful starting point before attempting to identify species calls and there are also some species that show relatively accurate acoustic separation from other species using the Frequency of Maximum Power (FreqMaxPwr). This is in agreement with the similar global analysis conducted by Roemer et al. (2021). Some of the species which are absent from this call library have had echolocation calls recorded in other areas of their range (Monadjem et al., 2020b), however it is important to explore potential regional differences. To improve the future use of PAM for research on bats, efforts should now be made to obtain echolocation calls for species that are not currently included in the call library (such as *Taphozous* species, as well as additional *Nycteris* and *Myotis* species to increase the data on a broader range of sonotypes) and to increase sample sizes so that species with similar call parameters can be studied further to identify more subtle differences that could be used to differentiate them acoustically.

6.2. Similar bat foraging activity across landscape, with subtly different responses to woodland by functional groups

The findings of [Chapter 2](#) enabled acoustic investigation into the activity of different functional groups recorded using PAM. The relatively wide area over which the bat activity surveys were carried out in commercial agricultural areas across Zambia in [Chapter 3](#), allowed broad patterns to be identified, which are more generally applicable rather than site-specific. Activity was highest for two functional groups: open and edge aerial bats. The prevalence of these functional groups in agricultural landscapes has also been seen elsewhere in the southern African region, for example in

macadamia crop dominated farmland in South Africa (Weier et al., 2021) and in sugarcane growing areas of Eswatini (Mtsetfwa et al., 2018).

Narrow flutter and edge trawling bats were also detected in this study, but activity levels were too low for further analysis. Narrow passive species, such as *Nycteris* spp have been recorded in these landscapes, through trapping with mist nets and locating roosts ([Chapter 4](#)), however, they were not detected during these acoustic surveys. Acoustic detection using zero crossing recording, is known to be particularly low for these species (Monadjem et al., 2017). Future acoustic surveys should use full spectrum recording combined with alternative methods in order to better assess their activity and habitat use (Russo et al., 2018).

Interestingly, activity levels in general were very similar over cropped and semi-natural habitats for both of the functional groups. Open aerial bats did show slightly lower activity in woodland habitats and in landscapes with more woodland, but at the largest landscape scale, this effect was not seen. In contrast, edge aerial bat activity was highest in woodland habitat and the wider landscape showed no influence on activity. Differing responses to habitat features in agricultural landscapes, between these functional groups, has been reported elsewhere, although have often indicated more extreme responses (Pocock and Jennings, 2008; Weier et al., 2021; Ancillotto et al., 2023). It highlights the need to consider functional groups, and even species, separately rather than merging bats into a single group for research or conservation purposes. This is not only because responses to habitat characteristics may vary, but the influential scale may also (Shapiro et al., 2020). For example, although local habitat characteristics seem to be important for both functional groups, open aerial bat species, with higher dispersal rates show some influence of landscape scale. The apparently contrasting responses to woodland by the functional groups in this study has implications for habitat management strategies so as to balance the needs of each functional group within the agricultural landscape. Maintaining heterogeneity in the landscape is a management strategy to encourage bats for the promotion of pest suppression has been recommended by other studies globally (Tuneu-Corral et al., 2023). Further research into the movement ecology of individual bats in the landscape would provide more insight into foraging preferences and also other resource requirements of these species, such as roost structures and commuting routes. This study can be used to inform such research as it identifies species and areas of interest for which to target capture and tagging efforts.

Although the survey timing did influence bat activity for both functional groups, this appears to be as a result of differences between cropping period surveyed (November to March) rather than within a cropping period. This could be as a result of the latent effects of weather and climatic differences between rainy seasons. So although logistics dictated that these surveys were carried out over several years, future comparative studies should be carried out within a cropping period. Long-term monitoring should also be carried out to explore links with weather and climatic fluctuations.

6.3. What do bats eat?

Increased understanding of interactions between natural predators and insect prey species, can help to inform land managers of Integrated Pest Management (IPM) approaches to make best use of ecosystem services and reduce pesticide applications. A successful IPM strategy should make use of multiple suppressive tactics, simultaneously targeting multiple pests, and informed by monitoring of both pests and natural predators, alongside evidence-based thresholds for pesticide application (Ehler, 2006). The literature on the inclusion of bats in IPM schemes is severely limited (Tuneu-Corral et al., 2023). However, understanding the roles that bats can play in IPM can be aided by analysing the diets of insectivorous bats. Genetic metabarcoding is increasingly being used in dietary analysis for a range of species, including bats, due to the relatively rapid and accurate identifications of barcoded prey items (Zeale et al., 2011; Pompanon et al., 2012). Despite this, there is a distinct lack of molecular dietary studies in the Afrotropical realm (de Sousa et al., 2019). In [Chapter 4](#), this study genetically identified insect prey taxa in the diets of functional groups of bats found in agricultural landscapes. There were relatively high proportions of dietary components which could not be allocated to species, or even to Order, which implies that this study is not able to present complete dietary descriptions. This is probably due to many of the Arthropods in this part of Africa not having been genetically barcoded; unfortunately this is even the case for some agriculturally important crop pests, such as *Gonocephalum simplex*. Other studies on African bat diet have come across this limitation (Bohmann et al., 2011). Research and industry collaborations, as well as funding, are needed to enact an increase in entomological barcoding for the region, which is essential for more accurate descriptions of the diets of insectivorous animals.

Despite limited data on dietary analysis to species level, there were indications that Coleoptera are an important dietary component for all three functional groups that were studied. Diptera were also

important for edge aerial and Blattodea for open aerial species. Lepidopteran prey were present in lower proportions for open and edge aerial species than expected, given the findings of some previous species-specific studies (Bohmann et al., 2011; Taylor et al., 2017; Nsengimana et al., 2023). This study also found that diets of narrow passive bats contained the highest proportions of Lepidoptera which is indicated by previous studies on these species (Findley and Black, 1983; Taylor et al., 2017). However, direct comparisons with other dietary studies were not possible for any of species included here, as they did not use the same molecular Percentage of Occurrence (POO) measure to quantify prey by order (Findley and Black, 1983; Seamark and Bogdanowicz, 2002; Bohmann et al., 2011; Taylor et al., 2017). The dietary width for edge and open aerial species were highest, indicating generalist predators, and for narrow passive bats, the dietary width was much lower, indicating specialist predators. Dietary overlap was also highest between open and edge aerial species.

As demonstrated by many studies elsewhere (Tuneu-Corral et al., 2023), the dietary analysis also showed that bats in these landscapes eat crop pests and although some were consumed by all functional groups, others were restricted to the diets of one or two of these groups. The majority of the crop pests detected in the diet were Lepidopteran or Hemipteran pest species. Many of the pest species detected here have also been reported from bat diets elsewhere e.g. *Nezara viridula* (Taylor et al., 2017), *Ectomyelois ceratoniae* (Aizpurua et al., 2018; Schäckermann et al., 2022), *Spoladea recurvalis* (Aguar et al., 2021), *Thaumatotibia leucotreta* (Nsengimana et al., 2023) and *Spodoptera frugiperda* (Whitby et al., 2020; Hughes et al., 2021; Clarkson et al., 2022; Liu et al., 2023).

The analysis of *Mops nigeriae* diet over time emphasised three main findings. Firstly that dietary components do change over time, even at order level, and this is likely to be due to prey availability, indicating that this species can be opportunistic. Secondly, it indicates consistently high levels of Lepidopteran consumption (with the exception of higher levels of Hymenoptera in December) in contrast to the highest levels of Blattodea and Coleoptera shown by the open aerial functional group to which it belongs. This finding emphasises that in addition to exploring functional group diets as a whole, there is a need to conduct species-specific dietary analyses. Some species within functional groups may show similar prey preferences (Bohmann et al., 2011). However, dietary niche partitioning has been found even in closely related species (Andriollo et al.,

2021) which may be due to prey preference or alternatively behavioural differences resulting in temporal or spatial partitioning. Intraspecific partitioning has even been recorded between males and females (Mata et al., 2016). Thirdly, the diet of *M. nigeriae* over time shows that consumption of crop pests can vary over the cropping period, with some pest species only found in the diet at certain times of the year, such as demonstrated by the Hemipteran pest *Nezara viridula*, again indicating opportunistic foraging behaviour. This seasonal effect on pest consumption has also been demonstrated by molecular dietary analysis for two crop pests (*Lobesia botrana* and *Sparganothis pilleriana*) consumed by bats in a Spanish vineyard area (Baroja et al., 2021).

6.4. Potential prey abundance is similar between crops

This study hypothesised in [Chapter 5](#), that insect orders consumed by bats would be present in similar quantities across crop types. There was no indication from the findings of [Chapter 3](#) that total insect abundance, or orders of highest abundance in light traps, influenced bat activity in cropped habitats. There was also evidence of generalist and opportunistic diets of open and edge aerial bats ([Chapter 4](#)), and in addition to making up relatively large proportions of the diets of the functional groups studied, Lepidoptera, Coleoptera and Hemiptera orders also contain crop pests that were identified in the light traps. These orders of insects did indeed show similarity in abundance across maize, soya and tobacco. This infers that there is similar potential prey availability across crops. Coleoptera abundance was influenced by survey date in a similar manner to the open and edge aerial bat activity shown in [Chapter 3](#), with evident differences between cropping periods. The study results also showed an influence of latitude on Coleoptera abundance ([Chapter 5](#)), with higher abundance at more southerly sites, which is similar to the influence of latitude on edge aerial bat activity ([Chapter 3](#)), and suggests an ecological link between latitude, this functional group and Coleoptera. This finding is supported by the relatively high proportion of Coleoptera found in the diet of edge aerial bat species ([Chapter 4](#)).

6.5. Where do we fly from here?

This study has built a foundation of understanding of the foraging ecology of functional groups of bats persisting, and potentially contributing pest control services, in commercial agricultural landscapes. The functional traits of the bat species able to take advantage of these landscapes should

now be explored further to aid assessments of extinction risk and inform conservation action to increase functional diversity. Finer detail is still required on habitat and landscape features that are important to the foraging ecology of species in these functional groups which can also be managed by landowners and decision makers as part of agroecological approaches. This can be conducted by tracking individual movements in the landscape, such as through telemetry techniques (utilising radio and GPS technology) (Teague O'Mara et al., 2014). In addition, investigation into resources required for other aspects of their ecology and behaviour (e.g. roosting) is needed.

Most importantly, for more comprehensive future PAM of bats to be conducted, further development of the acoustic call library is essential and relies on the sharing of knowledge between institutions, ecological consultancies and amateur naturalists working on bats across species ranges. Bats without Borders (BwB) is a driving force for the development of a collaborative network across the southern African region and is the point of contact for access and contributions to the call library (www.batswithoutborders.org).

Although seasonal periods were considered in all chapters of this thesis, there has been no consideration of the time outside of the main annual cropping period (from November to April). As this coincides with the dry period of the year, it represents a time of limited resource availability which could be important for bat survival and activity in these landscapes. Seasonal influences have been shown to differ between functional groups in a savanna habitat of Eswatini (Shapiro et al., 2020). In addition, due to increased use of irrigation for commercial agricultural production, the cropping period has been extended to throughout the year to include other crop types, such as winter wheat. Further studies that focus on changes throughout seasons will be invaluable in understanding habitat and landscape use in this context.

Functional group diet has been explored in this PhD and has highlighted prey insect orders of particular importance, as well as looking into diet width (Levin's index) and overlaps (Pianka's index). I was also able to confirm insect pest consumption in all of the functional groups analysed. This research has two main limitations, both need to be addressed to enable a more comprehensive description of diet to be reached. Firstly, there are biases introduced as a consequence of the number of arthropod sequences that could not be allocated to a species or even order (due to lack of barcoding data on insect species). This issue has also been encountered by other bat diet studies in

the African context (e.g. Bohmann et al., 2011). Barcoding efforts targeting insects in these local environments will significantly improve taxonomic resolution of bat diet using molecular methods, and will also mean that diet and prey availability can be more comparable at a local scale. Secondly, the consumption of insect prey by individual bats is not quantifiable by this method (just information on occurrence). A rudimentary quantification of pest consumption is given in this study in the form of Frequency of Occurrence (FOO). Nevertheless, other methods are needed to establish whether this level of pest consumption constitutes a pest control service and if it translates to an influence on yield and economic value. To conduct this research is challenging but should be the ultimate goal if we are to promote bats as providers of pest control services in the context of IPM.

Within this project, each of the chapters has focussed on functional groups of bats. Although this may be appropriate for some studies, such as this one focussed on identifying broader trends, this research has flagged up the importance of considering individual species as well. Dietary analysis in particular has highlighted the fact that assuming that species in the same functional group will target similar prey ignores the potential for dietary niche partitioning between species ([Chapter 4](#)). This was also emphasized by Clare and Oelbaum (2023) who suggest that oversimplified grouping of species, especially at this early stage of technological and statistical advances in dietary analysis, can cause the nuances of bat diet to be lost and means that ecological roles can be misrepresented or undervalued, which has consequences for research, conservation, and in this case, recommendations for IPM.

6.6. Concluding remarks

Agricultural landscapes have been highlighted as priority areas for African bat conservation (Smith et al., 2016). In agreement with other studies across the globe, this PhD research has reached the robust conclusion that insectivorous bats utilise commercial agricultural landscapes in this Afrotropical context, and that some functional groups thrive by foraging over cropped areas. It has also confirmed that in these landscapes, bats are predators of a range of insect orders and that their diets include economically important insect crop pest species, some of which have also been found in bat diet elsewhere. Future studies in these landscapes should utilise the advances in PAM technology, as well as develop the call libraries across species ranges. In addition they should build on the findings of this thesis by investigating species-specific predator-prey interactions and explore

‘effect’ traits, as well as ‘response’ traits related to environmental and biotic factors throughout all seasons and in the longer-term. Further understanding of the role of African bats in providing pest control services and their ecological requirements, will encourage agricultural and conservation practitioners across the continent to implement appropriate management strategies to benefit both biodiversity and agricultural productivity.

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Appendices

Appendix A: Mean, standard deviation (SD), minimum (Min) and maximum (Max) measures of five frequency parameters at key structural features of the call for all 22 species studied in [Chapter 2](#) regardless of sample size. Lines separate species of the same family.

Species	Frequency of Maximum Power (kHz)			Characteristic Frequency (kHz)			Frequency of the Knee (kHz)			Upper Knee Frequency (kHz)			Frequency of the Ledge (kHz)		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
<i>M. nigeriae</i> (N = 9)	24.6 (3.6)	20.7	30.3	21.0 (2.0)	18.8	23.9	25.7 (2.9)	21	29.8	29.3 (4.2)	22.8	33.5	21.5 (2.1)	19	24.8
<i>M. pumilus</i> (N = 6)	25.7 (4.0)	23	33.6	22.6 (0.8)	21.7	23.7	28.5 (1.4)	26.9	30.1	33.3 (3.7)	28.6	38.8	23.4 (1.0)	22.4	24.8
<i>Miniopterus</i> sp. (N = 12)	59.5 (2.3)	54.1	63	54.9 (1.9)	51.8	58.5	64.5 (3.3)	59.1	70.3	68.2 (4.7)	61	78.9	57.8 (3.7)	54.2	66.1
<i>A. nana</i> (N = 12)	70.1 (3.1)	65.7	76.9	67.7 (2.9)	62	73.1	75.7 (2.8)	71.6	80.4	76.8 (2.6)	72.5	79.3	70.5 (3.3)	66.7	76.3
<i>G. variegata</i> (N = 8)	37.6 (2.7)	34.6	42.6	34.8 (1.0)	33	36.7	42.0 (3.6)	36.2	46.4	45.0 (3.2)	38	49.1	37.2 (2.5)	34.2	41.1
<i>L. angolensis</i> (N = 11)	40.8 (3.4)	36.9	46.4	36.0 (0.7)	35.4	37.6	43.2 (3.0)	38.9	49.4	50.4 (3.7)	42.5	54.9	37.5 (1.2)	36.7	41
<i>L. capensis</i> (N = 46)	46.0 (4.3)	41.1	58.7	40.1 (1.4)	37.3	42.5	50.6 (2.3)	46.2	57	57.6 (5.3)	46.5	66.9	42.6 (2.1)	39	47.1
<i>M. bocagii</i> (N = 3)	47.6 (3.4)	44.9	51.4	35.8 (2.3)	33.3	37.9	46.4 (1.6)	44.9	48.1	50.1 (2.0)	47.9	51.7	39.1 (2.9)	35.8	41.5
<i>M. welwitschii</i> (N = 9)	39.7 (5.0)	34.7	49.9	31.7 (2.1)	28.6	34.3	47.4 (3.2)	41.7	52.6	54.6 (3.8)	49.7	61.6	36.6 (3.8)	30.9	42.4
<i>N. anchietae</i> (N = 16)	48.8 (3.1)	44.6	56.2	43.6 (1.0)	41.6	45	50.4 (2.0)	46.1	55.2	55.9 (5.0)	46.5	65.2	45.2 (1.4)	43.3	47.7
<i>N. schlieffeni</i> (N = 8)	48.5 (4.5)	43.4	57.2	44.0 (1.2)	42.7	45.7	51.5 (4.7)	43.3	59.8	53.1 (4.6)	44.1	58.8	45.6 (2.7)	42.7	51.2
<i>N. zuluensis</i> (N = 12)	52.8 (4.0)	45.3	57.9	49.1 (1.9)	45.4	52.2	55.6 (4.9)	47.8	62.5	57.1 (5.6)	48	65	49.9 (2.3)	45.7	53.6
<i>P. rusticus</i> (N = 18)	61.5 (4.5)	57.3	72.1	57.1 (1.4)	54.9	60.2	66.9 (3.1)	61.4	71.8	71.7 (3.8)	66.8	81.2	58.3 (1.6)	54.8	61
<i>S. dinganii</i> (N = 16)	37.7 (2.6)	32.2	43.3	32.8 (2.1)	29	36.8	39.8 (2.8)	34.9	44.2	45.7 (4.4)	36.9	51.8	34.4 (2.6)	29.2	38.1
<i>S. viridis</i> (N = 10)	48.3 (4.8)	42.2	58.3	41.4 (1.0)	40	43	50.6 (3.9)	45.7	59.7	62.2 (6.3)	51.1	73.7	43.7 (2.3)	40.3	47.6
<i>V. rueppellii</i> (N = 8)	49.9 (2.2)	46.5	53.7	46.1 (2.1)	43.3	50.4	54.8 (4.0)	50.4	60.9	56.5 (3.5)	51.2	61.5	48.3 (2.0)	44.8	50.7

	Frequency of Maximum Power (kHz)			Characteristic Frequency (kHz)			Frequency of the Knee (kHz)			Upper Knee Frequency (kHz)			Frequency of the Ledge (kHz)		
<i>H. caffer</i> (N = 1)	148.1 (NA)	148.1	148.1	145.6 (NA)	145.6	145.6	150.4 (NA)	150.4	150.4	150.7 (NA)	150.7	150.7	149.0 (NA)	149	149
<i>H. ruber</i> (N = 1)	133.4 (NA)	133.4	133.4	133.2 (NA)	133.2	133.2	133.4 (NA)	133.4	133.4	133.4 (NA)	133.4	133.4	133.3 (NA)	133.3	133.3
<i>M. vittatus</i> (N = 19)	64.4 (1.9)	60.5	66.8	64.1 (1.8)	60.4	66.6	57.6 (6.8)	43.5	65.2	57.7 (6.8)	43.5	65.3	57.5 (6.7)	43.4	65.1
<i>R. mossambicus</i> (N = 2)	38.5 (2.1)	37	40	38.1 (2.1)	36.6	39.5	38.5 (2.1)	37	39.9	38.5 (2.1)	37.1	40	38.1 (2.1)	36.6	39.6
<i>R. simulator</i> (N = 9)	77.9 (1.6)	75.7	79.9	77.6 (1.7)	75.5	80.2	76.7 (4.0)	66.7	80	76.8 (4.0)	66.7	80.1	76.3 (3.9)	66.5	79.7
<i>Nycteris</i> sp. (N = 1)	71.3 (NA)	71.3	71.3	64.9 (NA)	64.9	64.9	69.0 (NA)	69	69	69.0 (NA)	69	69	68.4 (NA)	68.4	68.4

Appendix B: Mean, standard deviation (SD), minimum (Min) and maximum (Max) measures of six frequency parameters along the call sweep for all 22 species studied in [Chapter 2](#) regardless of sample size. Lines separate species of the same family.

Species	Start Frequency (kHz)			End Frequency (kHz)			Highest Frequency (kHz)			Centre Frequency (kHz)			Lowest Frequency (kHz)			Bandwidth (kHz)		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
<i>M. nigeriae</i> (N = 9)	32.7 (5.0)	24.3	37.1	18.5 (2.5)	14.8	21.7	32.7 (5.0)	24.3	37.2	24.0 (2.3)	21	27.5	18.3 (2.5)	14.8	21.5	14.4 (5.2)	12.5	8.2
<i>M. pumilus</i> (N = 6)	36.3 (4.3)	30.7	42.9	20.2 (0.5)	19.4	20.7	36.3 (4.3)	30.8	42.9	27.3 (1.7)	25.1	30.3	20.0 (0.5)	19.1	20.7	16.3 (4.1)	10.9	22.2
<i>Miniopterus</i> sp. (N = 12)	90.6 (8.9)	101.4	99.7	51.9 (2.4)	47.8	54.8	90.7 (8.8)	101.4	99.7	61.6 (3.0)	55.6	65.9	51.9 (2.3)	47.8	54.5	38.8 (9.9)	22.1	50.6
<i>A. nana</i> (N = 12)	98.3 (4.8)	101.1	99.4	65.4 (3.6)	58.2	70.7	98.3 (4.8)	101.1	99.4	71.0 (2.2)	68.4	74.8	65.2 (3.6)	58.2	70.4	33.1 (6.8)	22.2	42.8
<i>G. variegata</i> (N = 8)	60.8 (8.5)	43.5	70	32.8 (0.9)	31.5	34.1	60.9 (8.5)	43.5	70	38.2 (2.0)	35.2	41.2	32.7 (0.9)	31.5	33.7	28.2 (8.8)	24.8	9.8
<i>L. angolensis</i> (N = 11)	65.7 (5.6)	52.9	70.4	33.8 (0.9)	32.3	35.4	65.7 (5.6)	52.9	70.4	42.4 (2.3)	38.6	45.8	33.8 (0.8)	32.3	35.2	31.9 (5.7)	19.2	36.8
<i>L. capensis</i> (N = 46)	79.0 (6.5)	62.1	93.5	36.8 (1.3)	33.9	39.1	79.0 (6.5)	62.1	93.5	47.9 (2.8)	43.6	54.7	36.8 (1.3)	33.9	39.1	42.2 (6.2)	26.8	54.6
<i>M. bocagii</i> (N = 3)	66.2 (5.7)	59.9	70.9	27.3 (1.6)	26.2	29.2	66.2 (5.7)	59.9	70.9	45.3 (3.2)	41.9	48.3	27.3 (1.6)	26.2	29.2	38.9 (4.6)	33.6	41.7
<i>M. welwitschii</i> (N = 9)	75.2 (8.3)	62.7	83.6	24.7 (2.2)	21.7	28.3	75.2 (8.3)	62.7	83.6	45.1 (4.2)	38.5	50.2	24.7 (2.2)	21.7	28.3	50.5 (7.7)	37.6	58.9
<i>N. anchietae</i> (N = 16)	79.8 (6.7)	61.4	89.4	41.5 (1.6)	37.8	44.6	79.8 (6.7)	61.4	89.4	47.8 (1.8)	45	51.3	41.4 (1.5)	37.8	44.1	38.4 (7.3)	17.4	48.2
<i>N. schlieffeni</i> (N = 8)	74.5 (11.6)	49.4	84.9	41.9 (1.1)	40.2	43.5	74.5 (11.6)	49.4	84.9	46.8 (2.4)	42.9	49.7	41.8 (1.0)	40.2	43.5	32.7 (11.4)	27.7	7.4
<i>N. zuluensis</i> (N = 12)	78.4 (14.4)	52.9	97.4	48.1 (2.3)	44.5	50.9	78.4 (14.4)	53	97.4	50.8 (2.7)	45.3	54.6	47.7 (2.1)	44.5	50.9	30.7 (14.6)	14.5	9.2
<i>P. rusticus</i> (N = 18)	91.4 (4.9)	80.8	99	54.5 (1.5)	52.2	57.3	91.4 (4.9)	80.8	99	60.8 (2.4)	56	67.2	54.4 (1.5)	52.2	57.3	36.9 (4.9)	26	44.2
<i>S. dinganii</i> (N = 16)	60.3 (5.7)	49.4	69.1	30.4 (1.8)	27.7	35.9	60.3 (5.7)	49.4	69.1	38.0 (3.1)	32	42.1	30.2 (1.8)	27.6	35.7	30.1 (5.6)	19.7	38.8
<i>S. viridis</i> (N = 10)	79.2 (4.7)	69.7	86.1	38.7 (1.1)	37.2	40.9	79.3 (4.8)	69.7	86.1	50.8 (4.5)	44.7	59.5	38.6 (1.1)	37.2	40.8	40.6 (5.4)	30.3	47.5
<i>V. rueppellii</i> (N = 8)	76.1 (7.8)	67	88.6	43.5 (3.1)	39.8	50.7	76.1 (7.8)	67	88.6	50.3 (1.9)	47.1	52.7	43.2 (2.5)	39.7	48.6	32.9 (8.6)	23.3	45

	Start Frequency (kHz)			End Frequency (kHz)			Highest Frequency (kHz)			Centre Frequency (kHz)			Lowest Frequency (kHz)			Bandwidth (kHz)		
<i>H. caffer</i> (N = 1)	149.6 (NA)	149.6	149.6	119.4 (NA)	119.4	119.4	151.0 (NA)	151	151	150.8 (NA)	150.8	150.8	119.4 (NA)	119.4	119.4	31.6 (NA)	31.6	31.6
<i>H. ruber</i> (N = 1)	132.5 (NA)	132.5	132.5	125.8 (NA)	125.8	125.8	133.5 (NA)	133.5	133.5	133.4 (NA)	133.4	133.4	125.8 (NA)	125.8	125.8	7.7 (NA)	7.7	7.7
<i>M. vittatus</i> (N = 19)	64.3 (1.9)	60.4	66.8	62.7 (3.0)	54	66.1	64.6 (1.8)	60.7	66.9	64.5 (1.9)	60.5	66.8	62.6 (3.0)	54	66	2.0 (1.8)	0.8	7.7
<i>R. mossambicus</i> (N = 2)	31.3 (1.6)	30.2	32.4	33.2 (1.8)	32	34.5	38.7 (2.1)	37.3	40.2	38.5 (2.0)	37.1	40	30.3 (1.0)	29.7	31	8.4 (1.1)	7.6	9.1
<i>R. simulator</i> (N = 9)	74.6 (3.4)	67.8	79	75.3 (2.4)	70.8	78.6	78.3 (1.7)	76.2	80.8	78.2 (1.7)	76.1	80.7	73.5 (3.5)	66.2	77.9	4.7 (3.1)	12.5	5.6
<i>Nycteris</i> sp. (N = 1)	84.1 (NA)	84.1	84.1	60.2 (NA)	60.2	60.2	84.8 (NA)	84.8	84.8	69.6 (NA)	69.6	69.6	60.2 (NA)	60.2	60.2	24.6 (NA)	24.6	24.6

Appendix C: Mean, standard deviation (SD), minimum (Min) and maximum (Max) measures of three time based parameters for all 22 species studied in [Chapter 2](#) regardless of sample size. Lines separate species of the same family.

Species	Calls per second			Ledge Duration (ms)			Call Duration (ms)		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
<i>M. nigeriae</i> (N = 9)	12.9 (13.8)	10.6	8.3	0.4 (0.0)	0.4	0.5	6.6 (2.2)	3.9	9.3
<i>M. pumilus</i> (N = 6)	8.3 (4.1)	10.7	6.7	0.4 (0.1)	0.3	0.5	7.5 (2.0)	10.4	9.4
<i>Miniopterus</i> sp. (N = 12)	15.5 (10.5)	10.8	6.7	0.5 (0.1)	0.3	0.7	3.8 (1.8)	1.9	7.3
<i>A. nana</i> (N = 12)	8.6 (4.0)	10.8	8.3	0.6 (0.1)	0.4	0.8	3.1 (0.9)	1.8	4.9
<i>G. variegata</i> (N = 8)	9.2 (3.5)	11	9.7	0.6 (0.1)	0.4	0.8	4.1 (1.1)	2.8	5.4
<i>L. angolensis</i> (N = 11)	10.8 (3.6)	10.8	9	0.4 (0.1)	0.3	0.6	3.4 (0.5)	2.6	4.3
<i>L. capensis</i> (N = 46)	11.0 (8.1)	10.7	9.9	0.4 (0.1)	0.3	0.6	3.5 (0.7)	2.1	5
<i>M. bocagii</i> (N = 3)	9.1 (4.8)	14.5	7.3	0.3 (0.0)	0.3	0.3	2.6 (0.4)	2.4	3.1
<i>M. welwitschii</i> (N = 9)	16.4 (12.4)	12.4	9.7	0.4 (0.1)	0.3	0.6	3.0 (0.5)	2.4	3.9
<i>N. anchietae</i> (N = 16)	7.6 (3.9)	10	9.6	0.5 (0.1)	0.4	0.6	3.6 (0.6)	2.8	4.9
<i>N. schlieffeni</i> (N = 8)	9.0 (4.3)	10.8	8.7	0.5 (0.1)	0.3	0.6	3.6 (1.2)	2.5	6.3
<i>N. zuluensis</i> (N = 12)	10.1 (4.0)	10.8	9.6	0.5 (0.1)	0.3	0.8	4.3 (1.0)	2.6	6
<i>P. rusticus</i> (N = 18)	8.6 (3.7)	10.2	8.9	0.5 (0.1)	0.3	0.6	4.2 (0.9)	1.9	5.4
<i>S. dinganii</i> (N = 16)	11.3 (3.6)	10.4	9.3	0.4 (0.1)	0.3	0.5	3.8 (1.5)	2.4	6.5
<i>S. viridis</i> (N = 10)	12.1 (3.2)	10.2	9.6	0.4 (0.0)	0.4	0.5	4.2 (1.2)	2.4	5.7
<i>V. rueppellii</i> (N = 8)	12.0 (5.1)	10.2	8.6	0.5 (0.1)	0.4	0.5	3.5 (1.1)	2.1	5.5

	Calls per second			Ledge Duration (ms)			Call Duration (ms)		
<i>H. caffer</i> (N = 1)	15.1 (NA)	15.1	15.1	0.4 (NA)	0.4	0.4	8.0 (NA)	8	8
<i>H. ruber</i> (N = 1)	23.6 (NA)	23.6	23.6	0.4 (NA)	0.4	0.4	8.0 (NA)	8	8
<i>M. vittatus</i> (N = 19)	16.5 (5.7)	11.3	9.7	1.3 (0.9)	0.3	3.3	12.6 (2.6)	10.1	9.3
<i>R. mossambicus</i> (N = 2)	16.0 (1.9)	14.7	17.3	0.4 (0.0)	0.3	0.4	34.3 (3.7)	31.7	36.9
<i>R. simulator</i> (N = 9)	13.6 (5.2)	14.7	9.5	0.7 (0.9)	0.3	3.1	24.1 (4.8)	18.8	30.1
<i>Nycteris</i> sp. (N = 1)	1.8 (NA)	1.8	1.8	0.5 (NA)	0.5	0.5	2.1 (NA)	2.1	2.1

Appendix D: Mean, standard deviation (SD), minimum (Min) and maximum (Max) measures of six slope based parameters for all 22 species studied in [Chapter 2](#) regardless of sample size. Lines separate species of the same family.

Species	Start Slope (kHz/ms)			End Slope (kHz/ms)			Dominant Slope (kHz/ms)			Steepest Slope (kHz/ms)			Lowest Slope (kHz/ms)			Slope at Characteristic Frequency (kHz/ms)		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
<i>M. nigeriae</i> (N = 9)	-4.0 (1.8)	-1.7	-6.5	-2.7 (1.9)	0	-5.7	1.9 (0.9)	1	3.7	4.5 (1.2)	2.5	6.5	1.1 (0.7)	0.1	1.9	1.5 (0.8)	0.5	2.9
<i>M. pumilus</i> (N = 6)	-3.1 (1.3)	-2.1	-5.5	-3.8 (1.3)	-2.1	-5.3	2.5 (1.0)	1.6	4	4.5 (1.8)	2.8	7.2	1.6 (0.5)	1	2.2	2.1 (0.5)	1.6	2.8
<i>Miniopterus sp.</i> (N = 12)	-24.0 (5.8)	-13.1	-38.2	-8.8 (4.0)	-10.1	-5.6	12.6 (8.5)	1.2	7.7	31.2 (9.4)	20.8	51.1	4.6 (3.5)	0.2	9.4	5.9 (4.2)	0.6	8.9
<i>A. nana</i> (N = 12)	-27.7 (5.1)	-19.1	-37.5	-8.2 (4.0)	-11.6	-8.4	7.5 (7.6)	0.7	7.3	33.5 (7.7)	20.9	49.6	2.7 (2.7)	0.2	7.6	4.0 (3.4)	0.5	8.9
<i>G. variegata</i> (N = 8)	-17.7 (7.3)	-12.1	-5.9	-6.4 (4.6)	-0.1	-4.7	5.0 (3.3)	1.1	9.8	22.8 (9.4)	16	6.3	2.1 (1.3)	0.1	4	2.8 (1.8)	0.7	6.3
<i>L. angolensis</i> (N = 11)	-16.0 (3.3)	-11	-21.6	-7.9 (2.6)	-11	-9.3	11.0 (3.4)	10.2	8.1	19.1 (3.9)	12.4	27.3	3.1 (1.4)	1.5	5.6	3.7 (1.5)	1.8	6.3
<i>L. capensis</i> (N = 46)	-23.0 (3.9)	-15.4	-31.5	-8.2 (3.3)	-1.4	-9.9	11.5 (5.3)	10.5	9.8	27.7 (5.2)	17.8	43.5	5.1 (2.1)	1.9	9.4	5.7 (2.2)	12.2	9.7
<i>M. bocagii</i> (N = 3)	-14.2 (2.9)	-10.8	-16	-20.2 (6.6)	-13.3	-26.4	15.3 (3.5)	11.5	18.3	19.8 (4.5)	14.7	23	8.9 (2.2)	10	6.4	10.8 (2.6)	12	7.9
<i>M. welwitschii</i> (N = 9)	-19.2 (3.7)	-14.1	-24.8	-18.8 (4.5)	-13.6	-25.9	18.1 (5.2)	12.2	9.4	25.5 (5.7)	16.5	33.9	10.9 (2.8)	10.5	6.3	11.6 (3.3)	10.7	6.4
<i>N. anchietae</i> (N = 16)	-22.6 (3.3)	-16.3	-27.6	-5.7 (2.3)	-0.9	-9.5	10.8 (4.8)	10.6	9	28.1 (4.6)	19.9	35	2.3 (1.7)	0.2	6.3	2.8 (1.7)	0.6	6.5
<i>N. schlieffeni</i> (N = 8)	-29.1 (9.8)	-24.1	-7.7	-5.7 (3.4)	-1.1	-7.1	5.9 (5.7)	0.7	4.5	34.0 (13.0)	24.7	7.8	1.9 (1.6)	0.2	4.8	2.7 (2.1)	0.7	6.8
<i>N. zuluensis</i> (N = 12)	-29.1 (12.7)	-18	-8.2	-2.7 (2.3)	-0.6	0.9	2.9 (2.5)	0.2	6.9	32.2 (15.4)	17.4	7.1	0.8 (0.9)	0	2.7	1.3 (0.8)	0.3	3

	Start Slope (kHz/ms)			End Slope (kHz/ms)			Dominant Slope (kHz/ms)		Steepest Slope (kHz/ms)			Lowest Slope (kHz/ms)			Slope at Characteristic Frequency (kHz/ms)			
<i>P. rusticus</i> (N = 18)	-23.9 (4.3)	-12	-29.3	-7.2 (3.8)	-1.7	-9.8	7.1 (6.1)	0.9	9.8	26.4 (5.1)	16.1	32.4	2.0 (2.1)	0.2	9.1	2.6 (3.0)	0.5	6.1
<i>S. dinganii</i> (N = 16)	-15.1 (2.8)	-10.4	-21	-6.7 (3.2)	-10.5	-9.8	9.8 (4.9)	1.9	8.6	19.2 (4.4)	11.4	27	3.3 (1.7)	0.7	6.4	4.1 (1.9)	1	7.3
<i>S. viridis</i> (N = 10)	-16.7 (6.7)	-13.5	-9.7	-6.4 (3.0)	-1.2	-9.6	11.6 (5.4)	10.1	9.2	21.1 (6.0)	11.6	31.9	4.3 (2.6)	0.6	8.8	5.1 (3.3)	0.9	9
<i>V. rueppellii</i> (N = 8)	-23.1 (4.0)	-19	-28.2	-7.4 (5.1)	-10.7	0.4	10.7 (5.4)	12.7	8.3	28.5 (5.2)	20	37	3.5 (2.3)	0.7	6.2	4.6 (2.5)	1	7.7
<i>H. caffer</i> (N = 1)	-0.1 (NA)	-0.1	-0.1	-36.9 (NA)	-36.9	-36.9	0.1 (NA)	0.1	0.1	7.4 (NA)	7.4	7.4	0.0 (NA)	0	0	8.2 (NA)	8.2	8.2
<i>H. ruber</i> (N = 1)	-0.1 (NA)	-0.1	-0.1	-12.7 (NA)	-12.7	-12.7	0.1 (NA)	0.1	0.1	0.5 (NA)	0.5	0.5	0.0 (NA)	0	0	0.5 (NA)	0.5	0.5
<i>M. vittatus</i> (N = 19)	-0.1 (0.0)	-0.1	-0.2	-1.7 (1.1)	-0.6	-4.7	0.0 (0.0)	0	0.1	0.5 (0.3)	0.1	1.1	0.0 (0.0)	0	0	0.7 (0.4)	0.3	1.3
<i>Nycteris</i> sp. (N = 1)	-17.7 (NA)	-17.7	-17.7	-16.5 (NA)	-16.5	-16.5	8.0 (NA)	8	8	31.1 (NA)	31.1	31.1	5.6 (NA)	5.6	5.6	8.4 (NA)	8.4	8.4

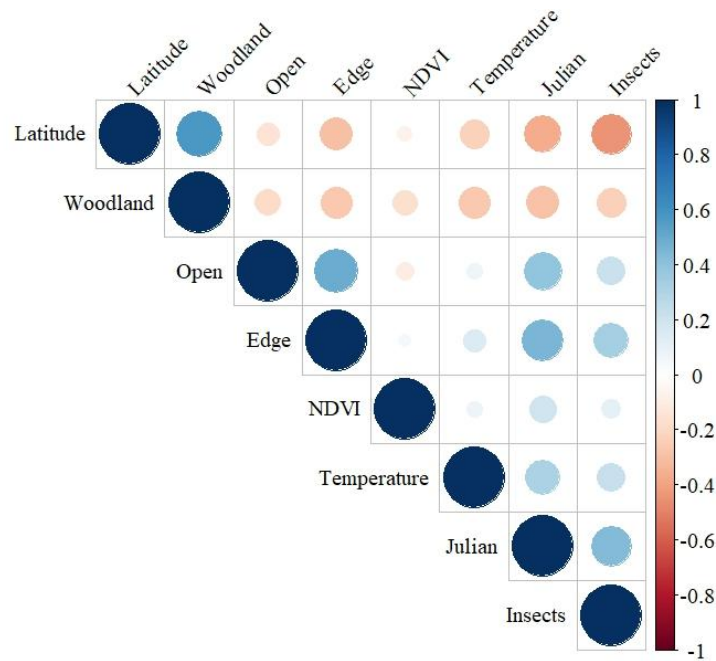
Appendix E: Linear Discriminant Function analysis (LDA) prediction summary of 17 species studied in [Chapter 2](#) with sample sizes of more than six individuals with predicted identifications of test individuals (Predicted) compared to the true identifications (Observed).

<i>Predicted</i>	<i>Observed</i>																
	<i>A. nana</i>	<i>G. variegata</i>	<i>L. angolensis</i>	<i>L. capensis</i>	<i>M. nigeriae</i>	<i>M. pumilus</i>	<i>M. vittatus</i>	<i>M. welwitschii</i>	<i>Miniopterus</i> sp.	<i>N. anchietae</i>	<i>N. schlieffeni</i>	<i>N. zuluensis</i>	<i>P. rusticus</i>	<i>R. simulator</i>	<i>S. dinganii</i>	<i>S. viridis</i>	<i>V. rueppellii</i>
<i>A. nana</i>	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>G. variegata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>L. angolensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>L. capensis</i>	0	0	2	12	0	0	0	0	0	4	1	0	0	0	0	2	0
<i>M. nigeriae</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>M. pumilus</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>M. vittatus</i>	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
<i>M. welwitschii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Miniopterus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>N. anchietae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>N. schlieffeni</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>N. zuluensis</i>	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>P. rusticus</i>	1	0	0	0	0	0	0	0	3	0	0	1	3	0	0	0	0
<i>R. simulator</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
<i>S. dinganii</i>	0	2	1	0	0	0	0	2	0	0	0	0	0	0	2	1	0
<i>S. viridis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>V. rueppellii</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>n (Test sample)</i>	3	2	3	13	2	1	5	2	3	4	2	3	5	2	4	3	2
<i>Balanced Accuracy (%)</i>	0.82	0.49	0.49	0.86	0.75	0.99	1.00	0.50	0.50	0.48	0.75	0.83	0.75	1.00	0.70	0.50	0.49

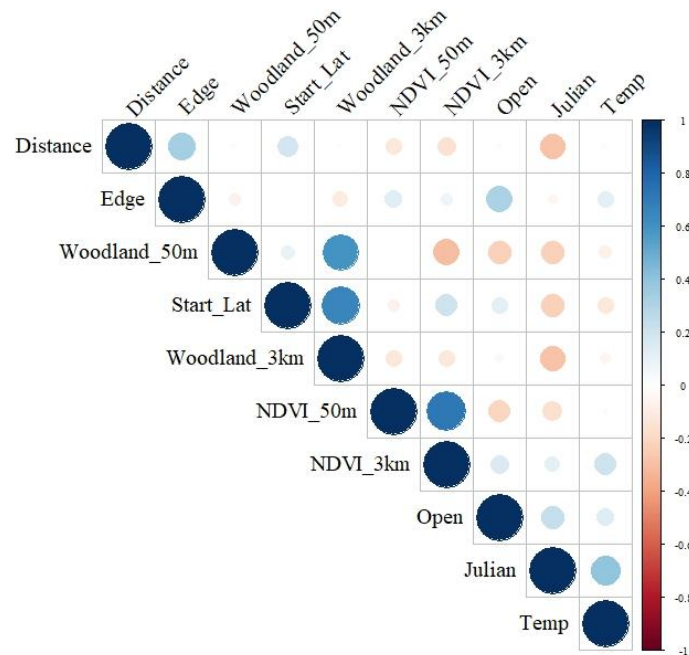
Appendix F: Comparisons of acoustic parameter Frequency of Maximum Power (FreqMaxPwr) studied in [Chapter 2](#) with the equivalent Frequency of Maximum Energy (FMaxE) given in the book ‘Bats of Southern and Central Africa’ (Monadjem et al., 2020b) which contains published parameters of echolocation calls of the species in this study. FreqMaxPwr was calculated by Sonobat software, whereas FMaxE was calculated manually using BatSound software. Overlap indicates whether minimum and maximum values show some intersection between the two datasets.

Species	This study mean FreqMaxPwr (kHz)	Monadjem <i>et al</i> 2020 mean FMaxE (kHz)	Overlap
<i>M. nigeriae</i>	24.6 (n=9)	17 (n=3)	No
<i>M. pumilus</i>	25.7 (n=6)	25.6 (n=11)	Yes
<i>Miniopterus</i> sp.	59.7 (n=12)	<i>M. natalensis</i> 49.7 (n=10) <i>M. mossambicus</i> 60.5 (n=2)	No Yes
<i>A. nana</i>	70.1 (n=12)	69.4 (n=10)	Yes
<i>G. variegata</i>	37.6 (n=8)	41.1 (n=1)	Yes
<i>L. angolensis</i>	40.8 (n=12)	NA	NA
<i>L. capensis</i>	46.0 (n=50)	39.4 (n=10)	Yes
<i>M. bocagii</i>	47.6 (n=3)	44.6 (n=5)	Yes
<i>M. welwitschii</i>	39.7 (n=9)	34 (n=1)	No
<i>N. anchietae</i>	48.8 (n=16)	55.7 (n = 1)	No
<i>N. schlieffeni</i>	48.5 (n=8)	42.5 (n=2)	No
<i>N. zuluensis</i>	52.8 (n=12)	48.4 (n=2)	Yes
<i>P. rusticus</i>	61.5 (n=18)	55.7 (n=10)	Yes
<i>S. dinganii</i>	37.7 (n=16)	33.6 (n=10)	Yes
<i>S. viridis</i>	48.3 (n=10)	44.3 (n=4)	Yes
<i>V. rueppellii</i>	49.9 (n=8)	37.3 (n=1)	No
<i>H. caffer</i>	148.0 (n=1)	142.3 (n=10)	No
<i>H. ruber</i>	133.0 (n=1)	NA	NA
<i>M. vittatus</i>	64.4 (n=19)	61 (n=?)	Yes
<i>R. mossambicus</i>	38.5 (n=2)	36.5 (n=?)	No
<i>R. simulator</i>	77.9 (n=9)	80.1 (n=10)	No
<i>Nycteris</i> sp.	71.3 (n=1)	NA	NA

Appendix G: Pearson's correlation matrix for [Chapter 3](#) static detector location variables with significant positive (blue) and negative (red) correlations. Darker colours indicate higher correlation.



Appendix H: Pearson's correlation matrix for [Chapter 3](#) transect variables with significant positive (blue) and negative (red) correlations. Darker colours indicate higher correlation.



Appendix I: Pest species present (quantified as Frequency of Occurrence (FOO) as a percentage) in the diet of *Mops nigeriae* studied in [Chapter 4](#) between December 2018 and May 2019

Order	Pest species	Common name	Dec	Jan	Feb	Mar	Apr	May
Hemiptera	<i>Nezara viridula</i>	Green vegetable bug	0.0	0.0	0.0	0.0	40.0	0.0
	<i>Rhopalosiphum padi</i>	Grain aphid	5.0	0.0	0.0	0.0	0.0	0.0
Lepidoptera	<i>Chrysodeixis acuta</i>	Tunbridge wells gem	0.0	0.0	0.0	5.0	5.0	5.0
	<i>Earias biplaga</i>	Spiny bollworm	0.0	0.0	0.0	0.0	0.0	5.0
	<i>Ectomyelois ceratoniae</i>	Carob moth	5.0	5.3	10.0	0.0	0.0	0.0
	<i>Marasmia poeyalis</i>	Lesser rice-leafroller	0.0	10.5	5.0	0.0	0.0	0.0
	<i>Marasmia trapezalis</i>	Trapeze moth	0.0	10.5	0.0	0.0	0.0	0.0
	<i>Maruca vitrata</i>	Legume pod borer	0.0	0.0	0.0	5.0	5.0	10.0
	<i>Spoladea recurvalis</i>	Beet webworm moth	0.0	5.3	0.0	5.0	0.0	0.0
	<i>Thysanoplusia orichalcea</i>	Slender Burnished Brass	10.0	15.8	0.0	10.0	10.0	0.0
	<i>Tuta absoluta</i>	Tomato leafminer	0.0	5.3	0.0	0.0	0.0	0.0
Orthoptera	<i>Gryllus bimaculatus</i>	two-spotted cricket	0.0	5.3	0.0	0.0	0.0	5.0